LINKS BETWEEN COGNITION AND FITNESS: MECHANISMS AND CONSTRAINTS IN THE WILD

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LINKS BETWEEN COGNITION AND FITNESS: MECHANISMS AND CONSTRAINTS IN THE WILD

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Editorial: Links between cognition and fitness: Mechanisms and constraints in the wild

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Editorial on the Research Topic
Links between cognition and fitness: Mechanisms and constraints in the wild

In the wild, animals frequently face environmental variations that can be predictable, for example seasonal climate variation, or not, such as habitat destruction or climate change due to the accelerating rate of anthropogenic activity. To cope with these variations, animals must adjust their decisions to the changing conditions. Cognitive abilities, widely defined as all the sensory, neurological, memory and decision processes used by individuals to interact with their environment (Shettleworth, 2001), can allow animals to gather and/or process information more efficiently, better exploit their environment and flexibly adjust their behavior to facilitate optimal responses to environmental changes (Wyles et al., 1983; Sol, 2008). Cognitive abilities can thus be expected to be a key component of animal fitness in the wild, shaping the potential for animal populations to rapidly adjust to a changing world.

A growing number of studies have recently explored whether cognitive performances are positively linked with fitness components in the wild, but the results are not always in line with such a prediction. Cognitive performances and fitness components can show positive links (e.g., Cauchard et al., 2013; Ashton et al., 2018; Sonnenberg et al., 2019), negative links (e.g., Mery and Kawecki, 2003), no links (e.g., Isden et al., 2013; Huebner et al., 2018), or even links dependent on the context or on fitness components suggesting trade-offs between investment in offspring and adult survival (e.g., Cole et al., 2012). Such varying results have frequently been attributed to differences in the design of the cognitive tasks used (which have to be adapted to the morphological and ecological constraints of the study model and site) and/or to other factors that can affect behavioral performance in general (such as personality traits, motivation, age, sex, etc.). However, once properly controlled for these potential biases (Schubiger et al., 2020), these varying results must above all reflect the complex relationships between

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cognitive abilities and selective pressures under various ecological and social contexts. Moreover, whether the links, when detected, are causal remains unknown in most cases. Yet, identifying the mechanisms underlying the links between cognitive performances and fitness components and the constraints acting on these mechanisms is crucial to understand and predict how selective pressures can shape the evolution of cognitive abilities in the wild. This is a major gap in our understanding about how and when cognition can help animals to adapt to their changing environments.

In this introduction to the themed issue "*Links between cognition and fitness: mechanisms and constraints in the wild*," we present an overview of potential mechanisms that could link inter-individual variation in cognitive ability and fitness components, and place the 15 contributions of this theme (5 reviews, 7 original research articles, 2 opinion pieces and 1 perspective) in context. Both direct and indirect mechanisms can link inter-individual variation in cognitive ability to fitness components. Direct mechanisms involve a causal link between cognition and fitness while indirect mechanisms involve cognition and fitness to be both influenced simultaneously but independently by a third variable, creating a correlational link between them.

Current literature on direct mechanisms suggests that individuals with better cognitive abilities might make a better use of their environment for fitness-related decisions, but evidence for such a causal mechanism is still very scarce, impeding our ability to draw general conclusions. Szabo et al. highlighted in their review the cognitive abilities relevant for species in conquering new habitats, targeting both invertebrate and vertebrate species, and examined which cognitive traits could give species an advantage in a competitive, novel environment. Going further, Cauchard et al. experimentally manipulated brood size in wild breeding great tits to explore causal mechanisms between reproductive success and the performance in solving a non-food motivated task presented at the nest. They showed that a significant increase or decrease in brood size did not affect problem-solving performance, thus excluding a direct causal relation through higher motivation to solve the task in more successful pairs. Yet within treatments, task solver pairs still reached higher reproductive success compared to non-solver pairs, which could at least partly be explained by a higher provisioning rate. These results are in line with the hypothesis that problem-solvers may achieve higher reproductive success through a better exploitation of the habitat. Such better habitat exploitation may require individuals to process information about the habitat more efficiently. In order to explore this question, White examined nest selection and its timing in nest-parasite brown-headed cowbirds (*Molothrus ater*). By experimentally manipulating the number of eggs present in mock nests and the timing of egg laying, White showed that female cowbirds relied on social information, i.e., information obtained from the presence, behavior or performance of others (Danchin et al., 2004), to plan where, when and how many eggs to lay in a given host nest. This ability to optimally use social information can be hypothesized to require different cognitive abilities to process such information. In line with this prediction, the study by Morinay et al. experimentally showed that the use of social information for small-scale nest site selection depended on learning performance in wild collared flycatchers (*Ficedula albicollis*). Collared flycatchers are known to rely on heterospecific social information from titmice for breeding decisions, which leads to fitness increase (Forsman et al., 2002). The study by Morinay et al. revealed here a relation between learning performance and the probability to copy nest preference by sympatric titmice. Overall, learning ability may be particularly important to process information, driving the capacity to optimally deal with environmental changes. To dig this idea deeper, a first comprehensive review by Barrett et al. presented a compilation of theory and empirical evidence on how social learning can help or hinder responses of organisms and thus species to human-induced rapid environmental changes and how these changes can interfere with the transmission of social information. More particularly, a second review by Greggor et al. focused on how learning in general may allow individuals to avoid ecological traps driven by human-induced environmental changes, depending on constraints, type of learning mechanism and individual factors such as personality.

The ability to better use habitat may affect not only reproductive success but also survival, especially in spatio-temporally varying environments. In their study, Mettke-Hofmann et al. explored the response to habitat novelty in the Gouldian finch (*Erythrura gouldiae*), a polymorphic species showing a link between head color and behavioral phenotypes. They showed that black-headed birds are more reluctant to enter a new dense habitat than red-headed birds, which may negatively affect long-term population persistence to habitat change since 70% of birds in the wild are black-headed. Yet, very little is currently known regarding the links between cognitive abilities and survival. One reason for this may be challenges when studying cognition in the wild (Morand-Ferron et al., 2015). In particular, most studies in nature rely on limited sample size, preventing reliable survival analyses. To address this issue in a laboratory setting, Matzel et al. took advantage of genetically heterogeneous mice that express individual differences in general cognitive ability to explore associated differences in behaviors known to be related to survival in this species. They found that mice with a higher general cognitive ability score also showed a higher survival-readiness score, and results suggested that heightened attention may drive this relationship. In their review, Rochais et al. explored the existing literature linking cognition to survival in the wild in order to highlight the cognitive traits that can be expected to be ecologically relevant for survival, as well as the individual characteristics that might influence these relationships. They discussed the challenges associated with investigating the links between cognition and survival in natural populations, and proposed a methodological approach to ward off these challenges.

Regarding indirect mechanisms, environmental variables such as habitat quality might affect both cognitive abilities and fitness components simultaneously but separately, outside any direct link between them. Using the extensive literature available on fish, Jacquin et al. highlighted in their comprehensive perspective article how exposure to pollutants from human-related activities can affect both cognition and fitness through various physiological and behavioral (personality) mechanisms. This study thus emphasized the urgent need for future studies to examine the links between ecotoxicology, cognitive ecology and evolutionary ecology in a multi-stress framework to improve our ability to predict the effects of anthropogenic stressors on wildlife. Parasitism is another environmental factor that can drive an indirect link between cognition and fitness. In their review article, Ducatez et al. proposed three scenarios on how cognition could affect the reciprocal pressures that hosts and parasites can exert on each other, shaping host-parasite eco-evolutionary dynamics. This review revealed the need for experimental studies to distinguish between direct (causal) and indirect (non-causal) effects of parasitism in the evolution of cognition.

Direct and indirect mechanisms may also operate simultaneously. For instance, in new habitats, new constraints should favor individuals with cognitive abilities enhancing their behavioral repertoire to cope with novel challenges and thereby achieve higher fitness. At the same time, new habitats may also host new stressors such as pollutants and parasites, or affect individual condition in general, impacting both cognition and fitness independently. In their comparative study, Sayol et al. showed that brain size was positively associated with urban tolerance, even if small-brained species can use alternative life history strategies, such as a higher number of low value reproductive events, to succeed in urban environments. Cognition-related differences in life-history strategies were also suggested in the study by Johnson-Ulrich et al. in wild female spotted hyenas (*Crocuta crocuta*), where innovativeness was linked to reproduction in multiple ways: innovative hyenas showed lower cub survival but higher annual cub production compared to non-innovative hyenas, leading to no overall difference between innovative and non-innovative hyenas in reproductive success. Another example where both direct and indirect mechanisms may operate together is between-species hybridization, whose effects on fitness have been frequently described, but potential influence on cognition is yet largely ignored. Adding to a previous paper (Rice and McQuillan, 2018) presenting how hybridization can negatively impact both hybrids' cognitive abilities and fitness, thus creating an indirect link, Rice's perspective discussed further how hybridization impact on cognition could lead to positive fitness consequences and indirectly affect the expression of cognitive traits. By discussing how trade-offs between investment in cognition and other important functions, coupled with individual variation, can complicate patterns of selection on hybrid cognition, Rice questioned the role of cognitive performance in the maintenance of species boundaries, and the links between hybridization and the expression of, and selection on, cognitive traits in the wild.

Finally, when facing environmental variation, selection may favor flexible adjustment ability, and this may also apply to cognitive performance. In a mini-review, Cauchoix et al. compiled current evidence for such plasticity in cognitive performance, called "cognitive performance plasticity," in response to environmental conditions and proposed methodological approaches to measure it, highlighting its role when exploring the repeatability of cognitive performance.

Overall, this body of research provides the first comprehensive overview of constraints influencing the evolution of cognition in the wild, highlights the multiple ways by which cognition can be linked to fitness and the needs for further research on this question. In addition to presenting novel results and methods, several authors presented a number of compelling ideas and perspectives that will help us to improve our understanding of this field.

Author contributions

LC wrote the first draft. Both authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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An Experimental Test of a Causal Link between Problem-Solving Performance and Reproductive Success in Wild Great Tits

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Recent studies have uncovered relationships between measures of various cognitive performances and proxies of fitness such as reproductive success in non-human animals. However, to better understand the evolution of cognition in the wild, we still have to determine the causality of these relationships and the underlying mechanisms. The cognitive ability of an individual may directly influence its ability to raise many and/or high quality young through for example its provisioning ability. Conversely, large and/or high quality broods may lead to high parental motivation to solve problems related to their care. To answer this question, we manipulated reproductive success through brood size and measured subsequent problem-solving performance in wild great tit parents. Our results show that brood size manipulation did not affect the probability to solve the task. Moreover, solver pairs fledged more young than non-solver pairs independently of brood size treatment in one of the two experimental years and they showed higher nestling provisioning rate in both years. Overall, it shows that problem-solving performance was not driven by motivation and suggest that problem-solvers may achieve higher fledging success through higher provisioning rates. Our study constitutes a first key step toward a mechanistic understanding of the consequences of innovation ability for individual fitness in the wild.

Keywords: brood size manipulation, motivation, *Parus major*, problem-solving performance, provisioning rate, reproductive success

INTRODUCTION

Human activities currently generate major and rapid environmental changes at various spatio-temporal scales (e.g., climate change, urbanization, habitat fragmentation) that can strongly impact individual fitness in wild populations. To limit the negative impacts of these changes, animals may attempt to cope with the unexpected problems or situations by innovating, i.e., using novel or flexibly adjust established behaviors (Reader and Laland, 2003; Tebbich et al., 2010). Such ability shapes behavioral changes that are thought to facilitate a rapid response to novel environmental conditions before adaptive evolution can take place (Duckworth and Badyaev, 2007; Sutter and Kawecki, 2009). Yet, research on the consequences of innovation on behavioral adaptation in non-human animals and its contribution to fitness in the wild is still in its infancy.

Innovation may influence fitness through different ways. For example, innovation can increase survival by facilitating the exploitation of new food sources during harsh conditions (Kozlovsky et al., 2015; Edmunds et al., 2016). It can also enhance mating and reproductive success by facilitating the display of a new behavior or phenotypic trait favored during mate choice (Keagy et al., 2009; Mateos-Gonzalez et al., 2011; Isden et al., 2013) or the exploitation of resources that will directly influence young growth and/or survival (Cole et al., 2012; Cauchard et al., 2013). The first empirical evidence for a positive association between innovation and reproductive success in the wild came from two studies conducted on two different populations of great tits (*Parus major*) (Cole et al., 2012; Cauchard et al., 2013). In these studies, problem-solving performance (a proxy of innovation, Griffin and Guez, 2014), measured either in captivity (stick-pulling task motivated by food, Cole et al., 2012) or in the field (string-pulling task motivated by nestling provisioning, Cauchard et al., 2013), was linked to various measures of reproductive success. Nests where at least one parent solved the novel task laid larger clutches (Cole et al., 2012; Cauchard et al., 2013) and fledged more young (Cauchard et al., 2013), although this effect was counterbalanced by problem-solving females being more likely to abandon their nest after human perturbation in one of the populations (Cole et al., 2012).

However, the mechanisms underlying potential reproductive benefits of problem-solving performance remain poorly explored. Moreover, as our understanding of the proximal causes of among-individual differences in problem-solving performance has considerably improved in the last decade, it has become apparent that various other factors may generate an indirect link between problem-solving performance and reproductive success. For example, studies have shown that individual traits such as age (Loepelt et al., 2016; Quinn et al., 2016), novelty response (Sol et al., 2011), stress level (Bókony et al., 2013) or motivation (Laland and Reader, 1999) as well as external factors such as predation (Taylor et al., 2012), competition (Overington et al., 2009) or habitat quality (Quinn et al., 2016) can affect both problem-solving performance and reproductive success independently.

Therefore, an experimental manipulation is critically needed to disentangle cause and effect in the relationship between problem solving performance and reproductive success. Here we manipulated the reproductive success (i.e., reduced, control, or enlarged brood size) and recorded parents' subsequent problem-solving performance as well as nestling provisioning rate in a natural population of breeding great tits. We predicted that if reproductive success drives parental motivation to solve the task, parents with experimentally increased broods should be more successful at solving the task than parents with control broods and parents with control broods should be more successful than parents with decreased broods. Conversely, if higher problem-solving performance *per se* allows parents to raise more young, our experimental brood size manipulation should not affect parents' success in solving the task and solving pairs should still achieve higher reproductive success compared to non-solving pairs independently of the brood size manipulation. Moreover, beside the brood size manipulation, if problem-solvers are more efficient in exploiting their habitat, we predicted that solver pairs should achieve a higher nestling provisioning rate than non-solver pairs.

MATERIALS AND METHODS

Study Site and Population Monitoring

Data were collected in a population of great tits breeding on the island of Gotland, Sweden (57°10'N, 18°20'E), between April and June 2012 and 2013. Great tits are small, monogamous passerines that breed readily in nest boxes, allowing us to record laying and hatching date, clutch size, hatching success, brood size at different ages and final number of fledglings. Nestlings were ringed at day 9, weighed and measured (tarsus length, to the nearest 0.1 mm) at day 14. Nestling body mass at day 14 is a good proxy of future recruitment in this species (Linden et al., 1992). Adults were caught within nest boxes when nestlings were 9–14 days old and identified using individually numbered rings.

Birds were caught, handled and ringed under a license from the Stockholm Museum Ringing Center. Behavioral experiments were authorized by the Swedish Committee for Experiments on Animals and conducted in accordance with international standards on animal welfare as well as being compliant with local and national regulations.

Brood Size Manipulation

In our great tit population, brood size range from 3 to 12 nestlings, with an average ± SE of 8.06 ± 0.13. In total, 150 broods were manipulated. We created enlarged ($N = 57$), reduced ($N = 54$) and control ($N = 39$) broods by adding or removing two nestlings (i.e., an average 25% increase or decrease in brood size) or exchanging two nestlings between broods without changing brood size. The difference between reduced and increased brood size treatments was thus on average 40% (6 vs. 9 nestlings, see **Table 1**), which seemed sufficient to allow detecting differences in parental care. Studies have shown that brood size manipulation using quantitatively similar changes in brood size has significant consequences on parental feeding behavior, with provisioning rate being lowest when broods were reduced in size and greatest when broods were enlarged (Sanz and Tinbergen, 1999; Garcia-Navas and Sanz, 2010). We excluded from this experiment nests with extreme brood sizes before the manipulation (<5 or more than 10 hatchlings on day 2) and assigned treatment (reduced, control, or enlarged brood) randomly with respect to initial brood size. Two days after hatching, nestlings were exchanged between broods that hatched on the same day and matched the same average weight (mean brood weight per nest ± SD: 2.72 g ± 0.47, nests were grouped when the mean difference among nests was <1 g). Whenever possible, we used triplets of broods: four nestlings were transferred from a first nest (nest A) to a second nest (nest B), then four other nestlings from nest B to a third nest (nest C),

TABLE 1 | Least square means ± SE for reproductive variables according to experimental treatments (reduced: $N = 54$; enlarged: $N = 57$; control: $N = 39$) and year (2012: $N = 93$; 2013: $N = 57$).

	Brood size treatment						**Year**			
	Enlarged		**Control**		**Reduced**		**2012**		**2013**	
	Least sq mean ± SE	**Tukey HSD**	**Least sq mean ± SE**	**Tukey HSD**	**Least sq mean ± SE**	**Tukey HSD**	**Least sq mean ± SE**	**Tukey HSD**	**Least sq mean ± SE**	**Tukey HSD**
Laying date	34.38 ± 0.59	a	34.93 ± 0.70	a	34.31 ± 0.62	a	28.33 ± 0.47	α	40.75 ± 0.58	β
Clutch size	8.93 ± 0.17	a	8.93 ± 0.20	a	9.03 ± 0.18	a	9.07 ± 0.14	α	8.86 ± 0.17	α
Brood size at day 2	7.93 ± 0.21	a	8.22 ± 0.26	a	8.20 ± 0.22	a	8.12 ± 0.17	α	8.12 ± 0.22	α
BROOD SIZE MANIPULATION										
Brood size at fledging	9.21 ± 0.22	a	7.96 ± 0.26	a	6.08 ± 0.23	c	7.56 ± 0.17		7.94 ± 0.22	α

Results of Tukey HSD tests testing effects of brood size treatment and year are presented with English and Greek letters, respectively; a different letter is attributed to significantly different groups.

and finally two other nestlings from nest C to nest A. We thus reduced brood size by two nestlings in nests A, increased it by two nestlings in nests C and left it unchanged in nests B, which functioned as a control for having foreign nestlings without changing brood size. All broods thus contained either two (nests A) or four foreign nestlings (nests B and C). When we could not match three broods, we used duos by skipping the control treatment (nest B), and when more broods could be matched, we used quadruplets of nests by repeating the control treatment (nest B). In great tits, the number of native *vs.* foreign nestlings in a nest does not affect provisioning rate (Neuenschwander et al., 2003).

Provisioning Rate and Problem-Solving Performance

We recorded provisioning rate when nestlings were 6 days old, using a camouflaged video recorder placed at a distance of ∼6 m from the nest box. The recording lasted 90 min and was performed during the daily peak of parental provisioning activity, i.e., between 06:00 AM and 02:00 PM. In great tits, both parents feed their young. Because distinguishing males from females on provisioning videos was difficult, we measured nestling provisioning rate per breeding pair. We calculated pair provisioning rate as the total number of parental visits to the nest during 1 h.

Problem-solving performance was measured directly during breeding. At this stage, it is however not possible to keep birds long enough to test them in captivity, in controlled conditions, without directly compromising their reproductive success. Therefore, we chose to conduct the problem-solving task directly in the wild. In this situation, food-motivated tasks cannot easily be used since food is more abundant in the environment at that time of the year than for the rest of the year and individuals show little motivation to interact with such tasks. To overcome this issue, problem-solving performance was thus measured using a string-pulling task attached in front of the nest box for which the solving motivation stems from parents' drive to feed their young during the nestling rearing period (Cauchard et al., 2013). The task consisted of a door placed in front of the entrance of the nest box. The door was by default closed. To enter, parents had to pull a string placed below the door using their feet to open it and then slip their body under the door. The door then closed automatically behind the bird, but could be simply pushed open from inside the nest box by parents to get out. The test was conducted during the peak of nestling food demand (i.e., when nestlings were 7–9 days old, between 07:00 AM and 04:00 PM), only when nestlings were satiated (e.g., not begging intensely at the beginning of the test). To avoid nestling starvation if parents were not able to solve the task, the test lasted 1 h but was repeated on two consecutive days. We randomly selected breeding pairs to be tested among pairs separated by at least 200 m from the nearest neighbors previously tested, to avoid social learning. We installed a camouflaged video recorder at a distance of ∼6 m in front of the nest box to record all the movements and interactions of parents with the task. Video recordings were scored by observers blind to the brood size manipulation. Because the entrance of the nest was closed during the test, birds had to stop on the nest and the gender was thus identified thanks to plumage features. Individuals who succeeded in solving the task (i.e., opening the door and entering the box) were considered to be solvers, while those who contacted the nest box but failed to enter were considered to be non-solvers (i.e., we defined problem-solving status as a binary variable).

Statistical Analyses

We first checked whether nests in different brood size treatments (i.e., reduced, control, or enlarged broods) differed in reproductive parameters prior to the brood size manipulation (i.e., laying date, clutch size and number of nestlings at day 2) using linear models (LM) including brood size treatment, year (i.e., 2012, 2013) and their pairwise interactions as fixed effects. We proceeded as well to check whether the brood size manipulation was successful in affecting the final number of fledglings.

We then tested whether brood size manipulation affected parental problem-solving probability (i.e., solvers vs. non-solvers) using generalized linear mixed models (GLMMs) with a binomial error and logit link function. The model included brood size treatment, year, sex and the pairwise interactions between treatment and cofactors as fixed effects, and pair identity as a random effect to account for the non-independence of pair members.

Finally, we tested whether problem-solving performance affected measures of reproductive success and provisioning rate independently from the brood size manipulation. We conducted these analyses at the pair level to avoid pseudoreplication since both parents had the same measures of reproductive success and provisioning rate. We tested whether pairs where both parents were non-solvers (NN pairs), pairs where only one parent solved the task (NS pairs) and pairs where both parents solved the task (SS pairs) differed in nestling mean nestling body mass at day 14, final number of fledglings and provisioning rate at day 6 using LMs. The models included pair's problem-solving performance, brood size treatment, year and their pairwise interactions with problem-solving performance as fixed effects. When analyzing mean nestling body mass, we added mean nestling tarsus length as a covariate to control for the effect of structural size on body mass. To check whether reproductive parameters prior to the brood size manipulation may account for the differences in final reproduction success and provisioning rate between pairs of different problem-solving performance, we also included laying date and clutch size as fixed covariates in the models described above. Inclusion of these covariates did not change qualitatively our results on effects of pair solving performance. Hence, hereafter we are only presenting the reduced models.

Sample sizes varied slightly between analyses because of missing data. To avoid pseudoreplication, we removed from our data all 2013 pairs in which at least one parent was tested in 2012 ($N = 10$). Non-significant effects were backward eliminated from the starting models. Normality and homogeneity of variance as well as residuals were visually checked and data transformed when needed (in this case, the transformation used is mentioned in the results). All the analyses, including power analyses, were performed using JMP® (Version *11*. SAS Institute Inc., Cary, NC, 1989–2007) at the exception of the GLMM tests that were performed using the *glmer* function in R cran (Bates et al., 2015). Tests were two-tailed, and $P < 0.05$ were considered significant.

RESULTS

Differences between Treatment Groups Before and After the Brood Size Manipulation

Prior to brood size manipulation, nests of different experimental treatments did not differ in laying date [$F_{(2,\ 146)} = 0.25, P = 0.78$], clutch size [$F_{(2,\ 146)} = 0.10, P = 0.90$] or number of nestlings at day 2 [$F_{(2,\ 143)} = 0.55, P = 0.58$], accounting for year (**Table 1**). As expected, brood size manipulation successfully affected the final number of fledglings [$F_{(2,\ 146)} = 50.59, P < 0.001$], accounting for year. More nestlings fledged from increased broods (least square means ± SE: 9.2 ± 0.2) compared to control broods (8.0 ± 0.3), and more in control broods compared to decreased broods (6.1 ± 0.2) (**Table 1**).

Effect of Brood Size Manipulation on Problem-Solving Performance

Of the 150 pairs tested, nine males and eight females did not participate in the problem-solving test. The brood size manipulation treatment did not influence parental probability to solve the task either alone ($\chi^2_2 = 1.20, P = 0.55$) or in interaction with year ($\chi^2_2 = 1.45, P = 0.48$) or sex ($\chi^2_2 = 1.00, P = 0.61$). The probability to solve the task only depended on sex ($\chi^2_1 = 11.21$, $P < 0.001$), with females being more likely to solve compared to males (number of solvers: 58 of 142 (40.8%) females vs. 32 of 141 (22.7%) males).

Links between Problem-Solving Performance, Provisioning Rate and Reproductive Success Independently from the Brood Size Manipulation

Mean nestling body mass at day 14 did not differ between SS, NS and NN pairs [$F_{(2,\ 137)} = 0.95, P = 0.39$], accounting for the positive effect of mean nestling tarsus length [$F_{(1,\ 137)} = 167.26$, $P < 0.001$] and for differences between years [i.e., nestlings were heavier in 2012 than 2013; $F_{(1,\ 137)} = 5.82, P = 0.017$]. Brood size treatment had no effect on mean nestling body mass at day 14 either alone [$F_{(2,\ 137)} = 0.68, P = 0.51$] or in interaction with year [$F_{(2,\ 137)} = 0.13, P = 0.88$].

The final number of fledglings differed between pairs of different problem-solving performance, but this effect depended on year [interaction between pair problem-solving status and year: $F_{(2,\ 139)} = 5.12$, $P = 0.007$; **Figure 1**], after controlling for the effect of brood size treatment [$F_{(2,\ 139)} = 54.92, P < 0.001$]. In 2012, SS pairs fledged more young than NS and NN pairs [$F_{(2,\ 87)} = 7.18$, $P = 0.001$; **Figure 1**]. In 2013, there was no difference in final number of fledglings between pairs of different problem-solving performance [$F_{(2,\ 50)} = 1.46$, $P = 0.24$]. *Post-hoc* power analyses suggest that the absence of difference in 2013 is also due to a lower effect of problem-solving performance on the final number of fledglings in 2013 than 2012 ($\delta = 0.35$ vs. 0.58) rather than merely due to smaller sample sizes in 2013 than 2012 ($N = 55$ vs. 92). The effect of pair problem-solving performance on the final number of fledglings was independent of brood size treatment [i.e., non-significant interaction between problem-solving performance and brood-size treatment: $F_{(4,\ 135)} = 0.86$, $P = 0.49$].

Provisioning rates also differed between pairs of different problem-solving performance [provisioning rates Box-Cox transformed; $F_{(2,\ 103)} = 5.20$, $P = 0.007$; **Figure 2**], after controlling for the effects of brood size treatment [i.e., tendency for higher rates in enlarged vs. reduced broods; $F_{(2,\ 103)} = 2.98$, $P = 0.055$] and year [i.e., higher rates in 2012 than in 2013; $F_{(1,\ 103)} = 10.38$, $P = 0.002$]. SS pairs and NS pairs showed higher provisioning rates than NN pairs (SS vs. NN pairs: mean difference ± SE = 11.74 ± 4.40, $P = 0.024$; NS vs. NN pairs: 6.80 ± 2.78, $P = 0.043$; **Figure 2**). Because provisioning rate can vary between males and females in this species (Pagani-Núñez and Senar, 2013), we checked whether the sex of the solver influences the link between problem-solving performance and provisioning rate. We ran the same initial model using both female and male problem-solving status as fixed factors instead of pair problem-solving performance. Results showed that both were significant [males: $F_{(1,\ 95)} = 4.9$, $P = 0.028$; Females: $F_{(1,\ 95)} = 4.3$, $P = 0.040$].

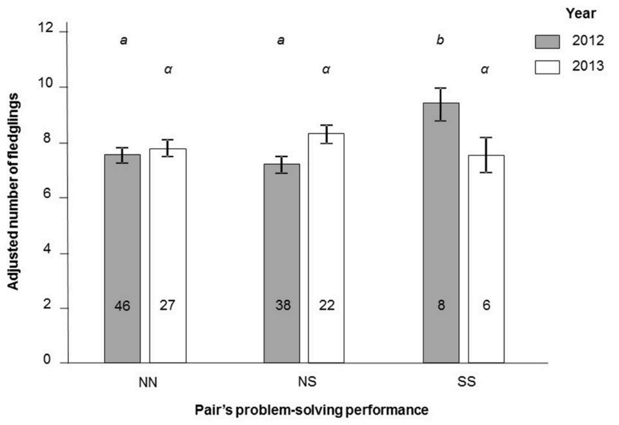

FIGURE 1 | Final number of fledglings (least square means ± SE) according to pair's problem-solving performance (NN, pairs where both parents were non-solvers; NS, pairs with one solver; SS, pairs with two solvers) and year (2012, 2013) in a natural population of great tits. Values are adjusted for the other significant effect of the model, i.e., effect of brood size treatment. Letters represent results of Tukey HSD test, where different letters are attributed to significantly different groups. Numbers are sample sizes.

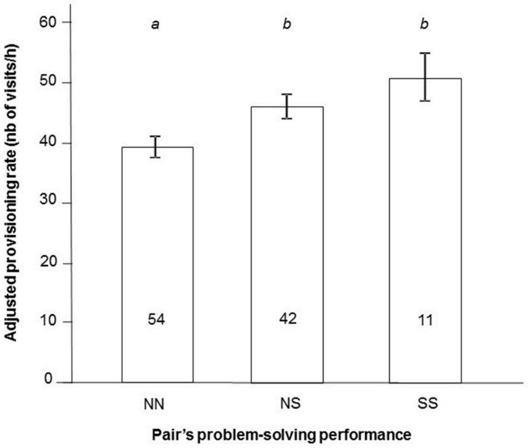

FIGURE 2 | Pair's provisioning rates (least square means ± SE) according to its problem-solving performance (NN, pairs where both parents were non-solvers; NS, pairs with one solver; SS, pairs with two solvers) in a natural population of great tits. Values are adjusted for the other significant effects of the model, i.e., effects of brood size treatment and year. Letters represent results of Tukey HSD test, where different letters are attributed to significantly different groups. Numbers are sample size.

DISCUSSION

Our first aim was to test the causality of the relationship between problem-solving performance and reproductive success in our study population. While the cognitive features of problem-solving (e.g., the cognitive and neurological processes of problem-solving) still need to be indentified, we experimentally showed here that parental motivation to solve the task, manipulated through the brood size manipulation (Sanz and Tinbergen, 1999; Garcia-Navas and Sanz, 2010), did not affect problem-solving performance, and thus could not generate the observed relation between problem-solving performance and reproductive success. Our results thus support the hypothesis that higher problem-solving performance *per se* might allow parents to raise more young. Accordingly, pairs' problem-solving performance was positively correlated to the final number of fledglings for each brood size treatment, although this relation was observed only in one of the two experimental years: in 2012, solver pairs fledged more young than pairs with at least one non-solver parent, beyond the brood size manipulation. Moreover, this positive correlation did not depend on brood size treatment (no significant interaction between problem-solving performance and brood size treatment). One could have expected problem-solving performance to affect the ability of the pair to cope with the manipulated reproductive effort differently depending on treatment, for example if solver and non-solver parents differ in their ability to cope with a change in parental work load and stress. On the one hand, all pairs could have achieved a similar reproductive success when brood size was decreased, i.e., when reproductive effort and thus the level of stress were low, while only pairs with high problem-solving performance may have been able to efficiently face an increased brood size if solvers better cope with stress. On the other hand, pairs with high problem-solving performance may have been able to face reproductive effort more efficiently than pairs with low problem-solving performance when brood size was reduced or unchanged, i.e., when the level of stress was low to moderate, but may not have been able to do so when the brood size was increased if solvers are not able to use their cognitive abilities adequately when stressed. Here, the ability of pairs with high problem-solving performance to achieve higher reproductive success than pairs with lower performance did not depend on the level of reproductive effort imposed through the manipulation, but depended on year. Taken together, these results provide support for the hypothesis that problem-solving performance may causally influence reproductive success in our study population, depending on environmental conditions.

At this stage, the origin of the difference in the relation between problem-solving performance and final number of fledglings between the two experimental years remains however unclear and deserves further studies. The absence of a significant difference between solvers and non-solvers in the final number of fledged young in 2013 was nonetheless not simply due to a lower sample size, but to a lower biological effect of problem-solving performance on reproductive success in that year. Although we cannot test this hypothesis because the experiment was performed in 2 years only, between-year variations in the environmental conditions might explain the difference between years observed. **Table 1** shows that birds laid eggs earlier in 2012 than in 2013 (which was an extremely late year for forest passerines in most parts of Europe), suggesting a difference in the environment between the 2 years because great tits synchronized their reproduction according to caterpillar (i.e., main food resource for nestlings) development (Naef-Daenzer and Keller, 1999). Moreover, nestlings were heavier in 2012 than in 2013, suggesting that the environmental conditions in 2013 might have been harsher than in 2012. In our study site, food availability during nestling rearing is the main environmental factor affecting reproductive success (nest predation is very low on Gotland due to the absence of mustelid species; Doligez and Clobert, 2003). The higher success in 2012 compared to 2013 suggests that environmental conditions were more favorable in 2012, but we have no direct measure of food availability in these 2 years. The observed difference between years in the link between pair problem-solving performance and reproductive success could therefore be due to higher costs paid by solving pairs in harsher conditions, but higher benefits in more standard conditions, possibly due to a higher ability to exploit the environment when provisioning nestlings. Although the link between pair problem-solving ability and provisioning rate was observed in both years, other variables related to parental care and thus influencing fledgling number might vary between solvers and non-solvers according to environmental variation (Récapet et al., 2016). Hence, the links between parental cognitive ability, food provisioning and fitness may be context-dependent and vary according to the environmental conditions. Further work is however needed at this stage to identify such traits. Exploring the relative role of environmental vs. individual quality would require performing the manipulation over many years to meet a larger range of environmental conditions.

Research in humans has shown that two types of motivation can affect the expression of any cognitive ability: intrinsic and extrinsic motivation (Sternberg, 1985). While the extrinsic motivation is generally defined as the process by which an expected reward (or punishment) drives a behavior, its intensity and direction, the intrinsic motivation originates from individual traits (e.g., curiosity, interest, perseverance) and does not require reinforcement (Sternberg, 1985). These two types of motivation are likely to also affect the performance to cognitive tests in non-human species too (Hull, 1933; Sol et al., 2012; Byrne, 2013). Sex, social status or satiety can affect an individual's motivational state that, in turn, can directly impact both performance on food-motivated tasks and reproductive success. Because the basic level of motivation is bound to differ between individuals, for example due to differences in metabolic rate and condition (e.g., total energy reserve, Clancey and Byers, 2014), controlling for the effect of such motivation in correlative studies may be difficult. Relying on non-food-motivated tasks to design problem-solving tests, such as a species' aversion to a particular color (Keagy et al., 2009) or parents' drive to provision their young (Cauchard et al., 2013), may thus provide interesting alternatives to food-motivated tasks to measure problem-solving performance while minimizing the effect of extrinsic motivation. Indeed, even if females were more likely to solve the task than males, reflecting a potential sex-bias linked to parental investment in intrinsic motivation to solve the task (i.e., males may be less motivated to invest and solve our task because of extra pair paternity frequently occurring in this species; Lubjuhn et al., 1999; Griffith et al., 2002; Doligez, pers. obs for the study population), this is unlikely to affect the link between problem-solving performance and provisioning rate in our study: both male and female solving status related to provisioning rate. Our task may have been intrinsically more motivating for females than males, because the reward (i.e., access to nestlings) was directly related to parental care (which has already been observed in another population of great tits: Preiszner et al., 2017). Fortuitously, such sex difference can easily be taken into account by modeling the effects of sex when studying problem solving performance. To better understand the role of intrinsic and extrinsic in problem-solving performance, further work is required based on experiments explicitly designed to quantify motivation sources, although this may again prove challenging in the field.

An important caveat is nevertheless that we cannot exclude that a third factor, thus far unidentified, independently influenced both problem-solving performance and reproductive success. The deleterious effect of oxidative stress along aging, for example, can negatively affect both cognitive performance and reproductive success (Finkel and Holbrook, 2000; Fukui et al., 2002; Bize et al., 2008; Monaghan et al., 2009), leading to a positive correlation between these two variables. A direct experimental manipulation of problem-solving performance would be needed to confirm the causal link to reproductive success, but this may involve procedures such as manipulating conditions during development to affect the ontogeny of cognitive abilities in future recruits, which may prove difficult to implement in the field. Further work is therefore needed to fully confirm that problem-solving performance shapes reproductive success. To better understand the evolutionary potential of innovation in the wild, a more comprehensive work is needed to examine its link with long term fitness (i.e., lifetime reproductive success) consequences and as well as its heritability level in natural populations, two questions that remain largely unexplored so far (Quinn et al., 2016).

The final aim of this study was to investigate provisioning as a possible mechanism underlying a potential causal link between problem-solving performance and reproductive success. Our results showed that, whatever the level of reproductive effort imposed, pairs with at least one solver consistently outperformed pairs with non-solvers on terms of food provisioning rate, which did led to greater number of fledgling in one of the two study years. Thus, the ability to innovate might allow parents to provision their young more efficiently, either by (i) choosing and/or securing a higher quality breeding territory, or (ii) finding and/or selecting more and/or higher quality preys (Cole et al., 2012). Accordingly, solver pairs fledged more nestlings than pairs with at least one non-solver parent, without having to trade-offs nestling numbers against quality, as mean nestling body mass was not lower for solver pairs. Previous studies in great tits also showed clear positive links of food provisioning with brood size, but not with mean nestling body mass (Mutzel et al., 2013), supporting the hypothesis that solvers were able to raise more nestlings, at least in some years, due to their greater capacity to provision their brood. Further investigations, with a particular attention to the importance of territory quality and/or provisioning efficiency, are needed to improve our understanding of the behavioral mechanisms underlying a potential causal link between problem-solving performance and reproductive success. By exploring the role of motivation on problem-solving performance and differences in provisioning behavior in relation to problem-solving performance in the wild, our study constitutes nevertheless a first key step toward a mechanistic understanding of the consequences of innovation ability for individual fitness in the wild.

AUTHOR CONTRIBUTIONS

LC and BD designed the study. LC, BA, NB, PB, and BD planned the research. LC and ML performed fieldwork. LC and PB analyzed data and all the co-authors contributed to write the paper.

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REVIEW
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Counter-Culture: Does Social Learning Help or Hinder Adaptive Response to Human-Induced Rapid Environmental Change?

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Human-induced rapid environmental change (HIREC) poses threats to a variety of species, and if or how it changes phenotypes is a question of central importance bridging evolutionary ecology and conservation management. Social learning is one type of phenotypic plasticity that can shape organismal responses to HIREC; it allows organisms to acquire phenotypes on a timescale that closely tracks environmental change while minimizing the costs of individual learning. A common assumption in behavioral ecology, is that social learning is generally an adaptive way to cope with HIREC by facilitating the rapid spread of innovative responses to change. While this can be true, social learning can also be maladaptive. It may hinder the spread of adaptive behavior by causing a carryover of old, no longer adaptive behaviors that slow the response to HIREC or even promote the spread of maladaptive behaviors. Here, we present a conceptual framework outlining how an organism's evolutionary history can shape cognitive mechanisms, social behavior, and population composition, which in turn affect how an organism responds to HIREC. We review quantitative theory and empirical evidence spanning the cultural evolution and behavioral ecology literature discussing how social learning helps or hinders organismal or species' responses to HIREC. We highlight how mismatch of social learning mechanisms and time-lags in a post-HIREC environment can slow or limit the acquisition of adaptive behavior. We then discuss how different pathways of cultural transmission and social learning strategies can help or hinder responses to HIREC. We also review how HIREC may interfere with the transmission process by altering the public information sent from sender to receiver through the environment before receivers acquire any public information. Lastly, we discuss gaps and future directions including how animals integrate personal and social information, the interaction between personality and social learning, and social learning between heterospecifics.

Keywords: social learning, rapid environment change, ecological trap, phenotypic plasticity, cultural evolution, communication, social learning strategies

1. INTRODUCTION

All organisms must respond to the challenges created by human-induced rapid environmental change (HIREC) including novel enemies (Mack et al., 2000), novel resources (Marczak et al., 2007), habitat change, loss/fragmentation (Goudie, 2013), human harvesting (Mace and Reynolds, 2001), novel contaminants (Walker et al., 2014), and climate change (Walther et al., 2002). While organisms have always encountered environmental change, HIREC is of particular interest because it is often characterized by changes that occur quickly and are more extreme; they are of a greater magnitude, occur more frequently, and affect larger spatial scales. HIREC also brings about a high degree of novelty (Candolin and Wong, 2012). Essentially, HIREC is an extreme, rapid change from that which animals have experienced in their evolutionary history. How well and how rapidly organisms adjust to these changes is critically important for both individual fitness and species persistence (Candolin and Wong, 2012; Sih, 2013; Wong and Candolin, 2015). Consequently, there has been increasing interest in examples of evolutionary responses to HIREC (Singer et al., 1993; Skelly et al., 2007) which often involve adaptive behavioral responses (Sih et al., 2011; Sih, 2013; Wong and Candolin, 2015). Notably, an animal's ability to learn and adjust behaviors within its lifetime might serve as a crucial mechanism that allows it to rapidly adapt to HIREC situations. That is, even if animals exhibit maladaptive initial responses to HIREC, if they survive, they can potentially adjust behaviors via learning (Sih et al., 2011). These learned behaviors, in turn, may be important for affecting a species' post-HIREC evolutionary trajectories (Baldwin, 1896; Maynard Smith, 1987; Chevin et al., 2010).

Social learning can serve as a key process through which information and adaptive responses spread within populations (Whitehead, 2010). Following Heyes (1994), we define social learning as "learning that is influenced by observation of, or interaction with, another animal or its products." This definition encompasses a variety of social learning processes where social factors influence the probability of acquiring public information (Danchin et al., 2004). Like individual learning, social learning is a type of phenotypic plasticity (West-Eberhard, 1989) that permits the acquisition of phenotypes on a timescale that more closely tracks environmental change, and with less of a time-lag, than genetic or epigenetic inheritance. Unlike individual learning, these phenotypes are inherited from others.

Quantitative models often assume that social learning has decreased costs and risks compared to individual learning; it outsources risk-taking and potentially costly mistakes to others (Boyd and Richerson, 1985; Aoki and Feldman, 2014). Cultural inheritance differs from genetic inheritance, as it occurs within an organism's lifetime and may utilize information from *multiple* demonstrators (or cultural parents), including genetically unrelated ones (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). Thus, the capacity for social learning to rapidly spread information and behaviors from a variety of demonstrators through a population makes it an important mechanism by which some species respond to rapid environmental change.

While there is compelling research on the ability of social learning to enhance responses to environmental change and its utility in conservation interventions (Whitehead et al., 2004; Whitehead, 2010; Greggor et al., 2016), our understanding of its potential to limit the spread of adaptive behavior in response to HIREC is lacking (Keith and Bull, 2017; Nieberding et al., 2018). The cultural evolution literature emphasizes the possibility that social learning leads to the spread of maladaptive behaviors or limits the spread of adaptive behaviors (Boyd and Richerson, 1985; Laland and Williams, 1998; Giraldeau et al., 2002). These limitations might be due to an over-reliance on social information after environmental change or the increased variance in fitness associated with social learning over individual learning. Social learning may also be maladaptive when an organism's social learning strategies, which evolved to allow individuals to cope with the volume and complexity of available social information in a population, lead to the acquisition of inaccurate information (Whitehead and Richerson, 2009). Additionally, social learning can result in maladaptive responses when offspring who rely on information from previous generations experience inertia, which hinders adaptive responses to change (Seppänen et al., 2007). This inertia, or time-lag, increases the likelihood that defunct information will be passed from demonstrators to observers, especially as the rate of environmental change increases (Rogers, 1988). Additionally, the interference of HIREC with the transmission of social information (i.e., the production, propagation, or detection of a signal) can result in a maladaptive response by an individual who is reliant on the disrupted signal (Patricelli and Blickley, 2006; Lürling and Scheffer, 2007; Ward et al., 2008). Broadly speaking, the overall benefit of social learning depends on the details of the social learning process, and how it is affected by HIREC.

Ultimately, whether a species' social learning response to HIREC is adaptive or maladaptive depends on its past environment (both within an individual's lifetime and on an evolutionary timescale), its current social learning pattern, and the type of HIREC it encounters. In this paper, we present a framework which connects these three factors to predict how social learning might facilitate or hinder organisms' adaptive responses to HIREC. Within this framework, we discuss the theory behind the evolution of social learning, the types of processes involved in social learning and the conditions under which particular types of social learning might make social learning maladaptive. These include the pathways of cultural transmission, or the generation from which an individual "inherits" the information, and social learning strategies, or the psychological mechanisms an individual uses to decide whom or what to copy. We also illustrate how HIREC might affect the propagation of social information through the environment from senders to receivers. Throughout the paper we present several HIREC scenarios and illustrate known examples, or potential examples, where social learning produces either adaptive or maladaptive responses to HIREC.

2. SOCIAL LEARNING AND HIREC: EMPIRICAL EXAMPLES

It may appear that the influence of social learning on individual responses to HIREC is well studied in behavioral ecology– particularly due to the pervasiveness of examples in popular culture like the spread of milk bottle-opening in blue tits (Hinde and Fisher, 1951). However, behavioral ecology lacks a cohesive framework for understanding when social learning facilitates adaptive responses to HIREC and when it results in maladaptive responses. **Table 1** summarizes empirical examples of social learning under environmental change associated with HIREC; it is not meant to be comprehensive but is instead a collection of case studies that illustrate the breadth of social learning responses to HIREC.

In addition to examples in which social learning is adaptive (Teitelbaum et al., 2016) and maladaptive (Szymanski and Afton, 2005) **Table 1** includes instances in which HIREC disrupts social learning from occurring (Shannon et al., 2013). Numerous human-induced changes, including pervasive environmental conditions (e.g., ocean acidification Ferrari et al., 2012, eutrophication (Fischer and Frommen, 2013) and culling of individuals (Shannon et al., 2013) can lead to a reduction in the availability of useful or accurate social information. This occurs either because information is never transmitted or because individuals no longer receive information that is transmitted.

Table 1 includes both lab and field studies. It is important to note that studying social learning in the field is extremely challenging both logistically and analytically (McElreath et al., 2008; Kendal et al., 2009b; Reader and Biro, 2010). Thus, despite the importance of field studies in understanding how social learning interfaces with HIREC, many of the current examples come from lab-based studies. In some cases, captive research may more clearly illustrate the nuances of social learning dynamics in a changing world, where researchers are able to understand detailed mechanisms that underlie learning processes (e.g., Chivers et al., 2016). However, manipulations in captivity are not always specifically or feasibly matched to realistic HIREC scenarios. To better understand the complexities of social learning in a changing world, more field and lab-based research is needed to examine social learning in systems currently experiencing HIREC or under conditions which closely mimic HIREC.

We excluded studies that address social learning in response to novelty or other environmental conditions not specifically linked to HIREC from **Table 1**. However, these excluded studies can help us generate predictions for how social learning leads to adaptive and maladaptive responses to HIREC. Thus, we include many of these excluded studies throughout this paper. As HIREC is a pressing source of change that numerous species will have to contend with, more work looking at responses to HIREC are needed. For example, studying cultural transmission from an anthropological comparative approach has stimulated much research effort toward understanding culture in non-human primates relative to other mammals. However, many 20th century primate studies are criticized for lacking ecological validity (Custance et al., 2002). Additionally, while many insects (e.g., bees) do socially learn (reviewed in Grüter and Leadbeater, 2014), we found few empirical examples with direct relevance to HIREC.

3. A FRAMEWORK FOR EXPLORING THE ROLE OF SOCIAL LEARNING IN SPECIES' RESPONSES TO HIREC

In this section and in **Figure 1** we present a framework for understanding the role of social learning in shaping individual, population or species level responses to HIREC. The specifics of an organism's social learning response begin with its evolutionary history (**Figure 1A**) where environmental traits, including the rate of environmental change, ease of innovation, benefits and costs of adaptive behavior, and social structure, shape three components of social learning: (1) the proportion of individual to social learners (**Figure 1B**), (2) social learning pathways (**Figure 1C**), and (3) social learning strategies (**Figure 1D**). HIREC may interact with these components, and make social learning a less adaptive strategy, by altering the environmental traits important to the efficacy of social learning mechanisms creating mismatches of previously adaptive learning mechanisms to a post-HIREC world or an increased time-lag to acquiring adaptive behavior (discussed in section 3.1.2). The effects of these mismatches and time-lags affect the frequency of individuals with adaptive behavior post-HIREC, q, (**Figure 1F**), which affects the rate of increase of adaptive behavior, dq/dt (**Figure 1G**). Prior to an animal acting upon social information and HIREC interacting with evolved social learning mechanisms, HIREC may also directly affect the transmission process (**Figure 1E**). It can interfere with the ability of the demonstrator to transmit social information, the propagation of social information through the environment, or the ability of a receiver to acquire and process transmitted information.

3.1. Rates of Environmental Change and the Evolution of Social Learning

To better understand how HIREC interacts with social learning, it is important to understand the conditions that favor the evolution of social learning and how learning relates to environmental change more generally. Learning, whether it is individual or social, is adaptive when environments change. A common intuition, particularly in behavioral ecology, is that social learning is adaptive *simply* because it saves organisms the costs or risks of individual learning. However, there are additional nuances to the evolution of social learning.

Individual learning is a form of phenotypic plasticity- it is often favored over fixed, innate behaviors when the environment changes (Stephens, 1991; Dukas, 2008). However, individual learning (also called "sampling" in the behavioral ecology literature) is assumed to come with some cost. These costs include time-costs and lost foraging opportunities (Stephens and Krebs, 1986) or increased predation risk (Sih, 1992; Griffin, 2004). Social learning and the utilization of public information is often assumed to be adaptive because it decreases the costs of individual learning by utilizing the experiences of others as

TABLE 1 | Empirical examples of how social learning interacts with HIREC for multiple taxa (mammals, birds, fish) and types of HIREC.

References	Year	Taxon	Common name	Species name	Type of HIREC	Adaptive/Maladaptive
Teitelbaum et al., 2016	2016	Bird	Whooping cranes	*Grus americana*	Climate Change/ habitat Change	Adaptive
Szymanski and Afton, 2005	2005	Bird	Mallards	*Anas platyrhynchos*	Human harvesting	Maladaptive
Hinde and Fisher, 1951	1951	Bird	Blue tit	*Cyanistes caeruleus*	Novel food	Adaptive
Ducatez et al., 2013	2013	Bird	Barbados bullfinch, lesser antillian bullfinch, bananaquit	*Loxigilla barbadensis, Loxigilla noctis, Coereba flaveola*	Novel food	Adaptive
Fischer and Frommen, 2013	2013	Fish	Three-spined stickleback	*Gasterosteus aculeatus*	Eutrophication	Unclear
Lienart et al., 2016	2016	Fish	Damselfish	*Pomacentrus moluccensis*	Increased temperature/habitat change	Maladaptive
Chivers et al., 2016	2016	Fish	Ambon damselfish, nagasaki damselfish	*Pomacentrus amboinensis, Pomacentrus nagasakiensis*	Introduced predator, habitat change	Maladative/Adaptive
Lindeyer and Reader, 2010	2010	Fish	Zebrafish	*Danio rerio*	Introduced predator, habitat change	Mixed
Ferrari et al., 2012	2012	Fish	Damselfish	*Pomacentrus moluccensis*	Ocean acidification	Maladaptive
Ward et al., 2008	2008	Fish	Banded killifish	*Fundulus diaphanus*	Pollution	Maladaptive
Fouda et al., 2018	2018	Mammal	Bottlenose dolphin	*Tursiops truncatus*	Habitat change	Mixed
Ohashi and Matsuzawa, 2011	2011	Mammal	Chimpanzee	*Pan troglodytes*	Human harvesting	Adaptive
Shannon et al., 2013	2013	Mammal	African elephant	*Loxodonta africana*	Human harvesting	Maladaptive
Mazur and Seher, 2008	2008	Mammal	Black bear	*Ursus americanus*	Novel food	Mixed
Sigaud et al., 2017	2017	Mammal	Bison	*Bison bison*	Novel food	Maladaptive
Schakner et al., 2014	2014	Mammal	Sperm whale	*Physeter macrocephalus*	Novel food/habitat change	Mixed
Schakner et al., 2016	2016	Mammal	California sea lions	*Zalophus californianus*	Novel food/habitat change	Mixed
Weinrich et al., 1992; Allen et al., 2013	1992; 2013;	Mammal	Humpback whale	*Megaptera novaeangliae*	Novel food/habitat change	Adaptive

The Adaptive/Maladaptive column shows if the response of social learning to HIREC is adaptive, maladaptive, mixed, or unclear. Mixed responses show evidence of adaptive and maladaptive responses. Examples that are unclear have or not had the consequences of social learning in response to HIREC thoroughly tested in the study are excluded.

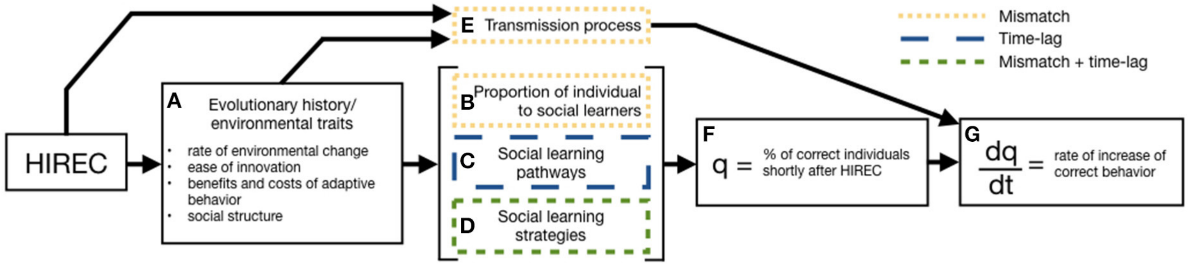

FIGURE 1 | Role of social learning in a species' response to HIREC. A species' evolutionary history, and the environmental traits associated with it, **(A)** shapes a number of factors important to social learning to produce an adaptive or maladaptive response. These factors include the percent of individual and social learners in a population **(B)**, the social learning pathways **(C)** and strategies **(D)** they exhibit, and the transmission of information between individuals **(E)**. HIREC can influence percent of individuals exhibiting the correct behavior shortly after HIREC **(F)** by changing environmental traits important for social learning mechanisms affecting the efficacy of these mechanisms and ultimately altering the rate of increase in correct behavior **(G)**. It can also impact the rate of increase by altering environmental traits which subsequently disrupts the information transmission process. HIREC disrupts these social learning traits by either creating a fitness mismatch (yellow, dotted boxes) between behaviors in the pre- and post-HIREC environments, by increasing the time-lag (blue, long dashed box), or a combination of the two (green, short dashed box).

proving grounds for whether a new behavior is adaptive. Thus, if the costs of individual learning relative to the benefits of adaptive behavior are sufficiently high, we might predict that social learning is likely to occur.

In addition to the cost of individual learning, innovating a novel solution can be very challenging. Innovations in wild populations are rather rare and many of them do not spread socially (Perry et al., 2017). There are also many "failed" innovations that must be tried before an adaptive one spreads (Miu et al., 2018) and social incentives (i.e., increased status in the eyes of others) might be important for their transmission (Arbilly and Laland, 2017). If adaptive innovation is rare, the evolution of social learning might be favored to propagate novel solutions.

A common intuition, particularly in behavioral ecology, is that social learning is adaptive *simply* because it saves organisms the above mentioned costs or risks of individual learning. However, there are additional nuances to the evolution of social learning. We explore these nuances with the aid of a development of one of the simplest and best-studied gene-culture coevolution models (Rogers, 1988). In contrast to Rogers' original model, this version assumes infinite environmental states and innovation error.

We use this model to discuss three factors that are widely thought to have an important role in affecting when or if social learning is advantageous relative to individual learning: (1) the cost, c, of individual learning relative to the benefit, b, of adaptive behavior, (2) the ease with which an adaptive behavior may be innovated, s, and (3) the rate of environmental change, u, in an organism's evolutionary history. These three factors affect how organisms respond to environmental change, and insights from this model can be used to explore the direct and indirect impact of these factors on responses to HIREC.

For simplicity we model two fixed phenotypes, social learners that exist at a frequency of p and individual learners that exist at a frequency of $1 - p$. Generations barely overlap- adults live just long enough to transmit behavior to juveniles before dying. The environment can change states once in each generation with a probability of u. This change, if it happens, occurs after individuals have an opportunity to socially learn, but before they use their strategy to cope with the environment. Individual learners, conversely, do not inherit adaptive behaviors from the previous generation. Instead, upon encountering a stimulus they try to innovate a solution and generate an appropriate novel phenotype. What was adaptive in previous environmental states or whether the environment recently changed does not affect their behavior. Adaptive behavior adds to baseline fitness a benefit of b. Non-adaptive behavior has zero benefit, leaving individuals with their baseline fitness, w_0.

Individual learning always has a cost, c, regardless of whether individuals innovate successful behavior. In addition to this cost, only s proportion of innovations, regardless of environmental state, are adaptive (i.e., increase fitness by b).

Assuming $b > c$ the fitness of individual learners is:

$$W(I) = w_0 + sb - c \tag{1}$$

Note that the fitness of individual learners is not affected by environmental change, nor does it change over time.

We assume social learners acquire their phenotype by randomly copying a member of the previous generation via oblique transmission. A proportion of behaviors Q copied from the previous generation are adaptive at time t. The fitness of social learners is a function of time and is determined by the frequency of adaptive behavior copied from the previous generation Q_t multiplied by its fitness benefit, b:

$$W_t(S) = w_0 + Q_t b \tag{2}$$

When adaptive behavior is common (Q_t is high), social learners can do well since most learn from other individuals that exhibit the adaptive behavior without paying the costs of innovation.

Q_t, the frequency of adaptive behavior in the current timestep copied from the previous generation has its own recursive dynamics and it is embedded in the recursion above:

$$Q_t = (1 - u)\big((1 - p)s + pQ_{t-1}\big) \tag{3}$$

Each phenotype produces offspring proportional to the above fitness functions. If the environment *does not* change after social learning at time t (i.e., $u = 0$), social learners may acquire adaptive behavior from individuals in the previous generation that existed at a frequency of Q_{t-1}. If the environment *does* change in the first time step (i.e., $u = 1$), then none of the behavior social learners acquired from the previous generation is adaptive. After an environmental change, only individual learners can innovate the new adaptive behavior. Thus immediately after environmental change, the frequency of adaptive behavior is proportional to $(1 - p)s$: the *(proportion of individual learners in the population)* $\times$ (*the ease of adaptive behavioral innovation*). However, by the next time step, juvenile social learners can learn the adaptive behavior from adult individual learners who successfully innovated immediately after change. If most individuals are social learners (i.e., individuals that do not innovate), then for some time after environmental change, most social learners continue to adopt the old, now maladaptive behavior, and thus do poorly compared to individual learners (Equation 2). This 'inertia of tradition' slows the population's response to HIREC (**Figure 1G**).

These dynamics are illustrated in more detail in **Figure 2**. In the first time step after each environmental change (before individual learners can innovate), the frequency of adaptive behavior drops to zero (**Figures 2A,C** in blue). Social learners thus learn the old, now maladaptive, behavior which decreases their fitness to baseline and decreases their frequency in the population relative to individual learners (**Figures 2B,D** in red). Each successive environmental change is marked by a number indicating the timestep and an arrow on the x-axis. Panels a and b show these dynamics in a relatively stable environment ($u = 0.05$), while c and d show dynamics in a more rapidly changing environment ($u = 0.25$). At the beginning of the simulation, the population is at $p = \hat{p}$, the steady state of the frequency of adaptive behaviors specified in Equation 4.

In the less stable environment, frequent environmental changes keep the frequency of social learners low (**Figure 2C**). However, because most of the population consists of individual learners who have a high chance (80% in this simulation) of innovating the new adaptive behavior, both the frequency of adaptive behavior and thus the fitness of social learners rebounds rapidly (**Figure 2D**). Because social learners avoid the cost of individual learning, they increase in prevalence. However, before the frequency of social learners can get high, the next environmental change occurs and knocks the proportion of social learners back down (**Figure 2D**).

In contrast, in relatively stable environments, if adaptive behavior has had time to become common (**Figure 2B**) social learners avoid the cost of individual learning while generally learning the adaptive behavior (from either individual learners or other social learners). As long as the environment does not change, social learners gradually increase in prevalence and after a long period of stability, may approach fixation (**Figure 2A**). However, after the next environmental change, if most individuals are social learners, only a few individual learners are present to innovate the new adaptive behavior. Social learners thus continue to adopt old, non-adaptive behaviors primarily from other social learners. The population then has a low dq/dt and exhibits low resilience following environmental change; in other words, it takes a long time for the frequency of adaptive behavior (**Figure 2B**, see, in particular, the lag in recovery after changes in time steps 25 and 80) and the fitness of social learners to rebound. During this recovery phase the frequency of social learners declines because the fitness of social learners is low. Still, as long as environmental change remains infrequent, social learners continue to stay common (**Figure 2A**) and this continues to reduce the population's resilience to environmental change.

Note that in a very stable environment, organisms can evolve to rely on adaptive, innate tendencies instead of learning (Stephens, 1991; McNamara et al., 2016) (e.g., on islands that have always lacked major predators, prey are often bold and do not readily learn about novel dangers). In contrast, low to intermediate rates of change tend to favor social learning while frequent, rapid change favors individual learning that allows for the rapid adoption of novel adaptive behaviors. This trend is a specific case of the conventional wisdom that organisms that have evolved with environmental change are more ready for HIREC.

Although ongoing environmental change produces a cycle of decline and recovery of social learners after each change, it is useful to solve for the long-term steady-state frequency of social learners, and the invasion conditions for social and individual learners as that may provide insight.

To solve for the genetic steady state of social learners, we may solve the simultaneous system of equations:

$$\begin{aligned} W_t(S) &= W(I) \\ Q_t &= Q_{t-1} \end{aligned}$$

for $\hat{p} = p$ and $\hat{Q} = Q_{t-1} = Q_t$ there is a unique solution for the equilibrium values (denoted by hats) of the frequency of social learners and adaptive behavior:

$$\hat{p} = \frac{1 - usb/c}{1 - u} \qquad \hat{Q} = s - \frac{c}{b} \tag{4}$$

Examining the invasion dynamics by setting $p \approx 0$ we find that social learners may invade a population of individual learners when $W(I) > \hat{W}(S)$ or:

$$u < c/sb$$

Setting $p \approx 1$, individual learners may invade a population of social learners when $W(I) < \hat{W}(S)$ or:

$$sb > c$$

It is easier for social learners to invade if they are sufficiently rare relative to individual learners (when p is small). This is a consequence of social learner fitness decreasing as p increases, yielding similar information-parasitism dynamics as the producer-scrounger game (Barnard and Sibly, 1981). A broad parameter space favors a mix of individual and social learners. Additionally, a substantial number of maladaptive

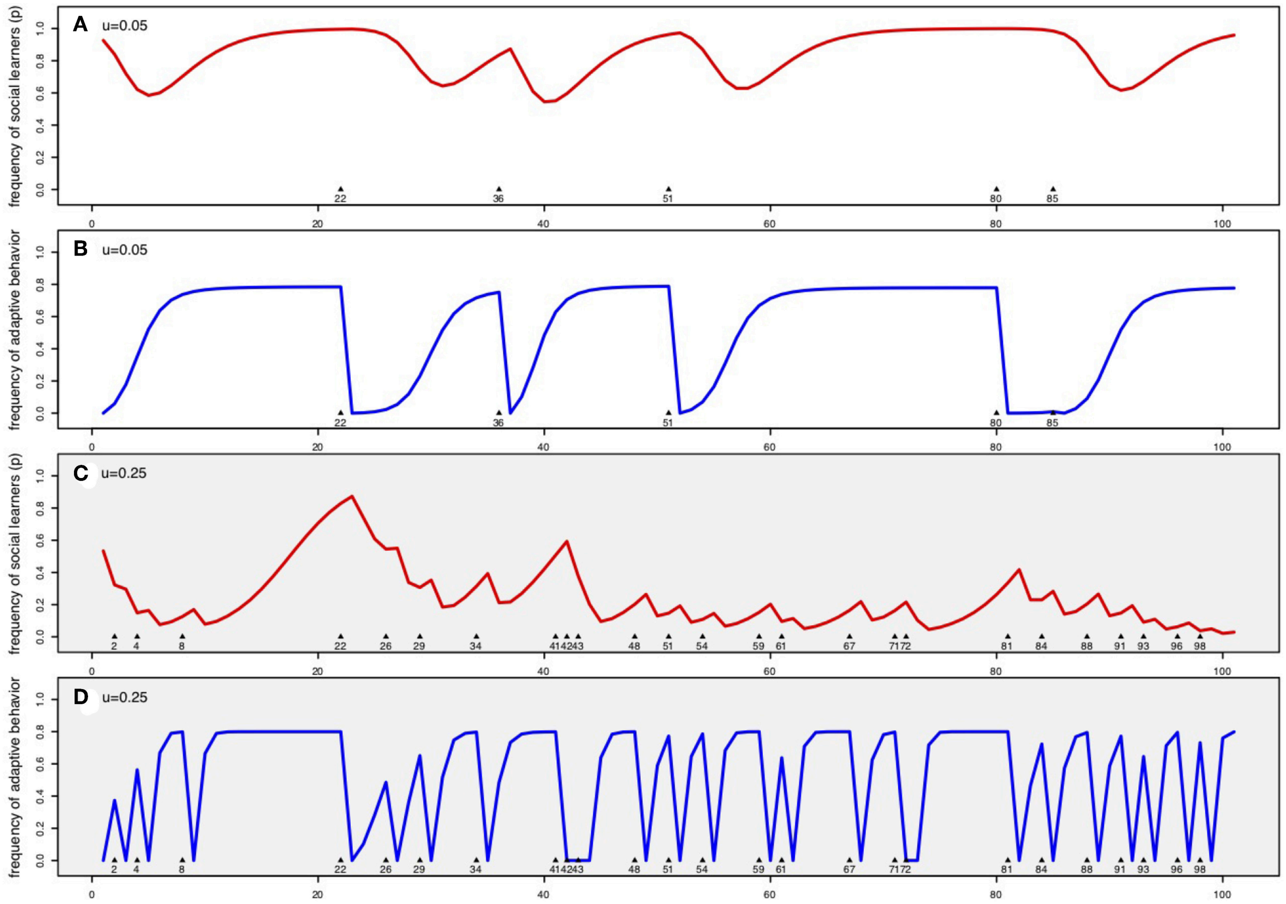

FIGURE 2 | Dynamics of the frequency of social learners, *p* (a,c in red) and the frequency of adaptive behavior *Q* (b,d in blue) under a continuous states version of the Rogers' model with innovation error. **(A,B)** (white background) are in a relatively stable environment where $u = 0.05$; **(C,D)** (gray background) are in a less stable environment where $u = 0.25$. Arrows on x-axis indicate where the environment changes states, rendering socially learned behavior from the previous generation non-adaptive. In this simulation $w_O = 1$, $s = 0.8$, $b = 3$ and $c = 1$. Simulations were initialized with $Q_{t=1} = 0$ and $p = \hat{p}$.

behavior and social learners can be maintained at equilibrium–particularly under a range of parameter conditions when both innovation is hard (i.e., lower *s*) and the rate of environmental change is moderate to high. Due to the risk of environmental change, a rare social learner is always better off in a group of individual learners whose frequency of adaptive behavior is unaffected by environmental change. This reduces the 'inertia of tradition' that affects social learners. This inertia is minimized in conditions that favor a lower $\hat{p}$– populations with fewer social learners on average. We might predict that organisms who evolved in ancestral conditions that favor a low $\hat{p}$ might fare better in HIREC scenarios as they may more quickly recover immediately after change.

Intriguingly, Rogers (1988) showed that at the mixed ESS conditions of $\hat{q}$ and $\hat{p}$, the mean fitness of social or individual learners is never higher than either pure equilibrium. This is also true when social learners selectively copy individual learners (Boyd and Richerson, 1995). This suggests that something other than simply saving the costs of individual learning is important for social learning to evolve. This observation is commonly referred to as "Rogers' Paradox."

Since the illustration of Rogers' Paradox, theoreticians have found multiple situations where social learning can raise population mean fitness such as spatial heterogeneity (Aoki and Nakahashi, 2008; Rendell et al., 2010), or when animals use "social learning contingencies" or combine individual with social learning (Boyd and Richerson, 1995; Enquist et al., 2007; McElreath et al., 2018). Under certain conditions, learning biases (e.g., a tendency to learn from successful individuals) often provide particular contexts where social learning is adaptive compared to random copying (reviewed in Aoki and Feldman, 2014). The broad point is that the specifics of social learning can have major effects on the adaptive benefits of social learning.

3.1.1. Evolutionary History Shapes Species' Response to HIREC

A key element in predicting a species' or population's response to HIREC is understanding the organisms' evolutionary history and how it shapes their ability to innovate adaptive behavioral responses to the novel conditions post-HIREC (**Figure 1A**).

If only individual learners can innovate, populations that have evolved to rely heavily on social learning will generally have a poorer response immediately after HIREC (see **Figure 2**). Of course, even populations with numerous individual learners will only respond well to HIREC if individual learners have a high probability of successful innovation, *s*. With regard to *s*, some species are simply better at domain general problem solving (Deaner et al., 2006; Reader et al., 2011) and likely have a higher probability of innovating adaptive behavioral responses to novel situations. In addition, all else the same, species that have evolved in highly variable environments (in space or time) will have experienced a history of selection favoring the ability to innovate that should result in higher *s*. This is the case unless they have typically experienced situations that are so novel that the required new behaviors have been exceptionally difficult to innovate (sometimes referred to as innovative "leaps" Miu et al., 2018). Notably, species that have experienced highly variable conditions should also have evolved a high proportion of individual learners (**Figure 2C**, Equation 4). The proportion of individual to social learners also depends on the cost of individual learning. Foragers that evolved in areas with high predation regimes or herbivores who evolved in areas with many toxic plants might have high costs of individual learning or sampling and thus be more likely to use social learning.

Evolved life history, social systems, and demographics are also important for understanding how social learning may affect species' responses to HIREC. At a basic level, generational overlap is necessary to provide access to older individuals who are repositories of knowledge to cope with ecologically rare events. However, older individuals may also have outdated information if environments change within their lifetime. More detailed effects of social systems can come via effects on patterns of interaction (social networks) that influence social learning pathways (e.g., horizontal vs. vertical or oblique transmission) and social learning strategies (section 3.3). That is, the evolved social system and life histories affect how many demonstrators are available to copy and what cues are available to utilize in a social learning strategy (e.g., a tendency to learn from others based on their age, sex, relatedness, or rank).

3.1.2. Mismatch and Time-Lags Affect Social Learning's Utility Post-HIREC

Immediately after HIREC, individuals and populations can suffer substantial reductions in fitness if their formerly adaptive behaviors are now mismatched and yield substantially lower fitness benefits than the new, adaptive behavior. While it is possible that previously adaptive behaviors are exaptations that happen to match adaptive behaviors post-HIREC (Gould, 1991), we focus here on mismatches. If the mismatch is severe enough it can cause population declines and even extirpation (Whitehead and Richerson, 2009).

As noted above, social learning can underlie maladaptive population responses to HIREC. For instance, social information about high quality resource patches or social facilitation (e.g., conspecific attraction) often permits animals to efficiently locate habitats with abundant resources (Valone and Templeton, 2002). HIREC, however, may render the use of social information less beneficial or even riskier (see **Table 1** for examples). This mismatch is often exploited by humans and is sometimes referred to as a "social trap." For example, hunters use spinning wing decoys which mimic the appearance and movement of their target bird, mallard ducks, to lure them to hunting sites (Szymanski and Afton, 2005).

At a population level, the fitness cost of mismatched behavior after HIREC is even larger if social learning contributes to a time-lag in the spread of adaptive behavior. The time-lag for adaptive behavior to spread depends not only on the frequency of social learners (as displayed in Equation 3 and **Figure 2**) but also on the population density, the species' life history (e.g., whether they have overlapping generations) and social system (e.g., group size and social networks), and what social learning strategy they employ (see section 3.2 for an example in rats). In order to display an adaptive social learning response and minimize time lag, animals must interact sufficiently frequently, exhibit key behaviors at the appropriate time, and have the capacity to adopt novel behavior at the time of their exposure (Beck and Galef, 1989; Pike and Laland, 2010; Slagsvold and Wiebe, 2011; Thornton and Clutton-Brock, 2011). Animals living in small social groups or with limited social interactions may be unlikely to observe adaptive behavior or be more prone to suffer from time-lag post-HIREC and fare poorly. Animals that learn from a broader pool of demonstrators might better respond to HIREC than those which might only learn from a subset of potential demonstrators in a population.

3.2. Social Learning Pathways

Social learning permits inheritance of behavioral phenotypes within and across generations from many cultural parents via different social learning pathways (**Figure 1C**) (Cavalli-Sforza and Feldman, 1981). Individuals may learn behavior from their biological parents, a process referred to as vertical transmission. They may also use oblique transmission, and copy behavioral phenotypes from all possible adults in the previous generation. Individuals may also acquire their behavior from cohort mates within their generation, a process known as horizontal transmission.

HIREC may favor oblique or horizontal transmission over vertical transmission. Vertical transmission is more prone to time-lag than oblique transmission, and therefore only evolves at low levels of environmental change. Oblique and horizontal transmission provide the advantage of better accessing individual learners, and they can more quickly respond to environmental change unless natural selection is strong. The ability of sampling a broader pool of individuals simply increases the odds of acquiring adaptive behavior over relying on gaining it from one or two parents. However when selection maximizes fertility, copying one's parents is more likely to be adaptive– a child's existence is an honest indicator that its parents were doing something right. Thus, the conditions where we would predict vertical transmission to evolve is in behavioral domains that affect fertility rather than survival, when the behavior's effective environment is stable, and when natural selection is strong

(McElreath and Strimling, 2008). In the context of HIREC, species that have limited access to oblique transmission (i.e., those that only interact within family-unit social systems) might respond poorly to environmental change given our predictions.

The hypothesis that oblique transmission copes with novelty better than vertical transmission is supported by empirical work in rats. Juvenile rats socially learn about the location of food and what to eat by following adults to food sources. Different species, however, rely on different social learning pathways and strategies. Norway rats have a tendency to incorporate foods into their diet that they smell on other adults via oblique transmission; they are very hesitant to consume foods they do not smell on other rats. In contrast black rats have a very strong preference for vertical transmission (mother to offspring) during a critical period. While both species are globally widespread, Norway rats have replaced black rats in recent years in many anthropogenically altered landscapes through much of the world. This may be in part because the rapid change at which novel food sources have been introduced in recent years may favor a flexible learning system such as oblique transmission over vertical transmission (Chou et al., 2000; Richerson, 2019).

Horizontal transmission, or copying age-mates, might also be less prone to time-lag issues than oblique and vertical transmission. This is especially true if organisms have a sensitive window (Fawcett and Frankenhuis, 2015) for social information, and older generations are less likely to sample or update information about the environment, as has been empirically supported in several species (Aplin et al., 2017; Barrett et al., 2017).

While oblique and horizontal transmission are typically prone to less time-lag, vertical transmission may be adaptive when historical knowledge about habitat quality and movement are important. The use of older individuals as repositories of knowledge has evolved in many social species and if the benefit of the information held by those individuals has not changed in a post HIREC world, their removal can be detrimental to a population's response to HIREC. The danger of removing the older, keystone individuals (Modlmeier et al., 2014) is particularly prevalent in transmitting knowledge about migratory pathways. Experimental translocations and relocations of bighorn sheep show that populations that maintained older, more knowledgeable individuals migrated more consistently and were able to find better forage (Jesmer et al., 2018). Herring develop migratory patterns early in life based on the migratory behavior of older conspecifics. However, fishing typically targets older, larger individuals. After some herring fisheries were reduced to two percent of their original size, the number of spawning sites reduced dramatically making populations of herring increasingly vulnerable to possible disturbances at the remaining spawning sites (Corten, 2002). Thus, the reliance on older individuals through oblique transmission may force individuals into maladaptive spawning decisions as a consequence of targeted over-fishing.

Ultimately, there exists an inherent tension in the costs and benefits of horizontal, oblique and vertical transmission. Individuals who have survived their juvenile stage almost certainly have some adaptive behaviors, making them a repository of information for rare events that have occurred within their lifetime. However, when the environment is likely to change, horizontal transmission may be more adaptive than oblique or vertical transmission, especially if age-mates are likely to innovate or if adaptive behaviors differ across age classes.

Perhaps one way to successfully cope with HIREC is to facultatively switch between transmission pathways. Experimental studies suggest that captive Zebra finches who were treated with cortisol, a stress hormone, relied primarily on oblique transmission when acquiring social information about a foraging task. Untreated control juveniles instead relied primarily on vertical transmission (Farine et al., 2015b). Vertical transmission often outperforms oblique transmission in very stable environments, whereas oblique transmission is better when the environment is changing. Thus switching from vertical transmission to oblique transmission might be adaptive if stress is a reliable cue that the environment has changed (i.e., juveniles are stressed because their parents fed them poorly in a post-HIREC environment).

3.2.1. Learning Pathways, Critical Periods, Sensitive Windows, and HIREC

Which social learning pathway to rely on becomes increasingly complicated if individuals change their propensity to socially learn within their lifetime. Critical periods are limited time windows in an organism's life where they are capable of learning, while sensitive windows are periods where individuals are more likely to update information and show plasticity within their lifetime (Fawcett and Frankenhuis, 2015). The ability to learn may decrease over development due to neurological changes or priorities shifting away from information acquisition toward other activities such as reproduction. The most well studied example of critical periods and social learning is bird song. Passerines, parrots, and hummingbirds learn songs via oblique or vertical transmission as juveniles. They then practice and refine this song. Later in development, testosterone causes neurological changes where the song types crystallize (Marler et al., 1988) and many, but not all (Nottebohm et al., 1987), birds lose the cognitive machinery to socially learn songs. In several species diet preferences (Terkel, 1996; Chou et al., 2000) and extractive foraging behaviors (Tebbich et al., 2001) may only be socially learned during critical periods.

Species that have a critical period or sensitive window, might fare poorly compared to open-ended, completely plastic learners post-HIREC. Juveniles that learn socially primarily when young (with little later updating) are more likely to copy older adults with outdated behavior. These same adults are also incapable of switching to a new behavioral optimum post-HIREC. If the environment changes, and cues that were learned to be useful during the juvenile critical period become less adaptive or dangerous, species with sensitive windows may do poorly. Thus, animal groups that are mostly comprised of post-critical period individuals, as a result of high survivorship from juvenile stage to adulthood or longevity, may do poorly post-HIREC. $\hat{Q}$ (the proportion of correct individuals shortly after HIREC) will be low and dq/dt (the rate of increase of correct behavior) will be slow.

3.3. Social Learning Strategies and Transmission Biases

Unbiased social learning might be an unrealistic expectation for many organisms. Some individuals may not have access to all available information in a population for reasons unrelated to cognition (Coussi-Korbel and Fragaszy, 1995; Barrett, 2018). More importantly, many organisms have transmission biases (Boyd and Richerson, 1985) or social learning strategies (Laland, 2004) that can help them hone in on adaptive behavior.

Social learning strategies refer to the psychological heuristics (or cognitive shortcuts) individuals use to choose whom or what to copy from a sea of multiple potential demonstrators and stimuli (Boyd and Richerson, 1985; Henrich and McElreath, 2003; Laland, 2004). These heuristics often have a speed/accuracy trade-off. Certain biases might help individuals hone in on an optimal (or good enough) behavior or demonstrator(s) to copy immediately post-HIREC. However, they also may have other risks associated with them as previously adaptive cues used in heuristic decision-making may not be adaptive post-HIREC (**Figure 1D**).

Various factors affect the costs and benefits of different social learning strategies. Individuals often must choose whom to learn from among *multiple* demonstrators who may differ in utility across social and ecological contexts. Acquiring and processing all available social information, when possible, may also be costly or impossible. Information acquired from particular demonstrators likely varies in utility among individuals (i.e., juveniles may not benefit from learning behaviors adaptive to adults). However, heuristics are not always optimal, and particular HIREC scenarios may render previously adaptive heuristics maladaptive. Various taxonomies have been made of the variety of social learning strategies (Henrich and McElreath, 2003; Rendell et al., 2011; Kendal et al., 2018). Here, we discuss in detail the ones most applicable to HIREC.

3.3.1. Frequency-Dependent Biases

Frequency-dependent learning refers to learning strategies where the probability of acquiring behavior depends upon its frequency in a population. Aside from random copying or unbiased learning, the most commonly studied variety of frequency-dependent learning is positive-frequency dependence– varieties of which include conformist transmission, conformity-biased learning, and majority-biased learning. [Note: we are not using conformity as defined by Asch (1956) where majority influence causes individuals to abandon accurate personal information; for debates and the history of terminology related to positive frequency dependence see Aplin et al. (2015a) and Van Leeuwen et al. (2015)].

Positive frequency-dependence is disproportionately copying the most common trait in a population, or more generally the use of some type of "consensus" information to inform behavioral choice (McElreath et al., 2013). This may be a function of copying the number of individuals or behaviors (Aplin et al., 2015a). Negative frequency-dependence is also possible, but less theoretically and empirically well explored (Vilhunen et al., 2005). Evidence consistent with positive frequency-dependence has been found in many species (Pike and Laland, 2010; van de Waal et al., 2013; Aplin et al., 2015b). The evolutionary rationale behind positive frequency-dependence is drawing on the wisdom of the crowd– arguably the most common behaviors are those that are beneficial to most individuals in the population. Otherwise, they would have been selected against.

Much theory, and some empirical work, suggests that positive frequency-dependence is a rapid means to acquire adaptive behavior and outperforms other learning strategies when adaptive behavior is common (Baldini, 2012, 2013; McElreath et al., 2013) and in spatially heterogeneous environments (Boyd and Richerson, 1985; Henrich and Boyd, 1998). However, under certain conditions conformist transmission may slow (Laland and Williams, 1998; Henrich, 2001) or prevent (Henrich and Boyd, 1998; Kendal et al., 2010) the spread of adaptive behavior. If the environment changes such that historically adaptive, common behaviors become maladaptive, a rare novel adaptive behavioral phenotype will be unable to spread through a population that consists of pure positive frequency-dependent social learners. Strong conformity may prevent any behavioral change and, essentially, has an infinite time-lag. If individuals undergoing change combine positive frequency-dependence with some other type of learning (i.e., individual learning), positive frequency-dependence may retard, but not prevent, the spread of new, adaptive behaviors.

Whitehead and Richerson (2009) show that conformist transmission can cause population collapse in realistic, temporally variable environments. For computational ease, analytical models typically assume disturbances resemble "white noise." Environmental disturbances are drawn from a normal distribution where extreme events at the tail are rare and occur with constant magnitude and variance over time. This often produces predictable phenomenon. However, "red noise" scenarios may more closely match realistic HIREC scenarios. Red noise produces environmental changes that occur with increased magnitude (more difference from previous environmental conditions), with increased frequency (extreme, novel events are more common), and less predictably (non-linear dynamics and sudden shifts to more extreme steady states are possible as mean and variance are not constant) than white-noise scenarios of environmental change (Richerson, 2019). Red noise distributions are commonly found when evaluating patterns of spatial heterogeneity or climate fluctuations– two scenarios that are extremely relevant to HIREC. Results from this model show that under certain red noise conditions, species cannot cope with environmental change if they are purely conformist (or potentially rank-biased). Populations that are smaller, or isolated from other groups due to social or geographic factors might be more likely to collapse particularly if they have evolved in a relatively stable environment and rely on conformity-bias. Limited migration from outgroups and drift in small populations may accelerate the near fixation of maladaptive behavior.

In short time scales conformity-biased learning has been shown to spread maladaptive behaviors. Lab studies with guppies (*Poecilia reticulata*) show that maladaptive information about foraging site location could spread in the population through conformity-biased learning, preventing these lab populations from exploiting the optimal path (Laland and Williams, 1998;

Kendal et al., 2004). Post HIREC, positive-frequency dependent learning strategies tend to cause a time-lag or prevent individuals from copying rare adaptive behaviors making it a seemingly risky learning strategy to employ under these circumstances.

3.3.2. Payoff-Biases

Payoff-biased learning includes learning strategies that utilize observable behavioral correlates of fitness (e.g., yield or efficiency) or outcomes of fitness (i.e., fecundity) to inform what or whom to copy. These behaviors are also sometimes contained under the umbrella of "success-biases," which also include using likely correlates of fitness associated with demonstrators such as rank or prestige (Baldini, 2012) to inform whom to copy (further discussed in the section 3.3.3 on model biases). Individuals may copy the most successful (on average) behavior, also known as "compare-means success-biased" (Baldini, 2013) or "pay-off-biased" learning (McElreath et al., 2008; Kendal et al., 2009a). Individuals may also copy the behaviors of the demonstrator with the best observable payoffs in a population (Baldini, 2013). Compare-means success-bias performs well when high-payoff behaviors are rare (Baldini, 2013), whereas "imitate the best" under performs when lower pay-off behaviors occasionally yield a high payoff due to stochasticity. Evidence consistent with success-biased learning has been found in one fish (Pike et al., 2010) and several primate species (Barrett et al., 2017; Vale et al., 2017; Bono et al., 2018).

If HIREC has directly observable fitness consequences like reducing foraging success or increasing opportunities for predation, evaluating the adaptive content of a behavior via pay-off biased learning is an excellent strategy for coping with HIREC. However, evaluating the content of seemingly successful behaviors or individuals might yield false positives because of stochasticity post-HIREC; we might predict this to be a problem when HIREC also decimates population size or the ability for individuals to acquire information from conspecifics. However, when successful behavior is particularly rare (Baldini, 2013), copying the single most successful individual might be the best strategy.

3.3.3. Model-Biases

Payoff-biased strategies appears to be underutilized in nature (Mesoudi, 2011), likely because evaluating the content of a behavior may be costly or impossible. If the inherent meaning of behaviors is not understood (i.e., bird song or displays used to attract mates) or is computationally costly, it may be adaptive to bias attention toward particular demonstrators or "models," who display cues (i.e., rank, health, fertility) that are likely to be correlated with adaptive behavior. Other times these cues may be indicative of phenotypic matching of socially learned behaviors (i.e., relatedness, age similarity, sex similarity). Additionally, when observable pay-offs are stochastic, then cues are sometimes a better proxy. Many of these cues, such as rank, abundance in a population, success of individuals, or mating success, are often coupled with fitness enhancing behaviors. Evolution might favor the use of particular social learning strategies that hone in on these cues if these cues are reliable over the course of evolutionary history.

HIREC may render model-biased learning maladaptive if it creates a mismatch by decoupling previously reliable cues from their fitness consequences, turning them from honest to dishonest signals. This can lead organisms into ecological traps (Schlaepfer et al., 2002), which will either cause some time-lag or entirely prevent an organism from switching to adaptive behavior. Additionally, behaviors that are socially learned, have high fitness consequences, and/or are only performed by individuals once (i.e., some mating or predation events) in their lifetime may be potentially prone to HIREC. For example, natural selection may favor the evolution of a learning strategy where an individual copies the oviposition or nestmaking site that was most common or chosen by the most fecund member of a population. If this decision is no longer adaptive post-HIREC, evolved social learning rules may become maladaptive unless organisms have some additional cognitive equipment or learned experience to bail them out.

Kin-biased learning (which also includes vertical transmission discussed in section 3.2) is one type of model bias. Kin-biased learning is common in many primates (Perry, 2009; Wrangham et al., 2016; Lamon et al., 2017) and carnivores (Mazur and Seher, 2008; Müller and Cant, 2010; Thornton and Clutton-Brock, 2011). In some cases, however, it is unclear whether this is a consequence of family-unit social systems or kin-biased social interactions rather than strategic social learning (Laland, 2004). In some species, kin-biases may drastically reduce the variety of social behaviors that an individual may acquire post-HIREC compared to social learning strategies that have them exploring outside of their family groups.

Furthermore, copying individuals that have indicators of success, such as rank, reproductive status, or physical condition may have longer time-lags than other social learning strategies if these cues are not equally relevant in the pre- and post-HIREC world. These indicators presumably take some time to be lost post-HIREC if they were reliable in the pre-HIREC world. Generally, we might predict that using social learning strategies which rely on a greater number of individuals may have a greater time-lag post-HIREC. However there exists an inherent tension; socially learning from multiple individuals reduces stochasticity due to sampling effects. Watching a seemingly successful behavior or individual might yield false results because of stochasticity, but can be adaptive when successful behavior is particularly rare (Baldini, 2013).

3.3.4. Content-Bias

Content- or direct-biased learning, is when individuals have genetic predispositions to acquire or attend to social learning about particular stimuli (Boyd and Richerson, 1985). This genetic predisposition is also referred to as 'evolutionary preparedness' (Seligman, 1971; Davey, 1995; Lindström et al., 2016). This may occur because natural selection biases organisms to attend to social information or copy behavior about evolutionary stable or important cues like predators (Galef and Laland, 2005) or mate choice (Nöbel et al., 2018). Examples of direct-bias include food taboos and dietary preferences (Fessler and Navarrete, 2003; Henrich and Henrich, 2010) and preferential retention of information about dangerous animals (Broesch et al., 2014).

Evolutionary simulations suggest that preparedness and social learning can coevolve in dangerous and stochastic environments. This coevolution may lead to suboptimal appearing behavior, although this is likely due to a tradeoff between flexibility and safety shaped by an organism's evolutionary history (Lindström et al., 2016). If HIREC reduces the reliability of ancestrally reliable cues upon which content-biases are based, this may strongly influence individuals to acquire outdated social information or choose a suboptimal behavior– a type of socially learned ecological trap (Schlaepfer et al., 2002).

3.3.5. Integrating Personal and Social Information

For much of this paper we have discussed social learning as a stand-alone mechanism for gathering information about the environment. In reality animals likely integrate social and individual information, a family of learning strategies known as social learning contingencies. Surprisingly, the interplay between social and individual learning in wild populations is not thoroughly explored, despite models suggesting that the integration of personal and social learning is what renders social learning adaptive over any fixed strategy (Boyd and Richerson, 1995; Enquist et al., 2007; Aoki and Feldman, 2014). Adaptive plasticity in learning strategies, where individuals switch from social to individual learning if they suspect the environment is changing was also common among the best strategies in a recent computer simulation based social learning strategies tournament (Fogarty et al., 2012).

The interplay between social and individual learning is subtle and takes several forms. Oftentimes social information is used to explore behaviors, while individual information is used to settle on behavior regarding the incorporation of novel diet items (Galef and Whiskin, 2001) and changing foraging behaviors to maximize yields (McElreath et al., 2005; Barrett et al., 2017). Social learning can also reverse earlier individual preferences, even if that socially acquired information is contradictory to individually acquired information. Norway rats that were taught an aversion to a food item then increased their intake of that food after interacting with a demonstrator rat that had consumed the aversive item (Galef et al., 1997). Later work showed that rats who learned that a food item was toxic or unpalatable ignored their personal knowledge and consumed an unpalatable or potentially toxic food item after interacting with a rat that had eaten that lower quality food (Galef and Whiskin, 2008). Similar experiments have demonstrated a social component to reverse feeding aversions in captive spotted hyenas (Yoerg, 1991) for previously learned unpalatable novel foods. Thus social learning might be an important mechanism for changing initial impressions– a type of reversal learning. However we need future studies and theory to understand the adaptive significance and limitations of this in the face of HIREC, as sometimes an over-reliance on one type of information over the other could lead to maladaptive decision making (Avarguès-Weber et al., 2018).

3.4. HIREC Intersects With Transmission Processes

In addition to altering the value of social information, HIREC can impair the transmission of information necessary for social learning to take place. For social learning to occur, a demonstrator must send information in the form of signals or cues through the environment to a receiver (Maynard Smith and Harper, 2003). This process has been shaped over evolutionary time, so when HIREC increases the mismatch between a population's current and ancestral environment, communication may be disrupted. Most research examining the maladaptive effects of social learning assume that the learner has successfully received a signal (Rieucau and Giraldeau, 2011). In reality, HIREC may disrupt the flow of information before it reaches the potential learner.

The transmission of information can be broken down into three phases: 1) production of information by the sender, 2) transmission through the environment and 3) detection by the receiver. HIREC may interfere with any of these phases. The production of signals by demonstrators can be impacted by anthropogenic activities in two main ways. First, HIREC often results in declining population or group size. This is particularly true with anthropogenic disturbances that target specific keystone individuals (Modlmeier et al., 2014) in a population. For instance, human harvesting that targets the largest, oldest, and most knowledgeable animals in a population can lead to a decrease in high quality demonstrators (Shannon et al., 2013). When social information is beneficial, HIREC can cause an information-based Allee effect, where a decrease in population size reduces the availability of useful social information that further exacerbates population decline (Gil et al., 2018). Second, HIREC can reduce information production per demonstrator. For example, high temperatures and low food availability decrease the ability of damselfish to produce chemical alarm cues (Lienart et al., 2016). Because food availability and climate are tightly linked, this has the potential to impact species that rely heavily on conspecific chemical alarm cues to learn about predatory threats.

Environmental conditions resulting from HIREC can also interfere with the propagation of signals. This is especially common in aquatic environments where conditions like low pH and turbidity impair chemical and visual signals from traveling between individuals (Semel and Sherman, 2001; Brown et al., 2002; Leduc et al., 2004; Fischer and Frommen, 2013). Signal propagation is also negatively affected by HIREC for many plants, as volatile cues transmitted between individuals are degraded by pollution, thus reducing their reliability (Blande et al., 2014). As diesel pollution affects the ability of honey bees to use chemical cues to locate nectar resources (Lusebrink et al., 2015), it is possible that olfactory signals transmitted between organisms through the air are also affected by atmospheric pollutants introduced by HIREC.

Anthropogenic activities can also inhibit the detection of signals by observers. This phenomenon has been studied extensively near urban areas and roads where noise pollution masks auditory signals (reviewed in Patricelli and Blickley, 2006). For instance, Parris and Schneider (2009) compared the effects of traffic noise on two species of bird: the grey-shrike thrush and the grey fantail. The thrush calls with a lower sound frequency than the fantail. Thus, with increased low frequency traffic noise, the thrush had to shift to singing at a higher frequency but the fantail was not disturbed. This underscores another important point: the degree that HIREC interferes with transmission depends on the mismatch between the pre- and post-HIREC environment. Still, at sites with high traffic noise the probability of detecting either bird decreased. Thus the magnitude of change is also important. Even if the noise is loud animals may be able to shift the timing of their calling to compensate for the increased noise if it only occurs during a specific temporal window (Fuller et al., 2007).

Importantly, HIREC often includes simultaneous changes on multiple aspects of the environment, which may limit the ability of animals to transmit information successfully in all three phases of the transmission process. Ultimately, an effective transmission process is necessary for a social learning response. If animals cannot effectively communicate to one another, then whether social learning is an adaptive or maladaptive response may be a moot point as it may be significantly reduced in a post-HIREC world.

3.4.1. Information Variation and Types of HIREC

For social learning to be an avenue for organisms to escape HIREC, there must be observable variance in fitness of information post-HIREC. To illustrate, imagine a novel pollutant is introduced to a stream that reduces reaction time of an aquatic critter to a predator. This species may notice that conspecifics upstream (where concentrations of the novel pollutant are lower) appear to be in a better state; they may use that social information to decide to move upstream. Now, imagine that the same pollutant is introduced to a pond, such that it exists in equal concentrations around the whole pond and equally affects all individuals. Individuals may evaluate their state compared to conspecifics, note that it is similar, and thus not have access to any social information that would allow them to escape this dangerous HIREC scenario. Thus types of HIREC that harm all individuals in a population equally may be particularly harmful, as they limit the utility of social learning as an escape. In such contexts, memory of conditions pre-HIREC might be the only source of variance that could inform them to leave their local patch and seek out better conditions.

4. CONCLUSIONS

Social learning is a complex phenomenon whose evolution and efficacy are influenced by a multitude of factors. Social learning allows individuals to gather information about their environment while avoiding the costs of sampling it directly through individual learning. However the ease of innovation, rate of environmental change, and proportion of individual to social learners are also important in maintaining the fitness of social learners in a given population. While models examining the evolution and prevalence of social learning have focused on these social learning traits, it is important to note that they often exclude the ability of individuals to integrate individual and social information, a scenario which likely occurs frequently in nature.

We provide a framework for understanding the expression of adaptive and maladaptive responses to HIREC. It demonstrates that a species' evolutionary history shapes components of social learning important in producing a response to HIREC. These components include the proportion of individual to social learners in a population, social learning pathways, social learning strategies and the information transmission process. These social learning traits are important in determining the proportion of individuals exhibiting the correct behavior shortly after HIREC and the rate of increase of correct behavior in a population, both of which determine the long-term social learning response to HIREC. HIREC can disrupt social learning by changing environmental traits important for the components of social learning, creating a mismatch or a time-lag.

We close by noting several avenues for expanding the analysis of effects of social learning on responses to HIREC. First, while we focused on social vs. individual learning as an isolated trait, social learning tendencies and strategies might usually be correlated with other phenotypic traits (e.g., age, size, condition, rank, or social network position). How social learning affects individual and population responses to HIREC might then be mediated by the correlation with these other traits. In particular, a developing literature examines how learning tendencies (social and individual) are associated with personality traits such as boldness, exploratory tendency or neophobia [(Sih and Del Giudice, 2012; Aplin et al., 2014; Carter et al., 2014; Trompf and Brown, 2014; Griffin et al., 2015); but see Morand-Ferron et al. (2015)]. If, for example, bold individuals tend to be individual learners (willing to expose themselves to risks to learn about novel options), this could result in high mortality of individual learners in the face of novel predators, making it particularly difficult for an adaptive response to these novel predators to spread. In contrast, if individual learners are cautious, they might be more likely to survive encounters with novel predators and then potentially transmit the information to social learners.

Second, we focused on learning from conspecifics, but social learning from heterospecifics also occurs (Dawson and Chittka, 2012; Gil et al., 2018) as has been historically shown for public information like predator risk (Seyfarth et al., 1980; Ito and Mori, 2010) and food patch quality and location (Parejo et al., 2005; Farine et al., 2015a). If social learning is beneficial, then heterospecifics that share information can be information mutualists (Gil et al., 2018), whereas if it is costly, then heterospecifics can contribute to cross-species social traps. Many of the points that we discussed about conspecific social learning can also apply for cross-species social learning (e.g., a key component could be heterospecific learning strategies, or which species and which members of other species one learns from). An intriguing idea is the possibility of keystone information providers - species that numerous other species learn from (Farine et al., 2015a; Gil et al., 2018). In general, a future area of study is what can be termed the 'community ecology' of social learning.

In addition, we assumed that any innovative behavior that provided an increase in fitness for social learners would benefit a population that utilizes social learning. However, effective innovation and its cultural transmission could result in over exploitation of resources and might lead to eventual population decline, a potential consequence which requires further research. While this topic is discussed in research integrating cultural evolution and sustainability science in humans (Kline et al., 2018), it may be a risk to some animals using social learning to cope with HIREC. Long tailed macaques living in archipelagos off the coast of Thailand rely on stone tools to open bivalves and other resources on resource limited islands– behaviors that are likely culturally transmitted. There is evidence that tool-users at sufficient population densities drive down both population size and composition, removing larger shellfish from the populations. Researchers estimate that given sufficient time, tool-aided foraging might no longer benefit these populations and might in fact further threaten their persistence (Luncz et al., 2017).

Finally, we focused our analysis on the initial, relatively short term response to environmental change. On longer time scales, by affecting fitness, the behavioral response to HIREC affects population dynamics. Social learning that slows responses to HIREC or even result in social traps can contribute to population decline (Hale et al., 2015). In contrast, when social learning spreads adaptive behavior quickly, this can not only rescue populations, it can result in population 'booms' (e.g., urbanized or invasive pests) that can be followed by overexploitation and subsequent 'busts'. And, in the even longer-term, post-HIREC, social learning tendencies and strategies might evolve and become a component of evolutionary rescue (Gonzalez et al., 2013). More empirical and modeling work on consequences of social learning for population (or even multi-species) dynamics, and for eco-evolutionary dynamics should be valuable and exciting.

AUTHOR CONTRIBUTIONS

All authors contributed to the formulation, writing, and revision of this manuscript and made direct intellectual contributions. They all approve of its publication.

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REVIEW
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Challenges of Learning to Escape Evolutionary Traps

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Many animals respond well behaviorally to stimuli associated with human-induced rapid environmental change (HIREC), such as novel predators or food sources. Yet others make errors and succumb to evolutionary traps: approaching or even preferring low quality, dangerous or toxic options, avoiding beneficial stimuli, or wasting resources responding to stimuli with neutral payoffs. A common expectation is that learning should help animals adjust to HIREC; however, learning is *not* always expected or even favored in many scenarios that expose animals to ecological and evolutionary traps. We propose a conceptual framework that aims to explain variation in when learning can help animals avoid and escape traps caused by HIREC. We first clarify why learning to correct two main types of errors (avoiding beneficial options and approaching detrimental options) might be difficult (limited by constraints). We then identify and discuss several key behavioral mechanisms (adaptive sampling, generalization, habituation, reversal learning) that can be targeted to help animals learn to avoid traps. Finally, we discuss how individual differences in neophobia/neophilia and personality relate to learning in the context of HIREC traps, and offer some general guidance for disarming traps. Given how devastating traps can be for animal populations, any breakthrough in mitigating trap outcomes via learning could make the difference in developing effective solutions.

Keywords: environmental change, learning, optimal sampling, stimulus-response contingencies, novelty, neophobia, set-shift

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INTRODUCTION

By altering food, predators and habitat, human-induced rapid environmental change (HIREC) presents organisms with new, survival-relevant decisions (Candolin and Wong, 2012; Sih, 2013; Wong and Candolin, 2015). On their first encounter with altered or novel situations (e.g., novel resources, habitats, or predators), animals often respond using their previously adaptive cue-response systems; e.g., respond to the smell of food by attacking, but respond to the smell or sight of danger by fleeing. One potential problem is that these previously adaptive systems may not continue to be adaptive post-HIREC. When previously adaptive cue-response pairings are mismatched with post-HIREC outcomes, animals can get drawn into ecological traps via maladaptive habitat preferences or range shifts (Battin, 2004; Hale et al., 2016), or commit themselves to evolutionary traps by mis-categorizing cues associated with novel food or predators (Robertson et al., 2013). The errors that cause traps can go "both ways." They include the underuse of good habitat or resources (Gilroy and Sutherland, 2007), and the overuse of poor habitat (Robertson et al., 2013) or toxic "foods" (e.g., cane toads, Shine, 2010); as well as the under-avoidance of novel predators (Sih et al., 2010; Miles et al., 2013), and the over-avoidance of situations and habitats that are safe, but appear dangerous (Hale and Swearer, 2017; Trimmer et al., 2017).

While ecological traps are habitat based, evolutionary traps involve a wider context of errors (Schlaepfer et al., 2002; Robertson et al., 2013). Both share the common feature of driving animals toward population decline due to maladaptive behavioral choices (Schlaepfer et al., 2002; Robertson et al., 2013; Hale and Swearer, 2016). However, not all animals get drawn into traps; some immediately respond adaptively to novel circumstances (Sih, 2013), others escape via phenotypic plasticity (i.e., plastic rescue; Snell-Rood et al., 2018). Key questions are thus: what explains the variation in response to traps caused by HIREC (Sih et al., 2011, 2016; Sih, 2013), and can they be disarmed either by animals themselves or by human intervention?

As a major form of phenotypic plasticity, learning gives animals flexibility to respond to changes in their environment. Indeed, learning can be an important precursor and facilitator of future evolutionary change (West-Eberhard, 2003, 2005; Brown, 2013; Dukas and Dukas, 2017). Learning can allow animals to escape ecological and evolutionary traps (Schlaepfer et al., 2002; Greggor et al., 2014). Operationally, learning is defined as a change in behavior as a result of experience, excluding changes that can be attributed to physiological adaptation or reflexes (Shettleworth, 2010). Almost all animals have an ability to learn (Shettleworth, 2010). Thus, many ecologists and conservation biologists might start with the *a priori* expectation that if animals initially respond poorly, they ought to learn to exhibit more appropriate behavioral responses to novel situations. Yet, many species (Ellenberg et al., 2007) or individuals (Ellenberg et al., 2009) often do not learn to adjust behavior after responding sub-optimally to an altered or novel cue, despite having the capacity to learn (Berger-Tal and Saltz, 2016).

We turn the *a priori* expectation on its head and argue that the main types of errors that animals make can be inherently difficult to correct by learning. Our argument draws on existing concepts from animal cognition, evolutionary theory and behavioral ecology to provide a conceptual framework for explaining variation in learning outcomes. We first acknowledge areas where learning may not be necessary to respond to HIREC and then focus on situations in which learning could improve outcomes. We classify these situations based on how animals should ideally respond, and examine the errors animals can make initially before they have the opportunity to learn. Taking a cognitive perspective of these errors reveals potential barriers to learning that arise due to processes such as the spatio-temporal structure of cues, costs of learning, and constraints of the types of associations animals make. This backdrop of learning barriers serves as the foundation for our framework that explains how organisms might learn in the face of traps: e.g., via adaptive sampling or generalizing. We then draw on literature using a cost-benefit approach to generate general predictions on how an organism's evolutionary or developmental history might explain variation in behaviors relevant for escaping traps—for example, the tendency to sample options that previously adaptive cue-response systems suggest are poor options, but after HIREC, are now beneficial. We also discuss the role of individual differences in behavioral tendencies, in neophobia/neophilia and in personality that might explain variation in the ability to learn to cope with the traps HIREC presents.

The principles we draw on are not restricted to novel situations that cause traps. They apply whenever animals mis-assess situations and make suboptimal or maladaptive decisions. However, these mis-assessments are often of critical importance following HIREC because the pace of change can be drastically faster than would have occurred over evolutionary time, and even minor increases in the rate of change can tip animals toward extinction (Botero et al., 2015). Also, we refrain from providing detailed, *specific* recommendations for managers. Providing workable management advice will require expert knowledge on specific situations. Instead we provide applied examples where learning, or the lack thereof, has influenced the success of a species, and we create a framework for how conservationists might think about learning in their systems, in the hope of encouraging the future development of specific learning-focused interventions.

PRELUDE: LEARNING AND LEARNING ABILITY ARE NOT ALWAYS THE KEY

Learning is not always necessary for organisms to avoid traps, and can even be deleterious. In some cases, animals' pre-existing, cue-response systems immediately produce an adaptive behavioral response (and thus little need for learning). For example, the "cue similarity" hypothesis (Sih et al., 2010; Carthey and Banks, 2016) notes that prey often immediately respond adaptively to exotic predators when those novel predators resemble familiar ones. Learning can even lead to traps when it predisposes animals to suboptimal behavior or human-wildlife conflict (Donaldson et al., 2012; Costa et al., 2016; Morehouse et al., 2016). For example, when seabirds first forage on discarded bycatch near fishing vessels, it may initially be a good choice since it allows them to gain food with little flight cost. However, when this becomes a learned cue—as has been documented for gannets (*Morus capensis)* and other seabirds—tracking fishing boats changes movement patterns (Oro et al., 2013), and can lead to an over-use of a lower quality food which is unsuitable for their chicks (Grémillet et al., 2008). Despite these costs, birds would be unlikely to change their behavior because it would require learning to avoid a seemingly rewarding stimulus, hence they are trapped. Similar patterns of learning around people emerge in other species such as bears (Mazur and Seher, 2008), suggesting that in many situations learning itself should not be considered a default survival tool.

Even if learning is not useful for all traps, how do we predict when and where learning could be beneficial? The breadth and flexibility in what organisms can learn clearly differs at both broad and narrower taxonomic levels, which makes predicting learning to escape traps based on species' learning ability a tempting prospect. For instance, primates can learn to flexibly respond to nuanced aspects of HIREC (Hockings et al., 2015) (e.g., deactivating snares) (Ohashi and Matsuzawa, 2011) in ways that are unlikely for snails. Meanwhile other species have more developmentally or contextually constrained learning abilities, which may only be effective in very well-defined contexts (e.g., flatworms' rapid anti-predator learning) (Wisenden and Millard, 2001). However, there can be variation in learning propensity even within narrower taxonomic groupings (e.g., among birds, amphibians, or primates), and surprising convergence between others (Emery and Clayton, 2004). Additionally, despite variation in the use of learning, it is not always the most cognitively flexible species (population or individuals) which succeed in using learning to avoid traps (e.g., even humans are susceptible to evolutionary traps, such as our insatiable attraction to sugar and fat) (Pijl, 2011). Therefore, learning ability alone can be a poor predictor of post-trap adjustment. Instead, we focus on the matches or mismatches between the types of traps HIREC produces and how likely animals are to perceive and respond to them. By taking a cognitive perspective on animals' responses, we can examine how evolutionarily-shaped learning and information gathering biases are likely to influence learning and trap outcomes.

We should note that although social learning is an equally valid means through which animals can gain information about escaping traps (see Barrett et al., 2019, this issue), this paper focuses on learning through individual experience. Social learning involves similar learning mechanisms to individual learning, but animals' use of social cues is subject to a different suite of biases than individual cues (Heyes, 1994, 2012). Therefore, we focus on individual learning to provide a simple foundation for learning to avoid traps, although we acknowledge some areas where social learning is likely highly relevant.

THE CONCEPTUAL FRAMEWORK: BREAKING DOWN THE STEPS REQUIRED FOR LEARNING

By definition, traps result from a mismatch between the cues HIREC produces and animals' resultant behavior (Schlaepfer et al., 2002). To figure out whether learning can play a role in escaping maladaptive behavior, we need to break down the learning process that can occur between the HIREC cues and animals' responses. In this context, learning involves several stages: (1) encountering and perceiving cues; (2) responding to them; (3) experiencing an outcome; and (4) adjusting behavior based on that outcome. Cues can involve single or multiple stimuli that animals use for decision making, e.g., a novel food type, or several markers of habitat quality.

How an animal responds the first time it encounters a cue post-HIREC is critical for determining not only whether it survives the experience, but also what it learns about that experience (**Figure 1**). If animals do not perceive the novel or altered cues, they cannot use the cue to respond or to learn. HIREC can alter the perception of cues, which can lead to ecological and evolutionary traps that give little opportunity for learning. For example, when HIREC interferes with perception by increasing turbidity, fathead minnows (*Pimephales promelas*) fail to perceive visual cues from novel predators well enough to learn to respond to them (Ferrari et al., 2010).

Assuming that the stimulus is perceived, signal detection theory (Green and Swets, 1966) has been used to make predictions about how animals initially respond when encountering known and unknown cues (Wickens, 2001; Trimmer et al., 2017), partly based on how closely those cues match evolutionary or experienced norms (Sih et al., 2011; Robertson et al., 2013). For example, native Australian bush rats (*Rattus fuscipes*) exhibit a stronger anti-predator response to novel predators that are more closely related to known predators (Carthey and Banks, 2016). Other factors that affect whether animals correctly categorize novel stimuli include the specificity of the cues, and the asymmetry of costs associated with over vs. under-responding (Macmillan and Creelman, 2005; Ehlman et al., 2019). For example, prey are more likely to correctly respond to novel predators (e.g., flee) without the need for learning if the prey evolved in environments with a broad diversity of predators (the "multiple predator hypothesis") (Blumstein, 2006), and if, in the past, the cost of under-responding was high (e.g., familiar predators were very dangerous), but the cost of over-responding (e.g., to non-predators that look like predators) was low. In such cases where animals respond correctly in their initial interactions, learning may not be needed for immediate survival, but could still be useful to fine tune their responses.

If animals perceive and attend to cues detected during initial encounters with novel or altered stimuli, they can respond in three basic ways: (1) avoid, (2) approach, or (3) ignore (no visible effect on behavior). As a generality, animals should have evolved to avoid bad options, approach or utilize good options, and ignore neutral ones. In **Figure 2** we outline a 3 × 3 matrix which plots the potential outcomes when animals respond (i.e., avoid, approach, or ignore) to stimuli that are defined by their fitness values (beneficial, i.e., good; neutral, or; costly, i.e., bad). This simple categorization allows us to organize HIREC scenarios to predict the experiences and type of learning (e.g., reinforcement learning, reversal learning, habituation) required for behavioral change when errors occur. As a rule, whether animals learn about the cues presented depends on the likelihood that animal's experiences with said cues yield the relevant, perceivable and useable information required for learning. The different types of learning required tap into ideas about optimal sampling regimes, generalization, reversal learning, habituation, neophobia, and personality for predicting learning and survival amid HIREC. In the following sections, we discuss each of these ideas and concepts in detail, with a focus on testable predictions.

In our simple matrix of responses (approach, avoid, ignore) and fitness values (good, bad, neutral), there are three main types of errors (orange boxes, **Figure 2**) that animals can make on their initial encounter with a novel or altered stimulus. Each of these errors can lead to detrimental traps if they are repeated on subsequent encounters or on single occasions by multiple individuals.

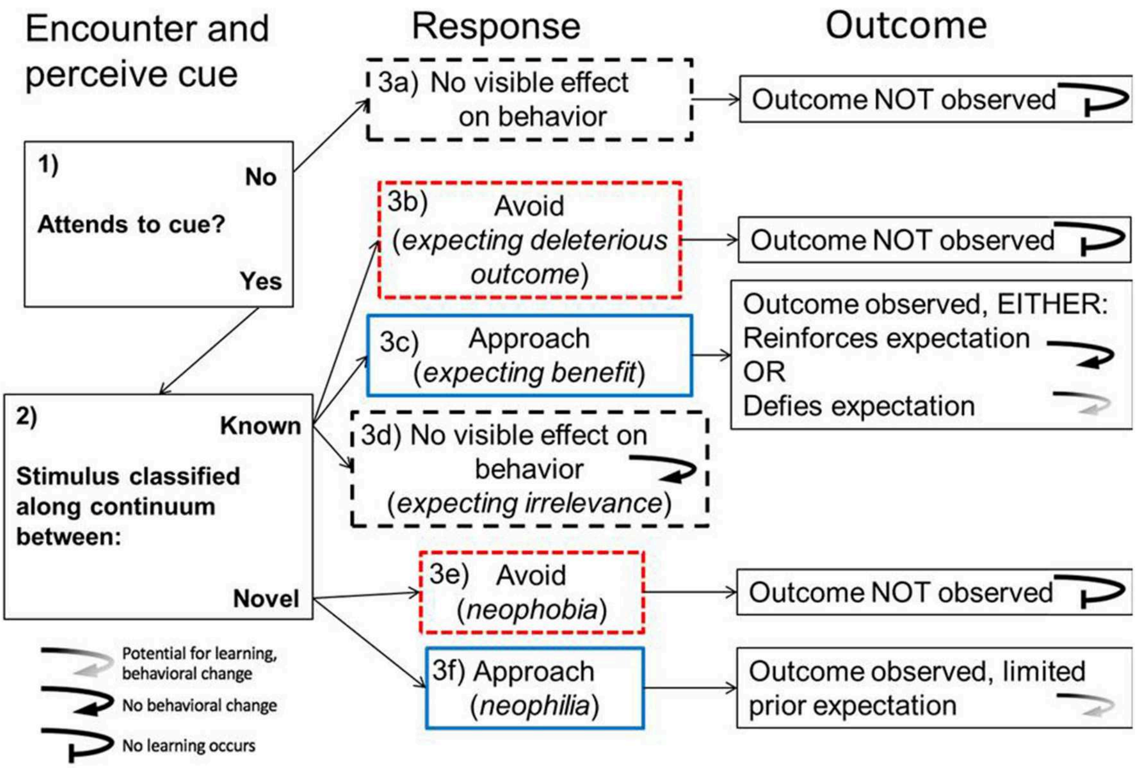

FIGURE 1 | Stages of responses to HIREC and potential for learning. Different underlying motivations can promote approach, avoidance and apparent neutrality toward a stimulus. The outcome of the animal's behavior will direct future responses to that same stimulus. Even when an animal makes the wrong choice, if the animal is not able to observe the outcome or does not perceive the outcome to be relevant to the preceding behavior, then it will not learn about it. Straight arrows imply the flow of response. Curved arrows symbolize the different responses animals will have on subsequent encounters. The greater the extent that an experience defines expectations, the higher likelihood there will be learning. In cases where there is no behavioral change, learning may not be overtly observed, but animals could still gain information that reinforces details of their response or associated outcome.

- Avoid or ignore beneficial options (e.g., avoid high quality restored habitats, Hale and Swearer, 2017; or novel foods, Pearse et al., 2013);
- Approach or fail to avoid stimuli with negative fitness outcomes (e.g., consume novel toxic foods, Crossland et al., 2008; oviposit on invasive plants, Keeler and Chew, 2008; or allow close contact with novel predators, Miles et al., 2013; or pathogens, Bouwman and Hawley, 2010);
- Fail to ignore neutral stimuli (e.g., avoid or be stressed by passing tourists unnecessarily, Ellenberg et al., 2007).

Upon an animal's first interaction with a stimulus, the animal does not know if it has encountered something that is good, neutral, or bad. Avoiding good stimuli or approaching bad stimuli both have obvious sub-optimal fitness consequences. Importantly, the mis-categorization of neutral stimuli may also carry significant opportunity and energy costs (Gwynne and Rentz, 1983; Ydenberg and Dill, 1986; Trimmer et al., 2017), many of which are only recently being realized (Geffroy et al., 2015). Although intuition suggests learning is beneficial for correcting errors and escaping traps, theory in animal learning suggests various constraints might limit learning.

Whether learning can help animals respond appropriately also depends on the type of trap. Some traps only offer a single opportunity for animals to respond in their lifetime, because an error is fatal, or the trap involves a choice they only make once, such as spawning. In these cases individual learning cannot occur and the initial choice alone determines whether they are trapped. In other cases, traps that offer multiple opportunities to respond have the potential to allow for learning, but can fail to offer animals the experiences they need to learn. When faced with multiple opportunity traps, the learning type and behaviors necessary for escaping errors can differ by error type (as listed in the arrows, **Figure 2**), and by the stimulus type in question. In the next section, we discuss general evolved constraints, or limits, on learning. Later, we distinguish solutions that are most relevant for the different types of errors listed above.

EVOLVED CONSTRAINTS ON LEARNING: WHY EXPERIENCE MAY NOT RESULT IN LEARNING

Learning hinges on experiencing *salient and reliable cues* that predict a relevant outcome, which can indicate a change in

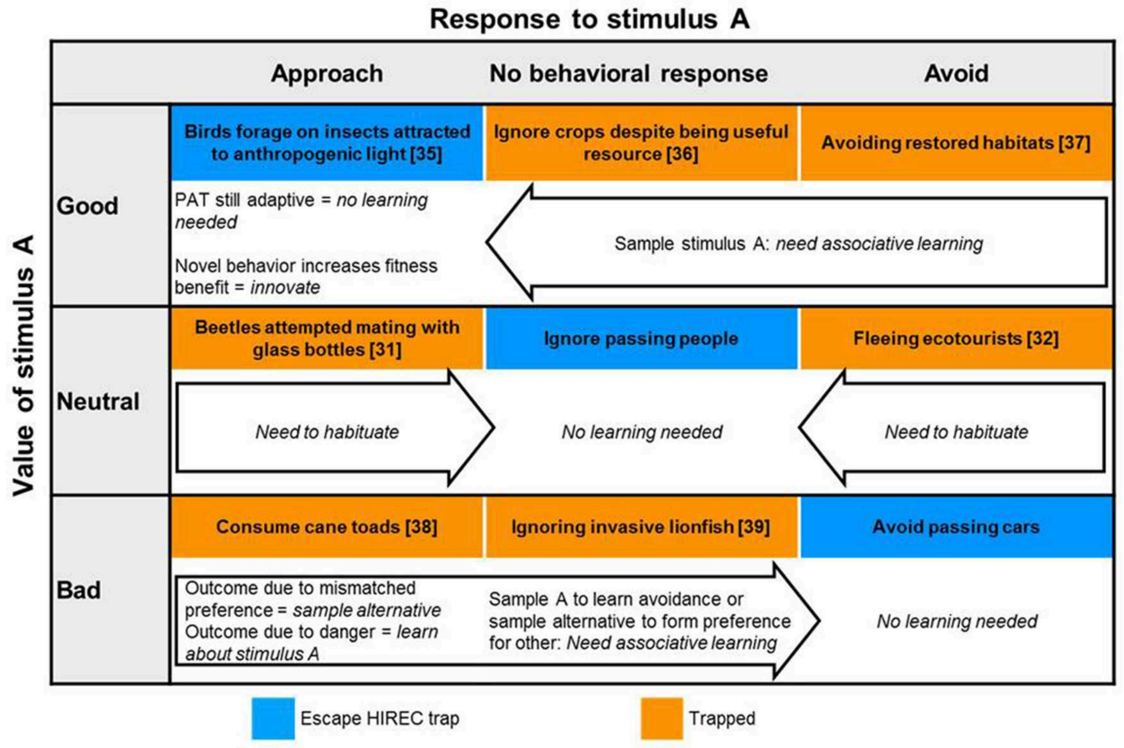

FIGURE 2 | Categories and example consequences for responding to stimuli post-HIREC. Adaptive responses in blue, potential traps in orange. Learning routes for behavioral adjustment listed in arrows. Learning can only occur if potential traps offer multiple opportunities for response. Sampling can involve gathering individual information or social cues.

the rewards or dangers of a given situation. Even if an animal can perceive cue changes post-HIREC, the changes may lack salience (and thus be ignored) because of historical correlations between that cue and its outcomes. First, a particular cue (that is now meaningful) may have been unreliable in predicting fitness outcomes in the past. For example, species for which winter temperature did not predict spring conditions ignore warmer temperatures in the winter, and rely instead on photoperiod to time the onset of spring breeding (Dawson et al., 2001). Second, animals that evolved in conditions where the best behavior was highly certain did not need cues to guide their behavior (e.g., island animals that evolved in predator-free environments did not need and thus often ignore predator-relevant cues). Dunlap and Stephens "flag model" predicts that organisms should use cues to guide behavior primarily when cue reliability is high and the certainty of the best behavior (without using reliable cues) is relatively low (e.g., Dunlap and Stephens, 2009). Over evolutionary time, cue reliability was also influenced by the rate it changed relative to the lifespan of an animal. A very slow change would select for tendencies toward fixed genetic traits, but changes within the lifespan of an animal could select for phenotypic plasticity and learning potential (Botero et al., 2015). As a result, animal's evolutionary history may render certain types of HIREC cues irrelevant to them, regardless of the consequences. Research into how quickly cue biases disappear in the absence of selective pressure is highly relevant to predicting which species may be ill-equipped to recognize novel HIREC cues (see Carthey and Blumstein, 2017 for relevant discussion relating to predatory cue responses).

When cues are relevant to survival, evolution shapes animals' cognitive biases to increase the salience of the cue-response relationship, and reduce the number of cue presentations necessary for learning (Shettleworth, 2010). For example, during a sensitive period of development salmonid fish rapidly imprint on the chemical signature of their home stream to help them return for breeding since it has historically been a reliable indicator of stream location, which they only experience during a set time period of their life (Dittman and Quinn, 1996). While evolutionary advantageous, dependence on olfactory cues makes salmonids particularly susceptible to chemical pollutants (Tierney et al., 2010), and thus makes them unlikely to learn to adjust to this interference. Switching to different cues for homing, such as visual ones, would require overcoming a highly-ingrained cue bias.

Even when HIREC-altered or introduced cues are salient, salience may not promote optimal learning if the cues historically triggered a fixed response. For instance, animals may not learn that a high intensity sound predicts the appearance of food if the loud sound is overly salient and causes a fixed startle response, which can lead to *sensitization* (increased response with repeated exposure, the opposite of habituation), and continued avoidance (Blumstein, 2016). Therefore, there may be certain types of intense HIREC stimuli, such as the abrupt crack of a firearm that animals never learn to ignore or to use as a cue.

TABLE 1 | Summary of future research questions.

- How quickly do different types of cue biases disappear in the absence of selective pressure? (section Evolved Constraints on Learning: Why Experience May NOT Result in Learning)
- Are species or individuals with lower sampling rates more likely to get trapped in HIREC scenarios that require them to approach beneficial options that they initially avoided or ignored? (section Solving the Problem of Avoiding or Ignoring Beneficial Options by Promoting Adaptive Sampling)
- Can patterns of generalization be predicted based on the risks of making mistakes? (e.g., Ferrari and Chivers, 2011, section Will Animals Generalize When Stimuli Change?)
- Under what conditions does habituation toward novel anthropogenic stimuli generalize in a dangerous way to reduce wariness toward genuine threats such as predators? (section Will Animals Generalize When Stimuli Change?)
- Do sympatric species that respond differently to HIREC show differences in their speed or propensity of habituation toward novel stimuli? (section Solving the Problem of Over-Responding to Irrelevant Stimuli)
- Does increasing the regularity and reliability of harmless, but disturbing, cues improve HIREC outcomes (Greggor et al., 2014) (section Solving the Problem of Over-Responding to Irrelevant Stimuli) and could it guide management action that addresses this type of trap (Hale and Swearer, 2016)?
- Under what contexts might set-shifting occur in the wild, and does it differ across species that vary in the number of cues they use? (section Reversal Learning and Innovation)
- To what extent does neophobia/neophilia influence interactions with multiple opportunity traps over time? (section Learning About Novelty)

Learning can also be limited if animals do not have the opportunity to assess the outcome of their response (Schakner and Blumstein, 2016), i.e., their experience is temporally disconnected from their initial choice. For example, frogs often leave after laying eggs in a pond. Even if climate change results in ponds drying sooner and mass tadpole mortality, female frogs might not have access to the consequences of their action and thus would be unlikely to learn to choose deeper or differently positioned pools. Conversely, if the outcome occurs too quickly after the cue, animals may not have time to respond or learn from their experience. For instance, approaching traffic or trains may not allow enough time between perception and consequence to elicit appropriate avoidance (Cassady et al., 2019) (however, when traffic can be perceived in time to escape, habituation can be a separate issue, Lima et al., 2015). Finally, even if the animal can perceive the outcome, the number of cue-outcome pairings needed for learning to occur depends upon the evolved strength of that association. Some associations have evolved to be learned quickly to avoid deadly outcomes (e.g., fear conditioning and taste aversion, Garcia et al., 1974; Griffin, 2004), but others like spatial foraging preferences may take longer to change because the cues are noisier or have fewer immediate fitness consequences.

PREDICTING POST-HIREC LEARNING DESPITE CONSTRAINTS

When faced with multiple-opportunity traps, reinforced, associative learning can help animals adjust to the errors outlined in **Figure 2**, assuming the outcome is salient. Different challenges to learning arise and thus different solutions are relevant, depending on whether the animals mistakenly avoid vs. approach the cue. We first address ways that animals might solve the mistake of avoiding novel beneficial options, and then move on to the problem of approaching or utilizing costly ones.

Solving the Problem of Avoiding or Ignoring Beneficial Options by Promoting Adaptive Sampling

When an organism's initial response is to avoid or ignore the novel or HIREC-altered stimulus, opportunities to learn are limited. If, however, animals sample novel foods or habitat, or approach novel organisms (that have not been identified as non-predators), this permits learning and potentially corrects initial errors. Thus, understanding when animals should sample (or not) is a key issue for predicting whether animals will gather information that allows them to escape traps associated with undervalued resources. Sampling rate is a previously adaptive trait shaped by past costs and benefits. Sampling benefits come in the form of additional information that can result in better future decisions, and costs include exposure to risks and wasted time and/or energy (i.e., opportunity costs).

Numerous models (Stephens, 1987, 2007; Dall et al., 1999; Eliassen et al., 2007) have explored simple scenarios where organisms may reduce uncertainty by sampling the environment. One such scenario gives animals the choice to stick with a known, mediocre (KM) option or sample a variable option (V) that is sometimes good, but sometimes bad. Even if the mean value of V is lower than the mean value of KM, frequent sampling is favored if the payoff of V in its "good state" is high enough relative to the payoff from KM, particularly if the cost of sampling is not too large. Thus, we predict animals to be more likely to sample and learn to use favorable options that they initially avoided if, in their evolutionary history, variable or unknown options were often exceptionally good relative to familiar, commonly utilized options. However, even if the "good" state of V is very good, highly stochastic reward schedules reduce useful information and are less likely to favor sampling. We also expect animals to not sample and thus remain ignorant about novel options if in the past, the cost of sampling was high; e.g., if it exposed animals to substantial risks of mortality or predation (Sih, 1992). In practice, for example, this theory would predict that species which live in environments with many poisonous potential prey items would be unlikely to sample a perfectly edible, invasive prey species.

Adaptive sampling also depends heavily on the rate of change in the value of the variable option. If V changes very rapidly, the organism does not have enough time to reap benefits before the option again becomes "bad"; there is no point in trying to track a rapidly fluctuating environment. If it changes very infrequently, sampling can be favored, but only occasionally. Thus, organisms should most readily sample and learn post-HIREC if they evolved in past conditions with a moderate rate of change, particularly when costs of sampling were low. Research that maps these change rates onto specific HIREC problems will be able to tap into a rich theoretical sampling literature. For example, there is evidence that urban populations sample more before switching foraging preferences, potentially due to living in a more variable environment (Griffin et al., 2016; Federspiel et al., 2017). Theory also predicts more sampling when organisms have a long lifetime to use information (Eliassen et al., 2007), when sampling reduces variation in fitness (Stephens, 1991) and when sampling substantially increases cue reliability (Abbott and Sherratt, 2013). Via these theories, we might logically predict that long-lived species with prior selection to learn about the type of HIREC-altered cue in question are going to be more likely to approach beneficial options that they initially avoided or ignored. In cases where gathering information individually is time-consuming or risky, social cues can also serve as a sampling mechanism (Rendell et al., 2011). Through this route animals can avoid having to personally sample potentially toxic foods (Thorogood et al., 2018), or interact with unknown predators (Griffin, 2004). Additionally, as a management technique, providing alternative cues that advertise the benefits of a given option, such as artificial social cues (e.g., Andrews et al., 2015), could help animals gain the experiences they need to stop avoiding or ignoring beneficial options.

Solving the Problem of Mistakenly Approaching Dangerous Options

Conversely, there are several reasons why animals that mistakenly approach dangerous options would have trouble learning to avoid these low fitness situations. First, they cannot learn to avoid single-opportunity traps if approaching the poor option kills them either immediately or via unrecoverable injury (e.g., Crossland et al., 2008), or they only make one choice in their lifetime (e.g., oviposition site choice in animals without parental care, Keeler and Chew, 2008). Second, they are unlikely to learn about multiple-opportunity traps if they cannot obtain information on the poor payoff of their choice, because they are not present, or because it is difficult to associate their behavior with the outcome (e.g., contracting an illness after interacting with a conspecific, Bouwman and Hawley, 2010). Finally, animals should be prone to approaching stimuli that HIREC has changed from good to bad if those options had historically been highly variable in short-term rewards, but stable in yielding good average returns; this is known as the partial reinforcement effect (Mackintosh, 1974; Houston et al., 1982). In that case, a run of poor payoffs could be viewed by the animal as simply a run of bad luck, and not an indication that the option has changed value. For example, many mammalian herbivores that commonly consume plants with varying levels of secondary compounds sample frequently (Freeland and Janzen, 1974), and thus may be more likely to continue sampling an unpalatable novel plant.

One way that animals might be less likely to "over-accept" poor options is if they become aware of highly attractive, beneficial, alternative options via sampling. This theory is used in practice when management action purposefully draws animals' attention toward alternative, beneficial options, such as encouraging settlement away from habitat sinks by broadcasting attractive cues in better areas (Patten and Kelly, 2010; Hale and Swearer, 2017). As discussed above, sampling rates should depend on the species' evolutionary history of costs and benefits, and individual differences (Pintor and Byers, 2015). In all cases, however, the effectiveness of sampling for producing optimal behavior depends on how much individuals generalize their sampling experience. For example, if an animal survives a negative experience eating a small, unpalatable, but not fatally-toxic cane toad, will it generalize to avoid a large cane toad carrying a fatal amount of toxin as the northern quoll (*Dasyurus hallucatus*) do (Kelly and Phillips, 2017)? How organisms categorize stimuli (e.g., safe vs. dangerous) is an important issue in cognitive ecology that can be critical for understanding how they respond to potential traps. Here, we summarize basic ideas on how a cost-benefit approach can be used to analyze adaptive generalizing.

WILL ANIMALS GENERALIZE WHEN STIMULI CHANGE?

An organism's evolutionary history shapes its ability and tendency to discriminate cues and generalize from experiences (Shettleworth, 2010). Animals must generalize to some extent every time they encounter a cue or suite of cues—even known cues will differ slightly (in rotational appearance, intensity, etc.). The degree of similarity needed for an encountered cue to be generalized depends on the costs of under- vs. over-generalizing. Generalizing broadly is expected to be favored in contexts of danger; e.g., horses will quickly generalize their fear responses toward unknown objects, startling even toward known objects if presented from a different spatial perspective (Hanggi, 2005). In contrast, there are situations where generalizing would be unfavorable. For example in birds distinguishing their own eggs from brood parasites', overgeneralizing is very costly—thus birds may notice and respond very differently to small details in egg size or shell patterns (Spottiswoode and Stevens, 2011). In most cases, however, generalization depends upon the degree of novelty of a new cue. For instance, if the difference between known and novel is large, animals are less likely to respond adaptively and need more cue presentations before learning adaptive behavior (Ferrari et al., 2007, 2016).

These ancestral differences in the costs/benefits of generalizing influence both the neural wiring of the brain and how those synaptic connections change with experience. Psychological and computer science fields have a rich literature addressing the statistical bases and learning mechanisms of adaptive generalization (Shettleworth, 2010). One approach to understand the neural processes underlying generalization utilizes neural networks, consisting of sets of linked input and output nodes (similar, in principle, to clusters of neurons and their connections; Mitchell, 1997) to determine optimal categorization responses. If animals' experiences (inputs) are costly (in time, energy, or risk), their neural networks should be constrained to use salient features of stimuli. For instance, foraging can be a costly endeavor, and therefore animals can often focus on a narrow set of cues for making foraging decisions that can easily be over-generalized. However, if salient features are no longer the most relevant post-HIREC, then animals may be slow to generalize, or not learn to distinguish the novelty they encounter.

For example, the narrowness of foraging cues becomes an issue when seabirds encounter ocean plastic because it emits dimethyl sulfide, a potent foraging cue (Savoca et al., 2016), and therefore many species are prone to errors of over-generalization based on a single cue error.

Responding appropriately to HIREC may require a change in the pattern of generalization. Whether that happens depends upon the cue type and learning type. For example, mis-categorizing predators as non-predators is costly. When an animal habituates to a predator-like cue, they habituate only to a precise cue presentation, which should not generalize to other predator-like stimuli (Hemmi and Merkle, 2009). In contrast, animals may readily generalize after a set of rewarding experiences. Chicks that experience numerous palatable novel foods are more likely to generalize about the palatability of a new food, reducing dietary wariness (Marples et al., 2007). A better understanding of generalization is important in scenarios ranging from the carryover of habituation from humans to natural predators (Geffroy et al., 2015), to the lethal mis-categorization of invasive species as native ones (Llewelyn et al., 2010). Experiments that assess to what extent the speed and breadth of category formation (as often measured in the lab) predicts accurate category formation around HIREC stimuli will be an important step in addressing these HIREC problems. For instance, the costs of overgeneralizing do not always map well onto the breadth of generalization tendencies as predicted (e.g., woodfrogs generalize to a similar extent in predatory and non-threatening contexts, despite the higher potential costs of generalizing around predators, Ferrari and Chivers, 2011).

SOLVING THE PROBLEM OF OVER-RESPONDING TO IRRELEVANT STIMULI

The third error type involves failing to recognize and learn the irrelevance of a stimulus; i.e., persistent over-responding (either avoiding or approaching) to options that are neither beneficial nor costly, and should be ignored. In essence, this is a problem of lack of *habituation*. Habituation is taxonomically widespread and in the strict psychological sense, it involves a reduced reaction to a specific, repeated stimulus through a simple form of learning (Rankin et al., 2009). Animals should habituate to irrelevant HIREC stimuli after repeated, predictable cues yield outcomes of little or no importance (Greggor et al., 2014). However, if animals always avoid novel stimuli (e.g., human habitats, human-generated noise, ecotourists), they will not experience the outcomes necessary for learning about irrelevance, and will not readily habituate to human activities. In addition, species' cognitive biases may make habituation toward some types and contexts of stimuli easier, even those that occur with equal frequency and strength (e.g., pigeons are less likely to habituate at night than during the day, Valentinuzzia and Ferraria, 1997). Compared to other learning types, research on habituation in the wild is in its early stages, and it is still unknown how many of the well-studied psychological habituation mechanisms apply in HIREC contexts (Nowacek et al., 2007; Blumstein, 2016; Schakner and Blumstein, 2016). Additionally it is unclear how habituation toward novel anthropogenic stimuli generalizes in a dangerous way to reduce wariness toward genuine threats such as predators (Geffroy et al., 2015; Trimmer et al., 2017). Testing differences in habituation speed/propensity between sympatric species that respond differently to HIREC (e.g., Blumstein, 2014) can help illuminate the extent to which habituation plays a role in their success and avoidance of traps. Meanwhile, testing the theory that increasing the regularity and reliability of harmless, but disturbing, cues should improve HIREC outcomes (Greggor et al., 2014), could guide management action that addresses this trap (Hale and Swearer, 2016).

REVERSAL LEARNING AND INNOVATION

Apart from considering the error type animals make, how the cue-reward relationship has changed due to HIREC may also influence how easily animals will learn to adjust. Are the same cues available, but new reward contingencies present, or does the animal need to respond to a novel cue with a novel behavior to access a reward? If reward contingencies are swapped, i.e., if previously unrewarding stimuli become beneficial or previously rewarding stimuli no longer carry benefits, then animals face the challenge of *reversal learning*. Such a scenario could occur, for instance, if previously palatable crops are routinely sprayed with dangerous pesticides. Although species ranging from honey bees to primates have demonstrated reversal learning (Komischke, 2002), how often and easily an animal will reverse an association is related to their level of inhibitory control, memory retention (Gonzalez et al., 1967), and sampling rate (Dunlap and Stephens, 2012). Inhibitory control allows animals to suppress a habitual or well-learned response—thus providing opportunities to gather information about alternative responses or stimuli—and has been shown to correlate positively with reversal learning abilities (Bond et al., 2007; Shaw et al., 2015), despite stemming from different brain regions (Aron et al., 2014). Meanwhile, higher levels of memory retention allow animals to remember prior change rates, i.e., that associations may have swapped in the past. Finally, a higher propensity for sampling, also makes it likely that species will occasionally try the previously unrewarded option (Dunlap and Stephens, 2012), which makes them more likely to discover when reward contingencies have swapped.

Alternatively, if a different cue set needs to be learned to predict a known outcome (e.g., shifting from daylight cues to temperature cues to determine the seasonal onset of spring), then animals face a more difficult problem of set shifting (Roberts et al., 1988). Set shifting involves different brain regions than reversal learning, at least in several mammal species (McAlonan and Brown, 2003), and can decline due to age because it incurs substantial attentional costs (Barense, 2002). Little is known about how often set shifting occurs in the wild, or across species that vary in the number of cues they use, but it could be the only escape route for many HIREC traps.

Beyond learning whether an option is good or bad, animals often also need to learn what behavior they should perform once they have approached or avoided a stimulus. Even if the animal makes the correct response (e.g., approach a beneficial food item), they may still fail to behave optimally (e.g., exhibit an inappropriate attack strategy) after approaching the stimulus. In some cases, when faced with novel situations, animals may need to exhibit a novel behavior or devise a novel solution to a known problem (e.g., a behavioral innovation, Reader and Laland, 2003; Ramsey et al., 2007; Tebbich et al., 2016; Dukas and Dukas, 2017). Not all innovations are equally as challenging to develop, which is why the magnitude of the innovation needed for an animal to escape a HIREC trap may determine how likely the animal is to adjust their behavior optimally (Arbilly and Laland, 2017). Low magnitude innovations that rely on employing an existing behavior in a new context (e.g., exploiting a new foraging patch of known food), could occur via sampling a novel cue and generalizing a known behavioral action. In contrast, a high magnitude innovation involves the creation of an entirely novel behavior. For example, a new foraging technique, such as opening milk bottles (Hinde and Fisher, 1951), may require a more extensive set of trial and error learning steps and a wider behavioral repertoire (Arbilly and Laland, 2017). Predicting innovations requires an understanding of how animals interact with, and learn about, novelty and is also conditional upon the properties of innovators and behavioral context of plausible innovations (Perry et al., 2017).

LEARNING ABOUT NOVELTY

Thus, far we have considered responses to altered or novel cues without explicitly considering how animal reactions might depend on their relationship with novelty itself. Although neophobia and neophilia are often thought of as ends of one spectrum, experimental work suggests that they are distinct psychological phenomena driven by different evolutionary pressures which influence repulsion or attraction to novel cues, respectively, both based on the historical costs and benefits of interacting with novelty (reviewed in: Greenberg and Mettke-Hofmann, 2001; Mettke-Hofmann, 2014; Greggor et al., 2015). In creating a fear response, neophobia would trigger avoidance, which may look similar to fear around known threatening stimuli (**Figure 1**, Greggor et al., 2015). Meanwhile, neophilic reactions would initially look similar to attraction to known beneficial stimuli. Neophobic individuals should be more likely than neophilic individuals to correctly avoid novel bad options, but less likely to adopt novel good options. In general, the underlying motivation for avoidance or approach would influence how the animal's response would change over time.

Although neophobia and neophilia have been suggested as important for predicting species' responses to changing environments (Sol et al., 2011), and to serve as potential conservation tools (Greggor et al., 2014), the extent to which neophobia/philia influence responses to ecological and evolutionary traps remains unknown. In theory, the influence of neophobia/neophilia could be critical in determining responses toward single-opportunity traps, but their effect on multiple-opportunity traps is less clear. Effects of novelty wear off with subsequent encounters; thus, both the initial levels of neophobia or neophilia and the rate at which attraction or repulsion toward novelty decays likely influence long-term responses. Additionally, the effect of neophobia on learning may depend on the learning type in question (Griffin and Guez, 2014). Innovative problem solving that requires persistence appears to be inhibited by neophobia, while learning that relies on inhibiting initial interactions, such as reversal learning could benefit from neophobia (Mathieu et al., 2012; Griffin and Guez, 2014; Guillette et al., 2014; Bebus et al., 2016). In contrast, neophilia can also influence learning if it increases sampling rate, but it can also increase the likelihood of an animal approaching a deleterious, novel cue. Additionally, whether animals have enough encounters to adequately learn adaptive choices once novelty is no longer the most salient cue depends upon the stimulus, memory retention, and lifespan of the animal. Even if animals make beneficial choices once novelty dissipates, there can still be opportunity costs in delaying their choices.

ANIMAL PERSONALITIES AND LEARNING IN RESPONSE TO HIREC

Finally, we consider how individual differences in "trapability" might also depend on the animal's personality or behavioral type (BT) as shaped by past selection and experience. Individuals within and between populations often differ consistently in their behavioral tendencies (e.g., aggressiveness, boldness, exploratory tendency) across time and ecological contexts (Sih et al., 2004; Réale et al., 2007). Although boldness, for example, clearly varies depending on ecological and social conditions, some individuals are consistently bolder and others consistently more fearful (shy, cautious) than others. In the context of HIREC, the animal's BT likely impacts each step in the formation of traps. As a broad generality, bold, exploratory animals are exposed more often to novel stimuli than shy, unexploratory ones (Cote et al., 2010; Spiegel et al., 2017). Therefore, bold, aggressive, or exploratory individuals should be more likely to approach and less likely to avoid novel cues. These effects of personality likely influence the relative success of individuals or populations in the face of traps, depending on how cues have changed. When HIREC produces novel dangers, the bolder species and individuals would be more likely to commit an error in approaching human-influenced stimuli, as can be the case for the individuals within populations that contribute to heightened human-wildlife conflict (Swan et al., 2017). In contrast, where HIREC produces novel, beneficial cues, such as access to new habitats, the less bold species and individuals would be more likely to commit avoidance errors. For example, invasive populations of cane toads, which are benefitting from approaching novel habitats, contain more bolder, exploratory phenotypes than native ones do (Candler and Bernal, 2015). In this way, even if traps do not lead to precipitous species or population decline, they may exert strong selection pressures based on personality phenotypes (e.g., recreational hunters can be more likely to catch bolder individuals, Ciuti et al., 2012; Madden and Whiteside, 2014).

With regard to subsequent learning, Sih and Del Giudice (2012) suggest and present evidence supporting the general hypothesis that high risk, high reward BTs might tend to be quicker to learn new activity-based tasks (and thus adopt novel resources or habitats that cautious individuals avoid), but tend to be slower to learn novel avoidance tasks, and slower to exhibit reversal learning. The animal's BT might directly affect learning tendencies, or both BT and learning might be associated with individual differences in hormonal stress response systems along a proactive-reactive axis (Koolhaas et al., 1999). Reactive animals tend to be more fearful (and thus less likely to explore novel situations), but more sensitive to (i.e., more likely to notice and learn about) environmental changes. Although these ideas seem intuitively plausible, they are probably oversimplified. A recent critique of the field connecting personality and cognition emphasizes that relationships are likely to be complex and both context and task- dependent (Griffin et al., 2015); nonetheless, a better understanding of within-species, individual differences in learning to better respond to HIREC should be insightful.

DISARMING TRAPS

Since there are many scenarios where animals will be unlikely to escape traps on their own, knowing where and when learning should be targeted could help disarm or prevent traps more effectively. In general it has been suggested that evolutionary traps can be disarmed by: reducing the attractiveness of poor resources, increasing the fitness value of these resources, or a combination of the two (Robertson et al., 2013). These suggestions can be made more specific when behavioral decisions and cognitive theory is considered in the process of disarming traps (Greggor et al., 2014; Hale and Swearer, 2016; Hale et al., 2018; Cassady et al., 2019). Throughout this paper we have identified areas of future research (**Table 1**), and illustrated a number of potential techniques. Although most of the techniques come down to the basics of attracting and repelling animals, we present them with the caveat that the most effective techniques for manipulating attraction and repulsion are still unknown (Greggor et al., 2016). Additionally, since the mechanism underlying an ecological trap can be a challenge to identify (Hale and Swearer, 2017), the relevant cues and experiences for a given trap may not be immediately apparent. Finally, the relationship between good and bad cues can be complex in the real world. HIREC changes can result in good cues (e.g., novel food resources) being presented alongside bad cues (e.g., new roads), and understanding how animals navigate these minefields of changes can require thinking about systems holistically. That being said, there are some guidelines that may be useful for thinking through solutions to traps.

Different approaches are likely necessary for disarming or preventing traps depending on whether they are single-opportunity or multiple-opportunity traps. Single-opportunity traps allow no space for individual learning. Therefore, animals must either be discouraged from interacting with the trapping cues initially by using deterrents (e.g., keeping marine mammals away from fishing nets, reviewed in Schakner and Blumstein, 2013), or drawing them to alternatives with rewards or social cues (Andrews et al., 2015). If traps are single opportunity traps because their cues occur too quickly for animals to respond (e.g., oncoming trains), then offering animals an additional warning cue may allow them to make associations which they otherwise would have been incapable of (e.g., giving bears a warning system that allows them to learn to avoid trains, Cassady et al., 2019). If none of the above is possible, single-opportunity traps need to be removed from the environment (e.g., changing the wavelength of light to prevent attractiveness for moths, or birds, Jones and Francis, 2003; van Langevelde et al., 2011).

Some multiple-opportunity traps may still be difficult to disarm with learning. For example, traps that result from interference with existing cues, rather than changes to the cue themselves (e.g., electromagnetic noise disrupting migrating birds' magnetic compass, Engels et al., 2014) are only likely to be alleviated by removal of the interference, since it can be a challenge for animals to set-shift to a new set of predicative cues. In contrast, there are a number of potential options for disarming multiple-opportunity traps when cue perception remains intact post-HIREC. However, their effectiveness will depend upon what type of error animals make. Encouraging animals to sample alternative options may help when animals approach bad options, or avoid good options. How one goes about encouraging sampling will depend upon the reason why it was not sampled in the first place, and whether we have any power to change the cues available. If animals have not sampled the beneficial option because they have not interacted with it spatially, then encouraging sampling by adding attractive cues to the beneficial option and repulsive cues to the detrimental option could help. In contrast, if animals approach bad options because those options themselves offer the most alluring cues, the only way to disarm the bad options is to remove the cues it offers. Finally, fixing errors relating to habituation may involve changing the repetition or predictability of cues to either encourage animals to ignore stimuli or facilitate their attention toward it. In all cases, understanding the mechanism underlying the trap will help determine if learning applies and target the correct learning ability if necessary.

CONCLUSIONS

There are many instances where learning can help animals avoid or escape potential traps caused by HIREC. In some situations, however, animals will not learn, or would do better by not learning. The error types we identify and the potential routes for learning they generate help highlight the circumstances where learning (or not) should be important for survival post-HIREC. While learning outcomes are challenging to predict, we are closer than ever to understanding the processes involved. Examining mismatches between the cognitive specializations that animals possess, and specific changes to cues may help explain why certain species commit errors post-HIREC. However, without greater attention toward patterns of sampling, generalization and individual differences in neophobia and personality, we will not understand when, or why, individuals or species escape their errors (or fail to do so). By focusing on the evolved constraints surrounding these processes we should better predict which animals will adjust to specific HIREC changes or need our help in disarming the traps we lay.

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All authors contributed to the ideas and writing of this review. All authors approved of the final submitted version.

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Fitness Consequences of Innovation in Spotted Hyenas

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Innovation is a well-studied cognitive phenomenon related to general intelligence and brain size. Innovative ability varies considerably within species and it is widely assumed that this variation must have important fitness consequences. However, direct evidence for a link between innovative ability and fitness has rarely been shown. Previous research examined variation in innovative problem-solving in wild spotted hyenas when confronting a novel puzzle box baited with meat. The earlier work revealed that variation in innovativeness in spotted hyenas was not related to age, sex, or social rank, but was predicted by neophobia, persistence, and diversity of motor responses to the puzzle. Here, we used the same dataset from wild spotted hyenas to investigate potential links between innovativeness and fitness. We found that innovative hyenas had lower offspring survivorship than non-innovators, but higher annual cub production (ACP). To test the hypothesis that high ACP can compensate for low offspring survival, we also measured annual cub survivorship (ACS) counting only offspring that survived at least 1 year. Here, there was no significant difference between innovators and non-innovators, which suggests that higher ACP does compensate for lower offspring survival, at least to 1 year of age. Overall, our data suggest that innovativeness may have both costs and benefits for fitness in wild spotted hyenas.

Keywords: innovation, fitness, spotted hyenas, survival, reproduction

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INTRODUCTION

Innovation, solving a novel problem, or using a novel behavior to solve a familiar problem, is widely studied in humans and animals (Kummer and Goodall, 1985; Reader and Laland, 2003). Innovation has been strongly linked to brain size across bird, primate, and carnivore species (Reader and Laland, 2002; Lefebvre et al., 2004; Benson-Amram et al., 2016). Innovation is also thought to be an important marker of high general intelligence (Ramsey et al., 2007; Reader et al., 2016) across a diverse array of taxa. Whereas the socio-ecological causes of inter- and intraspecific variation in innovative ability have been well-studied (reviewed in Reader and Laland, 2003; Reader et al., 2016), the fitness consequences of variation in innovativeness have rarely been examined despite growing interest (Morand-Ferron et al., 2015; Ashton et al., 2018; Boogert et al., 2018).

Innovative ability is typically measured on the species level by observing the rate of spontaneous innovations demonstrated in the wild (Lefebvre et al., 2013), and on the individual level by experimentally presenting captive or wild subjects with novel problem-solving tasks (Griffin and Guez, 2014; Reader et al., 2016), which typically require performance of a novel behavior to obtain a reward. Research suggests that innovativeness may be beneficial for adjusting to novelty and environmental change (Sol et al., 2016), an idea supported by correlations between innovation rates and generalist dietary or habitat preferences (Overington et al., 2011b; Ducatez et al., 2014). Furthermore, species that are more innovative appear more likely to invade novel habitats, including urban ones (Sol et al., 2005; Griffin and Diquelou, 2015). Finally, more innovative bird species tend to have slower life-histories and longer lifespans (Sol, 2009; Sol et al., 2016). Overall, this work suggests that innovativeness is likely adaptive for individuals responding to environmental change and novelty by enabling those individuals to express novel behaviors, exploit novel food sources, or avoid novel sources of mortality. Likewise, innovativeness is generally assumed to increase fitness through enhanced survival or reproductive success by buffering individuals against mortality-causing events (Sol, 2009; Sol et al., 2016), by increasing mating success (e.g., Keagy et al., 2009; Chen et al., 2019), or by increasing foraging rate, efficiency or quality. However, direct evidence supporting these assumptions is scarce.

Although innovation and general intelligence in humans have been consistently related to positive life outcomes (Plomin and Deary, 2015), the relationship between innovative problem-solving and fitness in non-human animals is much less clear. Across bird species, five studies have found a positive link between innovative problem-solving and fitness measures that included mating success, clutch size, hatching success, fledgling survival, provisioning rates, and offspring survival (Keagy et al., 2009; Cauchard et al., 2013; Preiszner et al., 2017; Wetzel, 2017; Chen et al., 2019). However, other studies of birds found no relationship between innovative problem-solving and mating success (Isden et al., 2013), or found that innovative problem-solving was correlated with lower competitiveness and higher nest desertion (Cole et al., 2012a,b). In the only study that has looked at innovation and fitness in a mammal, Huebner et al. (2018) found no link between more efficient problem-solving and any measure of fitness in mouse lemurs. Overall, the literature linking innovation and fitness in animals is very small, with limited taxonomic representation, and with largely mixed results. Here our goal was to examine the relationship between innovativeness and fitness in wild spotted hyenas.

Spotted hyenas are large African carnivores that have previously been established as a good model system for testing hypotheses about the evolution of cognition (Holekamp et al., 2007). Unlike most large carnivores in Africa, spotted hyenas are not endangered; their success may have been facilitated by their impressive behavioral flexibility. Spotted hyenas are generalist feeders; they eat everything from termites to elephants (Cooper et al., 1999; Hayward, 2006) and have established themselves in nearly every habitat in sub-Saharan Africa (Holekamp and Dloniak, 2010) including urban ones (Yirga et al., 2017). Earlier research found that spotted hyenas show innovative ability similar to that of wild vervet monkeys (Benson-Amram and Holekamp, 2012), and that hyenas also show high levels of innovativeness relative to other carnivores (Benson-Amram et al., 2016). In the present study we aimed to test the idea that innovativeness might be an adaptive trait in spotted hyenas by comparing their problem-solving performance to three measures of fitness. To do this, we used a subset of the data from Benson-Amram and Holekamp (2012) on innovative problem-solving in female spotted hyenas, and analyzed it in relation to our long-term data on reproduction and survival for each female. This subset included 29 female spotted hyenas, of which five were considered innovative.

Hyena fitness has been linked to both social and ecological variables. Dominance rank has large effects on lifetime reproductive success in hyenas; the highest ranking female in a clan may have up to five times more offspring than the lowest ranking female due to better access to food, younger ages at first parturition, shorter interbirth intervals, better offspring survival, and longer reproductive lifespans (Frank, 1986; Holekamp et al., 1996). Finally, ecological variables such as prey abundance and competition with lions also affect reproductive success and juvenile survival (Watts and Holekamp, 2009). Our goal here was to test the hypothesis that innovativeness is adaptive in regard to both reproductive success and survival in wild spotted hyenas; if true, we expected to see a direct positive relationship between innovative problem-solving and our measures of fitness.

MATERIALS AND METHODS

Subjects, Population, Location

The subjects were individuals from two neighboring clans (the Talek West clan and the Fig Tree clan) of spotted hyenas in the Maasai Mara National Reserve, Kenya. Individuals were identified by their unique spot patterns and other natural markings. Observations were conducted daily from 0530 to 0900 h and from 1700 h to 2000 h, on an average of 23.5 days per month. The Talek West clan was monitored continuously from May 1988 to December 2016, and the Fig Tree clan was monitored continuously from April 2007 to May 2015. All innovation testing took place between May 2007 and May 2008; during this period, the Talek West clan contained 46–48 members, including 12–13 adult females with their juvenile offspring and 10 adult males, and the Fig Tree clan contained 36–38 members, including 10 adult females with their juvenile offspring and 7–8 adult immigrant males. Additional information about the study subjects, methods and materials can be found in Benson-Amram and Holekamp (2012). Although innovativeness was tested in both male and female hyenas, in the current analysis we only included female hyenas for which we had reproductive data.

Problem-Solving Apparatus

We used a novel problem-solving apparatus to test innovative ability. The "puzzle box" used here measured 60 × 31 × 37 cm and was built from welded 10.5 mm steel rebar (**Figure 1**). The box had a single 30 × 34 cm door on one long side, large enough for a hyena to put its head inside the box, and handles in the center of each short side. When it was baited with roughly 2 kg of raw meat, the box weighed more than 35 kg. To obtain access to the meat, a subject had to slide a 12 cm steel bolt latch laterally using the mouth or forepaws, and the door would swing open. For more detail on the apparatus, see Benson-Amram and Holekamp (2012). Successful trials were those in which the puzzle box was opened. Unsuccessful trials included those in which

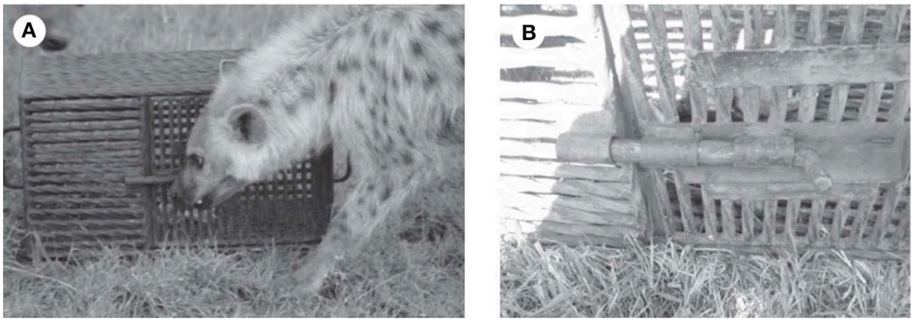

FIGURE 1 | (A) An image of the puzzle box apparatus used in the experiment. **(B)** A close-up image of the latch bolt that hyenas had to move laterally in order to access the meat inside the puzzle box. Republished from Benson-Amram and Holekamp (2012).

the hyena contacted the box, but failed to open it, as well as those in which the hyena did not interact with the box, despite spending time within 5 m of it (average duration in minutes spent within 5 m on the first trial $\pm$ $SD = 11.95 \pm 13.47$, $N = 29$). Previously, we found that 14.5% of all hyenas tested with this problem-solving task had at least one successful trial. Within this group of successful hyenas, 78% were successful on subsequent trials. Trial number was a significant predictor of latency to solve the problem, with hyenas generally solving the box faster in later trials, which suggests that hyenas learned how to open the box (see Figure 2 in Benson-Amram and Holekamp, 2012). Successful problem-solving also showed modest but significant repeatability after controlling for the effect of trial number ($R = 0.24$, SE = 0.12, CI = 0.03–0.41, $P < 0.0001$) (rptR package; Stoffel et al., 2017). Additionally, another study, with the same population of wild spotted hyenas, found that innovation was significantly repeatable across four novel problem-solving tasks ($R = 0.96$; Johnson-Ulrich et al., in review). Therefore, in the present study hyenas were defined as innovative if they had at least one successful trial and non-innovative if they had only unsuccessful trials.

Data Collection Protocols

Because we were working with a wild population, subjects for these experiments were chosen opportunistically, based on which animals were available at the time. However, every attempt was made to conduct equal numbers of trials with all the individuals in each clan, and to balance the number of participants in each age, sex and social rank category. When an appropriate subject animal was sighted in an accessible location, we parked our research vehicle ~100 m upwind of the hyena. The box was placed on the ground on the opposite side of the vehicle from the hyena in a location with good visual access, both for the subject, and for observers. The box was oriented with the door toward the hyena, with the latch protruding at 90° from the box, parallel to the ground. We then pulled the vehicle back ~50 m from the box and initiated observations. A trial began when a hyena approached to within 5 m of the box (thereby becoming a "focal hyena"); the trial ended when the hyena left the 5 m radius and remained outside of it for 5 min, or when it moved to at least 200 m from the box. All attempts were made to test subjects only when they were alone, but occasionally conspecifics approached and participated in a trial. However, the presence or absence of conspecifics did not significantly affect the likelihood of a hyena successfully opening the box (Benson-Amram and Holekamp, 2012), so this variable was not analyzed in the present study. All trials were videotaped in their entirety from our vehicle. For more detail on data collection protocols see Benson-Amram and Holekamp (2012).

Fitness Variables

Demography

We used several demographic variables to calculate survivorship and annual reproductive success. First, cub ages were estimated to ± 1 week based on their appearance when first observed (Holekamp et al., 1996), and date of birth (DOB) was calculated on that basis. Date of first conception (DFC) for each adult female was estimated by subtracting 110 days, the length of gestation in spotted hyenas, from the DOB of a female's first observed litter. Some females in the Fig Tree clan were adults when monitoring began; therefore DFC represents the first conception that researchers observed, but might not represent every female's first conception after reaching sexual maturity. Finally, date last seen (DLS) was recorded as the last day on which a hyena was seen alive or, if its body was found, the date on which it was found dead. Female hyenas remain in their natal clans throughout their lives (Kruuk, 1972) so females that had not been seen for at least 6 months were considered to be dead. Standardized social rank was measured as a continuous variable on a scale of 1 to -1 where a rank of 1 indicated the highest-ranking female in the clan and a rank of -1 indicated the lowest-ranking female in the clan. All individuals in a clan were assigned their own rank except for pre-weaning cubs and subadults who were assigned the rank of their mother. Ranks were assigned based on the clan hierarchy during the period from May 2007–2008, when innovation was tested. This hierarchy was generated using a dominance matrix ordering observations of aggressive or submissive behaviors within dyads of adult hyenas (Martin and Bateson, 1993; Holekamp et al., 2012). Rank hierarchies among spotted hyenas are convention-based such that offspring acquire ranks immediately below those of their mothers through a process of maternal interventions and social learning. Social ranks in spotted hyenas are relatively stable and rank reversals are rare (Strauss and Holekamp, 2019).

Offspring Survivorship

Offspring survivorship was calculated from birthdate and mortality data during the first 24 months of life. Mortality was recorded as a binary variable: dead vs. alive. Using this mortality data, the proportion of offspring surviving was estimated at each age (in months) up to 24 months of age. If offspring disappear before 24 months of age, this represents mortality, but this is not necessarily true after 24 months because 24 months represents the age at which hyenas reach sexual maturity and male hyenas begin to disperse then from their natal clans (Van Horn et al., 2003). Thus, disappearance after 24 months of age for male hyenas may be due to either mortality or dispersal.

Annual Reproductive Success

Offspring survivorship does not necessarily correlate with lifetime reproductive success because it doesn't account for the number of offspring produced. Therefore, the next measure of fitness we examined was annual reproductive success. We included two measures of annual reproductive success: annual cub production (ACP) and annual cub survival (ACS). ACP was calculated by dividing the total number of cubs born to a female during the study divided by her observed reproductive lifespan. Observed reproductive lifespans were calculated by subtracting a female's DFC from her DLS or the end date of the study. Annual cub survival (ACS) was calculated in the same manner as ACP, but instead of using the number of cubs born, only the number of cubs surviving to 1 year of age were counted.

Statistical Analysis

All statistical analyses were done using R version 3.5.0 (R Core Team, 2019). To analyze offspring survival we used a Cox proportional hazards model, which is ideal for analyzing right-censored time-to-event data. This model estimated the probably that subjects would survive to specific ages by using both the lifespan and mortality variables described in section Offspring Survivorship. Cox regression was conducted using the R packages "survival" (Therneau and Grambsch, 2000; Therneau, 2015) and "survminer" (Kassambara and Kosinski, 2018). For all other fitness analyses we used linear regression models built using the R package "glmmTMB" (Brooks et al., 2017). The dependent variables in each of our models were survival, ACP, or ACS. Every model included innovativeness as the independent variable. Subject rank, number of trials, and an interaction effect between innovativeness and number of trials were included as potential confounds in all models. We included rank to control for its previously demonstrated effect on reproductive success in spotted hyenas (Holekamp et al., 1996). We included the number of trials each hyena received prior to her first successful trial in each model to control for the number of opportunities each hyena had to open the puzzle box. If the hyena had no successful trials, this number represented the total number of trials in which she participated. Likewise, we added an interaction effect because subjects who solved the puzzle box on their first trial were potentially demonstrating a higher level of innovative ability than those who solved the box after many trials. That is, the effect of innovativeness on fitness might depend on the trial number. We also included a random effect of maternal ID in the Cox regression. Because proportions such as ACP and ACS might not fully account for the potentially confounding effect of length of the observed reproductive lifespan we also included the length of the observed reproductive lifespan as a covariate in these two models. Full output from each model is available in the Supplementary Material (**Supplementary Tables 1–3**). Model fit for each model was assessed using the R package "DHARMa" (Hartig, 2019). All models showed good fits as indicated by normally distributed residuals, non-significant DHARMa non-parametric dispersion tests, and non-significant Durbin-Watson tests for temporal autocorrelation.

RESULTS

Innovative Problem-Solving

Thirty-three female hyenas participated in trials with the puzzle box; however, the exact social ranks of two females were unknown, and two other females had incomplete reproductive data, so they were dropped from the analysis, yielding a sample size of 29 (**Table 1**). Of these 29 females, five females were able to open the box at least once, and were thus considered to be innovative. On average, female hyenas received 4.48 ± 4.16 trials (range = 1–14 trials) and opened the box an average of 1.62 ± 4.53 times (range = 0–18).

Offspring Survivorship

These 29 females produced 288 offspring across the study period and we confirmed 114 cases of mortality within the first 24 months of age. Using a Cox proportional hazards regression model, we found that offspring of innovative mothers had significantly lower survival rates during the first 24 months than offspring of non-innovative mothers (cox: $z = 2.31$, $P < 0.02$; **Figure 2**; **Supplementary Table 1**). None of the other covariates were significant in this model.

Annual Reproductive Success

On average, subjects gave birth to 9.6 ± 4.48 cubs (range = 3–19) during their observed reproductive lifespan. The average length of the observed reproductive lifespan was 8.24 ± 4.57 years (range = 1.73–20.00). Across all 29 females, without controlling for covariates, average ACP was 1.29 ± 0.35 cubs per year

TABLE 1 | Summary of number of subjects in each rank and age class combination.

	High-ranking	Mid-ranking	Low-ranking	Totals
Pre-weaning subadult	3	3	1	7
Post-weaning subadult	3	1	0	4
Adult	9	7	2	18
Totals	15	11	3	29

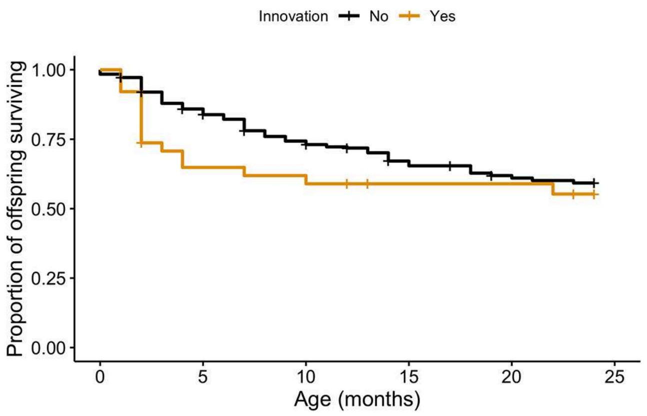

FIGURE 2 | Unadjusted survival curves calculated showing the proportion of offspring surviving at each age point between 0 and 24 months of age for non-innovative and innovative mothers.

(range = 0.60–1.93). In our model, innovative females produced significantly more cubs annually than did non-innovative females (LM: $z = 2.85$, $P = 0.004$; **Figure 3A**; **Supplementary Table 2**). Innovative females produced an average of 1.35 ± 0.24 (estimated marginal mean ± SE) cubs annually, whereas non-innovative females produced only 1.2 ± 0.07 cubs annually. The length of the observed reproduction lifespan (LM: $z = -3.42$, $P < 0.001$) and the interaction between innovativeness and trial number were also significant in this model (**Supplementary Table 2**). The effect of innovativeness on ACP was highest for female hyenas with the fewest trials (LM: $z = -0.44$, $P = 0.01$). When this interaction effect was not included the model, the effect of innovation on ACP was not significant (LM: $z = 1.04$, $P = 0.30$).

Next, we investigated the possibility that high ACP could compensate for low offspring survival by comparing the overall number of cubs surviving to 1 year of age between innovative and non-innovative females. On average, without controlling for covariates, females produced 0.81 ± 0.31 surviving cubs each year (range = 0–1.62). In our model, innovative females produced 0.94 ± 0.18 cubs annually and non-innovative females produced 0.79 ± 0.06 cubs annually, but this difference was not significant (LM: $z = 1.28$, $P = 0.20$), suggesting that innovative and non-innovative females produce similar numbers of cubs that survive to 1 year of age (**Figure 3B**; **Supplementary Table 3**). No other covariates were significant in this model (**Supplementary Table 3**).

DISCUSSION

We found that innovativeness was linked to fitness in variable ways in wild spotted hyenas. Innovative females had lower offspring survivorship, but gave birth to more offspring annually, than did non-innovative females. In addition, innovative and non-innovative females gave birth to similar numbers of cubs that survived to 1 year of age. This suggests that innovative females might be able to offset lower offspring survival with higher reproductive success. However, given our very small sample size of 29 hyenas (of which, only five were able to solve the puzzle box), our results should be interpreted cautiously. Our results are similar to those from other species suggesting that cognitive abilities may have both fitness costs and benefits. For example, guppies that were artificially selected for larger brains had better performance on cognitive tasks, but produced fewer offspring (Kotrschal et al., 2013), and more innovative great tits had larger clutches but also had higher levels of nest desertion (Cole et al., 2012a). Fitness trade-offs involving non-cognitive traits appear to be fairly common in animals (e.g., Sinervo et al., 2000; Ricklefs and Wikelski, 2002; Wolf et al., 2007; Barrickman et al., 2008; Lewin et al., 2017; Ducatez et al., 2019), so it should probably not surprise us to find that this may be true in regard to cognitive traits as well.

Life History Trade-Offs

Because innovative females had lower offspring survival (**Figure 2**), but higher ACP (**Figure 3A**) than non-innovative females, we considered the possibility that these correlations represented an adaptive trade-off between two alternative life history strategies where innovative female hyenas pursue a faster, quantity over quality, life history strategy and non-innovative females pursue a slower, quality over quantity, life history strategy. Previous research in wild spotted hyenas found that in juveniles, high insulin-like growth factor 1 (IGF-1) concentrations correlated with fast growth and earlier reproduction, but shorter lifespans (Lewin et al., 2017), suggesting that hyenas may invest differentially in reproduction and survival. However, innovation is generally thought to be associated with slower life histories across species (Sol et al., 2016). Instead of, or in addition to, alternative life-history strategies, it is also worth considering the possibility that innovativeness is an evolutionary stable strategy where the adaptive benefits of innovativeness are only realized at a specific ratio of innovative to non-innovative hyenas in the study population due to frequency-dependent selection. It is conceivable that the presence of a small ratio of innovative females could be beneficial at the scale of the entire clan if innovative females make previously unexploited resources available to the entire clan. Although spotted hyenas show only limited social learning of novel behaviors, feeding itself is highly socially facilitated (Yoerg, 1991; Benson-Amram et al., 2014).

Our result showed that innovative and non-innovative females have similar numbers of cubs surviving to 1 year, which suggests that higher birth rates in innovative females do indeed offset the significantly lower offspring survival rates. For spotted hyenas, mortality rates are highest in the first year of life; nearly half of all cubs born perish during their first year (Watts and Holekamp, 2009). Therefore, it seems reasonable to assume that the proportion of cubs that survive to 1 year would correlate with the overall proportion of offspring surviving to sexual maturity for female hyenas. This could be interpreted as evidence for equal adaptive value between being innovative vs. non-innovative; however, previous research on spotted hyenas found that, whereas annual reproductive success significantly predicted lifetime fitness, the length of the reproductive lifespan was the strongest determinant of lifetime fitness in spotted

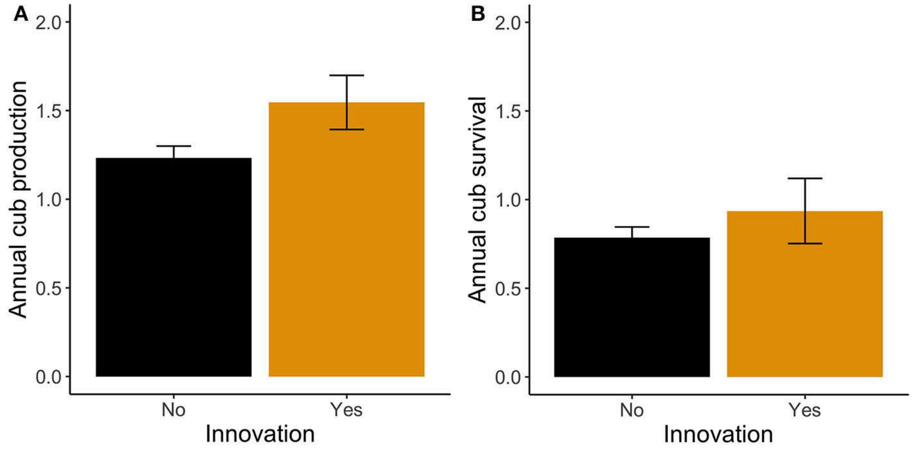

FIGURE 3 | Annual reproductive success for innovative and non-innovative females. **(A)** Average number of cubs produced annually by female hyenas. **(B)** Overall number cubs that survive to 1 year of age for female hyenas. Errors bars show standard error.

hyenas (Swanson et al., 2011). We were unable to calculate the actual reproductive lifespans of our female subjects because our dataset was both right and left-censored temporally; some of our subjects were adults females without known DOBs or dates of sexual maturity, and many were still alive at the end of the study period. However, the average observed reproductive lifespan in our dataset was 8.24 ± 4.57 years which, although censored for some subjects, is not significantly different from the average reproductive lifespan in our study population (7.13 ± 3.34 years, $N = 170$) (Swanson et al., 2011). Therefore, it is possible that innovative and non-innovative females have similar lifetime fitness, but, without actual lifetime fitness data on a larger sample of females, we cannot conclude this with any certainty.

Mediators of the Link Between Innovativeness and Fitness

Not only are researchers interested in the links between cognition and fitness, but also the mechanisms mediating such linkages. However, it is often unclear just why a specific cognitive ability might improve reproductive success or survival. The largest natural source of mortality for wild spotted hyenas comes from lions, both directly through conflict and indirectly through competition over food resources (Watts and Holekamp, 2009). In hyenas and other animals innovative problem-solving has been linked to greater boldness or risk-taking behavior (Webster and Lefebvre, 2001; Overington et al., 2011a; Benson-Amram and Holekamp, 2012; Audet et al., 2016; van Horik et al., 2017; Johnson-Ulrich et al., 2018), which in turn are correlated with higher mortality in wild hyenas. Hyenas that are bolder in the presence of lions, in particular, have a higher risk of mortality than conspecifics with intermediate or low levels of boldness (Yoshida et al., 2016), so lower survivorship among offspring of innovative females may be mediated by high boldness during conflict or competition with lions. In addition, greater risk-taking behavior in spotted hyenas, measured with a "mock intruder" test, is also correlated with a higher risk of mortality (Turner et al., 2019). Overall, if more proactive, bold, or risk-taking behavior, demonstrated by hyenas while interacting with problem-solving apparatuses, is correlated with their behavior in other contexts, it is possible that these traits mediate the link between innovation and survival.

The relationship between innovative problem-solving and reproductive success, on the other hand, has been linked in some bird species to the ability to forage more efficiently (Cauchard et al., 2017; Preiszner et al., 2017; Wetzel, 2017) but see Cole et al. (2012a). Access to food is a strong determinant of reproductive success among female hyenas; social rank is the strongest determinant of reproductive success because high ranking individuals enjoy the best access to high quality food resources (Holekamp et al., 1996). In addition, both average fatness, which usually indicates how recently a hyena has fed, and per capita prey availability also correlate with reproductive success in hyenas (Watts and Holekamp, 2009; Swanson et al., 2011). Social rank doesn't predict innovativeness in spotted hyenas (Benson-Amram and Holekamp, 2012); therefore, if innovativeness is correlated with the ability to access food in hyenas, then it is plausible that this would directly increase reproductive success.

Assumptions and Limitations

Our analysis of the relationship between offspring survival and female innovativeness is based on only a small sample and hinges on several assumptions. First, for innovativeness to be related to offspring survival, innovativeness must be transmitted from mother to offspring through genetic heritability or social learning. However, few studies have assessed the heritability of innovative problem-solving and one that has, in great tits, found no evidence for heritability (Quinn et al., 2016). If instead the relationship between innovative ability and offspring survival is mediated by a trait such as boldness, then boldness must be transmissible. Although the heritability of innovativeness in wild spotted hyenas has not been tested, previous research indicates that their boldness is heritable (Yoshida et al., 2016). Alternatively, it is also possible that innovative ability is entirely stochastic and has a direct effect on offspring survival through early-life effects or ongoing social support. Cubs usually wean between 12 and 18 months of age, but female hyenas provide ongoing social support to their mature female offspring throughout their lives during feeding competition and other social interactions with clan members (Watts et al., 2009; Smith et al., 2010; Vullioud et al., 2019). Thus, it is possible that variation in this support, if related to the ability to innovate, results in differential survival between offspring of innovative and non-innovative females.

Although our analysis of annual reproductive success in spotted hyenas doesn't hinge on assumptions about heritability, it is less robust than our analysis of offspring survival due to an extremely small sample size and censored windows of time during which we were able to monitor reproductive output for many subjects. Our total sample size consisted of 29 female hyenas, of which only five were innovators. Of these five individuals three were high ranking, one was mid-ranking, and one was low-ranking. In addition, three were adults at the time innovativeness was measured and two were pre-weaning subadults. Thus, these five innovative hyenas did not differ in any substantial measurable way from our overall sample of females, but our results should still be interpreted with caution because we cannot be sure that these five are not outliers in ways we did not measure. Maternal age might also have affected our measures of fitness. For individuals with known birth dates, the length of the reproductive lifespan would have controlled for this. Unfortunately, without knowing the birth dates for some of the females sampled ($N = 2$ innovators, $N = 5$ non-innovators), we have no way of knowing what their age was during the observed portions of their reproductive lives.

CONCLUSION

In summary, innovative female spotted hyenas were found to have lower offspring survival, but higher annual cub production, than non-innovative females. These results suggest there might be trade-offs among the costs and benefits of innovativeness, or that innovative and non-innovative females pursue different life history strategies. We would benefit from further study of the relationship between fitness and innovativeness in wild spotted hyenas. Ideally, long-term study would allow for measurement of lifetime reproductive success and assessing the heritability of innovativeness across generations. In addition, future work might investigate the mediators of the relationship between innovativeness and fitness by comparing innovativeness to other variables such as foraging ability, boldness, and social relationships.

DATA AVAILABILITY STATEMENT

The datasets and corresponding R code analyzed for this study can be found in the Knowledge Network for Biocomplexity (KNB) Repository: doi: 10.5063/F1D21VXP.

ETHICS STATEMENT

The animal study was reviewed and approved by Michigan State University Institutional Animal Care & Use Committee, Application no. 07/08-099-00.

AUTHOR CONTRIBUTIONS

LJ-U, SB-A, and KH designed the research and wrote the manuscript. SB-A collected the data on innovative problem-solving by spotted hyenas using an apparatus designed by KH. KH collected the data on spotted hyena demography. LJ-U performed all statistical analyses. This manuscript was submitted with the full knowledge and approval of LJ-U, SB-A, and KH.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00443/full#supplementary-material

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The Overlooked Influence of Hybridization on Cognition

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For many animal species, cognitive traits are important for fitness. Such traits may be especially important in rapidly changing environments, where innovation and learning about new challenges could mean the difference between persistence and extinction (Dukas, 2013; Mery, 2013). One factor that may affect cognitive performance is hybridization. Hybridization occurs when individuals from distinct species mate and produce offspring. It is widespread, with estimates suggesting 1–10% of all animal species hybridize (Mallet, 2005; Schwenk et al., 2008), and is expected to become increasingly common as species distributions shift due to climate change (Chunco, 2014). Yet, the extent to which hybridization affects cognition, and any resulting impacts on hybrid fitness, remain relatively unknown. Recently, Rice and McQuillan (2018) described several mechanisms by which hybridization could directly affect cognitive abilities and negatively influence hybrid fitness. Here, I also consider that hybridization's impacts on cognition could lead to positive fitness consequences, and *indirectly* affect the expression of cognitive traits. I further discuss how the trade-off between investment in cognition and other functions could have important implications for the ultimate evolutionary outcome of hybridization. Currently, little is known about hybridization's effects on the expression of and selection on cognitive traits, and I argue that this is an important area for future research.

WHAT WE KNOW ABOUT HYBRID COGNITION

The effects of hybridization on cognition have been poorly studied, particularly in cases of natural hybridization. A recent study tested the relative spatial memory and problem-solving abilities of black-capped and Carolina chickadees and their naturally-occurring hybrids (McQuillan et al., 2018). Chickadees are scatter hoarders, caching food throughout the environment during the fall. They rely on spatial memory to retrieve this food in the winter, and individuals with better spatial memory are more likely to survive (Sonnenberg et al., 2019). Although black-capped and Carolina chickadees performed equally well on an associative learning spatial task and a novel problem-solving task, hybrids were less able to remember the location of a food item or to solve the problem (McQuillan et al., 2018). Further testing is needed to determine whether other aspects of cognition are similarly affected. In contrast to the results in hybrid chickadees, mules—hybrids produced by crossing domestic horses and donkeys—exhibit enhanced visual discrimination and problem solving compared to their parental species (Proops et al., 2009; Osthaus et al., 2013). Although mules are not subject to natural selection, being domesticated, these findings demonstrate that hybridization can also lead to enhanced cognitive abilities compared to parental species.

Together, these examples illustrate the potential for hybridization to both positively and negatively affect cognition; however, much remains unknown. How frequently does hybridization influence cognition in other taxa? By what mechanism(s)? For a given hybrid cross, does hybridization have similar or variable effects on the diverse aspects of cognition? What are the net fitness consequences in wild populations across a range of environments? And how does selection on hybrid cognition contribute to the evolutionary outcomes of hybridization?

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DIRECT EFFECTS OF HYBRIDIZATION ON COGNITION

Cognition can be shaped by natural (e.g., Roth et al., 2012) and artificial selection (e.g., Mery and Kawecki, 2002), and individual variation in cognitive performance is repeatable (Cauchoix et al., 2018), leading to the conclusion that it has a heritable genetic basis (Croston et al., 2015). Therefore, hybridization should be expected to directly affect cognitive traits by the same mechanisms as it affects other traits.

Hybridization frequently leads to negative fitness consequences. Cognitive traits may be subject to genetic incompatibilities in hybrids (Dobzhansky, 1936; Muller, 1942; **Figure 1**), leading either to negative fitness consequences, or to asymmetric fitness consequences depending on the cross direction (Orr, 1995; Turelli and Moyle, 2007) or the sex of hybrid individuals ("Haldane's Rule," Schilthuizen et al., 2011). Likewise, when two parental species with cognitive abilities under divergent selection produce hybrids of intermediate ability, ecological selection may act against the hybrids (Hatfield and Schluter, 1999; McBride and Singer, 2010; **Figure 1**) following a classical "ecological speciation" scenario (Rundle and Nosil, 2005). Rice and McQuillan (2018) further elaborate on the direct mechanisms by which hybridization could affect cognitive traits, leading to negative fitness consequences and postzygotic reproductive isolation between parental species.

Hybridization could also directly affect cognition in ways that lead to positive fitness consequences, and facilitate adaptation to novel environments. The mule example above shows that in some cases, cognitive abilities may be enhanced in hybrids relative to parental taxa (Proops et al., 2009; Osthaus et al., 2013). Enhanced cognitive abilities could result from positive genetic interactions between loci in the parental species ("heterosis"; Dagilis et al., 2019), or from the recombination of additive alleles in F_1 and advanced generation hybrids ("transgressive segregation"; Rieseberg et al., 1999). Hybrids with enhanced abilities could experience high fitness (**Figure 1**), provided the fitness benefits of enhanced cognition in their specific environment outweigh any costs (Cole et al., 2012; Kotrschal et al., 2013). Such enhanced abilities, if caused by heterosis, may be transient, as it is less likely in advanced generation hybrids or back-crossed individuals (Barton, 2001). However, high fitness phenotypes in hybrids caused by transgressive segregation can persist across generations, as illustrated by the existence of stable hybrid species that are succeeding in novel or extreme environments, or are utilizing novel resources (e.g., Nolte et al., 2005; Gompert et al., 2006; Lamichhaney et al., 2018).

INDIRECT EFFECTS OF HYBRIDIZATION ON COGNITION

Hybrids often have lower success than parental species individuals in obtaining resources, or have less efficient metabolism, which could have indirect negative effects on cognition (**Figure 1**). Hybrids produced by parental species that have diverged in resource use may be intermediate in their

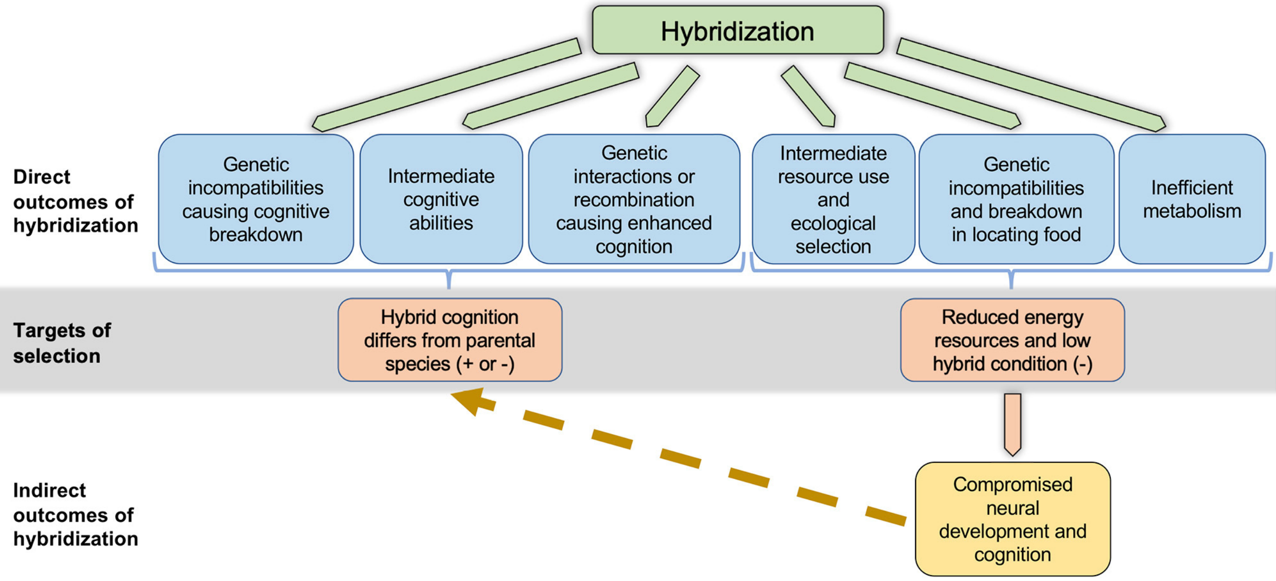

FIGURE 1 | Non-mutually exclusive pathways by which hybridization can affect cognition. Hybridization can have direct effects on cognition through positive or negative genetic interactions, or through combinations of additive alleles. Reduced, intermediate, or enhanced cognition may result in hybrids, and the fitness consequences could be either positive or negative, depending on a variety of factors (see text). Alternatively, or even simultaneously, hybridization can indirectly affect cognition through its direct effects on resource use phenotypes, metabolic efficiency, or abilities to locate food. All of these direct outcomes are likely to lead to reduced energy and low condition in hybrids, likely causing selection against hybrids. Reduced energy and low condition can subsequently lead to compromised neural development and cognition in hybrids, which can in turn cause hybrid cognitive abilities to differ from those in the parental species.

resource use phenotypes, and poor competitors in either parental environment (Hatfield and Schluter, 1999; Pfennig and Rice, 2007). Hybridization may also interfere with an individual's ability to locate food (Linn et al., 2004; Turissini et al., 2017). Such hybrids are likely to obtain fewer resources, and thereby experience reduced energy availability during development. Further, laboratory studies have demonstrated that mismatches between mitochondrial and nuclear genomes can affect metabolic function (Tieleman et al., 2009; Arnqvist et al., 2010; Hoekstra et al., 2013). Consistent with these findings, naturally-occurring hybrids from two different avian hybrid zones were found to be less efficient at energy metabolism (Olson et al., 2010; McFarlane et al., 2016). The fitness consequences of inefficient metabolism are likely to be environment dependent (Hoekstra et al., 2013), and could be further exacerbated if hybrids also have difficulties obtaining resources. Cognitive abilities and neural development are frequently condition dependent (reviewed in Buchanan et al., 2013). For example, birds experiencing restricted diets during development exhibited poorer spatial learning (Pravosudov et al., 2005) and auditory memory (Bell et al., 2018) as adults. However, poor nutrition does not necessarily affect all aspects of cognition similarly (Pravosudov et al., 2005). Given that hybridization can affect condition and energy availability through multiple mechanisms, indirect effects on some aspects of hybrid cognition are likely to be widespread (**Figure 1**).

TRADE-OFFS, THE ENVIRONMENT, AND SELECTION ON COGNITION

If hybrids differ from their parental species in cognitive performance, whether due to direct or indirect effects of hybridization or both (**Figure 1**), it will be important to estimate the magnitude and direction of selection on these traits. This will determine the impact of cognitive performance on the evolutionary outcomes of hybridization, which can include weakening or strengthening of species barriers, adaptive introgression, and even the creation of new hybrid species (Abbott et al., 2013).

Decreased cognitive abilities in hybrids could actually provide a fitness benefit in some environments, while enhanced cognitive abilities could result in lower fitness. This is because the energy demands of maintaining the brain tissue underlying cognitive abilities are expected to be high (Mink et al., 1981; Bordone et al., 2019), leading to a trade-off between investment in cognition and in other energetically costly functions and traits. For example, lines of *Drosophila* selected for enhanced learning ability experienced a decline in average lifespan compared to control lines (Burger et al., 2008). A consistent result was found in lines of guppies selected for large brains; the large-brained lines exhibited enhanced cognition (Kotrschal et al., 2013) but also shorter lifespan (Kotrschal et al., 2019). A trade-off between learning ability and competitive ability was uncovered in *Drosophila* as well (Mery and Kawecki, 2003), and families of cabbage white butterflies showing enhanced learning produced fewer eggs (Snell-Rood et al., 2011). Thus, the net strength and direction of selection on cognitive abilities will incorporate the costs to other functions important to fitness, and may differ among resource-poor and resource-rich environments. If hybridization occurs across a range of such environments and affects cognition, hybrids in certain environments may be strongly selected against, leading to a strengthening of species boundaries and potentially narrow hybrid zones, while the opposite could be true in other environments.

It is worth noting for at least three reasons, however, that hybrids may be particularly likely to find themselves in environments favoring enhanced cognitive abilities, even in the face of trade-offs. First, species range overlap is often associated with environmental gradients and can shift with the climate (Chunco, 2014; Taylor et al., 2015), such that the opportunity for hybridization may be especially high in variable or novel environments. Second, hybridization may facilitate the colonization of novel environments, either through the adaptive introgression of genes underlying functionally important traits, or as a result of transgressive segregation (Pfennig et al., 2016). Third, areas of sympatry, such as hybrid zones, are likely to be complex social environments, as animals must navigate and process both intra- and interspecific interactions and signals (Pfennig and Pfennig, 2012). Variable, novel, and socially complex environments are expected to favor enhanced learning, memory, and problem-solving (Sol et al., 2002; Dukas, 2013; Mery, 2013; Ashton et al., 2018), so that hybrids with such abilities could experience high fitness.

Selection on hybrid cognition is likely to be complex, and much additional research is required to assess how cognition contributes to the net fitness consequences of hybridization. Because hybrids may have reduced energy reserves compared to parental species individuals (see above), one interesting implication of the trade-off between investment in cognition and other functions is that the direction and magnitude of selection on cognition could vary between hybrids and parental species, even in similar environments. The optimal level of cognitive ability for a parental individual in a given environment might be higher than the optimal level for a hybrid—with reduced energy reserves—in the same environment. Expected patterns of selection are further complicated by the fact that individuals can vary in their performance across different aspects of cognition (DuBois et al., 2018; van Horik et al., 2018), and therefore hybridization may have variable effects on different aspects of cognition depending on which individuals are hybridizing.

CONCLUSION

Hybridization is likely to have important direct and indirect impacts on cognitive ability. Resulting cognitive performance in hybrids may lead to positive or negative fitness consequences. Further, the trade-off between investment in cognition and other important functions coupled with the potential for individual variation in performance across multiple aspects of cognition will complicate patterns of selection on hybrid cognition. The net strength and direction of this selection will determine how cognitive performance contributes to the ultimate evolutionary outcomes of hybridization. Currently, very little is known about hybridization's impact on cognition, and there is large scope for additional research. Important questions include: How frequently does hybrid cognition differ from parental species, and in what systems? Is it more common for hybridization to affect cognition through direct or indirect mechanisms, or both? What is the direction and magnitude of selection on hybrid cognition, and how does it vary across environments? Many study systems, across a broad range of taxonomic diversity, are well-suited for addressing these questions, particularly those with existing knowledge of traits affected by hybridization. Such research is needed if we are to evaluate the role of cognitive performance in the maintenance of species boundaries, or the links between hybridization and the expression of and selection on cognitive traits in the wild.

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Brain Size and Life History Interact to Predict Urban Tolerance in Birds

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Urbanization is a major driver of local biodiversity losses, but the traits that determine whether species are able to tolerate urban environments remain poorly understood. Theory suggests that a larger brain should provide higher tolerance to urbanization by enhancing behavioral flexibility to cope with novel challenges. However, assembling empirical evidence for a link between brain size and tolerance to urbanization has proven to be difficult, perhaps because the effect of the brain interacts with life history to influence persistence in urban environments. Here, we provide a global-scale assessment of the role of brain size on urban tolerance, combining quantitative estimations of urban tolerance with detailed information on brain size, life history and ecology for 629 avian species across 27 cities. Our analysis confirms the expected positive association between brain size and urban tolerance, but shows that the relationship is more complex than previously shown. While a large relative brain size generally increases urban tolerance, species with small brains can still attain high success in urban environments if they spread the risk of reproduction across multiple events (i.e., have a low brood value). These alternative strategies, although uncommon in natural conditions, seem to be favored in urban environments, fundamentally restructuring the composition of urban communities. Thus, our results support the notion that brain size mediates tolerance to urbanization, but also shows that there are alternative ways of exploiting urban environments. Our findings reconcile previous conflicting results regarding the effect of brain size on urban tolerance, and provide the basis for improved predictions of the responses of organisms to increasing urbanization over the coming decades.

Keywords: urban ecology, anthropogenic changes, avian communities, brain mass, brood value, biodiversity, urban exploiters, urban avoiders

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INTRODUCTION

Cities are home to almost 4 billion people and over the coming decades their populations and geographic footprint will continue to swell (Seto et al., 2011, 2012). Urbanization represents one of the most extreme forms of environmental change for biodiversity (Sala, 2000; McKinney, 2006; Newbold et al., 2015) and for the majority of organisms, entails severe fitness costs, with declines in population abundances or local extinctions (Grimm et al., 2008). However, for species capable of exploiting these novel environments, cities provide a potential cornucopia of opportunities, allowing increases in abundance far beyond those found in natural habitats (Sol et al., 2014). These urban tolerant species constitute the slim fraction of biodiversity with which most people have frequent contact and thus have a potentially disproportionate impact on the health and well-being of human societies. Although a number of factors have been identified to predict urban tolerance (Sol et al., 2014), the features that allow these animals to thrive in urban environments remain insufficiently understood.

Among the different explanations for why some animals are able to exploit urban environments, one that has recently received greater attention is the cognitive buffer hypothesis (Allman et al., 1993; Sol, 2009). According to this hypothesis, a large brain should enhance persistence in novel environments by facilitating the construction of behavioral responses to new challenges, an idea supported by growing evidence (Sol et al., 2005, 2008; Sayol et al., 2016b; Fristoe et al., 2017). Behavioral responses have been found to be particularly important in coping with the challenges of urban environments, being instrumental in facilitating the exploitation of new resources, avoidance of human disturbances, and improving communication in noisy conditions (reviewed in Sol et al., 2013). However, whether large brain size predicts success in urban environments remains controversial (**Table 1**), with early support for this hypothesis (Møller, 2009; Maklakov et al., 2011, 2013), challenged by later studies (Evans et al., 2011; Sol et al., 2014; Dale et al., 2015; Møller and Erritzøe, 2015), only to be re-affirmed by more recent analysis (Callaghan et al., 2019).

One explanation for why the effect of brain size has been challenging to resolve, is that a large brain size is only one of a number of traits that may influence urban tolerance (Sol et al., 2014). For example, a broader niche is expected to facilitate persistence in urban environments by increasing the likelihood of finding appropriate resources (Evans et al., 2011; Sol et al., 2014; Ducatez et al., 2018; Callaghan et al., 2019) while migratory behavior can promote the colonization of urban areas (Evans et al., 2012). Because brain size correlates with these traits, failure to properly account for such additional drivers may mask the effect of brain size on urban tolerance. For example, if a large brain affects tolerance to urbanization by facilitating broader niches (Ducatez et al., 2015; Sol et al., 2016), including a measure of niche generalism in the model can block the effect of the brain on urban tolerance. Given that migratory species tend to have smaller relative brains than resident species (see Sayol et al., 2016b, and references therein), including migration in the model may also reduce the effect of the brain on urban tolerance. An additional, less appreciated issue, is that brain size may interact with species life history in potentially complex ways to determine urban tolerance. For instance, previous work has shown that avian species that distribute their reproductive effort across a higher number of events—and hence give less value to any single event—are more likely to establish themselves in novel environments, including urban settlements (Sol et al., 2012, 2014; Maspons et al., 2019). By having a life history that prioritizes future over present reproduction, these species can spread the risk of reproductive failure over several breeding attempts and, if conditions become unfavorable, may skip reproduction entirely, thus saving energy for future reproduction. However, a low brood value can be achieved through a longer lifespan, but also by reproducing several times in a same breeding season. For these latter species—which have high reproductive efforts with a low brood value—investing in a large brain and enhanced behavioral flexibility may bring more costs than benefits (Maspons et al., 2019). However, their life history can still buffer individuals against the risks associated with an urban life. Because it is likely that there is no single strategy to become an urban dweller, life history and brain size should be studied together in order to understand how they interact to influence urban tolerance.

Here, we revisit the role of brain size on urban tolerance by combining quantitative estimates of tolerance to urbanization with measurements of brain size, life history, and ecology for 629 avian species. Our approach consists of two stages. In the first stage, we estimate urban tolerance of species by comparing the relative abundance of species in urban vs. surrounding wild habitats, using data from well-characterized communities (Sol et al., 2017). We then conduct phylogenetic-based analyses to explore how relative brain size interacts with life history and ecological traits previously linked to urban tolerance. In the second stage, we conduct a community-level analysis to explore how trait-dependent responses to urbanization alter the structure of urban assemblages. Our global analysis supports the hypothesis that a large brain promotes urban tolerance, but also reveals that the relationship is more complex than generally thought, depending critically on the interaction with species life history.

TABLE 1 | Summary of studies that have investigated the association between behavioral flexibility and urban tolerance in birds, in chronological order.

Sample size	Location	Response metric	Effect	References
31 species	Jerusalem	Presence inside the city (0/1)	n.s.	Kark et al., 2007
39 species pairs	W. Palearctic	Urban species (0/1)*	+	Møller, 2009
82 species	Europe	Breeds in city center (0/1)	+	Maklakov et al., 2011
88 species	UK	Relative density (continuous)	n.s.	Evans et al., 2011
108 species	Global	Urban species (0/1)*	n.s.	Møller and Erritzøe, 2015
358 species	Global	Relative abundance (continuous)	n.s.	Sol et al., 2014
90 species	Oslo	Relative frequency (continuous)	n.s.	Dale et al., 2015
477 species	Australia	Average night-time light (Continuous)	+	Callaghan et al., 2019

*n.s., Not significant. +, significant positive effect. *Defined based on monographs.*
The sample size and location of the study are shown, as well as the metric used to quantify urban responses and the reported effect of brain size. All studies used brain size as a proxy for behavioral flexibility, except Møller (2009), that used the frequency of behavioral innovations and Kark et al. (2007), that used both brain size and behavioral innovations.

MATERIALS AND METHODS

Species Abundance Data

We used a previously compiled dataset on bird abundances in 27 cities for which intensive surveys are available (Sol et al., 2017). We restricted our analysis to studies where abundance was measured in both well-defined urban settlements as well as in the surrounding non-urbanized wild habitats. In total, this dataset contained 1,036 observations of species in different cities (38.4 ± 3.5 SE species per city). Following Sol et al. (2014), we calculated an urban tolerance index for each species as the differences in log-abundances between urban and wild habitats [i.e., log(Urban abundance)-log(Wild abundance)]. A positive urban tolerance index indicates that a species is more common in urban compared to wild habitats while a negative urban tolerance index indicates that a species is more common in wild habitats. We calculated the urban tolerance index for each species × city combination. The raw abundance data for a given city could be recorded as either the number of individuals per unit of survey area or time. This, however, does not affect the calculation of the urban tolerance index, because this metric was computed for each city relative to the matched wild habitat sampled using the same methodology.

Species Traits Data

For the species present in our dataset we collected data on brain size as well as a number of ecological and life-history traits that could affect urban tolerance. Although the trait values of a given species may vary between locations (e.g., urban vs. wild habitats) and cities, information on such intraspecific variation in traits is generally lacking. However, evidence indicated that variation across species was substantially higher than within species, and so we gathered information at the species level. We were able to collate published data on brain volume for 524 of the bird species present in our avian assemblage dataset (See **Supplementary Data 2**, **Supplementary Table 1** to see source for each species). For 95% of these species, brain volume was estimated using the endocast method, which has been shown to give reliable estimates of brain size (Iwaniuk and Nelson, 2002). This method consists of filling an empty skull with lead shot or plastic microspheres, which are then weighed to infer the volume of the skull. For the remaining species ($n = 34$), brain size was measured as fresh brain weight and converted to volume using the density of fresh brain tissue (1.036 g/ml) (Iwaniuk and Nelson, 2002). We complemented these data with new skull measurements for 105 additional species from 51 families, measured at the Natural History Museum, Tring (UK), following the endocast method. Where possible, the values of measurements for male and female specimens were averaged to obtain an average brain size of each species (specimen measurements are available in **Supplementary Data 3**). In birds, the ability to construct novel behavioral responses is not related to brain size *per se*, but the extent to which the brain is either larger or smaller relative to body size (Lefebvre et al., 1997; Overington et al., 2009). We obtained body mass data from the same museum specimens, when available, complemented with estimates from the Handbook of the Birds of the World (Del Hoyo et al., 2018) and the Handbook of avian body masses (Dunning, 2007). We then estimated relative brain size as the residual from a log-log phylogenetic Generalized Least Square regression [using the "phyl.resid" function from R package *phytools* (Revell, 2012)] of absolute brain size against body mass. This relative brain size measure is strongly correlated with the sizes of pallial brain regions responsible for general-domain cognition, and hence is a good proxy for general behavioral flexibility (Lefebvre and Sol, 2008; Sayol et al., 2016a). As a measure of species life history, we used brood value, which measures the relative value of each reproductive event. To estimate brood value, we first collected information on the number of broods per year and maximum recorded lifespan (years) from various published sources (See **Supplementary Table 1**). With this information, we were able to obtain the potential total number of broods over the life of an individual, as the product of the maximum lifespan and the number of annual breeding attempts (broods). We then calculated the brood value as the logarithm of 1/total number of breeding attempts. Therefore, species that have fewer reproductive attempts over their lifetime, will have high brood values (i.e., each breeding attempt has a higher value), whereas species with many breeding attempts have low brood values (i.e., each attempt have a relatively smaller value). Although average life expectancy could be a more accurate metric to calculate the average number of breeding attempts per species, we used maximum lifespan instead because this metric has been recorded for a much larger sample of species. As a metric of niche breadth we used an index of habitat generalism based on the co-occurrence of species among different habitat types, which is available for all bird species (Ducatez et al., 2014). Global maps of species distributions (Birdlife International NatureServe, 2012) were used to identify migratory species as those that have some part of the population in different regions during reproductive and non-reproductive seasons. We also used these maps to classify the species in each city as exotic or native. In total, we obtained traits for 629 species, resulting in a final database consisting of 1,036 species per city records across 27 different cities (**Figure 1**, **Supplementary Data 1, 2**). When excluding all trait missing values (e.g., to run models with all factors at a time), our dataset contains 436 species and 816 observations.

Modeling the Predictors of Urban Tolerance

All of our analyses were based on Bayesian Phylogenetic Mixed Models (BPMMs) combined with Markov chain Monte Carlo approximations, as implemented in the MCMCglmm R package v2.20 (Hadfield, 2010). Prior to any analysis, all continuous traits were Z-transformed (Mean centered to 0). We first explored the association between urban tolerance index and brain size by constructing a BPMM with the urban tolerance index as our response variable (Gaussian error distribution) and relative brain size as the unique predictor. To control for phylogenetic effects, we used a maximum clade credibility tree (MCC) from the posterior sample of 10,000 trees with the Ericsson tree backbone (Jetz et al., 2012). We note that using the Hackett tree backbone led to quantitatively almost identical results and so is not reported further. Phylogeny, species and city were included as random factors, and we used an inverse-Wishart prior ($V = 1$, $\nu = 0.002$) to facilitate model convergence. We then ran additional models including several life-history and ecological variables as predictors of urban tolerance index. First, we ran models including relative brain size with either

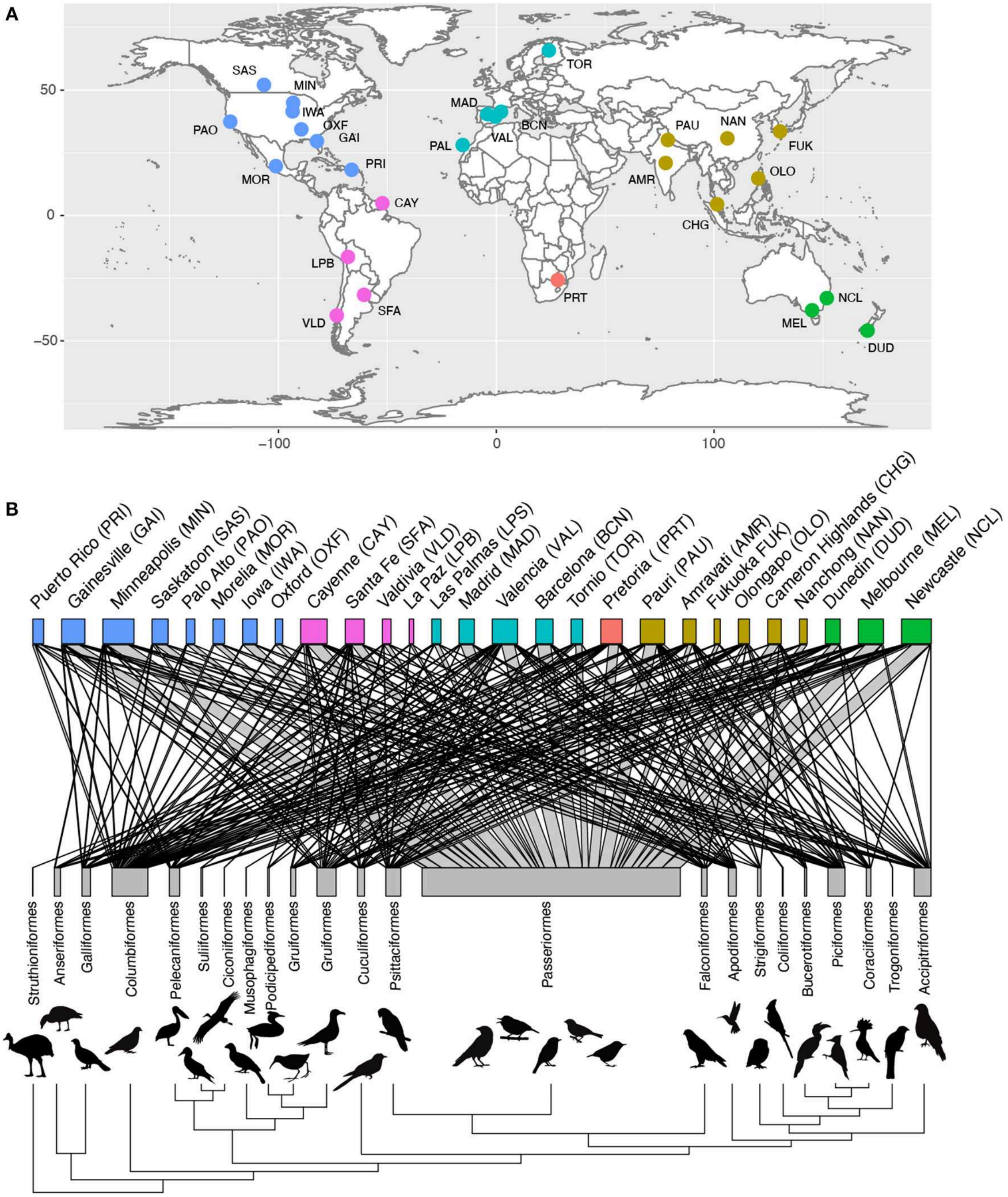

FIGURE 1 | Geographical and taxonomic coverage of the data. Our study includes abundance data from 27 cities from all the continents **(A)**. Abundance and brain size data was available for 629 species from 23 orders of birds including 1,036 unique city × species records. In **(B)** the distribution across cities of species from each taxonomic order are represented in a network, where the width of the links indicates the number of species from each order occurring in each city and the width of the bars indicates the total number of species in each city (top) and order (bottom). Silhouettes for each order are available at phylopic.org under a public domain license.

habitat breadth, migratory behavior and brood value to test for interactions between brain size and each of these traits. We ran three separate models with each variable in turn in order to maximize sample size. Finally, we ran a model including all variables as additive effects along with the significant interactions identified in previous models. Because the establishment success of introduced species—which are abundant in cities—is known to increase with brain size (Sol et al., 2005, 2008; Amiel et al., 2011), in this model, we also included whether the species was native or exotic to ensure that our results were not due to the effect of introduced species. We re-ran this final model after excluding species for which brain size was measured as fresh brain weight to check that the use of different methods did not affect our conclusions. Models were run for 1010,000 iterations, with a burn-in of 10,000 and a thinning interval of 1,000, resulting in a posterior distribution of 1,000 samples. We checked that the autocorrelation of samples was <0.1 and ran each model twice, assessing proper convergence using the Gelman-Rubin statistic, requiring models to have a scaling reduction factor below 1.1 (Gelman and Rubin, 1992). We report the posterior mean and the 95% credible intervals (CIs) for each variable, and assess significance according to pMCMC, which is the proportion of samples in the posterior distribution non-overlapping with zero. Because preliminary results suggested that species with different combinations of brain sizes and brood values have contrasting tolerances to urbanization, we examined how these two traits are related two each other at the species level. With this objective, we ran an additional BPMM with relative brain size as the response variable (Gaussian error distribution) and brood value as a predictor. We used identical prior and sampling options as for models of urban tolerance index, but in this case only phylogenetic structure was included as a random factor (the analysis is done at the species level, with a single value per species).

Exploring Brain Size Distributions in Urban and Wild Assemblages

Because brain size and life history were found to interact to predict urban tolerance, we performed additional analysis to further examine how the distribution of brain size changes between wild and urban assemblages and according to different life-history strategies. We calculated the mean urban and wild abundance of each species across all cities globally and classified each species as having either a high or low brood value, defined using the median brood value as the breakpoint (See resulting species averages in **Supplementary Data 4**). Then, we calculated the weighted mean and weighted standard deviation of brain size for both the global urban and global wild assemblage for each brood value group. To test for statistical differences in brain size between brood value groups we performed two-sample Weighted *T*-Tests (i.e., Welch tests) for each comparison, without significance-level correction for multiple testing. In addition, we also examined the relative extent to which differences in the weighted-mean brain size of wild and urban bird assemblages are driven by changes in species composition (loss or gain of species from wild habitats to cities) or changes in relative abundance of species that are found both in and outside cities (**Supplementary Figure 1**). To illustrate the types of species that are favored in urban communities, and how the brain size distribution is altered compared to natural assemblages, we ordered all bird families according to their mean tolerance to urbanization (using the mean urban tolerance index across their species). Then, we separately plotted the brain size distribution of urban exploiters (species from the 10 families with the highest tolerance) and avoiders (species from the 10 families with the lowest tolerance).

RESULTS

We found that relative brain size is positively related to urban tolerance (Posterior mean or ß, with 95% confidence intervals = 0.450 [0.115–0.818], pMCMC = 0.012), when included as a single predictor. In addition, we found that brood value and habitat breadth —but not migratory behavior— were also associated with urban tolerance when added to the previous model (See **Supplementary Tables 2–4** for more details). In particular, we found that a lower brood value (ß = −0.382 [−0.595 to −0.112], pMCMC < 0.001) and a broader habitat breadth (ß = 0.29808 [0.106–0.473], pMCMC = 0.002) were associated with increased tolerance to urbanization.

In the model including brood value, the main effect of relative brain size was no longer a significant predictor of urban tolerance. This in part reflects the existence of a weak negative association between brain size and brood value, so that species with relatively large brains were generally associated with low brood values (ß = −0.083 [−0.129 to −0.033], pMCMC < 0.001). However, there was a significant interaction between brood value and relative brain size (ß brain size*brood value = 0.272 [0.028–0.530], pMCMC = 0.028; **Supplementary Table 2**): Tolerance to urbanization was higher for species with relatively larger brains and low brood values, but the relationship between urban tolerance and brain size changed in species with high brood values (**Figure 2**). Thus, species with a high brood value (i.e., concentrating most reproductive effort in few events) have lower abundance in urban habitats when they have relatively small brains but have higher abundance when they have relatively larger brains.

The interaction between relative brain size and brood value was not due to the frequent presence of exotic species in cities (ß = 0.293 [0.044–0.542], pMCMC =0.024, **Table 2**, **Supplementary Table 5**). Similarly, the interaction between brain size and brood value was still significant when including the other ecological predictors (e.g., habitat breadth and migratory behavior) in the model (**Table 2**, **Supplementary Table 5**).

The previous analysis suggests that a species may become an urban dweller with different combinations of brain size and life history. However, what are the consequences for urban communities? We found that while the average brain size (mean weighted by abundance) of wild and urban communities were largely overlapping when all species were considered together (Wild community: −0.07 ± 0.71 SE; Urban community: −0.25 ± 0.85 SE), a clear shift in assemblage structure was evident when species with low and high brood values were examined separately. For wild habitats, the community-weighted average brain size was similar for both low and high brood-value strategies, whereas in urban environments, communities shift toward big-brained species with few breeding attempts over their lifetime and small-brained species with a high number of reproductive events (**Figure 3**). These shifts were primarily driven by the increase in abundance in cities of species with larger brains and high brood value or small brains and low brood value, but also to a lesser extent by the decrease in abundance or local extinction of species with small brains and high brood values (**Supplementary Figure 1**).

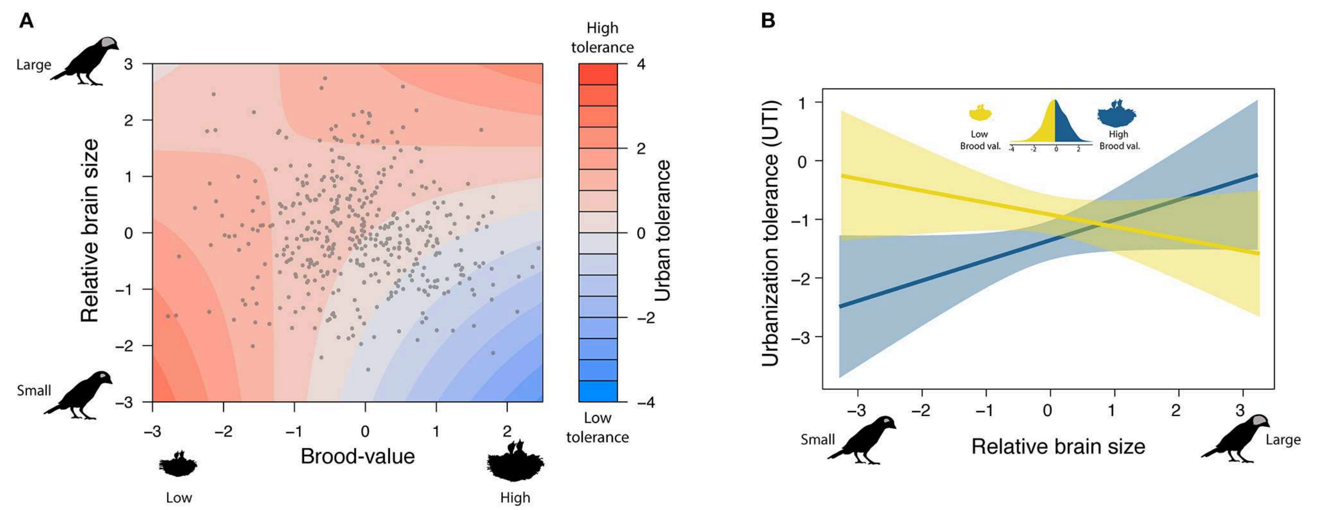

FIGURE 2 | Brain size interacts with brood value to predict urban tolerance. **(A)** Either species with lower brood values and small brains (bottom-left) or species with high brood values and big brains (up-right) are able to tolerate urban environments. **(B)** Splitting species into those investing in few breeding attempts (High brood value) or many attempts (Low brood value), helps to visualize the interaction: Brain size increases urban tolerance in species with high brood value but not in species with low brood value.

TABLE 2 | The effects of each predictor (Posterior mean with 95% credible interval) on the urban tolerance index, from a Phylogenetic Bayesian mixed model which includes the phylogenetic structure, species identity and city as random effects.

Model structure	Model parameter	Posterior Mean (with 95% C.I.)	pMCMC
Fixed effects	(Intercept)	−1.53 (−3.88 to 0.48)	0.164
	Relative brain size	0.33 (−0.11 to 0.78)	0.118
	Brood value	**−0.25 (−0.49 to −0.08)**	**0.042**
	Relative brain size * Brood value	**0.29 (0.04 to 0.54)**	**0.024**
	Status (exotic)	**1.45 (0.69 to 2.30)**	**<0.001**
	Habitat breadth	0.17 (−0.03 to 0.36)	0.094
	Migratory behavior	−0.29 (−0.85 to 0.24)	0.240
Random effects	Animal (Phylogenetic structure)	5.78 (2.82 to 8.81)	
	Species	0.28 (0.00 to 1.22)	
	City	0.28 (0.00 to 0.69)	

The full model was run with 816 observations from 436 species. Significant factors (pMCMC < 0.05) are shown in bold.

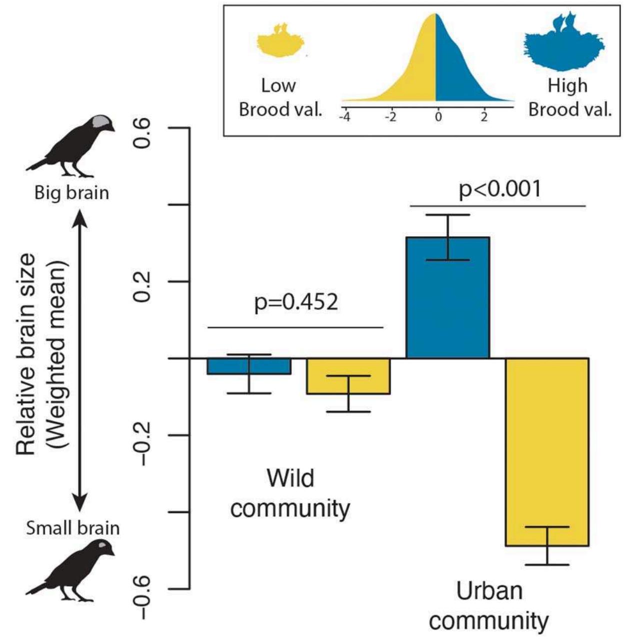

FIGURE 3 | Changes in the relative brain size of wild and urban bird communities. The community-weighted mean relative brain size of wild and urban communities is shown for both high (blue) and low (yellow) brood-value strategies, using the median of the brood value distribution as the breakpoint. *P*-values indicate the significance level from two-sample Weighted *T*-Tests (i.e., Welch tests).

DISCUSSION

Using a global dataset combining brain size and urbanization measures across cities, we show that relative brain size is an important predictor of species tolerance to urban habitats. However, our analysis shows that the direction of the effect of brain size is dependent on species life history, resulting in two alternative strategies for thriving in cities. In particular, species that invest in a high number of breeding attempts over their life (i.e., have a low brood value) are more tolerant of urbanization, even when having a small brain size. In contrast, for species that invest in few reproductive events, a brain that is larger than expected by their body size is key to provide urban tolerance. Although relatively uncommon in nature, these trait combinations seem to be favored in urban environments,

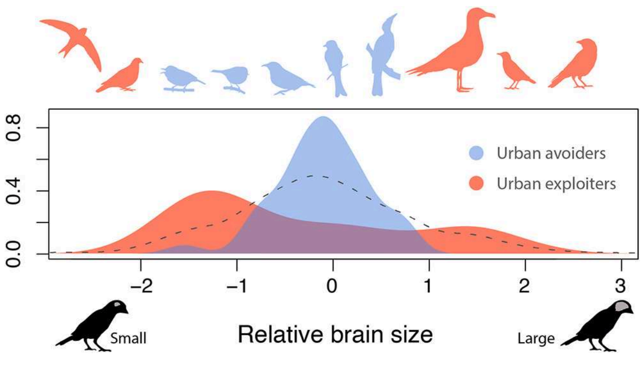

FIGURE 4 | Relative brain size distribution among urban exploiters and avoiders. Shown is the distribution of relative brain size across species from the ten families with the highest (urban exploiters) and ten families with lowest (urban avoiders) urban tolerance (see **Supplementary Figure 2** for results with additional families). Silhouettes provide examples of some of the families, ordered by brain size, from left to right: Apodidae, Columbidaee, Zosteropidae, Reguliidae, Coerebidae, Dicruridae, Meliphagidae, Laridae, Passeridae, Corvidae (available at phylopic.org under a public domain license). Gray dashed line shows the distribution of relative brain size for all the species contained in the dataset.

leading to a striking restructuring of avian assemblages in urban environments. These findings help reconcile previous conflicting results regarding the effect of brain size on urban tolerance and resolve the long-standing conundrum that urban exploiters (i.e., species that thrive in cities) include examples of both small brained (e.g., pigeons and swifts) and large-brained (e.g., crows, gulls, and starlings) species (**Figure 4**). The existence of multiple strategies to tolerate urban environments may also explain why recent work on mammals (Santini et al., 2019) found that a larger brain size promotes tolerance to urban habitat in some groups (e.g., carnivores and bats) but not in others (e.g., ungulates).

In our study, we found that larger brains are generally correlated (albeit weakly) with low brood values. However, we found that the few species that depart from this relationship are disproportionally represented in cities, revealing two trait combinations to tolerate urban environments: larger brains with high brood values and small brains with low brood values. These two alternative strategies could be seen as a choice between investing either in enhanced behavioral plasticity or in multiple reproductive events. There is indeed increasing evidence, both empirical (Sol et al., 2012, 2014) and theoretical (Maspons et al., 2019) that spreading the reproductive effort across many events can enhance the establishment success of populations in novel environments. Under these conditions, having multiple breeding opportunities can allow individuals to spread the risk through bet-hedging (Stearns, 2000) or to skip reproduction in favor of future events (Forcada et al., 2008), diminishing the costs of reproductive failure. In this case, having a large brain may entail net fitness costs due to the greater energy requirements and time constrains of spreading annual reproduction in several events (Sol et al., 2016).

In contrast, for species with fewer reproductive opportunities (i.e., with a high brood value for each attempt), dealing with urbanization pressures requires having a more plastic behavior, allowing them to respond to altered conditions (Lowry et al., 2013; Sol et al., 2013). There is ample evidence that urban bird populations tend to have greater innovation and problem-solving abilities (Liker and Bokony, 2009; Sol et al., 2011; Audet et al., 2016; Cook et al., 2017; Griffin et al., 2017; Kozlovsky et al., 2017)—traits that are closely linked to a relatively larger brain (Lefebvre et al., 1997; Overington et al., 2009; Benson-Amram et al., 2016)—and that this could potentially help animals to deal with novel challenges (Sol et al., 2007; Sol, 2009). These ideas are consistent with evidence that large-brained species tend to live in more variable environments (Sayol et al., 2016b, 2018; Vincze, 2016; Fristoe et al., 2017), and are more likely to establish when introduced to novel environments (Sol et al., 2005, 2008; Amiel et al., 2011). Although the exact mechanism linking brain size and urban success is not known, increased behavioral plasticity is likely useful in a variety of domains, including feeding innovations (Ducatez et al., 2015), recognizition of novel predation threats (Levey et al., 2009) and choice of the appropriate habitat (Clergeau and Quenot, 2007).

Our work reaffirms the importance of brain size in determining species responses to changing environments (Sol et al., 2005; Sayol et al., 2016b; Fristoe et al., 2017), but also highlights the need to consider behavioral flexibility in the context of life history (Sol et al., 2016; Fristoe and Botero, 2019; Maspons et al., 2019). These two factors must therefore be studied together in order to fully understand how organisms respond to current anthropogenic impacts. In this context, an important avenue for further work will be to explore how the interaction between brain size and life history affects the response of organisms to other kinds of anthropogenic threats such as habitat alterations (Shultz et al., 2005) and the potential consequences for global extinction risk (Gonzalez-Voyer et al., 2016; Tobias and Pigot, 2019). In the face of increasing urbanization, our findings can be used to predict those species that will better respond to the coming challenges as well-identify those species of greater sensitivity where conservation efforts should be concentrated.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

FS and DS conceived the study and collected the data on species traits and species abundances, respectively. FS and AP analyzed the data. All authors equally contributed to write the paper and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00058/full#supplementary-material

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Effects of Pollution on Fish Behavior, Personality, and Cognition: Some Research Perspectives

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Pollutants, and more generally, environmental stressors, are a neglected source of behavioral and cognitive variations in wild populations. Based on recent literature in fish, we highlight four interesting research perspectives to better understand the effects of pollutants on the links between fish behavior, cognition and fitness. First, (1) we review the neurotoxic effects of pollutants on fish behavior, personality, and cognition. These behavioral and cognitive effects could in turn affect the level of exposure to pollutants, potentially generating feedback loops that may amplify the effects of pollutants on fish fitness. Second, we propose that (2) the effects of pollutants should be studied in a multistress context, i.e., in realistic environmental conditions in combination with other stressors, because some stressors could amplify the behavioral effects of pollutants on fitness. Third (3), existing studies show that physiology, personality, cognition, and fitness components are often linked in syndromes. Pollutants could lead to syndrome disruption, which could affect the evolutionary trajectories of exposed populations. Future studies should thus focus on the complex links between traits to better understand the consequences of stressors on evolutionary trajectories. Fourth, (4) exposure to chronic pollution could lead to local adaptation or maladaptation, which could result into high intraspecific variability of sensitivity among wild populations. In addition, evolutionary responses to pollution could constrain, or be constrained by evolutionary responses to other stressors. We thus encourage future studies to use integrative approaches to bridge the gap between ecotoxicology, cognitive ecology and evolutionary ecology in a multistress framework to tackle these exciting questions and improve our ability to predict the effects of anthropogenic stressors on wildlife.

Keywords: temperament, contamination, global change, stress response, multistress, evolutionary ecotoxicology, local adaptation

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INTRODUCTION

Human activities are the sources of many organic and inorganic contaminants such as plastics, pharmaceuticals, pesticides, and metals that have alarming impacts on terrestrial and aquatic ecosystems (Scott and Sloman, 2004; Zala and Penn, 2004; Saaristo et al., 2018). However, our ability to accurately predict their effects on wildlife is limited by several scientific challenges. Direct effects of pollutants on animal physiology and mortality have been included as part of routine ecotoxicology studies (Butcher et al., 2006; Ashauer et al., 2013), but more complex behavioral effects on animal personality and cognition are less studied, especially in wild species and in realistic multistress conditions (Zala and Penn, 2004; Saaristo et al., 2018). In addition, the links between behavioral changes, cognitive performances, and individual fitness are rarely taken into account when studying contaminant effects, which limits our ability to predict the cascading long-term impacts of human activities on population persistence and evolutionary trajectories.

Here, we review the existing literature focusing on fish to investigate the behavioral effects of pollutants in a multistress perspective. Fish have been widely used for behavioral and cognitive assays (Brown et al., 2006), and are used as "sentinel" animals in ecotoxicology (Giulio and Hinton, 2008; Braunbeck et al., 2013). We thus summarized (non-extensively) the existing literature on the behavioral effects of pollutants in wild fish (**Table 1**). As shown in **Table 1**, most previous studies used ecologically relevant pollution levels, but they tested the effects of contamination alone, i.e., in a single stressor framework. However, pollution effects are often modulated by a concomitant exposure to other natural or human-induced stressors in the wild (Schinegger et al., 2016), which could result into synergistic interactions and/or amplified effects on fish fitness (e.g., Gandar et al., 2015, 2017a). Nonetheless, empirical data on multistress effects on fish behavior are still rare (**Table 1**). In addition, strong correlations often exist between traits (Réale et al., 2007; Conrad et al., 2011; Sih, 2011; Sih and Del Giudice, 2012), but most studies have measured behavioral traits in isolation (**Table 1**), and pollutant effects on syndrome structure are still unclear (Killen et al., 2013; Montiglio and Royauté, 2014). Finally, most previous studies used domestic species or a single population of wild species, so that the interpopulation variability and the evolution of behavioral responses to pollution are rarely taken into account (**Table 1**). Exploring the effects of pollutants on fish fitness through behavioral and cognitive alterations in wild populations and their evolutionary implications is thus an exciting scientific challenge for the next decades.

Based on the existing knowledge gaps, we highlight four promising research perspectives to better understand the effects of pollution on behavior, cognition and their consequences for fish fitness and population persistence (**Figure 1**). First, we propose that (1) pollution may alter several behavioral traits, as well as learning and memory abilities, with potential cascading effects on fish fitness. Pollution-induced behavioral alterations could potentially further increase the level of exposure to pollution in the wild, resulting in positive feedback loops that could potentially amplify pollution effects on fitness. Second, we propose that (2) exposure to multiple stressors might now be the rule, so that pollutants should be studied in combination with other stressors that often modify the effects of pollutants on fish behavior and fitness. Third, (3) stressors such as pollutants could affect the links between physiology and behavior, leading to syndrome disruption or reinforcement, with important consequences for evolutionary trajectories. Fourth, we discuss how (4) chronic pollution could lead to local adaptation or maladaptation, due to plastic and/or genetic changes caused by pollutants. Behavioral and cognitive responses are central in adaptive processes, because they are shaped by past evolution, and can in turn facilitate or impede adaptive responses to pollution and other stressors (Sih et al., 2011) (**Figure 1**). With this study, we hope to encourage future studies to use integrative approaches bridging the gap between behavioral, cognitive and evolutionary ecology to tackle these challenging questions and to better understand the impacts of current and future stressors on wild fish populations.

EFFECTS OF POLLUTANTS ON FISH BEHAVIOR AND FEEDBACK LOOPS

Many pollutants have direct and indirect effects on the behavior of terrestrial and aquatic organisms (Clotfelter et al., 2004; Zala and Penn, 2004; Saaristo et al., 2018), especially in fish (Scott and Sloman, 2004; Robinson, 2009; Sloman and McNeil, 2012). Inorganic and organic pollutants affect a wide array of behaviors such activity, exploration, avoidance, sociability, aggressiveness, sexual and feeding behaviors (summarized in **Table 1**). Some studies have also tested the effects of contaminants on behavioral types, or personalities, i.e., on consistent interindividual variations in behavior (Réale et al., 2007, 2010; Montiglio and Royauté, 2014). In addition, many contaminants affect fish cognitive performances (**Table 1**), with potential cascading effects on fitness (e.g., de Castro et al., 2009).

Some of these changes are underpinned by alterations of cholinesterase activity, neurotransmitter or hormone levels (Scott and Sloman, 2004; Brodin et al., 2014; Vindas et al., 2017). For instance, carbofuran pesticide alters neurofunction and activity in sea bass *Dicentrarchus labrax* (Hernández-Moreno et al., 2011). Fluoxetine antidepressant (Prozac) alters aggression, boldness and learning in the Siamese fighting fish *Betta splendens* by altering the serotonin system (Kohlert et al., 2012; Eisenreich and Szalda-Petree, 2015; Dzieweczynski et al., 2016). Other behavioral changes could be indirectly due to changes in energetic balance (Montiglio and Royauté, 2014), due to the costs of detoxification and stress responses (Sokolova et al., 2012; Sokolova, 2013). For instance, low doses of pesticides decreased activity in goldfish *Carassius auratus*, likely due to increased costs of detoxication and physiological defenses (Gandar et al., 2015, 2017a,b). However, more work is needed to fully understand the neuronal and physiological underpinnings of pollution-driven alterations of behavior and cognition (Brodin et al., 2014).

Interestingly, pollution-induced changes in behaviors could potentially increase further the level of exposure to pollution and result into positive feedback loops amplifying the negative effects of pollution on fish fitness. However, only indirect evidence exists so far. Indeed, spatial behaviors such as activity, exploration, and avoidance are key behavioral traits that are often affected by pollution. For instance, individuals living in metal polluted sites (lead and cadmium) and having higher levels of metal in their blood displayed slower exploration tendencies in great tits *Parus major* (Grunst et al., 2018, 2019). In another example, Trinidadian guppies *Poecilia reticulata* exposed to crude-oil had decreased exploration tendency in an experimental maze (Jacquin et al., 2017). Such impaired exploration tendencies could in turn affect fish ability to assess habitat quality,

TABLE 1 | Non-extensive summary of the existing literature on the link between pollution and behavior in fish.

Contaminant	Ecological relevance	Fish species	Behavioral traits	Multi-stress	Syndrome	Variability	Source
Plastics							
Microplastics	Yes	*Bathygobius krefftii*	Boldness, exploration	No	No	No	Tosetto et al. (2017)
Microplastics	Yes	*Acanthochromis polyacanthus*	Activity, feeding, aggression	No	No	Yes	Critchell and Hoogenboom (2018)
Nanoplastics	Yes	*Carassius carassius*	Activity, feeding, exploration	No	No	No	Mattsson et al. (2017)
Pharmaceuticals							
Oxazepam	Yes	*Perca fluviatilis*	Activity, boldness, sociality, feeding rate	No	Yes	No	Brodin et al. (2013)
Vinclozolin, flutamide (chemotherapy)	Yes	*Betta splendens*	Activity, shoaling, exploration, boldness	No	Yes	No	Dzieweczynski et al. (2018)
Ethinylestradiol	Yes	*Betta splendens*	Boldness, activity	No	Yes	No	Dzieweczynski et al. (2014)
Ethinylestradiol	Yes	*Poecilia reticulata*	Sexual behaviors	No	No	No	Bayley et al. (1999); Kristensen et al. (2005)
Fluoxetine	Yes	*Several species*	Antipredator behavior, boldness, aggression, associative learning	Yes	Yes	No	Eisenreich and Szalda-Petree (2015); Dzieweczynski et al. (2016); Eisenreich et al. (2017); Martin et al. (2017); Saaristo et al. (2017)
Various psychiatric drugs	Yes	*Several species*	Boldness, aggression, activity, feeding, anxiety	No	No	No	Brodin et al. (2014)
Oxazepam	Yes	*Salmo salar*	Migration	Yes	No	No	Hellström et al. (2016); Klaminder et al. (2019)
Mixture	Yes	*Neogobius melanostomus*	Aggression	No	No	Yes	McCallum et al. (2017)
Pesticides							
Cocktail of French pesticides (atrazine, metolachlor, isoproturon, linuron…)	Yes	*Carassius auratus*	Activity, foraging	Yes	No	No	Gandar et al. (2015, 2017a); Jacquin et al. (2019)
Vinclozolin (fungicide), DDE (DDT metabolite)	NA	*Poecilia reticulata*	Sexual behaviors	No	No	No	Baatrup and Junge (2001)
Carbaryl, chlordane, 2,4 DMA, DEF, methyl parathion, pentachlorophenol	Yes	*Oncorhynchus mykiss*	Activity, feeding	Yes	No	No	Little et al. (1990)
Chlorpyryfos		*Danio rerio*	Spatial learning	No	No	No	Levin et al. (2003)
Glyphosate	Yes	*Piaractus mesopotamicus*	Feeding	No	No	No	Giaquinto et al. (2017)
Glyphosate	Yes	*Danio rerio*	Exploration, locomotion, aggression, memory	No	No	No	Bridi et al. (2017)
Atrazine, linuron, metolachlor	Yes	*Oncorhynchus mykiss*	Aggression, locomotion	No	No	No	Shinn et al. (2015)
Ethoprofos	Yes	*Astyanax aeneus*	Avoidance, escape behavior	Yes	No	No	Sandoval-Herrera et al. (2019)
Carbofuran	Yes	*Dicentrarchus labrax*	Swimming activity	No	No	No	Hernández-Moreno et al. (2011)
Carbaryl, diazinon, malathion	Yes	*Oncorhynchus mykiss*	Swimming activity	No	Yes	No	Beauvais et al. (2001)
Other Organic Pollutants							
PCB, PeBDE	Yes	*Fundulus heteroclitus*	Activity, feeding	No	No	No	Timme-Laragy et al. (2006); Couillard et al. (2011)

(Continued)

TABLE 1 | Continued

Contaminant	Ecological relevance	Fish species	Behavioral traits	Multi-stress	Syndrome	Variability	Source
Nonylphenol (industrial surfactant)	Yes	*Fundulus diaphanus*	Shoaling, recognition	No	No	No	Ward et al. (2008)
Metals							
Mercury		*Danio rerio*	Activity, escape	Yes	No	No	Weber (2006)
Methylmercury MeHg		*Danio rerio*	Anxiety, locomotion	No	No	No	Maximino et al. (2011)
MeHg	Yes	*Fundulus heteroclitus*	Activity, feeding	No	No	Yes	Zhou and Weis (1998); Weis et al. (1999, 2001)
Metal mixture	Yes	*Pimephales promelas*	Swimming performance	No	No	No	Kolok et al. (1998)
MeHg	Yes	*Fundulus heteroclitus*	Sociality	No	No	Yes	Ososkov and Weis (1996)
MeHg	No	*Danio rerio*	Spatial learning	No	No	No	Smith et al. (2010)
Several metals (Cu, Zn,. . .)	No	*Several species*	Avoidance, activity	No	No	No	Atchison et al. (1987)
Ag	Yes	*Danio rerio*	Avoidance, swimming, spatial learning	No	No	No	Powers et al. (2011)
Cd	Yes	*Oncorhynchus mykiss*	Sociality	No	No	No	Sloman et al. (2003)
PCBs and PAHs	Yes	*Ameiurus nebulosus*	Aggression, activity, escape response	No	No	Yes	Breckels and Neff (2010)
Trenbolone (agricultural pollution)	Yes	*Poecilia reticulata*	Reproductive behaviors	No	No	No	Bertram et al. (2015); Tomkins et al. (2018)
PAHs Polycyclic aromatic hydrocarbons	NA	*Poecilia reticulata*	Exploration, activity, sociality	No	No	Yes	Jacquin et al. (2017)
Benzo[*a*]pyrene	NA	*Oncorhynchus kisutch*	Territoriality	No	No	No	Ostrander et al. (1988)
PAHs	Yes	*Neogobius melanostomus*	Competition	No	No	Yes	Sopinka et al. (2010)

The ecological relevance of the contamination level is indicated. Potential gaps regarding the testing of multistress effects, syndrome structure and population variability are also reported.

because exploration is a key trait enabling individual to gather information and cues about their environment (Reader, 2015). Social interactions are also often altered by contamination (e.g., Ward et al., 2008), which could decrease social learning and the acquisition of information from conspecifics (Laland and Williams, 1997; Brown and Laland, 2003).

Spatial cognitive abilities such as spatial memory and spatial learning ability are also often deeply impacted by contaminants. For instance, aluminum contamination impaired learning performance in a maze task in Atlantic salmon *Salmo salar*, which could decrease their ability to process information and cope with new environments (Grassie et al., 2013). Organic pollutants such as pesticides also disturbed activity and spatial memory in zebrafish *Danio rerio* and rare minnow *Gobiocypris rarus* (Hong and Zha, 2019). Such adverse cognitive effects are expected to have severe consequences for fish ability to learn and memorize information to escape predators, find food and mates, and to avoid polluted areas and food items. Contaminated fish could thus have difficulties to collect, process and memorize information about habitat and food quality, which might further affect their exposure to pollution and result into positive feedback loops. In addition, many pollutants affect dispersal and migration, which could affect the exposure of animals to pollution. For instance, pesticides and pharmaceuticals alter downward migration and homing behaviors in salmonid fish (e.g., Scholz et al., 2000; Hellström et al., 2016; McCallum et al., 2019), which could potentially expose them to higher levels of pollution if they cannot return to their clean home river. However, furher work is needed to test these hypotheses.

Pollution also affects fish boldness, appetite, foraging patterns, which could affect their level of dietary contamination (Montiglio and Royauté, 2014). For instance, perch (*Perca fluviatilis)* exposed to psychiatric drugs were more active and bolder than control fish and had a lower latency to feed (Brodin et al., 2013). These pollution-induced behavioral changes increased their foraging rate on zooplankton in the water column, which is a prey item potentially carrying a high dose of accumulated drugs (Brodin et al., 2013, 2014). In addition, organisms exposed to pollutants generally have higher metabolic rates and greater energetic needs, because detoxifying and repair processes are costly (e.g., McKenzie et al., 2007), which could increase their activity and foraging, and hence their exposure to dietary-transmitted pollutants (Montiglio and Royauté, 2014). For instance, crucian carp *Carassius carassius* exposed to dietary polystyrene nanoparticles through the food chain had altered activity and higher feeding time, likely due to increased energetic needs and/or altered brain structure (Mattsson et al., 2015, 2017). This could thus increase their exposure to further pollution in the wild, but empirical approaches are now needed to test this assumption.

In summary, pollution-induced alterations of exploration, sociability, memory, learning, appetite, boldness, and

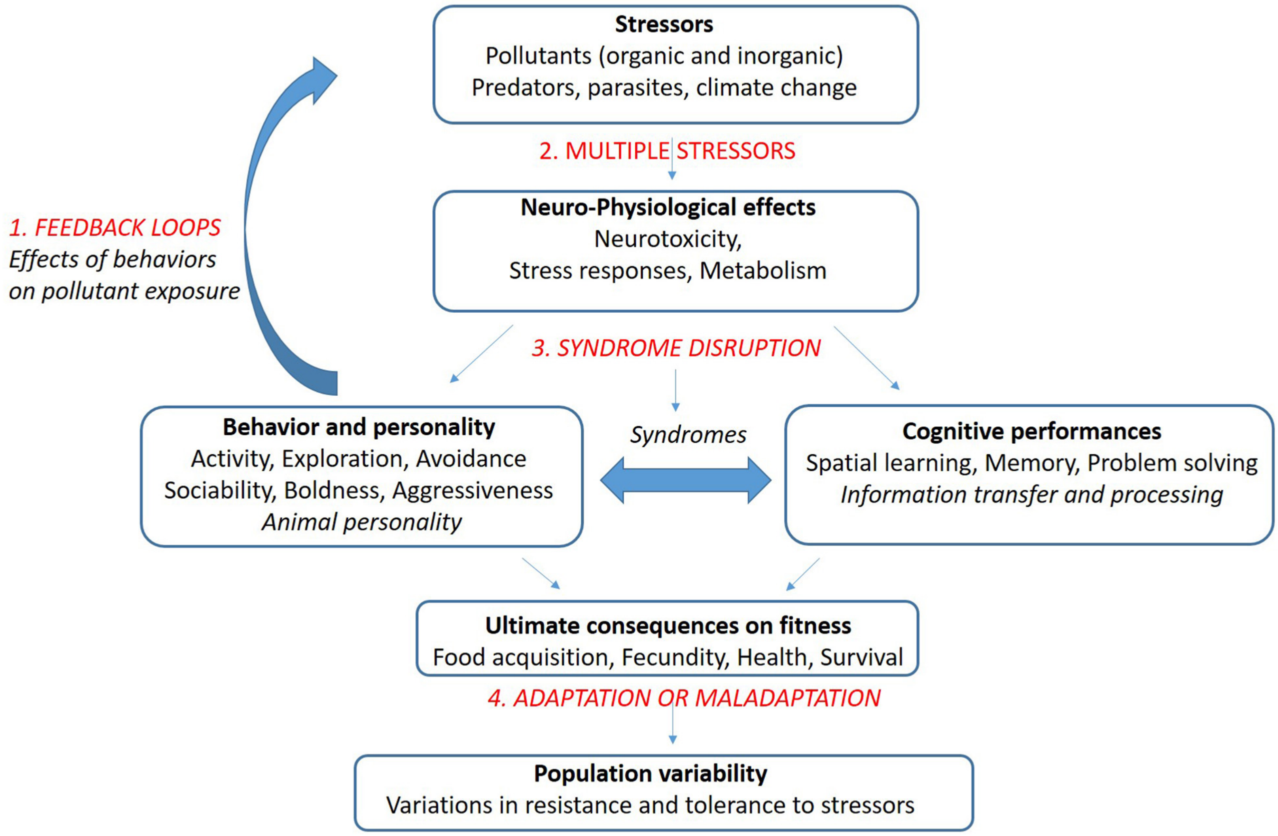

FIGURE 1 | Potential links between pollution, behavior and cognition, and proposed research perspectives (in red).

foraging could potentially in turn amplify fish exposure to environmentally or dietary contamination, and generate positive feedback loops (Montiglio and Royauté, 2014), with important implications for fish fitness. However, only indirect evidence exists so far, and further experimental studies are now needed to test this hypothesis.

MULTIPLE STRESSOR EFFECTS ON BEHAVIOR AND FITNESS

In addition, many behavioral disruptions caused by pollutants are amplified in the presence of additional abiotic and biotic stressors such as predators, parasites, or climate change. For instance, pollutants are likely to affect how efficiently individuals escape predators by altering activity, boldness, olfaction ability, and learning abilities (Weis et al., 1999, 2001; Lürling and Scheffer, 2007). Accordingly, copper impairs olfactory neurons in fathead minnow *Pimephales promelas*, which alters their ability to perceive alarm cues and increases their vulnerability to predation (Dew et al., 2014). In another study, banded tetra *Astyanax aeneus* exposed to an organophosphate pesticide had altered avoidance behavior and a lower ability to escape a predator attack (Sandoval-Herrera et al., 2019). As a result, the presence of predators can reveal the ecological effects of pollution on fish fitness through neuro-behavioral effects, resulting in lower fitness for individuals exposed to both pollution and predators.

Other biotic stressors such as parasites could also modulate the physiological and behavioral effects of pollutants. Indeed, resistance to pollutants and parasites are often based on shared neural and physiological pathways, which could result into significant interactions between these stressors (Thilakaratne et al., 2007; Blanar et al., 2009; Marcogliese and Pietrock, 2011). For instance, contaminants and parasites both involve important energetic, oxidative, and immune costs (e.g., Marcogliese et al., 2005), potentially leading to synergic or antagonistic effects depending on the metabolic strategy displayed (Sokolova et al., 2012; Sokolova, 2013; Petitjean et al., 2019). Pollution-exposed individuals generally invest more energy in costly detoxification processes (Du et al., 2018, 2019) at the expense of immunity (Dunier and Siwicki, 1993; Dunier, 1996), with potential consequences for parasite resistance (Arkoosh et al., 1991, 2001; Jansen et al., 2011; Rohr et al., 2013). For instance, three-spined stickleback *Gasterosteus aculeatus* exposed to a polymetallic stress were more susceptible to an immune challenge through changes in oxidative responses (Le Guernic et al., 2016). Parasites and their associated immune challenges could thus act as important biotic constraints altering the effects of pollution on fish behavior and fitness, but few studies experimentally tested this hypothesis, especially in fish.

Other stressors such as climate change and water warming could also modulate the effects of pollutants, either through direct effects on the chemical properties of pollutants, and/or through complex interactive effects on neurophysiological pathways (Schiedek et al., 2007; Noyes et al., 2009). For instance, exposure to pesticides and water warming in goldfish had complex interactive effects on goldfish *Carassius auratus* proteome and cell integrity (Gandar et al., 2017b; Jacquin et al., 2019), and resulted in antagonistic effects on fish foraging activity in fish exposed to multiple stressors compared to fish exposed to single stressors (Gandar et al., 2015). To conclude, pollution effects often depend on the concomitant exposure to other biotic and abiotic stressors (Dinh Van et al., 2013, 2014; Tüzün et al., 2015, 2017; Debecker and Stoks, 2019; Saaristo et al., 2019), underlining the need for multistress approaches to better predict the cognitive and fitness consequences of pollution on wildlife.

POLLUTION AS A REVEALING OR MASKING FACTOR OF BEHAVIORAL SYNDROMES

Rather than being one-dimensional, animal personalities often consist of a suites of interrelated traits, referred to as behavioral syndromes (Sih et al., 2004; Réale et al., 2007; Conrad et al., 2011; Sih, 2011; Sih and Del Giudice, 2012). In fish, several consistent behavioral traits such as boldness, activity exploration, and sociability are linked together in syndromes, with important implications for fitness and evolutionary trajectories (Conrad et al., 2011; Dochtermann and Dingemanse, 2013). For instance, three-spined sticklebacks *Gasterosteus aculeatus* that are bolder and more aggressive are more likely to escape predator attacks and survive, resulting in higher fitness compared to other trait combinations (Bell and Sih, 2007; Dingemanse et al., 2007). Behavioral syndromes are also important for information use and learning. For instance, sticklebacks that are more prone to explore a maze have also a higher tendency to follow trained conspecifics, with potential advantages for social learning (Nomakuchi et al., 2009). It is thus important to take these syndromes into account because they could help predict the effects of stressors on fish fitness and cognition.

Various mechanisms could explain the links between traits, such as genetic linkage, correlational selection, resource allocation trade-offs, genetic or physiological pleiotropy (Houston and McNamara, 1999; Aubin-Horth et al., 2012; Killen et al., 2013). In fish, physiological traits and personality traits are tightly linked. For instance, lineages of trout selected for low stress responses have a lower production of cortisol and higher metabolic rate, but are also bolder, more aggressive, with a lower ability of reversal learning, compared to lineages selected for high stress responses (Overli et al., 2002; Höglund et al., 2017; Vindas et al., 2017). Stress responses and energetic adjustments linked to metabolism thus seem central constraints in determining syndrome structure and the links between stable behaviors in fish.

Because pollutants often trigger important stress responses and changes in metabolism, they have the potential to affect the structure of behavioral syndromes, with consequences for cognitive abilities and responses to environmental cues (Killen et al., 2013). In particular, pollution can trigger a stress response (cortisol production) that strongly affects energy status, energy acquisition and metabolism (Schreck et al., 2016). By triggering stress responses and enhancing the energetic demand, pollution could thus alter the energy allocation between traits, creating the potential for divergence in correlated physiology-behavior nexus (Killen et al., 2013).

On one hand, stressors could have revealing effects on syndromes by strengthening the links between traits (Killen et al., 2013). Accordingly, the anxiolytic oxazepam drug induced a correlation between boldness and activity in perch *Perca fluviatilis*, which was only present after exposure to the drug (Brodin et al., 2013). On the other hand, the adverse neurophysiological effects of stressors could limit the capacity of fish to express the full range of behaviors, and reduce the phenotypic variations observed, thereby masking any relationship between traits that was apparent under mild or single stressor exposure (Killen et al., 2013). In this case, stressors could have masking effects on syndromes by weakening any link between traits. For instance, fluoxetine decreased the behavioral correlations across contexts in Siamese fighting fish *Betta splendens* (Dzieweczynski et al., 2016). In other cases, stressors had no effects on behavioral nor physiological correlations, such as in damselflies *Ischnura elegans* exposed to zinc (Debecker and Stoks, 2019). The effects of pollution on syndromes are thus not clear yet and deserve further investigations. The existing literature suggest that pollutants indeed affect the structure of syndromes (i.e., the links between traits) by affecting the physiological-behavior nexus, but their specific effects seem to depend on the nature/dose/duration of stressors.

In addition, syndrome structure can be shaped by past natural selection, and have important implications for evolutionary trajectories. Indeed, natural selection could select for particular combinations of physiological, behavioral and cognitive traits (Conrad et al., 2011; Sih et al., 2012). For instance, predation favors the correlation between boldness and aggressiveness in *Gasterosteus aculeatus* populations coexisting with predators, because fish that are bolder and more aggressive are more likely to escape predators and survive (Bell and Sih, 2007; Dingemanse et al., 2007). It is also possible that pollution could select for particular trait combinations, but few studies tested this hypothesis (see **Table 1**). In addition, behavioral syndromes could have different evolutionary implications depending on the underlying mechanisms such as genetic correlations or physiological trade-offs (Bell and Aubin-Horth, 2010; Conrad et al., 2011; Dochtermann and Dingemanse, 2013). For instance, genetic correlations resulting from gene pleiotropy could potentially constrain the evolution of behavioral responses to pollutants. In this case, behavioral correlations would be relatively stable across environments, because such correlations will be difficult to break apart via selection (Dochtermann and Dingemanse, 2013). On the other hand, syndromes resulting from physiological trade-offs resulting from resource allocation could potentially change across environments, so that different trait combinations could be found in natural populations depending on levels of pollution, resource availability and/or other stressors (Bell and Aubin-Horth, 2010; Killen et al., 2013). However, there is currently a lack of knowledge on the underpinnings of behavioral correlations and syndromes in wild fish exposed to pollution and their implications for evolutionary trajectories (Conrad et al., 2011) (**Table 1**). Because syndrome structure could facilitate or impede opportunity for adaptive evolution (Sih et al., 2012; Dochtermann and Dingemanse, 2013), further studies testing the effects of pollution on behavioral syndromes are now necessary to refine our ability to predict the evolutionary effects of pollution on behavior.

EVOLUTIONARY DIVERGENCE IN BEHAVIOR UNDER POLLUTION

Interestingly, the burgeoning literature in evolutionary ecotoxicology has shown that some fish populations having evolved under chronic pollution have divergent response to an experimental contamination, suggesting local adaptation to pollutants (Bélanger-Deschênes et al., 2013; Oziolor et al., 2016; Brady et al., 2017). For instance, killifish *Fundulus heteroclitus* from highly contaminated environments have evolved genetic-based physiological ability to cope with organic pollutants (Reid et al., 2016; Whitehead et al., 2017). Some studies also investigated the divergence in behavior caused by pollution, but empirical evidence of behavioral local adaptation to pollution through genetic evolution and/or plasticity is still scarce. For instance, brown bullhead fish *Ameiurus nebulosus* from a polluted river had a higher aggressiveness than fish from an unpolluted river, but only F0 fish collected in the field were tested (Breckels and Neff, 2010). In this case, it is difficult to disentangle the genetic and plastic components of the observed behavioral divergence in F0 generation, which limits our ability to predict the consequences of pollution across generations. In another study, guppies *Poecilia reticulata* having evolved in Trinidadian rivers polluted by polycyclic aromatic hydrocarbons (PAHs) had a lower exploratory tendency compared to fish from unpolluted rivers after several generations raised in common garden conditions (F1 to F3 generations), suggesting genetic-based behavioral divergence among populations (Jacquin et al., 2017). However, other studies on the same model species showed little evidence of adaptive plasticity that would limit the deleterious effects of pollutants on fitness, especially in unpolluted environments (Rolshausen et al., 2015; Hamilton et al., 2017). This suggests that adaptation to pollution might be maladaptive in unpolluted environments, but more studies are now needed to disentangle the relative role of plasticity and genetic-based evolution in this potential maladaptation (Rolshausen et al., 2015; Hamilton et al., 2017; Brady et al., 2019).

In addition, the evolutionary effects of pollutants remain difficult to disentangle from other environmental stressors in the wild, maybe because multiple stressors might exert conflicting selective pressures (Jansen et al., 2011; Saaristo et al., 2018). Adaptation to a particular stressor (e.g., contamination) might for instance impede the adaptation to another stressor (e.g., parasite). Thus, adaptation to pollution might come at a cost, depending on additional stressors (e.g., Dutilleul et al., 2017). For instance, tolerance to pesticides is associated with increased susceptibility to diseases in some amphibians and crustaceans (e.g., Hua et al., 2017; Jansen et al., 2011). In the same vein, European flounder *Platichthys flesus* populations living in contaminated rivers display a lower tolerance to thermal stress, although the underlying mechanisms remain to be determined (Lavergne et al., 2015). On the other hand, some physiological adaptations to one stressor could confer advantages against additional stressors (co-tolerance, Vinebrooke et al., 2004). For instance, some families of Atlantic salmon *Salmo salar* that are tolerant to high-temperature are also more tolerant to hypoxia, because of increased heart ventricle size and myoglobin levels, although the evolutionary implications are still unclear (e.g., Anttila et al., 2013). In another study, some *Daphnia magna* populations are co-adapted to warming and increased toxicity (Zhang et al., 2018). However, most previous studies focused on physiological and life-history traits, so that the evolution of behavioral traits in a multiple stress framework remains unclear. It is possible that some behavioral and cognitive responses to pollution could bring fitness benefits in polluted environments, but come at a cost in other environments. For instance, we could hypothesize that decreased exploration caused by pollution (e.g., Jacquin et al., 2017; Grunst et al., 2018) could limit toxicant uptake in polluted areas, but have detrimental effects when food becomes scarce, because exploration brings benefits in terms of foraging (Reader, 2015). In other words, pollution might change the balance between costs and benefits of information processing in animals, but the expected outcome for fish fitness and evolutionary trajectories might depend on several environmental and social factors that remain to be investigated.

Finally, plasticity (and hence behavioral plasticity) generally plays an important role in evolutionary responses to anthropogenic conditions (Price et al., 2003; Ghalambor et al., 2007; Hendry et al., 2008; Sih et al., 2011). Behavioral changes could drive evolutionary changes by exposing individuals to new conditions (so-called "behavioral drive") or in the contrary limit evolutionary changes if plastic behavioral changes are sufficient to mitigate the fitness effects of pollution (Huey et al., 2003; Sol et al., 2005). Plastic behavioral responses to pollution could thus promote or impede genetic selection depending on environmental conditions, by facilitating or limiting the move from one adaptive peak (e.g., past unpolluted environment) to another adaptive peak (e.g., new polluted environment) in the adaptive landscape (Price et al., 2003; West-Eberhard, 2003; Ghalambor et al., 2007; Sih et al., 2011). However, some emerging pollutants such as new pesticides, pharmaceuticals, plastics, and nanoparticles are new chemicals that fish have never encountered in their environment in the past, so that polluted environments might represent evolutionary novel conditions. Past evolution is thus unlikely to generate suitable behavioral responses to pollution that could enhance fitness, although this might strongly depend on the species and on the type and dose of stressor (Sih et al., 2011). Pollution-induced behavioral changes could thus potentially generate maladaptive effects and generate evolutionary traps (Sih et al., 2011; Brady et al., 2019), but this hypothesis remains to be tested.

CONCLUSION

To conclude, the existing literature underlines the need to take into account pollution and their associated behavioral, cognitive and fitness effects in a multistress context to better understand the complex responses of wild fish to pollution and their potential feedback loops. In addition, pollutants and multiple stressors can affect the physiology-behavior nexus and modify syndrome structure, which could generate interpopulation divergence in behavior and personality. Future work should now determine the evolutionary forces promoting such behavioral variability in the face of increasing pollution, and their implication for the evolutionary trajectories of wild populations. With this study, we hope to encourage future studies to bridge the gap between ecotoxicology, behavioral ecology and evolutionary ecology to better anticipate the effects of pollutants on evolutionary processes and population resilience in anthropized ecosystems.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/supplementary material.

AUTHOR CONTRIBUTIONS

LJ drafted the initial version of the manuscript. All authors contributed to the writing and revising of the manuscript.

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Host Cognition and Parasitism in Birds: A Review of the Main Mechanisms

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Parasites can have important detrimental effects on host fitness, thereby influencing their ecology and evolution. Hosts can, in turn, exert strong selective pressures on their parasites, affecting eco-evolutionary dynamics. Although the reciprocal pressures that hosts and parasites exert on each other have long been recognized, the mechanisms are insufficiently understood. Here, we discuss the role of host cognition in host–parasite eco-evolutionary dynamics. Theoretical advances have acknowledged the importance of behavior in shaping these dynamics, but how and why host cognition should affect and/or be affected by parasites is less clear. We propose three scenarios that may create causal and non-causal links between cognition and the richness, prevalence and intensity of parasites. First, host cognition may change the probability of exposure to parasites, either increasing (e.g., altering the relationship with the environment via innovative behaviors) or decreasing (e.g., influencing decision-making to avoid infected conspecifics) exposure. Second, parasites may change host cognitive performance, for example, by reducing host condition. Finally, host cognition and parasites can be associated via common causal factors (e.g., shared molecular pathways), energetic constraints generating trade-offs between cognition and immunocompetence, or trait co-evolution with life history, ecological, or social strategies. The existence of such a variety of non-mutually exclusive mechanisms suggests that host cognition has a great potential to affect and be affected by parasites. However, it also implies that progress in understanding these effects will only be possible if we distinguish between causal and non-causal links.

Keywords: behavioral plasticity, cognition, expensive tissue hypothesis, exposure hypothesis, immune traits, infection costs, parasite avoidance, pathogen

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INTRODUCTION

Cognition includes all ways in which animals collect information, process, retain and decide to act on it (Shettleworth, 2001, 2010). Because these cognitive functions deeply affect how animals interact with their environment, the study of cognition has long been recognized as central to understand the ecology and evolution of animals. Thus, cognition has been linked to a variety of key eco-evolutionary processes such as range expansions, niche shifts, population dynamics, and adaptive divergence (Sol et al., 2005; Ducatez et al., 2015; Sayol et al., 2016, 2019; Fristoe et al., 2017; Riotte-Lambert et al., 2017). Although cognition is also thought to be essential to eco-evolutionary dynamics in host–parasite systems, evidence remains scarce (but see, e.g., Ader et al., 2006; Gómez-Moracho et al., 2017).

Here, we argue that a major obstacle to understanding how host cognition affects and is affected by parasites has been the lack of a general theoretical framework for the different scenarios under which associations between parasites and cognition are expected. Developing such a framework has been particularly challenging because the causality of associations between parasites and cognition takes a variety of forms and can even change direction depending on the scenario, making it difficult to make unique, falsifiable predictions. Cognition can be affected by parasites: for example, most infections by pathogens can directly impair animal cognitive performance (Binning et al., 2018). However, cognition can also affect parasitism, e.g., by allowing a host to learn to avoid being exposed to pathogens (Zhang et al., 2005). Another mechanism through which cognition may influence parasitism is by promoting innovative behavior, which may increase (or decrease) exposure to parasites (Garamszegi et al., 2007). Although this predicts higher parasite loads, a long exposure to parasites may select for enhanced immune systems that reduce the intensity of infections. An association between parasites and cognition may even arise with no need for direct causal mechanisms. Cognition and parasite defenses may be associated as a result of indirect or common causes because they are co-selected in organisms with particular lifestyles (e.g., long-lived or generalist species, Overington et al., 2011; Ducatez et al., 2015; Sol et al., 2016) or because similar molecular pathways affect the two functions (Bilbo and Schwarz, 2012; Grindstaff, 2016). The main aim of our article is to organize the mechanisms expected to create parasite–host cognition associations in a common framework, hoping to build bridges between parasitologists, immunologists, behavioral ecologists and psychologists. Our ultimate goal is to provide a more solid basis for future investigations on the role of parasites in the evolution of cognition, and, conversely, the role of host cognition in the evolution of parasites.

To better understand the impact of parasites on eco-evolutionary dynamics, parasitologists have investigated patterns of variation in parasitism across a wide range of organisms (Poulin and Morand, 2000; Nunn et al., 2003; Lindenfors et al., 2007; Arriero and Møller, 2008; Bordes et al., 2009; Kamiya et al., 2014; Poulin, 2014). Two main theoretical frameworks determine the processes responsible for the main patterns of variation (Poulin and Morand, 2000), and can also provide insights to predict eventual associations between host cognition and parasitism. First, by considering individual hosts as "islands" that can be colonized by parasites, island biogeography theory (MacArthur and Wilson, 1967) offers explanations on, among other patterns, the increase in parasite species richness with host size and host geographic range (Kamiya et al., 2014). Second, by deriving the "basic reproductive rate" (R_0, defined as the average number of new cases of infections that arise from one infectious host), epidemiology models also provide clear predictions on the way host traits can affect parasitism (Anderson and May, 1979; May and Anderson, 1979). These models predict, for example that host population density, by affecting the probability of encounter with parasites, should increase parasite richness, a prediction supported by several empirical studies (e.g., Morand and Poulin, 1998; Arneberg, 2002; Kamiya et al., 2014). These two main theories suggest that host cognition can affect parasitism if it determines the host probability of exposure to parasites, or the probability of parasites' transfer among hosts. Clearly, the probability of transfer will also be determined by the host's (in)ability to eliminate the parasite, and thus by its defense mechanisms. These simple models are however complicated by the fact that parasite characteristics *per se* also play a central role determining parasitism and the interaction between cognition and parasitism, while the metrics used to measure parasitism (prevalence, infection intensity, species richness, etc.) also matter. Although still rarely tested, we discuss in the next paragraph how parasite characteristics may affect the association between parasites and their host's cognition, before focusing our review mostly on the host's perspective.

The mode of parasite transmission is especially likely to affect the interaction between cognition and parasitism. Whether the parasites are transmitted via direct contact with conspecifics (e.g., lice), via contact with the feces of conspecifics (e.g., coccidian parasites) or via a vector (e.g., mosquitoes for malaria) will determine whether and how host cognitive activities affect parasite transmission: for example, social learning may increase the level of social interactions, in turn favoring the exposure to socially transmitted parasites (McCabe et al., 2014; Kavaliers and Choleris, 2018). Host specificity will similarly be an important determinant of whether cognitive activities involving direct or indirect (e.g., via a vector, the predation of another species, or contact with feces) interactions with other species (e.g., foraging innovations and inter-specific social learning) can have an impact on parasitism. The virulence of the parasites is also likely to affect the association between cognition and parasitism, e.g., because a highly virulent parasite will globally decrease the performances of an individual, including its cognitive performance, whereas a less virulent one may not have any detectable effect. A highly virulent parasite may also trigger strong evolutionary responses by the host, including by devising new defenses allowing to limit the parasite effects, or avoid exposure (e.g., via associative learning; Zhang et al., 2005). The characteristics of the parasite's cycle may also be important. Especially, parasites may manipulate their host cognition if they need to be exposed to specific conditions, or to other hosts, to complete their cycle (as they manipulate their host's behavior; see Moore, 2002). Finally, considering metrics of prevalence, infection intensity or parasite species richness is likely to provide different information. For example, the prevalence of a parasite is mostly affected by the probability of encounter between a host and a parasite, whereas the richness of parasite species recorded on a given species is likely to be driven by the diversity of biotic and abiotic conditions encountered by the host, and by parasite specificity and diversification dynamics (Poulin, 2006).

We organize the review in three sections. In the first section, we briefly review empirical evidence for associations between cognition and parasites, distinguishing studies conducted within and across species. Although laboratory model organisms, such as rats (*Rattus norvegicus*) or *Caenorhabditis elegans*, provide key information with regards to the cellular and molecular mechanisms that can link cognition and defense against parasitism (e.g., see Anderson and McMullan, 2018; see also Ader et al., 2006), they are less informative with regards to the eco-evolutionary history of parasite/cognition associations. Studies in wild birds instead have led to fundamental discoveries in our understanding of natural host–parasite systems (see Clayton and Moore, 1997; Poulin, 2006), and have also been at the forefront of the recent advances in the ecology and evolution of cognition (e.g., Lefebvre et al., 1997; Sol et al., 2005, 2016; Morand-Ferron and Quinn, 2011; Cole et al., 2012; Cauchard et al., 2013; Morand-Ferron et al., 2016; Olkowicz et al., 2016; Rutz et al., 2016; Sayol et al., 2016, 2018; ten Cate and Healy, 2017; Ashton et al., 2018; Audet et al., 2018; Branch et al., 2019; Sonnenberg et al., 2019). We thus conducted a thorough review of the bird literature, mostly focusing on studies of wild birds, a relevant context to consider the eco-evolutionary dynamics of parasites and their hosts' cognition.

Several studies in insects (especially bees) have empirically demonstrated the effects of parasite infection on cognition (e.g., see Gegear et al., 2006; Mobley and Gegear, 2018). This research has been thoroughly reviewed and discussed recently, and we thus refer the reader to Gómez-Moracho et al. (2017) for more information. Research on other vertebrate taxa, including mammals (particularly primates and rodents, e.g., see McCabe et al., 2014; Kavaliers and Choleris, 2018) and fish (e.g., Kotrschal et al., 2016; Binning et al., 2018), have also been conducted, providing insights into the mechanisms that may also be at play in birds, and we discuss key results stemming from studies on other taxa when relevant. Our literature review (summarized in **Table 1**) shows that the association between host cognition and the richness, prevalence and intensity of parasites has rarely been investigated in wild birds. It also highlights that patterns of covariation can largely vary depending on the biology of the host and parasites. Parasites' mode of transmission and host specificity are, for example, key traits determining how cognition can affect host parasitism.

In the second section, we provide a framework explaining the observed associations between cognition and parasites (summarized in **Figure 1**). Specifically, we identify three scenarios under which an association between cognition and parasites is expected: cognition can causally affect parasitism, parasitism can causally affect cognition, or the association between cognition and parasites may not be causal, but instead be due to a third co-factor. For each scenario, we discuss the underlying mechanisms and provide examples (see also **Table 2**).

In the third section of this article, we identify gaps in knowledge on the role of cognition in host–parasite eco-evolutionary dynamics and discuss methodological challenges to guide future research.

COGNITION AND PARASITES IN THE WILD

Within-Species Analyses

Parasites have long been known to affect and be affected by host behavior. In a pioneering study, Wilson et al. (1993) found, for instance, that pumpkinseed sunfish (*Lepomis gibbosus*) caught in traps – perhaps reflecting their "bolder" or more "exploratory" personalities – had different levels of parasite infection than the average of the population. For one parasite (*Neascus* sp.), the load was higher in trapped fish, whereas the opposite pattern was detected for a second parasite, *Posthodiplostomum minimum*. This work demonstrated an association between parasites and host behavior, but mostly raised key questions with regards to the causality of the association, especially since it appeared to vary according to the parasite.

While the link between behavior and parasites is now well-documented, including in wild birds (e.g., see Barber and Dingemanse, 2010; Kortet et al., 2010; Poulin, 2013; Lopes, 2017; Sarabian et al., 2018; Sih et al., 2018), less effort has been devoted to identify the cognitive processes involved. Birds illustrate this point quite well (see **Table 1**). At the intra-specific level, we are aware of only five studies testing for associations between cognitive traits and either parasites or immune traits. In a study on house sparrows (*Passer domesticus*), birds that were faster at solving a problem also tended to have fewer coccidian parasites (parasites that infect the digestive tracts and are transmitted via contact with the feces of infected individuals; Bókony et al., 2014). However, this pattern only emerged in one of the four tasks measured, the one that was the most difficult to solve (only 22.8% of the tested birds solved it, compared to 72.4 to 83.3% for the other tasks). The pattern might reflect a negative effect of parasite infection on cognitive performance, although the observational nature of the study does not allow one to infer causality. In another study, Dunn et al. (2011) found a sex-dependent association between problem-solving performance and malaria prevalence in wild great tits (*Parus major*). Infected males showed an increased performance, whereas the reverse was true for females. Although the causality of these patterns could again not be inferred given the correlative nature of the study, the authors suggested that the increased performance of infected males may be explained by the higher exposure to parasites of problem-solvers, resulting from their more diverse foraging habits. Instead, the lower performance of infected females could be explained by a negative effect of malaria on their cognitive abilities, similar to the negative effect of coccidian parasites on sparrow cognition (Bókony et al., 2014). However, an experimental study did not confirm the latter interpretation. Cauchard et al. (2016) found that wild female great tits treated with an anti-malaria drug did not outperform control birds in a problem-solving task. Malaria infection thus did not seem to affect problem-solving

TABLE 1 | Patterns of covariation between cognitive traits and parasitism or host defense in wild birds from studies considering intraspecific or interspecific variation.

Host	Parasite	Parasitism measure	Transmission mode	Location	Cognition measure	Relationship	Causal relationship	Host defense	References
Intraspecific level studies									
House sparrow (*Passer domesticus*)	Coccidia	Load	Contact with feces	Hungary	Problem solving 1	–	Unknown		Bókony et al. (2014)
	Coccidia	Load	Contact with feces	Hungary	Problem solving 2	0	Unknown		Bókony et al. (2014)
	Coccidia	Load	Contact with feces	Hungary	Problem solving 3	0	Unknown		Bókony et al. (2014)
	Coccidia	Load	Contact with feces	Hungary	Problem solving 4	0	Unknown		Bókony et al. (2014)
Great tit (*Parus major*)	Malaria	Prevalence	Arthropod vector	Sweden	Problem solving	– in males, + in females	Unknown		Dunn et al. (2011)
	Malaria	–	Arthropod vector	Sweden	Problem solving	0	Experimental	Anti-malaria treatment	Cauchard et al. (2016)
Carib grackle (*Quiscalus lugubris*)				Barbados	Problem solving	–	Unknown	PHA	Ducatez et al. (2019)
				Barbados	Associative learning	+	Unknown	PHA	Ducatez et al. (2019)
				Barbados	Reversal learning	+	Unknown	PHA	Ducatez et al. (2019)
				Barbados	Detour reaching	+	Unknown	PHA	Ducatez et al. (2019)
Barbados bullfinch (*Loxigilla barbadensis*)				Barbados	Problem solving	0	Unknown	PHA	Audet et al. (2016)
				Barbados	Associative learning	0	Unknown	PHA	Audet et al. (2016)
				Barbados	Reversal learning	0	Unknown	PHA	Audet et al. (2016)
				Barbados	Detour reaching	0	Unknown	PHA	Audet et al. (2016)
Inter-species level studies									
45 Bird species	Haematozoa	Prevalence	Arthropod vector	Palearctic	Foraging innovation rate	+	Unknown		Garamszegi et al. (2007)
55 Bird species	Egg bacteria	Load	Direct contact?	Palearctic	Foraging innovation rate	+	Unknown		Soler et al. (2012)
107 Bird families	Amblyceran lice	Richness	Direct contact	Global	Foraging innovation rate	+	Unknown		Vas et al. (2011)
107 Bird families	Ischnoceran lice	Richness	Direct contact	Global	Foraging innovation rate				Vas et al. (2011)
107 Bird families	Amblyceran lice	Richness	Direct contact	Global	Brain size	+	Unknown		Vas et al. (2011)
107 Bird families	Ischnoceran lice	Richness	Direct contact	Global	Brain size	0	Unknown		Vas et al. (2011)
59 Bird species				Palearctic	Brain size	+ in males	Unknown	Bursa of Fabricius size	Møller et al. (2005)
127 Bird species				Palearctic	Brain size	+ in males	Unknown	Spleen size	Møller et al. (2005)
77 Bird species				Palearctic	Foraging innovation rate	+	Unknown	Bursa of Fabricius size	Garamszegi et al. (2007)
97 Bird species				Palearctic	Foraging innovation rate	+	Unknown	Spleen size	Garamszegi et al. (2007)
48 Bird species				Palearctic	Foraging innovation rate	+	Unknown	Thymus size	Garamszegi et al. (2007)

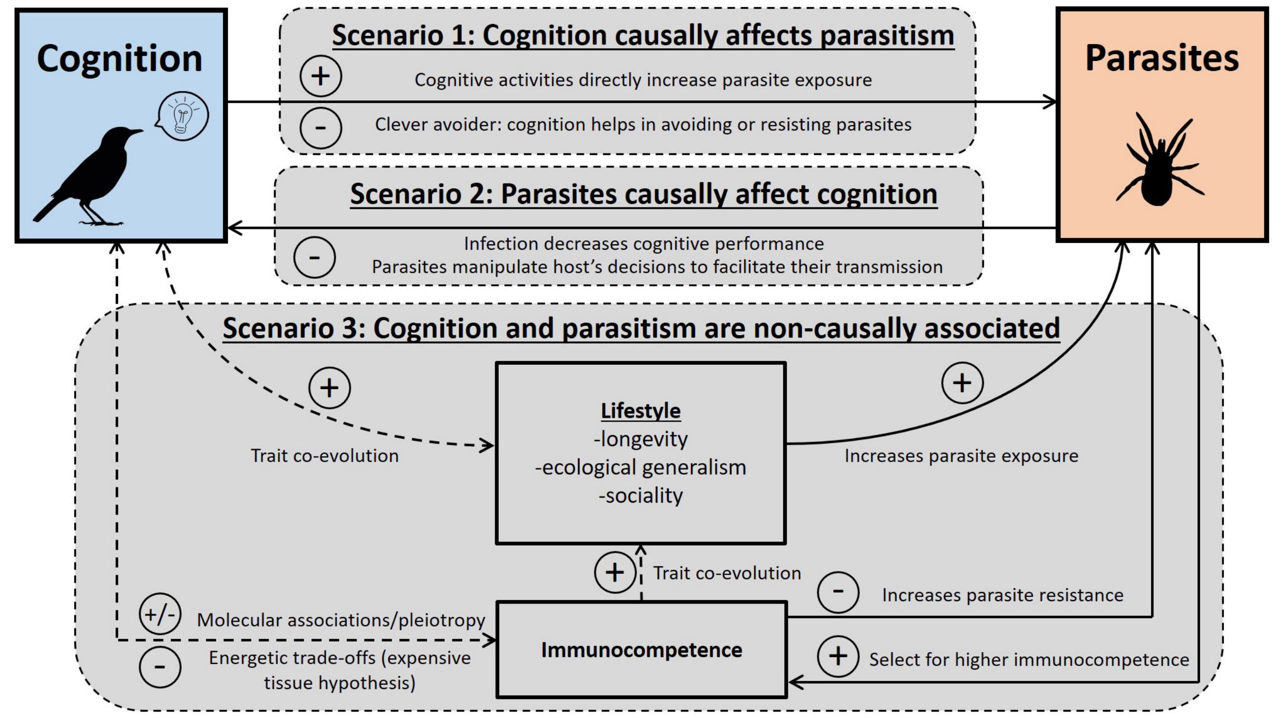

FIGURE 1 | Diagram presenting the different scenarios predicting associations between host cognitive traits and parasitism. Each of the three scenarios involves one or more different mechanisms. Solid arrow: causal association. Dashed arrow: non-causal association resulting from constraints or trait co-evolution. + : positive associations expected; – : negative associations expected; ± : both positive and negative associations expected.

performance in this system, although problem-solving was tested shortly after the drug injection, and long-term effects of infection could thus not be discarded (Cauchard et al., 2016).

Still at the intra-specific level, two studies tested for associations between cognitive performance and response to PHA, an immunoecological technique assessing general innate immunity, and to a lesser extent adaptive immunity (Martin et al., 2006). Artificial activation of immune responses, though very different from actual infections with pathogens, can be particularly informative to measure the covariation between traits affecting parasite resistance (i.e., immune traits) and cognitive performances. In Carib grackles (*Quiscalus lugubris*) from Barbados, individuals' response to PHA was associated with their performance in different cognitive tasks; PHA response was higher in grackles that were slow but accurate at problem-solving, associative learning and reversal learning tasks, and in grackles with better detour-reaching performance (Ducatez et al., 2019). The higher PHA response of slow-paced species detected by Martin et al. (2011) is in line with this result, suggesting that immunocompetence and cognition may co-evolve within a given lifestyle. However, the causality of the association remains untested, and other immune traits should be considered, as general immunocompetence is the result of a diversity of immune traits. In contrast, in a similar study on Barbados bullfinches (*Loxigilla barbadensis*), variation in performance at similar cognitive tests was not associated with variation in response to PHA (Audet et al., 2016). Despite the lack of association at the individual level, this last study detected co-variation at the population level: individuals from urban areas displayed both enhanced problem-solving performances and higher PHA responses as compared to their rural conspecifics. This result suggests that immunocompetence and cognition may respond to similar pressures (here, urbanization), even if they are not associated directly.

Together, these studies lead to the following conclusions. First, the results appear, at first sight, largely inconsistent from one study to another, as increased parasitism can either be associated with increased or decreased cognitive performances, or can be unrelated to cognition. Similarly, the association between a proxy of immunocompetence and cognitive performance was significant in one, but not in the other tested species. Second, except for one study, all analyses so far are correlative, making it difficult to determine the causality of the observed patterns. Third, even though several studies followed recent recommendations to characterize individual cognitive skills by measuring performance at a diversity of psychometric measurements (Rowe and Healy, 2014; Thornton et al., 2014), all of these studies focused on either one measure of immunocompetence or one type of parasite. Immune traits are labile and depend on past infection history and host–parasite co-evolution. In addition, different parasites differently affect their hosts. Future studies should thus favor experiments manipulating or controlling parasite infection

TABLE 2 | Main mechanisms predicting associations between parasitism and cognition, with examples from the literature and analyses/experiments required to provide more evidence for the different mechanisms.

	Mechanism	Published evidence	Future development	Important aspect to consider/ main difficulty
1.1	Cognitive activities increase exposure to parasites	McCabe et al. (2014) in primates; some correlative evidence in birds, but no test of causality (e.g., Garamszegi et al., 2007)	Comparative analysis: assess the causality of associations between cognitive traits and parasites which transmission mode is related to the cognitive activity considered using path analyses; e.g., birds foraging innovation rate and helminth species richness	Consider the confounding effects of diet and habitat breadth
1.2	Cognitive abilities help to avoid or respond to parasites	Zhang et al. (2005) in *C. elegans*; in birds, examples of innovative anti-parasite behaviors	Provide field and experimental evidence of parasite removal/avoidance using cognition; e.g., test whether birds can learn to avoid an area with high parasitism, or determine the role of cognitive mechanisms in the emergence of behavioral innovations limiting parasite effects	Demonstrate that innovative anti-parasite behaviors involve cognition
2.1	Cognitive cost of parasite infection	Binning et al. (2018) in Ambon damselfish; in birds, no evidence detected in Cauchard et al. (2016); effects of immune response on cognitive performance in zebra finch (e.g., Grindstaff et al., 2012)	Experimental manipulation of parasitism; e.g., infect or disinfect hosts with malaria or other parasites and measure the consequence on their cognition	The time scale can have strong importance (compare short/long term effects; compare the effects of manipulation during/after development)
2.2	Parasites manipulate their host cognition	Numerous examples of behavioral manipulations in taxa other than birds (e.g., arthropods; Moore, 2002); unclear how cognition is affected	Experimental infection; e.g., infect a host and measure its cognition in a context that affects the parasite's transmission	Determine how an eventual change in cognition following infection favors the parasite's cycle completion
3.1	Cognition is associated with lifestyles affecting parasitism			
	Social intelligence and social parasites	McCabe et al. (2014) use a comparative analysis to show an association between social learning and the richness of socially transmitted parasite species in primates	Comparative analysis: assess the causality of associations between social cognition and socially transmitted parasites; e.g., test for associations between lice species richness/prevalence and social learning performances in birds using path analyses	Consider social organization and interspecific interactions in the analyses
	Ecological generalism, cognition, and parasite exposure	Some correlative evidences in birds, but no test of causality (e.g., Garamszegi et al., 2007)	Comparative analysis: assess the causality of associations between cognition, parasites, and ecological generalism; e.g., test for associations between blood parasite richness/prevalence and general cognition in birds (innovation rate and brain size) using path analyses	Consider diet and habitat breadth
	Life history, cognition, and parasite exposure	Comparative analyses show associations between cognition and life history (e.g., Sol et al., 2016) and between life history and parasitism (e.g., Poulin and Morand, 2000)	Comparative analyses: assess the causality of associations between cognition, parasites, and life history; e.g., test for associations between parasite richness/prevalence and general cognition in birds (innovation rate and brain size) using path analyses	Consider different life history traits (especially longevity and breeding frequency)
3.2	Brain/immunocompetence trade-offs: the expensive tissue hypothesis	Kotrschal et al. (2016) in guppies – artificial selection on brain size also reduced innate immune response	Experimental selection on brain size and/or immune traits; such experiments may be easier to conduct on non-bird model species (e.g., guppies or arthropods); comparative analyses using path analyses can be considered in birds, e.g., relating brain size/innovation rates and immune traits	Consider a diversity of immune traits
3.3	Molecular associations and pleiotropy	Pleiotropic effects on immune traits and cognition in humans (MacMurray et al., 2014; Napolioni et al., 2014), no studies in wild animals	Using genomic and proteomic approaches to assess immune traits/cognition pleiotropy and molecular mechanisms affecting anti-parasite behavior in wild animals	Consider a large number of loci/genotypes and a variety of different cognitive traits

For each mechanism, we underline important aspects to take into account when developing experimental protocols or comparative analyses.

(ideally, over long periods of time), and consider a combination of parasitism measures and immune traits to relate to measures of cognitive performances.

Across-Species Analyses

In line with the paucity of studies within species, only a few comparisons have been conducted across species in birds. To our knowledge, only four comparative studies have looked for associations between proxies of cognition, immunocompetence, and parasitism (**Table 1**). Examining 45 bird species, Garamszegi et al. (2007) found a positive association between the prevalence of *haematozoa* parasites and species rate of foraging innovations. Similarly, in an analysis of 55 bird species, Soler et al. (2012) found that bacterial density on eggshells was increased in species with higher rates of foraging innovations. In a third analysis, working this time at the family level and considering 108 different families, Vas et al. (2011) found that the richness of amblyceran (but not ischnoceran) lice species was higher in more innovative families. The three studies thus reveal a similar pattern: an increase in either parasite species richness, parasite prevalence or intensity of infection in more innovative species. These patterns suggest that innovative species are exposed to more parasites, e.g., because innovativeness is part of a generalist lifestyle exposing individuals to a diversity of environmental conditions, or because foraging innovations *per se* increase the probability of encountering (new) pathogens. Vas et al. (2011) suggested that innovative species may also be more social, another factor that increases exposure to parasites by increasing conspecific contacts. Direct evidence for an association between innovativeness and sociality in birds is however lacking. In addition to associations between parasitism and foraging innovation rates, associations between proxies of cognition and immunocompetence have also been tested and detected at the inter-specific level. The relative size of the bursa of Fabricius (59 species) and spleen (127 species), two organs involved in immune defense, covaried positively with the relative size of the brain in male birds (Møller et al., 2005). Similarly, more innovative birds also had a relatively larger bursa of Fabricius (77 species), spleen (97 species), and thymus (48 species) (Garamszegi et al., 2007). These patterns thus suggest a higher investment in immune defenses in species with a larger brain and more innovative behavior. In line with the results considering parasites instead of immune traits, these associations thus also support the idea that a larger brain or a higher innovativeness involves a higher exposure to parasites, thus selecting for a better immunocompetence.

Contrary to the studies at the intra-specific level, inter-specific comparative analyses thus seem to yield relatively consistent results. However, it is important to notice three key aspects. First, all of these studies are either restricted to the Western Palearctic birds (Møller et al., 2005; Garamszegi et al., 2007; Soler et al., 2012) – reducing the generality of the results – or conducted at the avian family level (Vas et al., 2011) – thus ignoring within-family variation, although closely related species can show strong differences in cognitive abilities (e.g., Audet et al., 2018).

Second, the causality is again difficult to establish, especially because the link between the cognitive traits (here, foraging innovation) and the type of parasites considered is not obvious. Why foraging innovations should relate to the richness of lice species is unclear, for example, since the transmission mode of these parasites is not directly related to their host's foraging behavior. A more direct relationship between foraging innovativeness and food-related parasites (such as helminths) may be easier to interpret, but this association has not been tested. In primates, McCabe et al. (2014) showed that the richness of socially transmitted parasite species increased with the host rates of social learning, whereas the richness of environmentally transmitted parasite species increased with the diversity of extractive foraging behaviors, suggesting direct causal relationships. Considering parasites that have a clear link with the cognitive trait measured, e.g., because their transmission mode is likely affected by this cognitive trait, is a key step toward a better understanding of host cognition/parasites relationships.

Finally, previous studies linking cognition and parasitism not only focused on different types of parasites, but also adopted different metrics to quantify the level of parasitism. Prevalence (Garamszegi et al., 2007), intensity of infection (Soler et al., 2012), or species richness (Vas et al., 2011) were used in these studies, metrics that are likely affected by different parameters (Shaw et al., 2018) and cognitive traits.

DEVELOPING A CAUSAL FRAMEWORK

Most of the studies testing for associations between cognition and parasitism in birds are correlative, and inferring the responsible processes is still a challenge. In this section, we propose three scenarios and the associated mechanisms predicting different causal and non-causal associations between cognition, parasites, and immune traits (**Figure 1**). Our aim is to clarify the mechanisms that can explain associations between cognitive traits and either parasitism or immune traits. In addition, we provide examples and suggestions of future studies to better determine the importance of each scenario (**Table 2**). Note that the proposed scenarios are not mutually exclusive.

Scenario 1: Cognition Causally Affects Parasitism

Under the first scenario, associations between cognition and parasitism are expected because of a causal relationship: cognition causes a change in parasitism. Such a relationship can be due to two main mechanisms, either cognitive activities increase exposure to parasites, or cognitive abilities help in avoiding or responding to parasites.

Mechanism 1.1: Cognitive Activities Increase Exposure to Parasites

A higher exposure to parasites can be the causal result of the expression of a cognitive trait. Cognitive processes, by definition, involve the collection of information on the environment, which may entail an increased exposure to environmental pathogens. For example, as an individual expresses a new foraging behavior (either by ingesting a new type of food, or using a new foraging technique), it may at the same time be exposed to parasites that it would not have encountered otherwise. Activity and exploration level are indeed good predictors of exposure to parasites (e.g., Koprivnikar et al., 2012). Innovative individuals may thus experience a higher exposure to parasites as a direct consequence of their innovative behavior. Although the comparative studies mentioned in the previous sections suggest an increased parasite pressure in more innovative bird species, the causality of the association has not yet been demonstrated, and non-causal links cannot be excluded (see section "Scenario 3: Non-Causal Associations Between Cognition and Parasitism").

Mechanism 1.2: Cognitive Abilities Help to Avoid or Respond to Parasites

Host cognitive abilities can, in some cases, directly help a host to either avoid or resist parasites. By exploiting habitats or developing foraging behaviors that are not used by most of their conspecifics, innovative individuals may, for example, limit their contacts with conspecifics, decreasing their exposure to parasites. Evidence for this pattern is however missing. In addition, individuals may learn to recognize and avoid infected individuals – as in mandrills which can recognize the smell of individuals infected by protozoan parasites, and avoid grooming them (Poirotte et al., 2017; see also reviews on parasite avoidance behaviors: Hart and Hart, 2018; Kavaliers and Choleris, 2018; Sarabian et al., 2018). Hosts can also learn to avoid contact with pathogens – as in the Nematode *Caenorhabditis elegans* that learns to associate the smell of a pathogenic bacteria with a hazard (Zhang et al., 2005). Innovativeness may also yield novel ways of counteracting external and internal pathogens. In primates, a growing literature on self-medication suggests that several ape species ingest plants that have anti-parasitic properties. Chimpanzees, for example, chew the piths of *Vernonia amygdalina* and swallow *Aspilia* leaves, which are thought to facilitate the expulsion of intestinal nematodes and cestodes (Huffman, 2001). Gibbons in Thailand are also thought to use *Gironniera nervosa* leaves for similar purposes (Barelli and Huffman, 2017). A recent comparative analysis found that primate species with a larger absolute brain are more likely to self-medicate, suggesting that self-medication is, to some degree, cognitively demanding (Neco et al., 2019).

More direct evidence for a link between cognition and parasite avoidance comes from studies in birds. Several reports suggest, for instance, innovative ways of dealing with external parasites and nest pathogens. Over 200 avian species frequently apply formic acid secreted by ants during preening (Bush and Clayton, 2018). Occasionally, "anting" innovations have been observed, where substances likely to have anti-parasite effects are also applied. Cimadom et al. (2016) report that warbler finches (*Certhidea olivacea*) in the Galapàgos tear off leaves of *Psidium galapageium* and preen with them either directly or after chewing and applying a mixture of saliva and mashed leaf. Several species of grackles have also been described "anting" with different substances (e.g., mothballs, Borgelt, 1960; Clark et al., 1990; or lime, Clayton and Vernon, 1993; see also Parks, 1945; Groff and Brackbill, 1946; Laskey, 1948). Another use of innovative techniques by birds to combat pathogens involves the incorporation of substances like cigarette butts and fumigated cotton to avian nests. Suárez-Rodríguez et al. (2013) found that 80% of house sparrow and house finch nests at an urban site in Mexico contained cigarette butts, while Knutie et al. (2014) witnessed Darwin's finches taking cotton from laundry lines, leading the researchers to install field dispensers of cotton fumigated with permethrin that the birds bring back to their nests.

The role of cognition in the emergence of these anti-parasite innovations needs to be demonstrated. Importantly, if behavioral plasticity is a general trait that can apply to multiple situations, we would expect novel anti-parasite responses to occur in the same species that show high rates of innovation in the most intensively studied domain, foraging (Lefebvre, 2011). House sparrows, who incorporate tobacco in their nests, Darwin's finches, who take cotton from laundry lines, and grackles, who ant with mothballs, are among the birds with the highest rate of foraging innovation (Overington et al., 2009). Foraging innovations in birds (and primates, Reader and Laland, 2002) are associated with larger neural substrates, especially association areas (Lefebvre et al., 1997; Timmermans et al., 2000; Overington et al., 2009). This suggests that the enhanced cognitive processing associated with larger association areas might also apply to anti-parasite responses.

Similarly, while there is considerable evidence of anti-parasitic behaviors, their efficacy has not been demonstrated and we cannot eliminate the possibility that their usage is simply based on random use of materials. "Anting" substitutes never seem to involve neutral objects (Clark et al., 1990), but many birds incorporate plastic and other anthropogenic substances into their nests even if they do not have any anti-parasitic properties. In a recent review, Bush and Clayton (2018) stressed that rigorous experimental demonstrations of the purposefulness and efficacy of substitute anti-parasitic substances are still lacking. A few studies have however provided intriguing results on the anti-parasitic properties of several of the substances. Cimadom et al. (2016) showed that extracts from the *P. galapageium* leaves used in Darwin's finch "anting" have negative effects on both mosquitoes and invasive hematophagous fly (*Philornis downsi*) adults and larvae. Clayton and Vernon (1993) exposed lice-infested pigeon feathers to both lime juice and lime rinds and found that the latter had a strong negative effect on them, a finding supported by Weldon et al. (2011). Suárez-Rodríguez et al. (2013) found that mite traps containing cellulose from smoked cigarette butts attracted significantly fewer ectoparasites than traps with non-smoked cellulose. Care is therefore needed in interpreting observations of anti-parasite innovations in birds, but experimental evidence suggests that Simmons (1966) skepticism on the functionality of substitute substances, which he saw as developmental errors in the learning process of anting responses, might be unfounded. Paradoxically, the exposure to pathogens that is associated with flexible, opportunistic generalist feeding could thus be greater than we think, because innovative anti-pathogen behaviors, if frequent enough, might be reducing the parasite loads we are actually measuring on innovative feeders.

Scenario 2: Parasitism Causally Affects Cognition

The second scenario also considers a direct causal relationship between cognition and parasites, but the direction of the causality is reversed: parasites change their host cognition.

Mechanism 2.1: The Cognitive Cost of Parasite Infection

In line with the idea that host behavior can be altered by pathogen infection, especially via a change in the host state (e.g., body condition), pathogen infection may cause a decrease in cognitive performance. For example, in the Ambon damselfish (*Pomacentrus amboinensis*), experimental infection with gnathiid parasites decreased individual performance at a visual discrimination test (Binning et al., 2018). To our knowledge, there is no direct evidence of a change in cognition after a pathogen infection in wild birds. This is however most likely due to a lack of studies: we are aware of only one study that aimed at changing parasite infection to test its effect on cognition in wild birds; as mentioned earlier, Cauchard et al. (2016) found no effect of an anti-malaria drug on problem solving performance in great tits. In a study on a captive population of zebra finches (*Taeniopygia guttata*), Grindstaff et al. (2012) showed a long-term effect of an immune challenge during the juvenile stage on the learning performance of adult males. Also working with captive zebra finches, Uysal et al. (2018) demonstrated that the morphology of adult brains was affected by a simulated viral infection during the hatchling stage. The activation of the immune system in response to a pathogen infection can thus have long-term effects on the host cognition, and additional studies would likely bring valuable information on the immediate and long-term effects of pathogen infections on wild bird cognition. Some pathogens are also known to directly infect the nervous system; in birds, they have mostly been investigated in veterinary sciences, using poultry as model species (e.g., the paramyxovirus responsible for the Newcastle disease in chickens; Butt et al., 2019). Experimental infection and treatment of infected individuals, ideally on wild birds, are likely the best approaches to further test the importance of this mechanism.

Mechanism 2.2: Parasites Manipulate Their Host Cognition

Parasites may also directly alter their host decision-making to facilitate their own transmission. A diversity of studies have demonstrated that some parasites manipulate their host behavior for their own benefit (e.g., to favor their transfer to another host, Lafferty and Morris, 1996; Moore, 2002). Host cognitive responses could be similarly affected by parasite manipulation. For example, parasites could reduce a host's ability to learn about aversive consequences of its dietary choices, facilitating repeated ingestion despite cues that would normally lead to food avoidance. However, to our knowledge, this idea has not been tested directly.

Scenario 3: Non-causal Associations Between Cognition and Parasitism

Non-causal associations between cognition and parasitism are also expected, e.g., because they are both affected by a third factor. The following three mechanisms predict such indirect associations.

Mechanism 3.1: Cognition Is Associated With Lifestyles Affecting Parasitism

Animals' lifestyles are known to affect their exposure to parasites for several reasons. Since cognition co-evolves with lifestyles (e.g., see Ducatez et al., 2015; Sol et al., 2016), indirect associations between cognition and parasites are expected. Three trait features of animals' lifestyles are especially likely to affect their exposure to parasites and co-evolve with cognition: sociality, ecological generalism, and life history.

Mechanism 3.1.1: social intelligence and social parasites

As expected under the "social intelligence" hypothesis (Byrne and Whiten, 1989; Whiten and Byrne, 1997), an increased complexity of social organization may select for cognitive skills favoring social interactions (e.g., Ashton et al., 2018). Since social interactions are also likely to favor the transfer of socially transmitted pathogens, associations between social cognition (e.g., social learning) and socially transmitted pathogens are expected. In primates, the higher richness of socially transmitted parasites in species where social learning is more often recorded is in line with this idea (McCabe et al., 2014). Other cognitive traits may also be indirectly associated with socially transmitted parasitism, because of co-variation between these traits and social cognition (e.g., see Reader et al., 2011; see also Villa et al., 2016). Note however that sociality may also, in some cases, decrease parasite pressure, for example, via social defenses such as allogrooming/allopreening, or because of dilution effects (see Mooring and Hart, 1992), in which case social species should be less parasitized (e.g., Bordes et al., 2007). Innovative species with allogrooming and with close social contact leading to dilution thus need to be singled out here, with the prediction that their parasite loads should be lower than species without the social effects.

Mechanism 3.1.2: ecological generalism, cognition, and parasite exposure

Ecological generalists are often characterized by their higher cognitive abilities (e.g., larger brain or higher innovation rates; Overington et al., 2011; Ducatez et al., 2015). Because occurring in a wider diversity of habitats or exploiting a higher diversity of foods is likely to increase the diversity of parasites a given organism is exposed to (e.g., Gutiérrez et al., 2017, 2019), the generalist lifestyle of organisms with higher cognitive abilities should increase the rate of parasitism.

Mechanism 3.1.3: life history, cognition, and parasite exposure

Large brains, relative to body size, are more likely to evolve in long-lived species (Allman et al., 1993; Van Schaik and Deaner, 2003; Ricklefs, 2004; Sol et al., 2007; Lefebvre and Sol, 2008; González-Lagos et al., 2010). Similarly, innovation propensity covaries with life history in birds, long-lived species being also more innovative (Sol et al., 2016). Differences in parasitism associated with variation in life history could thus indirectly result in associations between parasitism and cognition. Host longevity is, for example, a predictor of parasite richness in some taxa, long-lived species tending to accumulate a higher diversity of parasite species (Poulin and Morand, 2000). Indirectly, large-brained and more innovative species should thus have an increased parasite species richness.

It is noticeable that these different lifestyles are not only associated with differences in cognition and parasite exposure, but also with differences in immunocompetence (see **Figure 1**; we consider here a broad definition of immunocompetence, i.e., the ability to produce an immune response following exposure to an antigen). For example, the pace-of-life syndrome hypothesis suggests that animals differ in a suite of physiological traits (including immune traits) that have coevolved with particular life histories (Ricklefs and Wikelski, 2002). Behavioral (Réale et al., 2010) and cognitive (Sih and Del Giudice, 2012) traits are also expected to be part of this general syndrome, shaping variation in cognition, behavior, and physiology according to an organism's life history. As a result, immune and cognitive traits may be associated because of co-selection processes, e.g., because in long-lived species, both a higher investment in immunocompetence and in learning abilities are favored. Long-lived species may thus, as a result, have a lower rate of parasitism because of their investment in better immune defenses, while also benefiting from better learning abilities. Modern comparative methods such as phylogenetic path analyses (Hardenberg and von Gonzalez-Voyer, 2013), based on large numbers of species and including data on parasitism, immunocompetence, cognitive performances, life history and/or ecological generalism and/or sociality are likely to bring new advances in our understanding of the causal relationships between these different compartments. For example, an association between foraging innovation rate and helminth richness may be mostly due to the higher diet generalism of innovative birds which may expose them to a higher diversity of helminths, rather than to their higher cognitive abilities *per se*. A path analysis should help in disentangling the causality of this eventual association, and determining whether, after taking into account the effect of diet breadth, foraging innovations still causally affect the richness of helminth species (see also **Table 2**).

Mechanism 3.2: Brain/Immunocompetence Trade-Offs: The Expensive Tissue Hypothesis

Anti-parasite defenses are energetically costly (Sheldon and Verhulst, 1996; Hanssen et al., 2004), resulting in evolutionary trade-offs between investment in anti-parasitic defenses and other energetically costly functions (Sheldon and Verhulst, 1996). The brain is especially costly to build and maintain (Aiello and Wheeler, 1995; Isler and van Schaik, 2009), so that a trade-off between investment in cognitive vs immune functions is theoretically expected. In line with this hypothesis, experiments using artificial selection on brain size in guppies (*Poecilia reticulata*) found that individuals selected for relatively larger brains had a reduced innate (but not adaptive) immune response as compared to fish selected for relatively smaller brains (Kotrschal et al., 2016). Evidence for this hypothesis remains however scarce and the association between brain size and parasites or immune traits is inconsistent. In rodents, species brain size was not associated with either flea or helminth richness (see Bordes et al., 2011). In birds, the relative size of the brain and of organs involved in the immune system tend to be positively correlated (Møller et al., 2005; Garamszegi et al., 2007). This apparent contradiction may relate to methodological and taxonomic differences. Especially, such energetic trade-offs may be difficult to detect via inter-specific comparisons. Long-term trait co-selection, for example, of cognition and immune traits if higher cognitive performance tends to increase parasite exposure, may have led to the evolution of both larger brains and stronger immunocompetence in some species, even if both traits require important energy inputs. Experimental approaches, including artificial selection experiments, are likely a more powerful approach to test the importance of this mechanism (e.g., Kotrschal et al., 2013).

Mechanism 3.3: Molecular Associations and Pleiotropy

The immune system and the central nervous system share numerous cell types, signaling molecules, processes, pathways and genes. There is considerable communication between the nervous and immune systems, among others through the blood–brain barrier, a semi-permeable cellular boundary between the brain and the circulating blood flow that allows cells, proteins, and molecules – such as leukocytes, cytokines, and chemokines – to travel through it (Abbott et al., 2010).

In humans, the intimate connection between cognition and the immune system is relatively well understood (e.g., see Bilbo and Schwarz, 2012). A wide range of neuropsychological disorders such as schizophrenia, learning disabilities, depression, anxiety, and stress disorders are characterized by abnormal or modified levels of immune components, namely cytokines, growth factors, inflammatory markers, synapse proteins, and immune cell numbers (reviewed in Bilbo and Schwarz, 2012; Theoharides et al., 2013). The modification of a wide variety of inflammatory components, either during development or in adults, is also known to affect both cognitive and immune traits (Bilbo and Schwarz, 2009, 2012; Donzis and Tronson, 2014).

Pleiotropic effects may also explain associations between cognitive and immune traits. Pleiotropy is the influence of a single gene on multiple unrelated phenotypic traits (Tyler et al., 2009). Two studies reported separate pleiotropic effects of two genes, INFG and ACP1, which affect both extravert behavior and immune functions (MacMurray et al., 2014; Napolioni et al., 2014). Other loci were found to display pleiotropic effects on immune system and neuropsychological conditions or diseases that include cognitive impairments. For example, genome-wide association studies (GWAS) have identified several loci in the major histocompatibility complex (MHC) – an acquired immune system component – that were associated with schizophrenia and multiple sclerosis

(Stefansson et al., 2009; Schizophrenia Psychiatric Genome-Wide Association Study (Gwas) Consortium, 2011; Gourraud et al., 2012; Ripke et al., 2013). Other non-MHC related but immunologically relevant genes have also been linked with multiple sclerosis (Sawcer et al., 2011). The above examples suggest that pleiotropic genes affecting both immune function and cognition are also likely to exist in wild animals, causing associations between immune and cognitive traits.

KNOWLEDGE GAPS IN THE PROPOSED FRAMEWORK

We have proposed three main scenarios under which associations between parasitism and cognitive traits are expected. The mechanisms detailed under these scenarios are not mutually exclusive and can even have opposite effects, increasing the difficulty of developing falsifiable predictions that can distinguish them. Providing a precise guideline on how to thoroughly test the relevance and generality of each mechanism is particularly challenging and beyond the scope of this article, but we discuss here several points that we think should help future studies to provide a mechanistic understanding of cognition–parasite associations (see also **Table 2**).

One key to further develop our understanding of these interactions is to combine different approaches (including observations, experimental, and comparative studies), while also targeting parasites, metrics of parasitism and cognitive traits that are relevant to test a given mechanism. Empirical studies on captive birds, e.g., experimental infections to test both short term and long-term effects on cognition, would for example be especially informative for mechanisms such as the infection cost. Similarly, artificial selection experiments should favor a better understanding of the importance of energetic trade-offs. In contrast, some mechanisms such as the indirect effects of lifestyles may only be detectable at higher taxonomic levels, using inter-specific comparative analyses. The mechanism of parasite transmission is especially important here, as different host behavioral and cognitive strategies will have different effects on parasites being transferred via direct contact between conspecifics, contact with specific food items, or vectors such as mosquitoes (see **Table 2** for examples of studies that could bring new elements to understand the importance of the different mechanisms).

Host–parasite interactions are dynamic processes, involving eco-evolutionary processes such as feedback loops and arms races between parasites and their hosts (Price, 1981; Poulin, 2006). Such processes are likely to have major effects on the association between cognitive traits and parasitism, especially via changes in host immunocompetence (though these effects may depend on the host specificity of the parasites considered, see Poulin, 2006). For example, if highly innovative individuals are exposed to more parasites, natural selection is likely to favor innovative individuals that are better able to respond to these parasites. As a result, innovative individuals may evolve better immune defenses. Ultimately, these stronger immune defenses may result in lower parasite prevalence or infection intensity in more innovative individuals. This type of evolutionary feedback loop is a key aspect of host–parasites dynamics (Ezenwa et al., 2016), and can affect both the host and the parasite's evolution, involving changes in host defense, parasite pathogenicity or parasite diversification (Poulin, 2006). Considering both metrics of parasitism and immune traits is thus important to provide integrated information on how cognition and parasites are associated. Immunocompetence is complex and involves a diversity of traits, and investigating interactions between cognitive traits and immunocompetence also requires careful consideration of the immune traits measured. Measurements such as the PHA response are easy to take on wild individuals, but only cover a small part of the story, and a diversity of other immune traits should be considered (Monceau et al., 2017). Studies considering both innate and acquired immune responses would, for example, provide more complete information on the importance of previous exposure to pathogens in shaping associations between cognition and immune traits (e.g., see Kotrschal et al., 2016).

Finally, note that we focused on the most likely mechanisms based on the literature, though other mechanisms may also play a role. For example, extra-pair copulation was more likely to occur in innovative than in non-innovative female great tits (Bókony et al., 2017), which could indirectly increase exposure to sexually transmissible pathogens in more innovative birds. Our review has also mostly been written from the perspective of the host, although cognition may also be relevant for the parasite. Although the justification is that most current studies focus on the role of cognition in hosts, the viewpoint of the parasite is particularly relevant considering that some of the mechanisms linking cognition and parasitism are expected to vary depending on the biology of the parasite – notably its virulence, mode of transmission and ability to respond to the host defense.

CONCLUDING REMARKS

The studies that have investigated associations between parasites and cognition do not yet allow us to rank the relative importance of the different mechanisms and scenarios explaining how and why cognitive traits and parasitism interact. This is likely to change in the near future, with the growing availability of fully resolved phylogenetic trees on large taxonomic groups (e.g., see Jetz et al., 2012 for birds; Upham et al., 2019 for mammals), together with the existence of large datasets on species cognitive traits, immunocompetence and parasites, especially in birds. Combined with modern advanced phylogenetic methods, this information provides the opportunity to test some of the mechanisms proposed in our framework at unprecedented large taxonomic and geographic scales. Experimental studies are also strongly needed. The main challenge is likely to distinguish between causal and non-causal effects, and thus to design experiments to falsify competing predictions. Both for comparative and experimental approaches, progress will largely depend on carefully selecting the measure of parasitism (prevalence, infection intensity, or species richness), the characteristics of the parasites (host specificity and parasite transmission mode), the type of cognitive trait (e.g., innovativeness and social learning), and the type of defensive trait (e.g., innate or acquired immunity) measured. Understanding these causal effects is essential in assessing the role of parasites in the evolution of cognition and, conversely, the role of host cognition in the evolution of both hosts and their parasites. Ultimately, acquiring a better understanding of causal effects in cognition–parasite associations may provide fundamental information on the role played by cognition in zoonoses and disease dynamics.

AUTHOR CONTRIBUTIONS

SD wrote the first draft of the manuscript. All authors contributed to the formulation, writing, and revision of this manuscript, made direct intellectual contributions, and approved its publication.

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MINI REVIEW
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Cognition in Context: Plasticity in Cognitive Performance in Response to Ongoing Environmental Variables

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Cognition has evolved to allow organisms to process, use and store information in their natural environment. Yet, cognitive abilities are traditionally measured in controlled laboratory conditions to obtain consistent and accurate measurements. Consequently, little is known about the actual effect of natural environmental variation on cognitive performances. Being able to modify cognitive performance according to environmental conditions (e.g., plasticity of attentional performances according to current predator densities) could provide evolutionary advantages. In this mini-review, we compile evidence for what we call "cognitive performance plasticity" (i.e., flexible adjustment of cognitive performance in response to the current environment). We then discuss methodological approaches associated with measurement of cognitive performance plasticity and cognition in general. Finally, we discuss the implications of acknowledging plasticity in cognitive performance, including a better understanding of the reproducibility crisis observed in cognitive sciences (Open Science Collaboration, 2015) and new lines of inquiry into the evolution of cognition and the adaptive value of cognitive performance plasticity.

Keywords: cognition, cognitive plasticity, evolution, environment, reaction norm

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WHY CONSIDER CONTEXT IN COGNITIVE SCIENCES?

The recent growing interest of cognitive ecologists in an evolutionary ecology of cognition (Cauchoix and Chaine, 2016; Morand-Ferron et al., 2016; Boogert et al., 2018) and the emergence of environmental psychology (Stern, 2000; Sörqvist, 2016) raises the question of how current social or ecological conditions influence measures of cognitive performance. Whereas the impact of early environmental conditions on the development of cognitive abilities has recently been examined (Ebbesson and Braithwaite, 2012; Buchanan et al., 2013; Murphy et al., 2014; Ashton et al., 2018), we still know little about the effect of ongoing environmental variation on cognitive performance. Indeed, cognitive scientists traditionally conduct tests in controlled laboratory environments with homogenous social and physical contexts (Fize et al., 2011; Roitblat, 2014). By contrast, natural environments where cognitive traits have evolved are complex and dynamic such that cognitive performances recorded in one setting might not describe all possible expressions of the cognitive ability of interest but only its expression in that particular setting (**Figure 1A**).

Laboratory conditions during testing might thus only represent one of many possible environments, or worse, be out of the range of natural environments for a given species (Niemelä and Dingemanse, 2014) such as isolating gregarious species, increasing stress levels by taking individuals in captivity, or removing predation risk for prey species. Consequently, cognitive

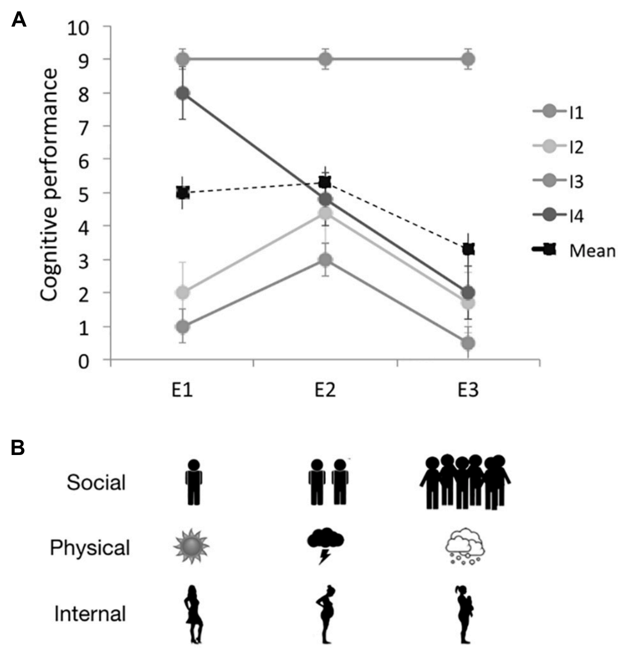

FIGURE 1 | Examples of reaction norms for plasticity in cognitive performance elicited by current environmental factors. **(A)** Cognitive performance from each of four individuals (I1–4) and the population response (Mean) as a function of three different environmental conditions (E1, E2, and E3). Vertical lines represent standard errors across trials on the same individual in the same environment and highlights the need for repeated measurements of cognition for each individual in each environment. If individuals are tested in E2 only, little variation in cognitive performances would be detected among individuals. If a different lab tests individuals in a similar, but not identical environment (e.g., E3), there would be a clear lack of correspondence in results contributing to the reproducibility crisis at both the individual and population levels. **(B)** Examples of environmental factors that might influence cognitive performance including social factors (e.g., number of observers/group size), physical factors (e.g., weather/season) and internal factors (i.e., reproductive status/hormonal state).

performance recorded under such conditions may not reflect cognitive performance expressed in nature (Niemelä and Dingemanse, 2014; McCune et al., 2019; but see Cauchoix et al., 2017). Furthermore, individuals might differ in their response to laboratory testing conditions if, for example, there are individual differences in response to stress (Ebner and Singewald, 2017).

An alternative to highly controlled laboratory settings is to acknowledge that cognitive performance might vary with environmental conditions and to measure and report those variations (i.e., cognitive performance plasticity). Therefore, instead of testing an individual in one standardized condition, we could measure an individual's cognitive performance in different natural (or artificial) conditions (e.g., social vs. non-social, temperature gradient, etc.) to take into account plastic responses at the individual and population levels (Voelkl and Würbel, 2016; Barragan-Jason et al., 2018a; Caza and Atance, 2018). Such an approach would not only enable a more accurate measure of cognitive abilities, teasing out repeatable and plastic components (Dingemanse et al., 2010), but could also help us better understand the adaptive value of plastic cognitive responses. Plasticity in cognitive performance follows the concept of phenotypic plasticity in evolutionary biology which describes how a given genotype expresses different phenotypes under different environmental conditions (Bradshaw, 1965; Pigliucci, 2001; West-Eberhard, 2003). Plasticity in cognitive performance could borrow the conceptual framework from the field of "behavioral plasticity" which refers to the ability to flexibly adjust a behavior in response to environmental variations (e.g., temperature, elevation, etc; Dingemanse et al., 2010) including the notion of "social competence" which refers to the ability to flexibly adjust a behavior to best match a given social context (Taborsky and Oliveira, 2013). We believe that by focusing on plasticity in cognitive performance, rather than trying to limit variation during measurement of cognitive performance, we stand to gain a much richer understanding of cognition as a whole, how it is used in natural environments, and how it evolves under natural selection.

EVIDENCE FOR PLASTICITY IN COGNITIVE PERFORMANCE

A number of different environmental factors could cause shifts in cognitive performance for the same individual or genotype. We provide examples below divided into three broad categories - social context, physical environment, and internal factors - as a first step in synthesizing and then better understanding plasticity in cognitive performance (**Figure 1B**).

The effect of the current *social context* on cognitive performance includes some of the best documented examples of plasticity in cognitive performance (**Figure 1B**). For instance, nine-spined sticklebacks engaged in a social learning task are more likely to copy the foraging choice of the larger of two groups they observe (Pike and Laland, 2010). Indeed, across a broad variety of species from insects to humans, the age, sex, size and social status of demonstrators also influence social learning (Rendell et al., 2011). Similarly, partner characteristics in chimpanzees (Suchak et al., 2018) and the social environment (presence or absence of female observers) in humans (Tognetti et al., 2016; Kelsey et al., 2018) greatly influences performance in cooperative and altruistic tasks. Less intuitively, social context can also modify performance in non-social cognitive tasks. For example, group size (number of individuals present on the site) seems to affect the efficiency of passerines engaged in a problem solving task in the wild (Chabaud et al., 2009; Morand-Ferron and Quinn, 2011) as well as success in a spatial discrimination task (Langley et al., 2018) in pheasants. In human children, the presence of an experimenter in a testing room modulates the expression of self-control (Barragan-Jason et al., 2018b). Similarly, the presence of conspecifics in baboons affects performance in a cognitive control task (Huguet et al., 2014). While most of the above studies contrast groups of individuals placed in each context, the last three (pheasants, children, baboons) specifically tested the same individuals in two different social contexts and clearly demonstrate how current/ongoing environmental variables can modify cognitive performance at the individual level (Huguet et al., 2014; Barragan-Jason et al., 2018b; Langley et al., 2018).

The current *physical environment* can also modulate cognitive performance (**Figure 1B**). Weather, pressure and temperature can affect working memory performance in humans (Keller et al., 2005) and mate choice copying in fruit flies (Dagaeff et al., 2016). Similarly, exposure to extreme environments (e.g., heat, hypoxia, and cold stress) impacts the expression of a number of cognitive functions in humans (Taylor et al., 2015). The emerging field of environmental psychology attests to growing interest in how the environment impacts cognitive performance (Stern, 2000; Sörqvist, 2016). One striking result from this new literature is that in humans, experiencing nature seems to almost instantaneously affect learning performances (Kuo et al., 2019). Changes in the physical environment of an area due to season can likewise influence cognitive performance. Seasonal plasticity in bird brains and in particular in the adult song system has been known for decades (Tramontin and Brenowitz, 2000). Increases in song rate during spring when males need to attract mates and defend territories is supported by important plasticity in neural nuclei involved in song production (Ball et al., 2004). New evidence suggests that brain activity related to executive function (i.e., working memory) tasks is also affected by season in humans (Meyer et al., 2016). Similarly, season modulates attention and spatial performance in african striped mouse (Maille et al., 2015). At a finer time scale, time of day can affect learning and memory performance in rats (Winocur and Hasher, 1999).

Internal factors, such as health, reproductive status, stress, motivation, mood, and hunger among other possibilities could also dramatically affect cognitive performance (**Figure 1B**). The impact of motivation on cognitive performance has been a preoccupation of cognitive scientists for decades (Padmala and Pessoa, 2010; Morand-Ferron et al., 2016;, Cauchard et al., 2017). For example, short-term fasting decreases psychomotor speed and executive functioning in humans (Sansone and Harackiewicz, 2000; Benau et al., 2014). On the contrary, short-term high fat food intake can deteriorate performance of rats in a maze test (Murray et al., 2009). Effects of stress on learning, memory, and cognitive flexibility is also well documented (Roozendaal et al., 2009; Schwabe et al., 2012; Seehagen et al., 2015; Goldfarb et al., 2017). Infection may also affect cognitive performance in humans (Boivin and Giordani, 1993; Kihara et al., 2006), mice (Desruisseaux et al., 2008), and birds (Dunn et al., 2011). Other internal factors such as reproductive status and hormonal levels modify both cognitive performance and neurophysiological activity (**Figure 1B**; Buckwalter et al., 1999; O'Reilly et al., 2004; Amin et al., 2006; Little, 2013; Sundström Poromaa and Gingnell, 2014). Finally, exposure to hazardous chemicals can also have important effects on cognition. For instance, acute exposure to even a low dose of pesticides directly impairs working memory in bees (Samuelson et al., 2016).

It is important to acknowledge that during cognitive testing all these environmental factors, grouped here in social, physical and internal categories, are likely to play a role in cognitive performance (Morand-Ferron et al., 2016). Furthermore, these different factors might also interact and produce different effects on cognition depending on their combination. For instance, the effect of weather on cognition is season dependent in humans (Keller et al., 2005). Positive relationships between higher temperature or barometric pressure (i.e., pleasant weather) on memory (i.e., digit span) modulated by the time spent outdoors only holds during the spring. In fact, the testing environment will always contain a specific value for each environmental category and most if not all combinations are possible. While understanding the simple effects of a given factor should be an initial goal in studies of plasticity in cognitive performance, we can already begin thinking about the more complex experimental designs needed to look for interactive effects of two or more environmental factors on cognitive performance.

METHODS TO MEASURE PLASTICITY IN COGNITIVE PERFORMANCE

In order to understand the causes and consequences of individual differences in cognitive abilities, cognitive ecologists are increasingly interested in measuring cognitive performance of animals directly in their natural environment (**Figure 2A**; Pritchard et al., 2016; Cauchoix et al., 2017; Boogert et al., 2018). Such an approach is ideal to evaluate how natural variation in the environment affects cognitive performance (Morand-Ferron and Quinn, 2011) but it requires a large number of repeated measurements on given individuals across contexts, which is challenging. The development of new technologies for automated and voluntary testing of cognitive abilities on free-ranging animals directly in their natural environment (**Figure 2A**) now allows us to record large numbers of trials for individuals in the wild (Fagot and Bonté, 2010; Gazes et al., 2013; Morand-Ferron et al., 2015; Cauchoix et al., 2017; Sonnenberg et al., 2019), although some bias may still exist in which individuals choose to participate. Moreover, the same kind of RFID (radio frequency identification) testing device (**Figure 2A**) which automatically identifies an individual during testing can be used to measure fine grained social interactions of free ranging birds and infer social structure or dominance hierarchy (Aplin et al., 2012; Evans et al., 2018). Such systems could be coupled with environmental sensors that constantly monitor physical environmental variables ranging from simple meteorological variables to air pollution (Ripoll et al., 2019) or even sensors to monitor individual weight as a proxy for condition (Larios et al., 2013; Hou et al., 2015). Together, these types of data provide us with repeated measures of cognitive performance for given individuals under a broad array of social and environmental settings which can then be used to understand plasticity in cognitive performance using the "behavioural reaction norm" approach (Dingemanse et al., 2010; Morand-Ferron et al., 2016). A similar approach in human cognitive psychology could use real-time tests and environmental sensors on smartphones (Dufau et al., 2011; Harari et al., 2017).

The correlational nature of such measurements in the wild do, however, have some limitations that could be complemented with experiments conducted in the laboratory or large semi-wild enclosures under controlled settings. Measurements of free ranging animals in the wild described above make it difficult to

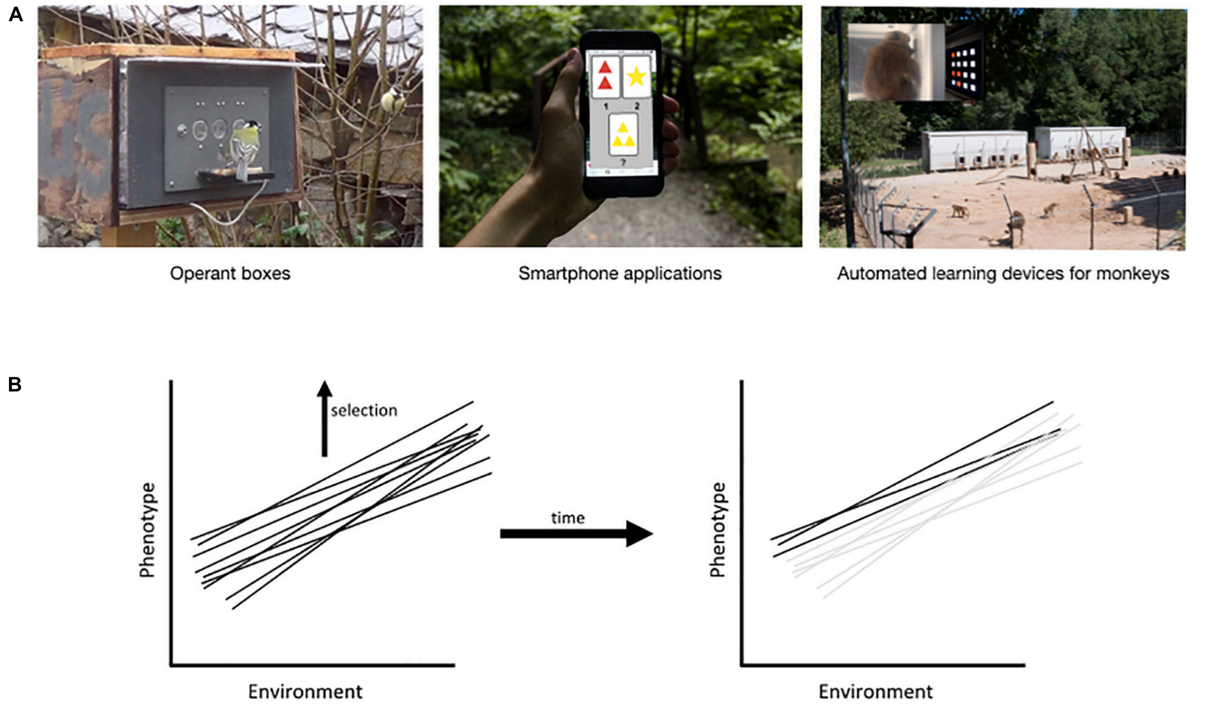

FIGURE 2 | Methods to study plasticity in cognitive performance and its adaptive value (i.e., evolution of reaction norms). **(A)** Automated cognitive testing devices can gather repeated data from the same individual in natural contexts. Examples include operant boxes to study associative and reversal learning in wild birds (Morand-Ferron et al., 2015; Cauchoix et al., 2017), smartphone applications for cognitive tasks (e.g., executive function task), and automated learning devices for monkeys: ALDM (Fagot and Bonté, 2010; Claidière et al., 2017). **(B)** Plasticity can then be described by linear (or non-linear; e.g., **Figure 1A**) reaction norms. Selection can act on phenotypically plastic traits just as with normal traits except that selection will act on the reaction norm rather than a specific trait over the long term. Here we illustrate a population of genotypes that show a plastic expression of the phenotype across different environments (each line), and if selection favors increased values of the phenotype, the reaction norms that produce lower phenotypes will be eliminated over time. Note that selection can act primarily in one environment and therefore on the phenotype expressed in that environment, regardless of expression in other environments. Under such conditions, selection could be less efficient or slower in causing population change. In the case of cognition, the variety of expressions possible for an organism that is frequently in different environments could cause selection to act much more quickly on the shape of the reaction norm rather than exclusively on expression in one environment.

infer causality and may make it impossible to test independent effects of each environmental gradient. In such cases, controlled experiments that manipulate the social, physical or internal environment in the lab, as initially developed for rodent studies in biomedical research (Turner and Burne, 2013), could provide a complementary understanding. Virtual reality (Schoeller et al., 2018) or video playbacks (Snijders et al., 2016; Smit and van Oers, 2019) could provide an ideal tool to document responsiveness of cognitive performance to artificially controlled contexts in the lab. Other methods could include testing the same individual in a few different controlled environments by manipulating physical features (e.g., temperature), ecological features (e.g., predation risk), social context (e.g., group size), or internal state (e.g., hormonal manipulations) in the lab. Such experimental manipulation in the wild may also be possible. For instance, Cauchard et al. (2016) manipulated infection status of nesting great tits to evaluate the impact of parasitism on problem-solving performances. Finally, controlled experiments are the only way to understand how different contexts interact to influence cognitive performance through fully factorial designs crossing multiple levels of each environmental feature. Such experiments are ambitious in scale, but would provide us with a unique understanding of whether each environment has additive effects on cognition or complex non-linear impacts.

In practice, measuring plasticity in cognitive performance implies measuring one cognitive ability (e.g., attention, memory, etc.) in a few different contexts (**Figures 1**, **2B**). Such contexts can be different categories (i.e., in presence or absence of a predator) or contexts that vary quantitatively in a specific dimension (e.g., temperature, group size; **Figure 1B**). Sample sizes depend on the goals of the project, but linear descriptions of plasticity, called reaction norms (Dingemanse et al., 2010), require multiple measures of each individual in each testing environment, which can be a challenge (Martin et al., 2011). For example, a study including 3 environments might ideally have 3 or more measures for each individual in each environment to control for the effects of noise or measurement error, implying more than 9 tests per individual. Such standards might be possible to reach for cognitive tasks in which individuals usually go through a high number of trials (Fagot and Bonté, 2010; Morand-Ferron et al., 2015) and often perform successive cognitive tasks (Cauchoix et al., 2017). Data from either observational or experimental approaches can then be analyzed much like behavioral plasticity using a mixed-model approach borrowed from quantitative genetics to partition phenotypic variation into its between-individual and within-individuals components (Dingemanse et al., 2010; Dingemanse and Dochtermann, 2013). This so called 'behavioral reaction norm' approach allows us to disentangle measures of individual consistency (personality or repeatability) and responsiveness to the environment (plasticity; **Figures 1A**, **2B**). We recently used this approach to document the repeatability of individual differences in cognitive performances (Cauchoix et al., 2018) but it has not been applied yet to document plasticity in cognitive performance within a population. A powerful feature of this approach is that inclusion of a random slope in the mixed model allows individuals to vary differently according to environmental conditions which generates a description of plasticity for each individual (**Figure 1A**). The slope or shape of these individual reaction norms provides us with a trait - plasticity in cognitive performance - that can then be related to other features such as success later in life (**Figure 2B**; for a discussion of the benefits and challenges of this approach, see Houslay and Wilson, 2017).

IMPLICATIONS AND FUTURE DIRECTIONS

If plasticity in cognitive performance is more than just noise as we have argued here, then directly studying it could provide new insight into past findings and would open whole new lines of research in cognitive sciences and cognitive ecology. For example, plasticity in cognitive performance could help resolve the reproducibility crisis in psychological sciences through an understanding of environmental variables that might generate differences between studies (Van Bavel et al., 2016; Voelkl and Würbel, 2016). Indeed, although recent studies report that some factors including contextual sensitivity (i.e., variations in time, culture and location) influence reproducibility, the effect of many other environmental factors on cognitive performance still need to be tested (Voelkl and Würbel, 2016). In addition, we still do not know how often cognitive performance is actually sensitive to the environment (i.e., plastic), if some cognitive abilities are more sensitive than others, and to what degree individuals vary in cognitive performance plasticity. While direct study of this phenomena would be ideal, systematically recording and reporting environmental variables in cognitives studies would enable future meta-analyses to answer such questions on a large scale.

If such plasticity is common, as we believe it is, there are important implications for the evolution of cognition. There is now a growing interest in linking individual variation in cognitive performance to fitness in wild non-human populations (Boogert et al., 2018), but plasticity in cognitive performance would modify our view of how selection acts on cognitive traits. Under what social and ecological conditions do we expect to see the evolution of plastic cognitive performance rather than fixed, invariant performance? The degree of plasticity in a population depends primarily on how stable the environment is and whether there are reliable cues to make plastic adjustment advantageous (Pigliucci, 2005). Variable environments with predictable cues to trigger plastic expression will favor high plasticity whereas stable environments or a lack of reliable cues will favor fixed phenotypic expression. Similarly, we might expect that the benefits of plastic modification of cognitive performance will depend on natural environmental variation which make it adaptive or maladaptive (Greggor et al., 2019). For instance, being able to modify attentional performance according to level of predation risk that can vary among seasons, time of day, and foraging areas, would enable an individual to allocate more time to feeding rather than vigilance (Lima and Bednekoff, 1999).

Furthermore, selection on plastic cognitive performance would act on reaction norms (**Figure 2B**) rather than the mean trait which can have important implications for evolutionary trajectories (Price et al., 2003; Duckworth, 2009). A stable environment will lead to low plasticity since selection will act on expression in one environment rather than the whole reaction norm which can lead to canalization of the trait in the long term. However, if the environment is naturally variable, then plasticity can be preserved as selection acts on different expressions of the phenotype in each environment and therefore on the shape of reaction norms rather than the mean. Likewise, plasticity will be preserved only if shifting the phenotypic expression provides a good match to the given environment and this match depends critically on reliable environmental cues to generate the correct phenotypic expression. These considerations will have important consequences for the role that cognition plays in adaptation to new environments including both colonization and climate change (Chevin et al., 2010; Chevin and Hoffmann, 2017). If the prior environment was variable, there might be sufficient plasticity to allow a decent fit to the new environment if the environmental cues triggering phenotypic expression are still appropriate (Lyon et al., 2008). In this case, plasticity could buffer against the negative effects of a new environment relative to a fixed phenotype, but will also mean the population takes longer to adapt to that new environment since selection on a reaction norm is generally thought to be weaker (Forsman, 2015).

Ignoring plasticity in cognition also carries costs such as concluding that there is low within population variation in cognitive performance (E2 in **Figure 1A**) or incorrectly describing evolutionary dynamics on plastic traits (Chaine and Lyon, 2008). In contrast, adopting a plasticity perspective adds complexities to experimental protocols, but has no influence on interpretation when traits are fixed. Given the potential for new insights into both cognition and ecology, we believe that a shift in perspective to plastic rather than fixed cognitive performance is critical.

AUTHOR CONTRIBUTIONS

All authors have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Avian Egg Timers: Female Cowbirds Judge Past, Present, and Future When Making Nest Parasitism Decisions

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The cognitive demands associated with brood parasitism are substantial. Not only must female parasites locate nests and assess their suitability for parasitism, they must also time parasitism to correspond with the breeding behavior of the host. Keeping track of the reproductive state of hosts for a variety of nests allows the parasite to select a nest where their egg can be incubated successfully. Thus, nest selection decisions are integral to obligate brood parasites' reproductive success. In captive breeding flocks of brown-headed cowbirds (*Molothrus ater*), I provided females access to mock nests that varied in the number of eggs present. By changing the number of eggs added to nests across days, I studied (1) females' abilities to time a host nest's readiness for parasitism and (2) the timing of females' nest selection decisions. I found that cowbirds can attend to the amount of time that elapsed since a host egg was added to a nest and can use that information to choose a nest for parasitism. Females made their choice of nest during prospecting the day before they laid, and, once decided, they did not update their decisions on the day of laying. Taken together, the results reveal that female cowbirds process substantial amounts of information about location, time, number, and rate in order to plan for future parasitism. This research program reveals that species-typical decisions integrate a variety of general and specialized cognitive abilities to allow females to behave adaptively and maximize reproductive success.

Keywords: cowbird, cognition, timing, nest parasitism, egg laying

INTRODUCTION

Understanding the animal mind has been of keen interest to researchers and laypeople for centuries (Dewsbury, 1989; Shettleworth, 2010). Research into how animals acquire, process and act on information has come in fits and starts across this time; there have been decades of tremendous interest and others of complete disregard. Currently, due to renewed interest from both biologists and psychologists working in the lab and field, and integrating function with the underlying mechanisms controlling decision processes, advances are being made in our understanding of animal cognition at a pace unmatched in the past (Bouton, 2007; Pearce, 2008).

Functional perspectives into cognition consider the information processing skills that animals possess to be specialized adaptations, evolved to deal with species-specific ecological demands (Sherry and Schacter, 1987). For example, the requirements to remember locations associated with habitats, mates, or stored food could lead to the evolution of enhanced spatial memory abilities (Sherry, 1982; Smulders et al., 2010), or the needs to navigate social hierarchies might produce new skills like transitive inference (Bond et al., 2003; Paz-y-Mino et al., 2004; Maclean et al., 2008). One of the critical implications of this perspective is that cognitive performance in real-world tasks is under selection pressure, and thus heritable variation in cognitive performance must relate in some manner to fitness. Thus, work under this perspective is often done examining species-typical behavior in the animals' natural habitat. And, while the connection between cognition and fitness is only starting to be discovered in some animal systems (see Sol et al., 2005; Cole et al., 2012; Cauchard et al., 2017; and other articles in this special issue) the evolutionary perspective provides a powerful organizing perspective.

Mechanistic perspectives approach animal cognition with less interest in ecology or evolution, and instead use a few animal species that are well suited for the laboratory as model systems for studying learning, behavior, perception, and action in order to shed light on universal aspects of cognition. Thus, even though both perspectives examine cognition, functional perspectives tend to focus on specializations while mechanistic perspectives tend to focus on domain-general processes (Heyes, 2012). These approaches need not be in conflict, however, it is possible for both specialized and general mechanisms to exist and interact. For example, there could be general aspects of problem-solving that can be coopted and enhanced by a specific ecological demand (Sherry and Schacter, 1987; Sherry, 2006). Tracking time, for example, is a general ability ubiquitous to animals, but for some species, certain ecological demands may enhance and specialize the ability to remember elapsed time or track it more precisely.

Another point of conflict between Psychologists and Biologists is methodological. Psychologists often explicitly avoided the examination of behaviors that relate to reproductive success. For example, the study of spatial memory in rodents is often measured using behavioral tests that are foreign to the activities of the animal, for example using computerized touch screens or water-mazes (Choi et al., 2006; Bussey et al., 2008). The argument against studying species-specific behavior found in the animal's repertoire is that such behavior might be under control of some sort of simple "instinctive" tendency, and thus such behavior is lacking in generalizability to other species (e.g., Domjan, 2010). It is, however, a mistake to think about species-specific behavior as simple instinctive reflexes. The biological validity of the instinct concept itself is severely limited (Lehrman, 1953), and merely because a behavior may be specific to a species does not therefore mean there is no underlying complexity in the cognitive processes that control it. Indeed, behaviors that relate directly to reproductive success would be most subject to selection, potentially leading to the evolution of complex levels of information processing.

My students and I have been studying the decision processes involved in selecting nests for parasitism by female brown-headed cowbirds (White, 2019). We use a procedure and a theoretical perspective that integrates both adaptationist and psychological perspectives to understand the cognitive abilities female cowbirds possess that allow them to select a viable nest in which to lay their eggs and for their young to develop to independence.

Finding and selecting a nest is critical for a parasite's reproductive success. Classic work has shown that female cowbirds have enhanced spatial memory skills compared to closely related non-brood parasites, or to conspecific males (Guigueno et al., 2015) and this is reflected in the neuroanatamy of hippocampus (Sherry et al., 1993), an area of the brain considered critical for spatial memory abilities. Beyond having the ability to find and remember the locations of nests, cowbirds are also sensitive to a remarkable number of features of hosts that relate to the chances that their offspring successfully fledge the nest. For example, cowbirds attend to the characteristics of the nest, the type and quality of the host, and the existing offspring (Clotfelter, 1998; Banks and Martin, 2001; Hauber, 2001; Grant and Sealy, 2002; Hauber et al., 2002; Hoover and Robinson, 2007; Louder et al., 2014, 2015; Swan et al., 2015).

Research from the wild, tracking individuals of closely related cowbird species, provides evidence that cowbirds are consistently monitoring nests over time to assess host defenses, host parenting abilities, and hosts' readiness for incubation (Fiorini and Reboreda, 2006; Gloag et al., 2013; Fiorini et al., 2014; Scardamaglia et al., 2016). Acquiring, prioritizing, and recalling this diverse information when selecting a nest can create a significant cognitive load and we have found natural variation among females in their ability to make these decisions effectively (Davies and White, 2018). Since these decisions relate directly to reproductive success, these cognitive abilities can be subject to selection pressure.

We study wild-caught cowbirds in large outdoor aviaries where they live and breed in patterns similar to the wild (Rothstein et al., 1986). These conditions allow us to examine female cowbirds' prospecting and egg-laying patterns while controlling information about the quality of nests. We do not provide actual hosts in our conditions but we have found that by manipulating the number, size, and visual characteristics of mock eggs in mock nests in the aviaries, we can change female cowbirds' nest selection preferences and manipulate the cognitive challenges associated with choosing the highest quality nest (White et al., 2007, 2009, 2017).

Our most frequently used manipulation involves changing the number of eggs in nests (White et al., 2007, 2009). We have found that cowbirds have distinct preferences for nests containing different numbers of eggs. Overall, all other factors being equal, females prefer nests containing more eggs to nests containing fewer eggs (at least in the range of 0–3 eggs; White et al., 2007). But much more important to females is whether nests change in egg number over time (White et al., 2009). Nests that increase in egg number from the day before are vastly preferred to nests that do not change from 1 day to the next. We have interpreted these findings as a mechanism that allows females to time their parasitism effectively, because hosts typically lay one egg each day until their entire clutch is laid. It is at that point that they commence incubation. Development starts with incubation and thus a nest where incubation has begun can be a bad place for a parasite's egg, as this late egg would be at a developmental disadvantage and could potentially not even hatch. Keeping track of the timing of egg laying by the host would be one means by which a cowbird could avoid the dangers associated with laying in a nest too late. To do so, however, requires the cowbird to attend to and process substantial amounts of information, including information about space, number, and time and using information about personal experiences to guide behavior, so-called what-where-when, or episodic-like memory (Clayton and Dickinson, 1998; Griffiths et al., 1999; Hampton and Schwartz, 2004).

Animals represent time in different ways, from evaluating very short timescales, to days, months and years (Gallistel, 1989; Dibner et al., 2010). We have conducted several studies in which we have given female cowbirds the opportunity to track nests that change or do not change across days (White et al., 2009). In these experiments, females preferred to inspect and preferred to lay in nests that changed in egg number corresponding to the number of days that had elapsed. We have never explicitly tested females' ability to track time in these experiments, however. Females could have performed these experiments merely by using numerical abilities and showing preferences for nests that change more than any other nest. In the first experiment here, I keep changes in egg number constant across nests and vary only the amount of time that had elapsed from one visit to another to assess whether females are indeed using time as part of parasitism decisions.

Not only is the timing of the hosts' reproductive behavior important, but it is also important for the cowbird to time her nest selection decision appropriately so that the host and parasite's reproduction are synchronized. Cowbirds typically lay at first light then spend the rest of the day investigating other nests (Friedmann, 1929). While we have found that the time females spend investigating a nest the day before laying relates to the likelihood of that female actually laying in the nest the next day (White et al., 2009, 2017; unpublished observations), it has not been explicitly tested whether females are actually choosing a nest on the prospecting day, or instead selecting a nest the morning of laying. If they are making the decision in advance in order to plan for their future egg laying (sensu Raby et al., 2007), then this is yet more information that must be processed when selecting a nest. Cowbirds may need to maintain a cognitive map of nest options at different stages of readiness so that they can respond selectively when ready to lay. In experiment 2, I change nest characteristics at different times between the prospecting day and the egg laying day to determine the timing of the nest selection decision.

MATERIALS AND METHODS

Experiment 1: Timing Host Behavior

I examined whether female cowbirds were sensitive to the amount of time that has elapsed since they had examined a nest and whether they could use information about time and the number of host eggs encountered to select a nest for parasitism.

Subjects

Twelve wild-caught female cowbirds served as subjects for this experiment. These females were wild caught in Montgomery County PA as adults (i.e., they had experienced at least one breeding season in the wild in 2010–2011) and had been living in aviaries for at least 1 year prior to the experiment. Each female wore individually distinct combinations of colored leg bands to permit identification. Prior to experimentation, birds were housed with other females and with males in large outdoor 18 × 6 × 4 m aviaries.

For testing, birds were removed from their home aviary at the beginning of the breeding season (May 1–June 30, 2012) and housed in 4.26 × 1.67 × 2.13 m outdoor flight cages. The flight cages were divided into a holding area and a testing area by a wire mesh barrier (**Figure 1**). The test area could also be divided in half with a removable hardware cloth barrier which was used during the pretest phases (see below). The main dividing barrier between holding and test areas had two 12 × 12 cm doors in the top corners that could be opened or closed externally from the cage to allow females to enter either side of the testing area.

The cage was outdoors. It had a grass floor and a variety of perches throughout. The holding area contained food, a roof shelter, and water. The test area also contained perches as well as two mock canary nests that contained grass and white Plaster of Paris mock eggs created from casts of cowbird eggs. Each egg had a plastic-coated paperclip affixed into its base so that it could be anchored into the nest and thus would not allow the cowbird to remove it. The number of eggs in the nests varied depending on experiment and day (see below). Nests were affixed to the side of the flight cage approximately 1 meter from the bottom of the cage. Each nest was covered such that females had to perch immediately in front of the nest and peer into it to examine the contents of the nest.

Procedure

Experiment 1a (see **Table 1**). Two days prior to the beginning of the experiment (Pretest day1), the door separating the holding area and one side of the test area was opened allowing a single female to enter. On this day, the female would find a nest containing two eggs. After 15 min elapsed from the time she first put her head into the opening of the nest, she was encouraged to fly back into the holding area and the door was closed. She remained in the holding area for the rest of the day. Only one female was housed in the flight cage for any given trial, but after

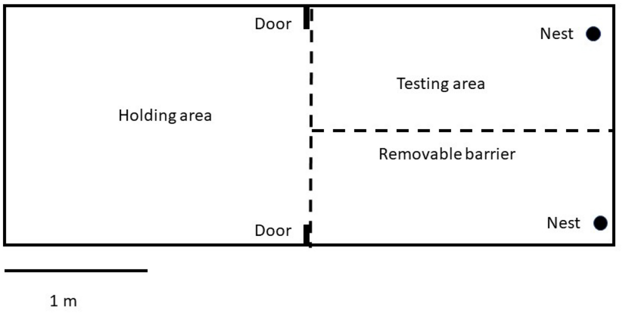

FIGURE 1 | Scale representation of the testing apparatus for experiments 1A–C.

TABLE 1 | Outline of egg numbers in experimental manipulations.

	Day			
	1	2	3	4
Experiment 1A				
Pretest1	2		3	
Pretest 2		2	**3**	
Experiment 1B				
Pretest 1	0			**3**
Pretest 2		2		3
Experiment 1C				
Pretest 1	2		4	
Pretest 2		2	3	

Numbers of eggs in each of the two nests in each of the 3 or 4 days of experiments 1A-C. Bold indicates where there were significant preferences on the test day.

testing, groups of 6 females were housed together in the holding areas for the night.

The next day (Pretest day 2), she entered the other side of the testing area and encountered a nest also with two eggs in it. Again, after 15 min starting when she investigated one nest, she was returned to the holding area for the rest of the day.

On day 3 (Test day), she again could enter the testing area but now there was no barrier separating the two halves and she was given 15 min to spend time investigating the same two nests that she encountered on the two pretest days. During the test, however, both nests contained three eggs. Thus, both nests had increased by one egg, but the Pretest1 nest increased by one egg with 2 days elapsing, whereas the Pretest2 nest increased by one egg with only 1 day elapsing. I tested the 12 females in this experiment counterbalancing the sides they entered in the two pretest days. One female did not visit nests during the pretest days. She was removed from testing.

Statistical Analysis

I measured the amount of time females spent on the two nests on the test day. While it would be preferable to measure actual egg laying patterns from the subjects to definitively determine their preferences, female egg laying in these flight cages can be so unpredictable that it would be impossible to run the experiments in reasonable time. Fortunately, we have found in past experiments that the preference to spend time on a nest when prospecting reflects females' preference for laying in that nest (White et al., 2007, 2009, 2017; unpublished observations). Thus, we used time females spend on nests when prospecting as an assay of their preferences to lay in those nests. Time spent on the two nests were compared within-females using paired sample t-tests using SPSS software. All tests were two-tailed.

Experiment 1b and 1c: Controlling for a Recency Bias

I conducted two control experiments to assess whether females might be simply showing a preference for a nest they had visited more recently in the past. I used the same 12 females and the same apparatus in these two experiments with a similar procedure as the first experiment (see **Table 1**). In experiment 1b, females encountered an empty nest on Pretest day 1 and a two-egg nest on Pretest day 2. There was an extra delay day added between Pretest day 2 and the Test day during which females remained in the holding area. On the test day, females again encountered the two nests, and similar to experiment 1, each nest contained three eggs. Thus, the nest from Pretest day 1 had increased by three eggs across 3 days and the nest seen on pretest day 2 increased by one egg across 2 days. If females were merely spending more time on the nest they had encountered more recently, then they should spend more time on the pretest day 2 nest. If, however, they were attending to the nest that had increased in egg number in the same ratio as days elapsed, then they should prefer the Pretest1 nest.

In experiment 1c, I kept the rate of change consistent across the two nests (see **Table 1**). The Pretest1 nest contained 2 eggs on day one, the Pretest 2 nest contained 2 eggs on day 2. One day elapsed before the Test day. On the Test day, females observed Pretest1 nests now contained 4 eggs and Pretest2 nests now contained 3 eggs. Thus, both nests increased by one egg per day since they had encountered them. If females preferred the nest they most recently encountered, they would prefer the pretest 2 nest. If they preferred nests with more eggs to fewer, they would prefer the Pretest1 nest, and if they preferred nests that changed commensurate with the number of days that had elapsed, then they should show no preference.

Experiment 2. Timing of the Parasitism Decision

The results of past work have revealed that female cowbirds are sensitive to the timing of eggs being laid by hosts (White et al., 2007, 2009). We have measured this both using females' prospecting patterns as well as their actual propensity to lay in nests in aviaries. We have never conclusively tested, however, whether females were actually making nest selection decisions during prospecting. Given that they would not be laying an egg until at least the next day, if they were making decisions on the prospecting day, they would be effectively planning for their future parasitism behavior. This form of 'mental time travel' represents an ability that many have considered to be an ability that few non-human animals possess (Tulving, 2002). An ability to do so nevertheless would suggest that part of the decision process females make involves a coordination between their own reproductive behavior and that of the hosts. Indeed, it would be difficult to account for the impressive abilities of female cowbirds in the wild to keep track of nests without such an ability (Fiorini and Reboreda, 2006; Gloag et al., 2013; Fiorini et al., 2014; Swan et al., 2015; Scardamaglia et al., 2016).

While we had never tested the timing of the parasitism decision in the past, some conundrums in egg laying patterns found over the years have suggested that the decision may indeed be made the day before laying. Two particular patterns have defied explanation until now. First, early in testing egg laying patterns in aviaries, I had not yet implemented the paperclip in the mock eggs to affix them into nests. It was often the case that in the mornings of egg collection, females would remove some of the mock eggs from the nests prior to other females laying. These other females, however, were still able to do the experiments effectively; they laid in the nests that followed their prospecting patterns from the day before. It was as if they were no longer sensitive to the number of eggs in nests on laying day.

Second, we had found that when nests are experimentally parasitized with a mock cowbird egg (a speckled egg added to a clutch of white eggs), females show very strong aversions to prospect or lay in the nests. When given a choice to lay in experimentally parasitized or non-parasitized nests, as many as 90% of eggs were laid in non-parasitized nests (White et al., 2007). Cowbird young are very aggressive at begging for food and thus a nest already containing a cowbird baby would be a very competitive nest for another cowbird, thus it makes sense to avoid such a nest (Kilner et al., 2004). This aversion, however, is so strong, with so many females avoiding experimentally parasitized nests, that routinely multiple females in an aviary will lay in the same non-parasitized nests. While this makes sense for the first female, all subsequent females are effectively laying in already-parasitized nests. Again, it is as if females do not attend to the characteristics of the nests in the morning when laying.

In experiment 2, during the breeding season of 2013 (May 4–June 10), I made a number of manipulations to nests in aviaries at different times to document the time at which females made their nest selection decisions. To do so, I set out twelve nests in each of six outdoor aviaries containing six to eight adult female and six to eight male cowbirds in the breeding season. All nests contained three white mock eggs affixed with paperclips to the nests. In a series of manipulations across days I experimentally parasitized half of the nests (P nests) in each aviary by removing one of the white eggs and replacing it with a speckled egg. To control for manipulating the nests, I removed a white egg from the non-parasitized nests (NonP nests) as well and replaced it with a new white egg. I varied the time at which I parasitized the nests such that females could examine the presence of the specked egg either during prospecting the day before laying, or only during the morning of laying. The different routines of experimental parasitism were as follows:

Trial 1: Parasitism occurred at 11:00 a.m. of the prospecting day (the day before egg collection).
Trial 2: Parasitism occurred at 11:00 p.m. of prospecting day (the night before egg collection).
Trial 3: Parasitism occurred at 11:00 a.m. of prospecting day. All eggs were then removed at 11:00 pm.
Trial 4: Parasitism occurred at 11:00 a.m. Parasitized eggs were then swapped at 11:00 p.m. such that the parasitized nests from the prospecting day became non-parasitized on the laying day and vice versa.
Trail 5: All nests were completely empty until 11:00 p.m., then half were filled as non-parasitized and half were filled as parasitized.

I collected all eggs laid in the aviaries between 5:30 and 7:00 a.m. each morning of the laying day and used the number of eggs laid in each type of nest as a measure of nest type preference for each of the trials. Because in each trial half the nests were experimentally parasitized and half were not, I calculated two-tailed binomial probabilities for the number of eggs laid in Non parasitized nests based on a null hypothesis of $p = 0.5$. Importantly if any nests were parasitized multiply, I only counted the first egg for data collection purposes because it was unclear whether other cowbird eggs in the nest in the morning would be a factor influencing subsequent females. There were too few cases of multiple parasitism over the course of this experiment (4 eggs total) to examine this question.

RESULTS

Experiment 1a: Females spent 1.77 (±0.65) min investigating the nest on Pretest day 1, and 1.62 (±0.39) min investigating the nest on Pretest day 2 [paired samples *t*-test $t(10) = 0.25$, NS]. On the test day, females showed a significant preference to investigate the Pretest2 nest (the nest that had increased by one egg after 1 day of delay) compared to the Pretest1 nest (the nest that had increased by one egg after 2 days of delay). Mean min spent on Pretest1 nest: 1.12 (±0.32) min, Pretest2 nest: 2.30 (±0.53) min; paired samples $t(10) = 3.16$, $P < 0.01$ (**Figure 2**). This manipulation revealed that when females had information only about time elapsed (because equal numbers of eggs were added to two nests) they selected the nest where the number of eggs added corresponded to the number of days that had elapsed since prospecting. This result is consistent with experiments where we kept time consistent but changed the number of eggs encountered in the nests (White et al., 2009).

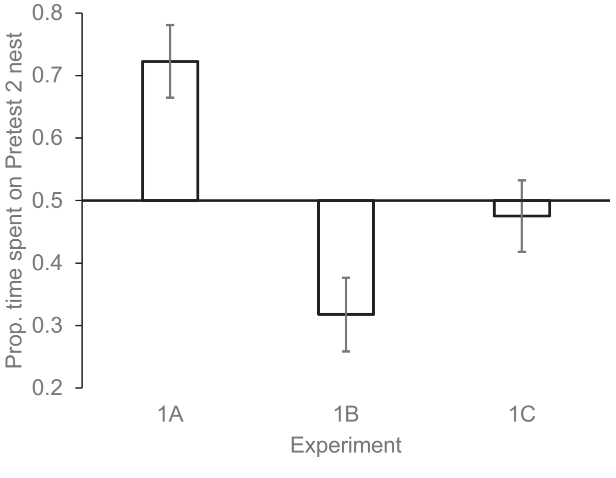

FIGURE 2 | Mean (±1 SEM) proportion of nest visiting time females spent investigating the Pretest2 nest (the nest encountered on the second pretest day) in each of the three phases of experiment 1. Experiment 1A: Pretest2 nest had higher rate of change (eggs being added across days) than the Pretest1 nest. Experiment 1B: the Pretest1 nest had a higher rate of change than the Pretest2 nest. Experiment 1C: The two nests changed at equal rates. *N* = 11 females, in 1A, 9 females in 1B, 12 females in 1C.

Experiment 1b: Three females failed to investigate at least one nest during the pretest phase. They were removed from testing. Females spent 1.13 (±0.11) min investigating the Pretest1 nest and 1.27 (±0.71) min investigating the Pretest2 nest during the pretest phases (paired samples *t*-test $t(8) = 0.34$, NS).

On the Test day, females spent significantly more time on Pretest1 nest compared to the nest that had more recently been investigated (Pretest2). Mean min spent on Pretest1 nest: 1.64 (±0.31) min, Pretest2 nest: 0.91 (±0.33) min; paired samples $t(8) = 2.55$, $P < 0.05$ (**Figure 2**).

Experiment 1c: All females investigated nests in this experiment. They spent 1.01 (±0.09) min investigating the Pretest1 nest, and 0.94 (±0.14) min investigating the pretest2 nest during pretest days [paired samples *t*-test $t(11) = 0.12$, NS].

On the Test day, females did not show a significant preference to spend more time on one nest vs. the other. Mean time spent on Pretest1 nest: 1.52 (±0.32) min, Pretest2 nest: 1.39 (±0.31) min; paired samples *t*-test $t(11) = 0.52$, NS (**Figure 2**). The two control experiments revealed that females preferred nests where the same number of eggs had been added as days had elapsed since their first visit and showed no strong preference for a nest if both nests had changed in egg numbers from their last visit. These conditions demonstrated that the effect in experiment 1a was not a function of a recency bias in nest encounters from past days.

Experiment 2

Trial 1: Females showed a strong aversion to lay in experimentally parasitized nests when the speckled egg was added in the morning of the prospecting day. Eggs laid in NonP nests/total eggs = 16/18, Binomial test probability, $p = 0.002$ (**Figure 3**).

Trial 2: When experimental parasitism occurred at night and thus there was no opportunity to see where parasitism occurred prior to the laying day, females showed no aversion to lay in parasitized nests: Eggs laid in NonP nests/total eggs = 13/23 Binomial test probability, $p = 0.678$.

Trial 3: When nests were emptied at night such that there was information gained during prospecting day, but no egg information present on laying day, females laid in the nests that were NonP on prospecting day. Eggs laid in NonP nests/total eggs = 11/13, Binomial test probability, $p = 0.022$.

Trial 4: When the nests that were parasitized on prospecting day were reversed at night, such that they became non-parasitized on laying day, females showed an aversion to the nests that had been parasitized on prospecting day, not the nests parasitized on laying day. Eggs laid in NonP (laying day)/total eggs = 4/18. Binomial test probability, $p = 0.031$.

Trial 5: When nests were empty until the night of prospecting day, and then half the nests were parasitized for laying day, females showed no aversion to the parasitized nests. Eggs laid in NonP nests/total eggs = 6/10. Binomial test probability, $p = 0.754$. Taken together, this series of trials reveals strong evidence to suggest that the nest selection decision is made the day before laying and is remarkably resistant to change afterward; even when there is conflicting (Trial 4), or no valuable information (Trial 5) on prospecting day. Females do not use information from laying day to inform their nest selection decisions.

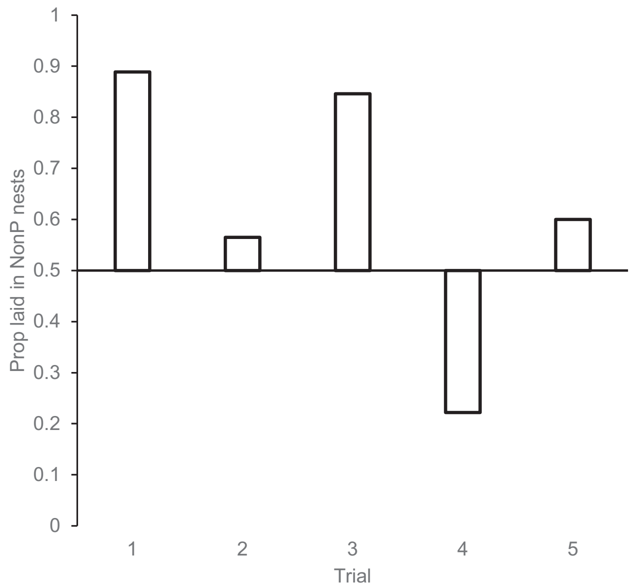

FIGURE 3 | Proportion of eggs laid in nests that had not been experimentally parasitized the day (or night) before for each of the trials in experiment 2. Trial 1: Experimental parasitism occurred during prospecting day. Trial 2: Experimental parasitism occurred at night after prospecting. Trial 3: Experimental parasitism occurred during prospecting day; all eggs removed that night. Trial 4: Experimental parasitism occurred during prospecting day; all nests were reversed in condition that night. Trial 5. All nests were empty until after prospecting day.

DISCUSSION

The results of these experiments provide two new insights into the nest prospecting decision processes of female brown-headed cowbirds. First, females have an ability to track time elapsed between nest visits and use this information in concert with numerical information- egg number changes- to measure the rate of eggs added to nests. They then can compare rates of change across nests to select the nest where the rate of eggs added corresponds with, or at least is not less than, the number of days that had elapsed since first encountering the nests. Second, experiment 2 reveals compelling evidence that females are assessing nests and deciding on the nest best suited for parasitism during the prospecting day prior to egg laying. They are, in effect planning for the future (Suddendorf and Corballis, 1997; Raby et al., 2007).

Timing Hosts

We have found very reliable effects across numerous experiments showing female cowbirds track how nests change in egg number across time as a cue to select a nest for parasitism (White et al., 2007, 2009, 2017). The current experiments for the first time directly reveal that cowbirds use the time elapsed between nest visits to assess rates of egg laying. Prior to this work, a simpler mechanism could have accounted for the effects involving females selecting nests where the most eggs were added. This hypothesis is refuted by experiment 1, where both nests increased by the same amount but not at the same rate. The patterns in experiment one could not be explained by a simpler mechanism of just preferring the most recently encountered nest (see also White et al., 2009), though the possibility remains that females use a variety of different decision heuristics such that they weigh different types of information in each circumstance in which I placed them.

These findings provide numerous possibilities for future study of both the functional and mechanistic processes involved in the cognitive processes of timing. From the functional perspective, the cognitive demands associated with tracking the rates of change of eggs in numerous nests, in the wild, comparing among them, integrating this information with the other important characteristics of hosts and nests all to choose one nest would be a remarkable cognitive load. The relationship between variation in these abilities and reproductive success is currently under study (Davies and White, 2018). These patterns seen in the lab with numerous variables controlled and removed, do fit with findings in the wild where cowbirds of closely related species consistently visit nests to synchronize breeding patterns with hosts (Fiorini and Reboreda, 2006; Swan et al., 2015).

From a mechanistic perspective, it could be that tracking time, space, and number – aspects of cognition ubiquitous to animals that are essential in a wide variety of contexts (Davis and Perusse, 1988; Gallistel, 1989; Clayton and Dickinson, 1998; Brannon, 2006) may be specialized in cowbirds, allowing them to be more sensitive to representations of time and number or to remember them longer. How they keep track of the amount of time elapsed is an important future question, as it does seem the delays they could deal with in experiments 1 and 2 are longer than what most animals can attend and remember in lab-based delay interval experiments (Domjan, 2010). This offers many lab-based possibilities for testing stimulus control of behavior and to investigate the underlying neural processes that may govern these abilities.

Timing of Decisions

Results of experiment 2 suggest that information acquired and processed about nests during prospecting time is fundamentally different than during laying time. Females appeared incapable of updating their decision processes in the morning of egg laying, even when information was lacking during prospecting. Cowbirds lay at first light and can enter a nest and lay an egg in as little as one second. Perhaps the demands associated with cryptically getting in and depositing their egg so quickly is so important (Friedmann, 1963), selection actually favors ignoring nest contents when laying. This is another pattern of prospecting that appears in the wild in closely related cowbird species (Scardamaglia et al., 2016).

We are now using radio frequency identification on nests in order to investigate every prospecting event females make so that we can track in real time how they investigate nests, whether different females use different strategies, whether females who are going to lay the next day prospect differently than females who are not going to lay that day, and whether highly fecund females prospect differently than less fecund females.

Ecology and Evolution of Cognition

Taken together, these experiments on the decision processes associated with nest selection provide an integration of biological and psychological traditions. We study a species-specific natural behavior that requires no training or reinforcement and is directly connected to reproductive success. While we do still use a laboratory environment for testing, and it necessarily removes a wide variety of the important variables that are undoubtedly important in the cowbirds' nests selection decisions (most notably the behavior of hosts), we do provide them the stimuli necessary to court, breed and lay eggs. This allows us to maintain a high degree of control over stimulus presentations and prior experiences. This approach has provided us insights into many different aspects of the form and function of cognition in nature.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the Institutional Animal Care and Use Committee of the University of Pennsylvania (#800439), and the Animal Care Committee of Wilfrid Laurier University (#17000).

AUTHOR CONTRIBUTIONS

DW conducted all research and wrote the manuscript.

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Can Cognitive Ability Give Invasive Species the Means to Succeed? A Review of the Evidence

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Invasive species are a global conservation problem that have an enormous economic cost. Understanding the attributes of invasive species and what makes them successful at colonizing and flourishing in novel environments is therefore essential for preventing and ameliorating their negative impact. Learning ability and behavioral flexibility—the ability to adjust behavior flexibly when conditions change including to learn to solve novel problems or existing problems in a novel way, are thought to play a key role during invasions although cognitive ability is rarely considered in studies of invasive species. We begin by reviewing the evidence that flexible learning and problem solving can influence invasion success in both invertebrates and vertebrates. We also review brain size as an index of cognitive ability with respect to invasion success. We then focus on the specific attributes of cognition that are likely to be important for species entering novel environments as they learn the location of resources (e.g., food, shelter), and as they encounter and interact with conspecifics, heterospecifics, and potential predators. We suggest that enhanced spatial learning ability in conjunction with behavioral flexibility are likely to be adaptive. Furthermore, good memory retention and the ability to learn from others (both conspecifics and heterospecifics) are beneficial. Finally, we suggest future directions for studying the link between cognition, fitness, and invasion success. Studies of closely related "invasive" and "non-invasive" species, as well as invasive populations and their source, should provide important baseline information about the potential role of cognitive ability in determining invasion success. We also advocate an experimental approach. In particular, we borrow methods from experimental evolutionary ecology. We suggest that experimental studies in which potential invasive species can be assayed for behavior and their cognitive ability measured prior to population-level release on small islands will help inform us about the potential role of cognitive ability in determining the fitness of invasive species. The idea that cognitive ability may determine invasion success is only now starting to gain traction. This is a rich field worthy of further study that will help us better understand what makes a successful invasive species.

Keywords: biological invasions, behavioral flexibility, mammal, bird, fish, amphibian, reptile, integrative review

INTRODUCTION

Human society is changing the world at an alarming rate. Overpopulation, globalization, and climate change have led to unprecedented levels of habitat transformation resulting in negative effects on species, populations, and entire ecosystems. Consequently, many species living in altered environments either need to rapidly adapt or potentially face local extirpation (WWF, 2018). Conversely, some organisms may benefit from anthropogenic environments and human activity. For example, some species can take advantage of the existing vast global transport networks and use it to hitchhike and colonize new locations and thereby expand their range (Chapple et al., 2012; Lockwood et al., 2013; Lewis et al., 2016). This invasion process is complex, and encompasses multiple stages. Each stage poses a different set of obstacles that animals need to overcome in order to become invasive (Blackburn et al., 2011). A species that fails at any stage of the process will thus not become invasive (**Figure 1**). Nevertheless, biological invasions have been steadily increasing in the last century (Essl et al., 2011; Lewis et al., 2016), and therefore, understanding why some species are successful invaders is of great interest.

Whether an organism needs to adapt to changes in their current environment, or whether they are introduced into a completely novel environment, they need to be able to adapt or change their behavior quickly in order to survive (Tuomainen and Candolin, 2011). While selection may favor particular phenotypes and behavioral types, the degree to which an organism can plasticly adjust behavior (behavioral plasticity) may also be crucial in determining the outcome of an invasion (Chapple et al., 2012; Griffin et al., 2016). In addition to behavioral plasticity, cognitive ability can plausibly give some species an advantage in the invasion process because an ability to use resources and to learn and retain the location of resources and threats should be adaptive in novel environments (Shettleworth, 2001, 2010). It is thus not surprising that cognitive ability is increasingly being recognized for the potentially important role it may play in selection affecting fitness (Cole et al., 2012; Thornton et al., 2014; Budaev et al., 2019), which highlights the importance it can have on the success of invaders.

Behavioral flexibility–the ability of an individual to adapt its behavior to changes in the environment (Brown and Tait, 2015) by, e.g., stopping current behavior and initiating new behavior (Brown and Tait, 2015), solving a novel problem (problem-solving) or solving an existing problem in a novel way (innovation) is likely associated with invasion success (Reader and Laland, 2002; Sol et al., 2002; Shettleworth, 2010). This is because being more flexible can help an individual to better cope with novel habitats, predators, or resources (Sol et al., 2002; Wright et al., 2010; Chapple et al., 2012), which can ultimately increase their fitness (Sol et al., 2002). Measuring behavioral flexibility is challenging, but some metrics include the ability and speed with which animals conduct reversal learning (e.g., Brown and Tait, 2015; Lea et al., 2020) and their ability to deal with response inhibition (e.g., Diamond, 2013; Daniels et al., 2019), proficient problem solving across multiple domains (e.g., Logan, 2016a,b; Chow et al., 2018; Daniels et al., 2019; Lea et al., 2020), and the frequency of learning innovations (e.g., Sol and Lefebvre, 2000; Sol et al., 2002; Lea et al., 2020). A link between brain size (as a proxy of behavioral flexibility) and invasion success has been reported for invasive birds (Sol et al., 2002, 2005), mammals (Sol et al., 2008), amphibians and reptiles (Amiel et al., 2011). These reviews and comparative studies are powerful because they give us the big picture of how widely distributed a trait or relationship may be and sets the stage for later hypothesis testing. Another approach is to compare the cognitive ability of closely related species that may

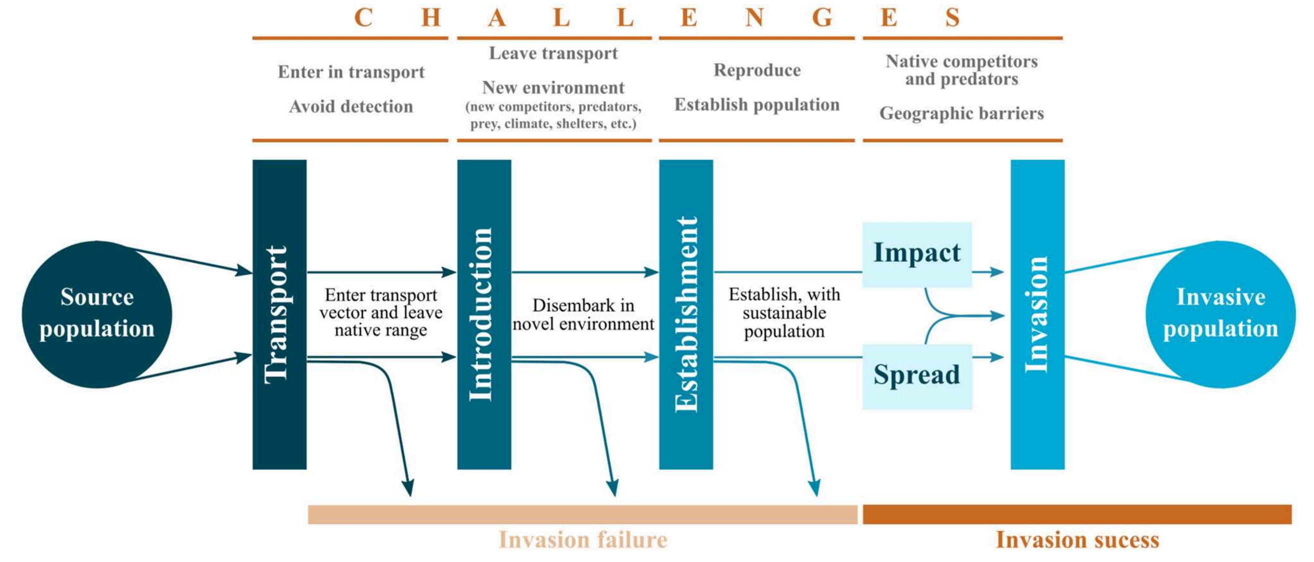

FIGURE 1 | The resulting invasive population consists of the filtered individuals that were able to overcome all obstacles in all stages successfully. Based on Colautti and MacIsaac (2004), Blackburn et al. (2011), and Chapple et al. (2012).

compete for the same resources, particularly when one species is native and the other is invasive (e.g., Roudez et al., 2008; Bezzina et al., 2014; Griffin and Diquelou, 2015; Chow et al., 2018). These studies typically address how species compete for ecological resources but differences in their ability to exploit resources may be independent of direct competition and may instead be a consequence of behavior and/or cognitive ability (e.g., Foucaud et al., 2016). Because cognitive abilities are often correlated with other factors such as motivation, personality, feeding ecology, sociality and life history (e.g., Tebbich et al., 2010; Carere and Locurto, 2011; Titulaer et al., 2012; van Horik and Madden, 2016; Dougherty and Guillette, 2018), disentangling the role of cognition in determining invasion success is challenging.

In this review, we have the following aims: (1) to review the evidence that cognition can influence invasion success; (2) characterize the features of cognitive ability that are likely to give individuals an advantage during the invasion process; and (3) propose future directions for studying the link between cognitive ability, fitness, and invasive success. To this end, we first conduct a systematic review of the literature on cognitive abilities that likely relate to invasion success (behavioral flexibility, problem solving, learning and memory) in both invertebrates and vertebrates. We also review the literature on brain size (as a proxy for cognitive ability) as it relates to invasive species. We then examine cognitive traits that could give species an advantage in a competitive, novel environment. Last, we describe an experimental approach to studying the role of cognition in determining invasive success and outline ways in which we can properly link invasive ability and cognition in a fitness framework.

SYSTEMATIC LITERATURE COMPILATION

We searched Web of Knowledge, Scopus and ProQuest for publications on biological invasions (using the keywords "invasi*," "invad*," "establish*," and "introdu*"), cognition (using the keywords "cogni*," "learning," "flexi*," and "innovat*") and fitness (using the keywords "fitness," "surviv*," and "reprod*") focusing on animals (using the keyword "animal*"). To refine our very broad search, we excluded publications based on the keywords "educat*," "child*," "physic*," and "gluco*" (**Figure 2**). To get the largest possible number of hits with these search terms, we made sure that we included all words starting with these terms by applying *. Additionally, we used the built in options each database provided to further refine our searches (for more details see electronic **Supplementary Material**).

We downloaded 4,737 references as RIS files to import into EndNote (version X9.3.2) of which 892 were removed as duplicates. Only 2,000 of the 8,254 entries identified in Scopus could be downloaded (sorted by relevance). Of the remaining 3,845 we selected 61 based on the title. To be included in our sample, the title had to include any mention of cognitive ability such as learning, cognitive or behavioral flexibility, memory, inhibition, etc. To ensure no publications

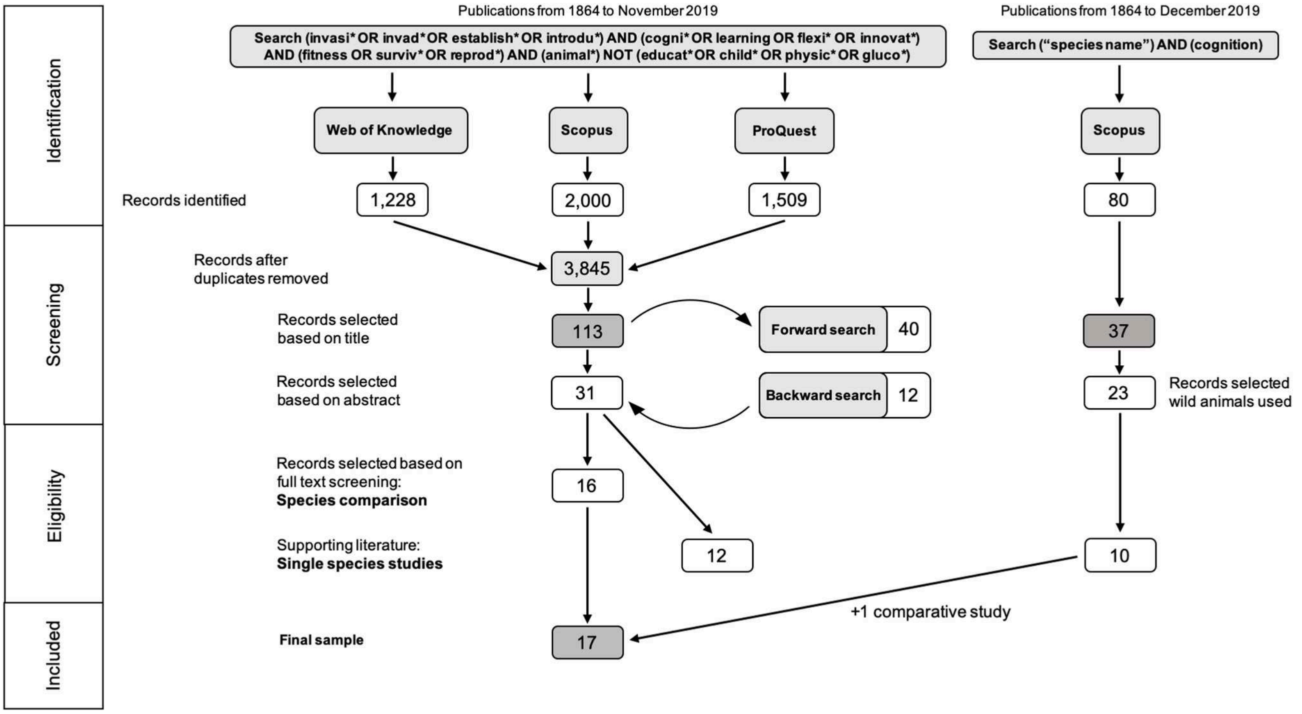

FIGURE 2 | Graphical representation of the systematic literature compilation (PRISMA diagram) including details on search terms, databases searched, number of entries found, and number of entries selected at each step.

were missed, studies on behavior (which might encompass some cognitive ability) were included as well. Furthermore, the title had to mention either that the behavior or cognitive ability has a fitness or adaptive value (or increases reproductive success) and that it was tested in an invasive species or a species that successfully invaded an urban habitat. This ensured a broad selection of publications. We then conducted a forward search on these 61 entries resulting in an additional 40 entries (selection based on title). After full text download we looked at the abstracts of the 101 articles (61 + 40 = 101) and selected 27 as being relevant for our review. We included articles if the abstract (1) described a cognitive ability (studies solely looking at behavior were excluded at this stage); and (2) focused on invasiveness (an invasive species, comparing performance between invasive and native species or comparing performance between individuals from the source population and invasive population). We then conducted a backwards search (based on title) on the 27 selected articles resulting in an additional 11 publications. A second forward search on these 11 articles resulted in no new entries. Finally, we conducted a second backward search (resulting in one additional entry) and a final forward search (resulting in no new publications). We identified 113 articles based on title and selected 31 of those based on their abstract (**Figure 2**).

We then proceeded to read the full text of these 31 articles. Based on content, they were then divided into articles comparing species cognitive ability either directly ($N = 10$) or through a proxy such as brain size ($N = 6$) and articles looking at cognitive performance of a single invasive species ($N = 12$). The other three articles were reviews. Although studying the cognition of a single invasive species is interesting, without a comparison, it is unclear if the tested ability is associated with enhanced invasion success, consequently, some were used as examples to help identify possible useful cognitive abilities associated with invasion success ($N = 10$) but were not part of the main literature review.

Our review, therefore, focuses on those studies that make a comparison. To get a comprehensive picture of the cognitive abilities of the invasive species on which these comparative studies focus, we did an additional search for studies testing further cognitive abilities in these invasive species. We conducted these additional searches in Scopus using the species name (common or scientific) and “cognition” as the search terms (see electronic **Supplementary Material** for details). Studies were included if they were conducted on wild animals (either in the wild or testing wild caught individuals) and on a task that measured problem solving, innovation, behavioral flexibility, social learning, associative learning of ecologically relevant stimuli (food or threat) or spatial learning. We identified an additional 10 studies to those found in our initial search ($N = 12$). One of these studies was a species comparison which our initial search had missed and was included in our final sample. Overall, we identified 17 studies comparing performance between species and 21 studies testing cognitive performance on a single species (supporting literature). All searchers were conducted in November and December 2019 (**Figure 2**).

INVADER SMARTS VS. NATIVE KNOW-HOW: A COMPARISON

To investigate if successful invaders possess enhanced cognition, a comparison of their cognitive ability to that of their congeneric non-invasive counterparts can give some indication of how cognition aids biological invasions. Although this seems a straightforward way to tackle the question if cognition benefits invasive species, only a small fraction of research has focused on a direct comparison between native and invasive congeners and even fewer have compared performance of the source population to the invasive population. Luckily, these few studies span a wide range of taxa from invertebrates such as crabs (Roudez et al., 2008; Ramey et al., 2009), crayfish (Hazlett et al., 2002) and flies (Foucaud et al., 2016), to vertebrates including mammals (MacDonald, 1997; Sol et al., 2008; Chow et al., 2018), birds (Sol et al., 2002, 2005; Diquelou et al., 2015; Griffin and Diquelou, 2015), fishes (Drake, 2007), reptiles (Amiel et al., 2011; Bezzina et al., 2014) and amphibians (Amiel et al., 2011) and provide a good first insight into how cognition may enhance invasive species success (**Supplementary Table 1**) in competing with the resident species assemblage already adapted to the invaded environment.

Comparison of Cognitive Performance Among Invasive vs. Native Species

Invertebrates

Invasive green crabs (or shore crabs, *Carcinus maenas*) learnt to locate a prey item (a ribbed mussel buried in the sand) faster over five test days compared to native blue crabs (*Callinectes sapidus*). Additionally, a larger proportion of green crabs were successful on the last three test days but both species showed similar memory of the trained location after a 10-day break (Roudez et al., 2008). Green crabs are a highly successful invader (Roudez et al., 2008). They have a high salinity and temperature tolerance, a high reproductive rate, and a long larval stage (Roman and Palumbi, 2004). They were able to transfer learnt prey handling techniques to novel prey items (Hughes and O’Brien, 2001) and were good spatial learners when tested in a complex maze (Davies et al., 2019). Invasive green crabs were also better at spontaneous alternation behavior compared to native blue crabs. Spontaneous alternation is the tendency of an individual to visit a location not previously visited or which has not been recently visited (Hughes, 2004) and can facilitate the discovery of new habitats, resources, or mates (Ramey et al., 2009). This was tested in a submerged plus-shaped maze. Only if an individual entered a novel arm four out of five times in a row was a successful spontaneous alteration recorded; otherwise it was unsuccessful. Invasive crabs made significantly more spontaneous alterations than native crabs, and only the green crabs’ performed significantly above chance (Ramey et al., 2009). Spatial learning and memory, besides other traits (see above), therefore appears to play some role in invasive success in green crabs.

Apart from remembering the location of food in a new place, learning about novel predators and remembering cues associated with the threat also improves individual survival.

Hazlett et al. (2002) investigated the memory for learnt predator odor in two pairs of invasive-native crayfish; the North American *Orconectes virilis* and its invasive competitor *O. rusticus* and the Italian *Austropotamobius pallipes* and its invasive competitor *Procambarus clarkii*. Individuals were either exposed to goldfish odor (an unfamiliar, herbivorous fish species unlikely to be recognized as a predator) combined with conspecific alarm chemicals (created by crushing a conspecific) for 2 h (short-term treatment) or 24 h (long-term treatment) or to a control treatment in which no goldfish odor or alarm chemicals were presented. The reaction of each crayfish to (1) water, (2) food odor (thawed cod), and (3) goldfish odor was then recorded for several weeks. Control animals did not react to goldfish odor indicating that goldfish are not innately recognized as predators, whereas trained crayfish showed a predator avoidance reaction when experiencing goldfish odor. Invasive O. *rusticus* ceased responding to goldfish odor after 4 weeks, whereas native O. *virilis* stopped responding after 1 week (2 h treatment) and 4 weeks (24 h treatment). Similarly, the native Italian *A. pallipes* stopped showing predator avoidance behavior 2 weeks after training no matter the treatment, whereas the invasive P. *clarkii* still recognized goldfish as a threat 3 weeks later when initially exposed for 24 h. Moreover, the two invasive species (*O. rusticus* and *P. clarkii*) responded as strongly to heterospecific as to conspecific alarm odors (Hazlett, 2000; Hazlett et al., 2003) while the native Italian *A. pallipes* did not (Hazlett et al., 2003). Further studies on *O. rusticus* showed that they have good spatial learning ability when escaping a T-maze, performing few wrong turns and with a low latency to exit (Tierney and Lee, 2011). Crayfish used both place learning by relying on maze cues and a response strategy when visual cues were provided within the maze. Furthermore, animals remembered the way out of the maze for 1 week (Tierney and Andrews, 2013). Finally, crayfish had a harder time learning to find the exit if conflicting cues were present and showed flexibility in learning during a spatial reversal (Tierney et al., 2019). These studies reveal that invasive crayfish species are more effective in using alarm cues provided by congeneric species and remember a predator odor for longer than native competitors. These results again suggest that better cognitive performance (here the memory of a predator odor) could provide an advantage in novel environments, consistent with conditions during invasion.

Comparing invasive species abilities to those of the native species they displace is one way to demonstrate which traits may be important for successful invasion. However, such studies are constrained by the fact that they focus on an invaders ability after it has already established itself and may have limited insight into abilities that might inherently make a species a good candidate to invade a new habitat. A comparison between female fruit flies (*Drosophila subobscura*) from their native range in Europe and from an area where they were introduced (in Chile) in the 1970s revealed that learning to select the correct oviposition site (medium without quinine, a bitter tasting compound) was not enhanced in the invasive population, but fecundity (number of eggs laid overall) was greater in females from Chile (Foucaud et al., 2016). Although invasive fruit flies were not better at selecting an appropriate oviposition site, tests looking at other cognitive abilities could give insight into if and how a range of cognitive abilities could be involved in predicting invasion success.

Vertebrates

Similar to invertebrates, a number of studies have used species comparisons to look for enhancements in learning and problem solving in invasive species. The Australian delicate skink (*Lamprohpolis delicata*) is a successful invader while their related congener, the common garden skink (*Lampropholis guichenoti*), is not. Both have frequently been discovered by biosecurity authorities within cargo but only the delicate skink has, so far, managed to establish viable populations outside their native range. Both species show very similar phenotype and behavior; however, delicate skinks are more exploratory and hide more (Chapple et al., 2011). Both species were tested on their ability to learn the location of food within a Y-maze. Lizards were provided with visual cues such as arm color and pattern as well as spatial intra-maze cues such as left/right position of the correct arm and distal extra-maze cues. Both species decreased the time taken to locate the hidden food but no difference was found between species. Additionally, they did not progressively take a more direct route within the maze indicating no learning had taken place (Bezzina et al., 2014). Based on these data, delicate skinks do not possess better cognitive ability than common garden skinks; however, learning ability was compared on a single test in this study. Additional work in delicate skinks showed that these lizards can learn to find a "safe" refuge to escape a simulated predator attack within a similar Y-maze using color cues (Kang et al., 2018), and that urbanized skinks are not better learners than individuals from natural areas (national park; Kang et al., 2018). Finally, behavioral phenotype affected learning performance: fast-type lizards (i.e., more active and exploratory) made more errors during learning (Chung et al., 2017; Goulet et al., 2018). Importantly, lizards were sourced within their native range to be tested in these different studies. Without data from the invasive population of the delicate skink it is still unclear if learning ability is a trait selected for during the establishment process.

Another Australian study compared the problem-solving ability between the native noisy miner (*Manorina melanocephala*) and the introduced common myna (*Acridotheres tristis*) in a foraging context. Problem solving may involve cognitive mechanisms such as associative learning, inhibitory control and cognitive flexibility (Diamond, 2013; van Horik and Madden, 2016); however, it can also involve a range of non-cognitive abilities such as motivation, persistence and motor skill (Diquelou et al., 2015; van Horik and Madden, 2016; Lermite et al., 2017). Although noisy miners are a very successful native honeyeater species, able to outcompete other small avian species when occurring in large numbers, common mynas are very opportunistic and able to occupy niches that native species cannot (Lowe et al., 2011; Sol et al., 2012a). Indeed, mynas are listed as one of the "100 World's Worst Invasive Alien species" (by the International Union for the Conservation of Nature; Boudjelas et al., 2000). To study problem-solving ability in these birds, three tasks were given in a random order in which birds had to use different techniques to open transparent food containers (task 1 and 2) or extract food from within a Styrofoam cup which was transparent on top (task 3). Overall, the invasive common myna outperformed the native noisy miner. Common mynas were faster to solve these tasks and showed greater motor diversity and flexibility, which were highly repeatable. Common mynas also showed repeatability in their persistence when solving the tasks compared to the noisy miners (Griffin and Diquelou, 2015). These result indicate that mynas show consistent, high levels of persistence, motor diversity, and flexibility, while miners do not. Furthermore, in a later study, task directed motivation (making more contact with an apparatus) and exploratory behavior (moving less within an open space) predicted task success in mynas (Lermite et al., 2017) confirming these traits to be important during problem solving. Moreover, invasive mynas can learn to remove lids from food wells (motor innovation) and motivation and neophobia were the best predictors of successful motor innovation (Sol et al., 2012b). Individuals from highly urbanized habitats were faster problem solvers and were also less neophobic and more exploratory (Sol et al., 2011), behavioral traits that covary with individual cognitive styles (Carere and Locurto, 2011; Sih and Del Giudice, 2012). Mynas were also good observational learners. They remembered a "dangerous" human after observing a staged catching event (Diquelou and Griffin, 2019) and became more wary (increase in locomotion) in the location of such an aversive event (Griffin and Boyce, 2009). Observing the behavior of an alarmed conspecific when the source of the threat was not visible, however, did not affect the observers behavior (Griffin et al., 2010).

Following Griffin and Diquelou (2015), transparent food containers (same as task 1) were presented to seven different Australian bird species: Australian ravens (*Corvus coronoides*), Australian magpies (*Cracticus tibicen*), magpie larks (*Grallina cyanoleuca*), common mynas (A. *tristis*), noisy miners (M. *melanocephala*), European starlings (*Sturnus vulgaris*), and crested pigeons (*Ocyphaps lophotes*) in the wild. As with common mynas, European starlings are highly invasive and should perform well in problem-solving tasks if problem solving indeed is a trait enhanced in invasive animals. Although this was true, Australian ravens were the best problem solvers closely followed by common mynas and European starlings. Except for the Australian magpie (another native species like the Australian raven), none of the other species showed much skill in solving the presented task. Motor flexibility (range of motor actions) predicted problem-solving probability across all species (Diquelou et al., 2015). These studies are great examples of how simple tests on wild birds can reveal striking difference in a range of abilities (cognitive and non-cognitive) and can give some indication of how learning, memory and flexibility are helping invaders colonize novel habitats.

Another species amongst the "100 World's Worst Invasive Alien species" (Boudjelas et al., 2000) is the gray squirrel (*Sciurus carolinensis*). In the UK, they outcompete and replace the native red squirrel (*Sciurus vulgaris*) with which they share a number of ecological traits (Koprowski, 1994; Gurnell et al., 2004; Lurz et al., 2005). Wild gray squirrels were better problem solvers compared to wild red squirrels. Animals were given an easy task in which they had to displace lids to gain access to a reward (nut), and a hard task in which they had to push or pull a bar to make a nut drop down to the bottom of a box, making it accessible. In the easy task, more gray squirrels were first-time solvers than red squirrels, and invasive gray squirrels were also faster solvers. In the hard task, more gray squirrels were solvers but both species showed the same performance, were similarly persistent (number of attempts), and used similar proportions of effective behaviors; red squirrels were even more efficient (sum of the duration of all attempts to solve the task until it was successfully solved; Chow et al., 2018). These results indicate that although both species exhibit similar levels of persistence and motor diversity (non-cognitive factors important for successful problem solving) other factors such as cognition might explain why more gray squirrels solved the tasks. Invasive wild gray squirrels also had longer lasting spatial memory of caches made by a human experimenter compared to native wild red squirrels (MacDonald, 1997). However, low sample sizes reduced statistical power and results need to be interpreted with caution. Furthermore, the difference could have been caused by the fact that gray squirrels rely more on caches (MacDonald, 1997) and could have a more specialized hippocampus, an essential brain area for spatial memory. The results of these studies indicate that learning and memory could help explain why gray squirrels have been such successful invaders although both species have good problem-solving abilities. Future studies could investigate if gray squirrels are innately better learners and problem solvers by comparing individuals from the native and introduced range. Moreover, gray squirrels have been introduced to Italy more recently (20th century; Bertolino et al., 2008) and a comparison to the UK population (introduced in the 19th century; Chow et al., 2018) could provide new insights into how selection shapes cognitive (and non-cognitive) traits during the invasion process.

In summary, comparative research in both invertebrates and vertebrates suggests that cognitive abilities such as learning and memory might help favor invasion success. However, not all studies have found differences between the tested species (Bezzina et al., 2014) or populations (Foucaud et al., 2016). Furthermore, non-cognitive factors are clearly causing differences between species in task performance (Diquelou et al., 2015; Griffin and Diquelou, 2015). It is therefore crucial to take such factors into account to avoid drawing the wrong conclusions about the role of cognition in invasion success. Studies in birds and mammals mainly test problem-solving ability focusing on non-cognitive factors such as motivation and persistence but less on cognitive factors such as inhibition and flexibility. Studies focusing on species or population comparisons are rare, which underscores how we are only just starting to understand how cognition might aid the invasion process. Moreover, if species innately possess beneficial abilities that help them invade novel habitats or if these abilities emerge as a result of selection is unclear. The degree to which cognitive abilities are beneficial in the invasion process and if these are general across different invasive species is also unknown.

Comparison Based on Relative Brain Size in Vertebrates

A link between cognitive ability, innovative behavior (feeding and problem solving) and brain size has emerged in a range of taxa (e.g., Lefebvre et al., 1997, 2004; Bouchard et al., 2007; Güntürkün, 2012; Griffin et al., 2013). Recently, comparative studies have examined the relationship between behavior, cognition, and brain size with a focus on how innovative behavior and cognition might benefit invasive species (Sol and Lefebvre, 2000; Sol et al., 2002, 2005, 2008; Drake, 2007; Amiel et al., 2011). By using data on relative brain size and invasion success after human translocation, Amiel et al. (2011) suggested that those species of amphibians and reptiles with larger relative brains are more successful in establishing a population in a novel environment. This trend was consistent geographically except for Australasia. Here, the opposite trend was observed, species with smaller brains were more successful (Amiel et al., 2011). In birds, there is a strong link between relative size of the hyperstriatum ventral (which serves a similar function to the mammalian neocortex) and cognitive flexibility (Timmermans et al., 2000) but it is still unclear if larger brain size confers similar cognitive enhancements in amphibians and reptiles. A large-scale analysis of relative brain size, fecundity, parental investment and invasion success in fishes revealed no correlation between brain size and establishment success in a novel environment (Drake, 2007). Empirical work on fishes has demonstrated a positive link between brain size and cognition (numerical associative learning; Kotrschal et al., 2013a,b). In these studies, however, fishes were artificially bred for larger brain size; if selection acts in a similar manner in natural populations is unclear, and if so, a correlation between brain size and cognitive ability might be much weaker and harder to detect. In birds, the first study looking at how establishment/invasion success relates to brain size and foraging behavior was restricted to species introduced to New Zealand. It revealed, that species with larger relative brain size were more likely to successfully invade New Zealand and that successful invaders also showed a higher number of foraging innovations. Other traits were also associated with invasiveness: the number of individuals introduced (introduction effort), migration (migratory, partially migratory, or sedentary) and developmental mode (nidicolous vs. nidifugous) (Sol and Lefebvre, 2000). Following this study, the inclusion of a much wider range of bird species revealed a similar trend. Again, species that were successful invaders had larger relative brain size and showed more foraging innovations. As before, additional variables were associated with invasion success: order a species belongs to, plumage (monochromatic or dichromatic), nest location (ground, bush/tree or hole) and if a species was also found in urbanized habitats (Sol et al., 2002). Anthropogenic environments differ greatly from natural environments and are subject to greater change and disturbance (Lowry et al., 2013). It is not surprising to find species that establish themselves in a human dominated environment to also have larger relative brains possibly to deal with these challenging environmental conditions. Sol et al. (2005) confirmed the relationship between brain size and successful adaptation to environmental change (brain size—environmental change hypothesis) first in birds. They found that birds with larger relative brains were more successful at establishing a population in novel environments and this invasion propensity was also associated with innovativeness; invasive species had more feeding innovations. Additional analyses showed the success of invasive species in coping with novel environments was due to an increase in their cognitive ability and no other mechanisms (Sol et al., 2005). The brain size-environmental change hypothesis was also confirmed in mammals. Establishment success was higher in mammals with relatively larger brains and was also associated with introduction effort and habitat generalism (Sol et al., 2008). Contrary to birds, however, no proxy for cognitive ability (e.g., feeding innovations) was included in the analysis. Nevertheless, a link between relative brain size and cognitive ability has already been established in some mammalian groups (e.g., Lefebvre et al., 2004; Güntürkün, 2012).

Across taxa, the analysis of large multi-species datasets has been useful for investigating the generality of different hypotheses about how cognition could help species become successful invaders. While a link between larger relative brain size and enhanced cognition has been established for some taxa, more effort is still needed to test for the existence of a similar relationship in other taxa. Importantly, studies using brain size as a proxy for cognitive ability run into a number of constraints and results should be interpreted with caution. Evidence suggests that brains are heterogeneous across taxa and the degree of enlargement and neuron densities of specific brain areas can differ greatly (e.g., Olkowicz et al., 2016 cited by Logan et al., 2018). Furthermore, selection may change specific brain areas without an increase in brain size (see Does Selection Act on Brain Size? in Logan et al., 2018). Moreover, analyses are hampered because the relationship between brain size and body size is not linear in all taxa [e.g., Fitzpatrick et al. (2012) cited by Montgomery et al. (2013), Logan et al. (2018) cited by Logan et al. (2018)] and often, brain measures used in comparative studies are based on a few individuals (Logan et al., 2018). Results of such comparative studies using brain size are, therefore, better used as a starting point for more detailed investigations looking at how individual differences in cognitive ability translate to brain anatomy within species (e.g., Audet et al., 2018) followed by investigations into differences between closely related species (e.g., Aamodt et al., 2020) to better understand how changes in brain size and structure are related to cognition and behavior (Logan et al., 2018).

COGNITIVE ABILITIES THAT CAN INCREASE INVASION SUCCESS

During invasion into a new habitat, animals will inevitably face environmental conditions which are novel and to which they are not optimally adapted. The faster way to adapt to changing conditions is through behavioral plasticity and flexible behavior. Shifts in behavior most likely follow after experience with a certain situation allowing the individual to learn an appropriate response. Animals might innovate solutions to problems by modifying existing behavior, come up with new behaviors, or learn socially from conspecifics or even native congeneric heterospecifics (Wright et al., 2010; Damas-Moreira et al., 2018). Cognitive ability can play an important role during the different stages of the invasion process, but which abilities increase invasion success within or across stages? Below, we provide some examples of cognitive abilities which are likely to be involved in increasing the likelihood that a species becomes established in a novel environment (based on work presented in the previous section).

Behavioral Flexibility, Innovation, and Problem Solving

Although we can assume that a cognitive ability might not carry the same advantage when facing novel or changing conditions across species, behavioral flexibility, the ability to adapt flexibly to changes in the environment (Brown and Tait, 2015), is a trait likely to be advantageous to most, if not all, invaders. Behavioral flexibility is often described together with innovation and problem solving such that species or individuals that are innovators or problem solvers are behaviourally flexible (Lea et al., 2020). A key component of behavioral flexibility is that it can be adaptive in a given situation (Brown and Tait, 2015). Inventing new behaviors or techniques to solve problems such as being confronted with novel foods or having to extract edible foods from within inedible casings (e.g., shells, soil, wood) will improve survival. Furthermore, being behaviourally flexible in the traditional sense, by flexibly adjusting behavior in situations when old behavior becomes unsuccessful, also carries fitness advantages. Therefore, our definition of behavioral flexibility encompasses any change in behavior that helps individuals to adapt to changing conditions and can be measured using innovation rates, different techniques to solve puzzle box tasks (i.e., problem-solving techniques), reversal learning and similar tasks (e.g., serial reversal learning or set-shifting) that cover multiple cognitive domains. Wright et al. (2010) proposed the "Adaptive Flexibility Hypothesis" in which they relate behavioral flexibility and its usefulness (adaptive value) to the different stages of the invasion process and propose that behavioral flexibility will be most beneficial during the initial stages of an invasion in which novel problems are most likely to be encountered. For example, wild North American racoons (*Procyon lotor*) caught in their native range, possessed flexible problem-solving skills. They were tested on a multi-access box which could be opened in three different ways. Across nights, access points were blocked to force animals to abandon old solutions and find new ways to access the reward. Seven of the 20 racoons tested solved the box using all three ways showing high levels of problem-solving ability and flexibility in their use of behaviors to open the box when an old solution became ineffective. Exploratory behavior and persistence were robust predictors of solving success. Inhibitory control was also assessed by looking at the time spent interacting with a newly locked access point but it did not predict differences in solving success between night two and three. This shows that this species possess an innate ability to solve problems which might be the reason why it is such a successful invader (Daniels et al., 2019). Not all successful invaders, however, are great problem solvers. Great-tailed grackles (*Quiscalus mexicanus*) showed behavioral flexibility during reversal learning and varying degrees of problem-solving ability. Birds learnt to reverse their preference for finding food in a golden tube to choosing the previously unrewarded silver tube during a reversal stage. Fast learners were, however, not more flexible (Logan, 2016a). Problem solving was tested using the Aesop's fable paradigm (dropping stones into water to raise the water level and bring a reward closer; Logan, 2016a), a stick tool-use task (to extract a piece of bred from between two transparent walls) and a horizontal and vertical string pulling task (in which a string has to be pulled to bring a reward close enough to reach it; Logan, 2016b). Although grackles were unable to spontaneously drop stones, use sticks or pull strings to access a reward, birds could learn to drop stones to reach a reward (Logan, 2016a,b). However, they could not learn to use stick tools (Logan, 2016b). They were also flexible in learning which strategy to use during the Aesop's fable paradigm. Initially birds preferred heavier stones but when these became ineffective, they switched strategy to use lighter stones in higher numbers Logan, 2016a. Individuals tested in these tasks were wild caught from within their introduced range. If great-tailed grackles are innately good problem solvers has still to be investigated. So far, no direct link between cognition, its fitness value, and invasion success has been demonstrated. Nonetheless, increasing numbers of studies show how behavioral flexibility is enhanced in successful invaders as compared to species that did not establish a viable population in a novel environment (e.g., Sol and Lefebvre, 2000; Sol et al., 2002, 2005, 2008) and how problem-solving ability, innovation, and behavioral flexibility influence reproductive success (e.g., Cole et al., 2012; Cauchard et al., 2013, 2017; Ashton et al., 2018) and survival (e.g., Dayananda and Webb, 2017; Madden et al., 2018). Conflating these areas of research will further our understanding of if and how behavioral flexibility aids biological invaders.

The Fast Acquisition of Information Through Learning

Learning enables an individual to acquire new information and compensate for shortcomings that might arise from entering a new environment to which it is not adapted, or even maladapted. Theoretical models predict that, if the initial founder population is small, adaptation (through genetic change) alone is not fast enough to result in a sustainable population; however, learning can help a population persist even if it is initially maladapted to the novel environment (Sutter and Kawecki, 2009). Importantly, the benefit of learning to buffer differences in fitness between habitats and to increase mean fitness in the novel habitat is higher when the difference between the native and novel habitat is large (Sutter and Kawecki, 2009). This means that learning could be more beneficial for introduced species than it is during a gradual range expansion. Learning about the characteristics of a novel habitat has the potential to increase the probability that even a small founder population can persist in a new environment. Fast learning is present in invasive species, as compared to native competitors (see earlier discussion of green crabs, common mynahs and gray squirrels). In addition, invasive American bullfrogs (*Lithobates catesbeianus*), which experienced threat (scent of the novel largemouth bass, *Micropterus salmoides*, combined with conspecific alarm cues) as embryos within the egg, hid more inside a refuge when experiencing the threat later in life (as larvae after hatching). No effect could be detected in untrained control larvae (Garcia et al., 2017). These studies give some indication that enhanced learning ability may facilitate invasion success; however, we do not know if these learning abilities have actual fitness consequences (increased survival and reproductive success) or if these species are innately better learners.

Social Learning and the Spread of Knowledge

When entering a novel habitat that is dissimilar to the environment in which an individual developed and has adapted to, collecting information about predators, what to eat and where to hide, can be crucial for survival. Trial-and-error learning can be associated with high costs when sampling noxious foods or encountering dangerous predators, possibly leading to death after first contact. It can therefore be beneficial to rely on the knowledge that other individuals have already accumulated. Social learning is considered a shortcut to accessing important information that has already been vetted and is beneficial (Galef and Laland, 2005). During the early stages of the invasion process, the only individuals with relevant information might be congeneric native individuals. Some invasive species are known to use the behavior and alarm signals of native species to quickly learn about food (e.g., Camacho-Cervantes et al., 2015) and novel threats (e.g., Hazlett, 2000; Hazlett et al., 2002, 2003). For example, lab-reared female guppies that watched the behavior of either a small group of conspecifics or heterospecifics (butterfly splitfins, *Ameca splendens*), when food scent was introduced, changed their behavior accordingly. Observer fish showed similar behavior to demonstrators by spending more time in the upper layer of their aquarium. When no demonstrators were present or water was added instead of the food odor, observers did not change their behavior showing that their behavior was guided by that of the demonstrators irrespective of whether demonstrators were conspecifics or heterospecifics (Camacho-Cervantes et al., 2015). Furthermore, a recent study showed that invasive Italian wall lizards, *Podarcis sicula*, readily learn stimuli associated with a food reward (in an artificial foraging task using differently colored food wells) from both conspecifics and heterospecifics and made fewer errors when learning socially as opposed to individually (Damas-Moreira et al., 2018). Social learning has, however, limitations. It is only really beneficial if the environment is largely stable and information stays relevant for extended periods of time and if animals are selective about what information they learn (Galef and Laland, 2005). Nonetheless, it might be a powerful tool to spread important information rapidly through an invasive founder population and increase the likelihood that a large enough number of individuals survive and can reproduce.

Choosing "Smart" Mates

In some species, smart individuals are preferred as mates (e.g., Keagy et al., 2009, 2011; Chen et al., 2019) although cognitive abilities do not always provide direct benefits to the choosing sex (e.g., Keagy et al., 2011). If a cognitive ability or innovative behavior enhances survival within a novel environment and if these abilities are heritable then choosing a "smart" mate would increase offspring survival and fitness, and in the long run, help establish a population in the new location. There is evidence that cognitive ability (e.g., Galsworthy et al., 2005; Hopkins et al., 2014) and learnt behavior (e.g., Kelly and Phillips, 2017, 2018) are heritable, but this is not always the case (e.g., Quinn et al., 2016; for a review see Coston et al., 2015). Mate choice for individuals with enhanced cognitive ability has received little attention (for a review see Boogert et al., 2011) and none in relation to invasion success. It has also been shown that a number of species have to learn about intraspecific sexual traits to successfully mate and reproduce (Ryan et al., 2009). During the invasion process, animals might come in contact with congeners that are not dissimilar to themselves. On the one hand, if courting and mating with congeneric species are costly, enhanced learning for intraspecific traits that help distinguish between species could help avoid such costs and help an establishing population to grow to a sustainable size. On the other hand, hybridization can enhance cognition and adaptability to novel environments through backcrossing of favorable genes acquired from the native species into the parent lineage or through the development of extreme phenotypes that increase fitness in a novel habitat (Rice, 2020).

LINKING COGNITION, FITNESS AND INVASION SUCCESS—FUTURE DIRECTIONS

The way forward is multi-faceted, but a good starting point is studies that compare invasive and non-invasive species, source and invasive populations, and experimental studies which link or test for links between fitness, cognitive ability, and invasive ability. Ten years ago, no longitudinal studies of invasive populations were available (Wright et al., 2010), a big gap that has not been filled. Additionally, we found only one study comparing learning (female fruit flies choosing between oviposition sites) between individuals from the source and invasive population (Foucaud et al., 2016), an approach also listed by Wright et al. (2010). We need more baseline data on differences between invasive and non-invasive species pairs (i.e., congeneric species) and between invasive and source populations. The challenge will be to conduct direct tests of how cognitive ability affects fitness with links to either survival or reproductive success in the future as manipulation of cognitive ability will likely also change associated abilities (cognitive and non-cognitive; e.g., Cauchard et al., 2017). This will create a clearer picture of what attributes make a species a more successful invader than less invasive species.

Simple cognitive tests that can be used in the wild and on a wide range of species would be especially valuable, although bringing wild caught individuals to the lab and testing an array of cognitive abilities also has merit. Careful consideration should also be given to which cognitive abilities to investigate, based on a species' ecology and sociobiology. We need to think in terms of aspects of cognition that are most likely to be beneficial during an invasion event. At the same time, cognition often correlates with non-cognitive traits including motivation or neophobia (e.g., Sol et al., 2011, 2012b) which should be measured simultaneously. Moreover, correlation between cognitive traits might occur warranting additional controls for such co-variation. We also would like to highlight that, so far, fitness benefits of enhanced cognitive ability have often been implied, but less often directly studied (e.g., Thornton et al., 2014; Dayananda and Webb, 2017; Ashton et al., 2018). Studying the value of cognitive ability during biological invasions is not an easy task but certainly one that has a substantial pay-off.

Future research could look to studies of *Anolis* lizards (anoles) for insight on how to experimentally study the role of cognition in invasions. Anoles have become the poster child of experimental vertebrate evolution because large numbers of known individuals can be introduced on to small islands and they have sufficiently short generation time to study selection in "ecological" time. Their survival and fitness can then be measured for a range of traits and island conditions (e.g., predator vs. predator-free, different habitats, etc.), thereby creating a picture of how selection acts on traits in novel environments. As it turns out, the brown anole (*Anolis sagrei*) is now a common invasive species documented in far flung locations from Florida (USA) to Taiwan, including regions such as Hawai'i. Florida is also home to a large number of invasive species including many species of lizards because of its tropical climate and an historically lax control of animal imports. We highlight this because Florida is a potential epicenter for a range of studies on how cognitive ability may link to invasive ability because the spread of these species can be easily monitored. This state also has a large number of artificial islands in their inter-coastal waterways which are used for selection studies (e.g., Fargevieille et al., 2019). We suggest using these same islands for experimental studies involving the release of anoles of known cognitive ability to monitor their survival and replicate it among islands. Likewise, both invasive brown anoles and native green anoles of known cognitive ability could be released on to the same islands. These islands are small and can be easily manipulated. For example, in addition to introducing pairs of native and invasive anoles, the native green anole could first be introduced and established before subsequently releasing brown anoles. This would replicate real-world conditions where invasive and native species come into contact. Likewise, common garden experiments in which native and invasive anoles are first raised under the same conditions before being released onto islands would control for any variance contributed by the developmental environment. We also suggest assaying all individuals for behavior, such as boldness, exploratory behavior, and propensity to disperse (this can be done in large outdoor arenas). Furthermore, traits such as motivation and persistence should be measured during cognitive testing to ensure that these traits are not causing differences between species rather than cognition. It is important to be able to disentangle the effects of cognitive ability and behavior on invasive ability. And with respect to cognitive ability, although time consuming, we suggest multiple tests that focus on spatial learning and give a measure of behavioral flexibility because these traits are likely to be crucial to survival in novel environments.

In summary, there is increasing evidence that cognition influences fitness (e.g., Cole et al., 2012; Cauchard et al., 2013, 2017; Dayananda and Webb, 2017; Ashton et al., 2018; Madden et al., 2018). In the case of biological invasions, when organisms are exposed to new environments, cognitive ability is predicted to improve the probability of successful establishment. In this scenario, individuals with better cognitive ability are therefore more likely to be selected for. This hypothesis requires testing and we have suggested a potential experimental paradigm using *Anolis* lizards, but there are many others. We also encourage more empirical work comparing pairs of invasive and non-invasive species that are closely related and more studies comparing populations at the invasion source and the invasion front in order to better understand invasions and the role of selection. Understanding invasions in light of a species' cognitive ability and the relative fitness of potential behavioral and cognitive styles is a field with great potential. We hope this review will help stimulate innovative research in this direction.

AUTHOR CONTRIBUTIONS

BS did the integrative review and wrote the bulk of the paper, ID-M wrote the bulk of the introduction and MW wrote the bulk of the future directions section. All authors contributed to writing and revising all sections of the manuscript. All authors conceived the framework for the paper.

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SUPPLEMENTARY MATERIAL

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Cognition in a Changing World: Red-Headed Gouldian Finches Enter Spatially Unfamiliar Habitats More Readily Than Do Black-Headed Birds

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Human activities are increasingly confronting animals with unfamiliar environmental conditions. For example, habitat change and loss often lead to habitat fragmentation, which can create barriers of unsuitable and unfamiliar habitat affecting animal movements and survival. When confronted with habitat changes, animals' cognitive abilities play an important, but often neglected part in dealing with such change. Animals must decide whether to approach and investigate novel habitats (spatial neophilia) or whether to avoid them (spatial neophobia) due to potential danger. For species with strict habitat preferences, such as the Gouldian finch (*Erythrura gouldiae*), which is an open habitat specialist, understanding these novelty responses may be especially important for predicting responses to habitat changes. The Gouldian finch is a polymorphic species, with primarily red or black head colors, which are linked to differing behavioral phenotypes, including novelty reactions. Here we investigate responses to novel habitats (open, dense) in the Gouldian finch, manipulating the color composition of same-sex pairs. Two experiments, each consisting of novel open and novel dense habitat, tested birds in opposite head color combinations in the two experiments. We measured the number of approaches birds made (demonstrating conflict between approach and avoidance), and their entry latency to novel habitats. Gouldian finches showed more approach attempts (stronger approach-avoidance conflict) toward the dense as compared to the open habitat, confirming their open habitat preferences. Black-headed birds also hesitated longer to enter the dense habitat as compared to the open habitat, particularly in experiment 1, appearing less neophilic than red-headed birds, which showed similar entry latencies into both habitat types. This is surprising as black-headed birds were more neophilic in other contexts. Moreover, there was some indication that pairings including at least one black-headed bird had a stronger approach-avoidance conflict than pairings of pure red-headed birds. Results suggest that the black-headed birds use a cognitive strategy typical for residents, whereas red-headed birds use a cognitive strategy known for migrants/nomads, which may cognitively complement each other. However, as 70% of the population in the wild are black-headed, the spatial wariness we document could be widespread, which may negatively affect population persistence as habitats change.

Keywords: exploration, fear, specialist, decision-making, color polymorphism, nomad, conformity, conservation

INTRODUCTION

Most species experience environmental variation to some degree, but organisms are increasingly exposed to climatic and human-induced environmental change at a rate much higher than evolutionary time scales. For example, habitats are altered, fragmented and/or lost, which can affect movement patterns (Riotte-Lambert and Matthiopoulos, 2019), such as dispersal, migration, and movements for foraging and breeding (e.g., Norris and Stutchburry, 2001; Shadbolt and Ragai, 2010; Stouffer et al., 2011; Amos et al., 2014). The ability of individuals to respond to such changes is paramount for their survival and long-term population persistence. Therefore, an understanding of animal behavior can help predict responses toward varying types of environmental change (Wong and Candolin, 2015), including movement in response to habitat-related changes (Knowlton and Graham, 2010). In fact, a better understanding of impediments to animal movement and their influence on the functional connectivity of habitat has been flagged as a high priority for conservation behavior research (Greggor et al., 2016a).

Movement decisions inherently involve cognition. In moving into a habitat, animals must perceive a given space and assess available predator and foraging cues, relative to experience or an ingrained bias; all of which involve cognitive mechanisms (Shettleworth, 2010). Cognitive biases consistently guide how animals make often imperfect assessments of their environment (Marshall et al., 2013) and are, therefore, instrumental in understanding responses to habitat change and the downstream effects on survival. This is especially true when animals are faced with evolutionarily novel conditions because their responses and decisions may not be easy to predict without considering underlying perceptual abilities and learning tendencies (Greggor et al., 2019).

Organisms confronted with habitat change, such as a newly fragmented landscape, must decide whether to approach and investigate the new habitat or whether to avoid it. The decision to approach or avoid the novelty associated with change is governed by two independent motivations, both of which are cognitive by nature. Neophobia, the fear of any novelty, leads to avoidance and protects an animal from potentially dangerous situations. Neophilia, the attraction to novelty, results in approach, investigation and information gathering (Mettke-Hofmann et al., 2002). The two motivations are independent of each other (Wood-Gush and Vestergaard, 1993) and have different gene expressions (Powell et al., 2003; Weisstaub et al., 2006). However, they are both elicited when an animal is confronted with novelty, resulting in four possible extreme combinations of neophobia and neophilia (2-Factor model, Greenberg and Mettke-Hofmann, 2001). (A) An individual can show high neophilia and low neophobia, resulting in a fast approach of the novel situation without hesitation, followed by information gathering. (B) Likewise, low neophilia (no interest in novelty) can be combined with high neophobia, leading to a delayed approach and little information gathering. (C) However, a lack of approach can also result from a combination of low neophilia (no interest) and low neophobia. Accordingly, the delayed approach is driven by the low interest in the novel situation rather than fear. (D) Finally, a high level of neophilia and neophobia can be in conflict with each other, in which there are repeated approach attempts (reflecting the conflict between the two motivations; Mettke-Hofmann et al., 2009). Approach attempts in this scenario will result in information gathering (to some extent) and in later exploration. The relative expression of neophobia versus neophilia is a species level trait, with considerable individual variation, and has evolved in relation to the costs and benefits of approaching or avoiding a certain type of novelty (e.g., novel spaces, objects or foods, Greggor et al., 2015). Accordingly, neophobia and neophilia are often correlated with other traits such as learning speed and problem solving (e.g., Seferta et al., 2001; Benson-Amram and Holekamp, 2012).

Spatial neophobia and neophilia have been shown to differ between habitat generalists and specialist species. For example, butterfly species with a more local distribution were less likely to explore new habitats, showed greater avoidance of unfamiliar habitats (i.e., low spatial neophilia and high spatial neophobia) and consequently hesitated longer to enter unfamiliar and deviating habitats than butterflies with a large distributional range (Norberg et al., 2002; Leimar et al., 2003). The authors concluded that spatial neophobia and neophilia can have consequences on the distribution of populations. Similar patterns appear in songbirds, where diet and habitat specialists have shown greater spatial neophobia to feed from novel micro habitats than closely related generalist species (Greenberg, 1983, 1989).

Spatial novelty reactions also vary with species' movement patterns. Migratory bird species are often confronted with unfamiliar environments and readily enter new habitats (high spatial neophilia) with few approach attempts (indicative of a low approach-avoidance conflict). However, as they only stay for short periods in each area, they only superficially explore unfamiliar areas (Mettke-Hofmann et al., 2009). In contrast, residents are more hesitant to enter new areas, and demonstrate high approach-avoidance conflict (Mettke-Hofmann et al., 2009) due to the potential danger of the novel environment. Residents thoroughly explore once they are in an environment as they can use information in the long-term

(Mettke-Hofmann and Gwinner, 2004; Mettke-Hofmann et al., 2005, 2012). Generally, residents are more flexible in their responses (e.g., innovations, Sol et al., 2005) and positive population trends have been linked to this higher flexibility (Mettke-Hofmann, 2017). Finally, dispersal decisions have been linked to the amount of spatial exploration (spatial neophilia, Selonen and Hanski, 2006).

Although novelty reactions are species-specific traits, they can also vary considerably intraspecifically, and are often linked to existing polymorphisms. Individuals can differ in their novelty responses due to individual coping styles or personalities (consistent individual differences), which can affect the genetic composition of populations (Dingemanse et al., 2003). Variation in novelty reactions can also be linked to other polymorphisms such as distinct differences in coloration in the same population. For instance, melanin-based polymorphism in siskins (*Carduelis spinus*) was linked to variation in the speed to approach a novel object with faster approach in individuals with a larger black bib (Mateos-Gonzalez and Senar, 2012). Polymorphism in general has been proposed to enhance ecological success, particularly in the light of environmental change, due to individuals utilizing different environmental resources and behavioral strategies (Forsman et al., 2008). Accordingly, a mix of personalities has been found to facilitate earlier entry into novel environments or better patch exploration in combination with improved group cohesion as compared to groups consisting of single personalities (Dyer et al., 2009; Aplin et al., 2014). However, other studies have challenged the adaptational advantage of polymorphic species due to constraints of correlational evolution of traits and interdependence of morphs (Bolton et al., 2015).

Overall, the interspecific and intraspecific variation in spatial novelty responses and the link to habitat specialization and movement suggest a potential mechanism for the maintenance of avoidance traits affecting decision-making and information gathering. Such persistent avoidance should therefore be useful for predicting how space use patterns will carry over into novel habitats.

The current study aimed to investigate how decision-making about engaging with unfamiliar environments is affected by spatial neophobia and neophilia in the ecologically highly specialized Gouldian finch (*Erythrura gouldiae*). Gouldian finches are color polymorphic in both sexes consisting of three distinct head colors (Brush and Seifried, 1968). Head colors signal personality, including responses to novelty. Black-headed birds were more explorative when facing environmental changes (object neophilia) and risk-prone in dangerous environments but less aggressive than red-headed birds (Mettke-Hofmann, 2012; Williams et al., 2012). Gouldian finches are classed as endangered by the Australian Government (EPBC, 2018) and as near threatened in the IUCN Red List (BirdLife International, 2016) due to habitat change (Legge et al., 2015; Weier et al., 2016). Knowledge about how the species responds to unfamiliar habitats in an increasingly fragmented landscape is important to understand population persistence, particularly as populations are far apart and an estimated number of only approximately 2,500 individuals remain in the wild (Legge et al., 2015; Weier et al., 2016; EPBC, 2018).

While the species shows low site-fidelity (Bolton et al., 2016) and is nomadic during the wet season, tracking resources over extensive areas (Dostine et al., 2001), little is known about its responses to habitat change and habitat fragmentation. However, from its ecology one would expect little hesitation to enter unfamiliar environments due to its nomadic nature, but this may only apply for suitable habitats due to its high habitat specialization. If Gouldian finches only readily explore habitats that they are specialized to use, their movements may be increasingly compromised or hindered by continuing habitat fragmentation. The role that cognitive and behavioral differences between the color morphs may play in orchestrating novelty reactions is currently unknown. We aimed to investigate (a) whether morphs differ in their spatial neophobia/neophilia affecting information gathering and decision-making to enter unfamiliar environments that differ in their ecological suitability and (b) whether the morph combination (same head color or different head colors) in a group affects these decisions. Considering morphs will provide a more nuanced picture of the species' cognitive ability to respond to habitat change and its ability to overcome gaps in suitable habitat availability.

We exposed the black-headed and red-headed morphs to two unfamiliar environments – one simulating an open habitat in correspondence with their habitat preference, the other one a dense habitat. We measured each bird's number of attempts to approach the novel habitat before entering (revealing their level of approach-avoidance conflict, Mettke-Hofmann et al., 2009), and their latency to enter the novel habitat. Due to the highly social nature of the species and to address our second aim, birds were tested in pairs of same sex birds. The following predictions were made.

(1) As an open habitat specialist, we expected Gouldian finches to enter the open habitats earlier than the dense habitats and to show a lower approach-avoidance conflict for the open habitat (due to less spatial neophobia).

(2) Morphs often differ in behavior and cognition. We therefore expected black-headed birds to enter the novel habitats earlier than red-headed birds as the former are more neophilic toward changes in their familiar environment (Mettke-Hofmann, 2012; Williams et al., 2012) which may translate to novel spaces. Consequently, the number of approach attempts before entering may differ as a function of differences in spatial neophilia, despite similar neophobia levels (Mettke-Hofmann, 2012).

(3) Group composition can affect behavioral responses (Dyer et al., 2009). We expected head color combination to effect decision-making with mixed head colors entering faster than pure head color combinations. If black-headed birds are faster to enter, they may facilitate faster entry in red-headed birds with or without reducing the number of approach attempts in red-headed birds.

MATERIALS AND METHODS

Gouldian finches are diet and habitat specialists preferring open savannah woodlands with suitable breeding trees and understory dominated by annual grasses for foraging on seeds

(Dostine et al., 2001; Dostine and Franklin, 2002; Weier et al., 2016). Their color polymorphism consists of about 70% black-headed, 30% red-headed and less than 1% yellow-headed birds in both sexes in the same population (Brush and Seifried, 1968). The red/black polymorphism is located on the z chromosome with the red allele being genetically dominant (Toomey et al., 2018). Population declines have been attributed to habitat change caused by current fire regimes and cattle grazing affecting resource availability (Legge et al., 2015; Weier et al., 2016).

Experiments were conducted under controlled conditions in the laboratory. Thirty-two wild type, parent-reared Gouldian finches originating from 12 private breeders took part in the study. Ages ranged from 1 to 6 years and the sex ratio was equal with 16 males (eight of each head color) and 16 females (seven red-headed and nine black-headed). Birds were housed in flight cages (1.20 m × 0.80 m × 1.00 m) in groups of five to six birds of mixed age, sex and head color. The only exception were ten 1-year old birds, which were housed in same sex groups to avoid harassment. All birds were purchased when 1 year old and knew each other from changing group compositions linked to experiments and moving birds between holding cages. Cages consisted of a mixture of natural branches and perches. Food was offered in feeders consisting of a mixture of Astrilden Spezial, Amadinen-Zucht Spezial, and Red Sibirica millet (all products from Blattner-Heimtierfutter, Ermengerst, Germany). Additional feeders contained grit (Blattner-Heimtierfutter) and egg shells. Water was available *ad libitum*. Birds were kept at 24°C with full spectrum light at a light:dark cycle of 13:11 h. All birds took part in a food neophobia test (Eccles et al., unpublished) which ran the week preceding the spatial neophobia/neophilia testing and novel object experiments conducted in the morning before the spatial experiments.

Experimental Setup and Procedure

Experiments were conducted in six experimental cages (1.20 m × 0.70 m × 1.00 m) located in a separate room from the holding cages. Each experimental cage had three wooden walls with wire mesh on the front and the ceiling. Cages were arranged in two rows of three cages, each. Birds from the two rows could not see each other. The outer two cages in a row were used as the home cage during the experiment. Home cages consisted of two perches left and right in the cage 30 cm away from the side wall and a perch running parallel to the front wire. Food and water were offered at the front of the cage. Each home cage had a movable partition (15.5 cm × 19 cm) in one sidewall providing access to the middle cage with the new spatial environment. The new spatial environment simulated an open or dense habitat. For both habitat types, the novel room had three perches, the two outer ones at the same height as the lower border of the partition and the middle one about 10 cm higher (**Figure 1**). Furthermore, six cardboard tubes (4 cm × 45 cm) were attached to the ceiling. In experiment 1 for the open habitat, these tubes were decorated with green eucalyptus leave garlands made of soft plastic tightly woven around the tube. They covered relatively little area in the novel spatial environment (**Figure 1A**) simulating an open habitat. For the dense habitat, silken Daisies were used consisting of green leaves and yellow/white flowers. Daisies were loosely woven around the tube occupying much more space in the novel spatial environment representing a denser habitat (**Figure 1B**). The dense habitat deviated from the birds' preferred habitat, potentially increasing neophobia, and was also more complex than the open habitat, potentially hiding more threats (Mettke-Hofmann et al., 2006). In experiment 2, the open habitat consisted of silken green vine leave garlands (**Figure 1C**) tightly woven around the tube and the dense habitat of silken roses consisting of dark green leaves and red flowers loosely woven around the tube (**Figure 1D**). All birds experienced all four habitats.

Pairs were strategically formed for the experiments to help control for variables such as age and sex, and to test our hypothesis about the influence of partner head color. Pairs were formed with same sex individuals, matching partners for size (average tarsus length 15.02 mm, mean difference 0.64 ± SE 0.10 mm) and body mass (average mass 20.11 g, mean difference 2.4 ± SE 0.35 g) as much as possible. Age has been shown to affect object neophobia (Mettke-Hofmann, 2012). As we could not match same-sexed birds of the same age due to unequal age distribution, we decided to have all pairs of different age for consistency. Birds in a pair were at least 2 years apart.

To address our hypothesis about group composition, all birds were tested with a partner of the same head color and a partner of the different head color in separate experiments. Half of the birds were first paired with a partner of the same head color and half with a partner of the different head color (experiment 1). This was reversed in the second experiment which started once all birds had been through experiment 1. The interval between experiment 1 and 2 ranged from 3 to 18 weeks for individual birds. In each experiment, half of the pairs were exposed to the open habitat first, whereas the other half experienced the dense habitat first balanced for head color combination and sex. The two open and dense habitats could not be balanced across experiments due to the re-pairing of the birds. As we had more black-headed than red-headed females and also uneven numbers within head colors, two black-headed females were tested with partner birds in both experiments that had gone through their own testing already (hereafter named experienced partner bird). In experiment 2, two additional black-headed females and one red-headed female were tested with experienced partner birds. Only the responses of the focal birds were included from these pairings, whereas for all other pairings both individuals in a pairing were considered.

Four pairs could be tested simultaneously with head color combination and sex balanced across cages. Overall, four batches with four pairs each were tested over a period of 8 weeks. Pairs were moved to the experimental cages for 2 weeks, first undergoing food neophobia testing (week 1) as part of a separate experiment. Spatial neophobia experiments commenced on day 11 or 12 as two pairs each had access to the same novel environment from different sides. On day 13 or 14 birds got access to the other habitat than experienced before. Birds were given access to the novel habitats for 3 h from 12:00 to 15:00, by temporarily removing the partition separating the two cages. Behaviors were video recorded with digital video cameras using GeoVision 1480 for later analysis.

FIGURE 1 | Novel environments representing open and dense habitats. In the first experiment, pairs of Gouldian finches got access to an open habitat simulated by soft plastic eucalyptus leaves tightly woven around cardboard tubes **(A)** and a dense habitat simulated by silken daisies **(B)**. The pictures show the habitats from outside with access for the birds from either the right or left side. Experiments were repeated with different pair compositions and silken vines for the open habitat **(C)** and silken roses for the dense habitat **(D)**. The pictures show the view for the birds through the opened partition.

Data Preparation

Data preparation and statistical analyses were performed in R version 3.6.0. (R Core Team, 2019). Raw data can be found in the **Supplementary Materials** (S1). We extracted two response variables: (1) number of approach attempts before entering the novel environment and (2) latency to enter the novel environment. An approach attempt was recorded when the bird landed either on the perch closest to the open partition (30 cm from the opening) or on the lower part of the opening without flying into the novel environment. The number of approaches provided a measure of the approach-avoidance conflict between the motivation to enter and explore the novel environment (neophilia) and the motivation to avoid the novel environment due to potential danger (neophobia; Mettke-Hofmann et al., 2009). Latency to enter the novel environment was measured as the time between removing the partition and the bird flying into the novel environment. Birds that did not enter a habitat within the 3 h were given the maximum time of 10,800 s. The two response variables were not correlated (Pearson correlation: $r = 0.314$, df = 29, $P = 0.09$). Due to unrelated circumstances, one bird died after the first experiment and was not included in the analyses resulting in a sample size of 31 birds.

Statistical Analysis

Initially, we fitted linear mixed models using the R package 'lme4' version 1.1-20 (Bates et al., 2015) to analyze our two response variables: number of approaches and entry latency. For number of approaches, transformation did not improve distribution and therefore we specified a Poisson family error distribution with log-link function in a generalized linear mixed model (GLMM) for the untransformed data. For entry latency we log transformed data to improve the distribution and used the default family error structure (Gaussian) in a linear mixed model (LMM).

For each response variable, we built two full models: one model to address hypotheses 1 and 2 regarding novelty responses to the two habitat types and the effect of morph on these reactions, the other model to address hypothesis 3 about social effects of morph composition. The analyses were separated into these two models for each response variable to avoid inclusion of too many variables in any single model. All explanatory variables were factors with two levels. To test our hypothesis about the relationship between habitat type and morph response (model 1), we entered into each model two predictor variables: habitat type (dense and open) and head color (black and red); and two control variables: age (1 year old, older than 1 year; to control for age effects linked to experience; Langham, 2006; Benson-Amram and Holekamp, 2012; Mettke-Hofmann, 2012; Biondi et al., 2013) and experiments (1, 2; to account for the repeated testing). We included the three-way interaction between habitat type, head color and experiment because novelty responses to the open and dense habitat may differ between morphs (stronger differences toward the more deviating and complex dense habitat) and these differences may be particularly prevalent during the first experiment as the entire situation was new. Sample sizes in the three-way interaction for all comparisons were $n = 31$ birds (124 rows of data) as all birds were tested in both head color combinations and both habitat types. Where the three-way interaction was not significant, its component two-way interactions were tested and retained in the final model only when significant: habitat type × head color, experiment × head color and habitat × experiment. To test our third hypothesis about effects of social factors (model 2), we entered into each model two predictor variables: head color (black and red) and partner head color (black and red) and one control variable: relative age within each pairing (younger or older to account for age effects within pairings as found in earlier studies; Mettke-Hofmann, 2012). We included the two-way interaction between head color and partner head color because the combination of morphs may matter (e.g., Dyer et al., 2009). Bird identity, partner identity and cage number were entered as crossed random effects in all models (crossed rather than nested because assigning birds to new pairings for experiment 2 precluded birds being tested in the same cage as in experiment 1). To account for using the same data in both models we used sequential Bonferroni adjustments were necessary (Rice, 1989; Chandler, 1995).

We inspected interaction terms, retaining all interactions that were $P < 0.05$ and excluding all others, in a stepwise model simplification, following Crawley (2012). Orthogonal data are robust to stepwise removal of interaction terms as variation attributable to each factor is constant at each stage of the stepwise simplification (Crawley, 2012). All main predictor and control variables were retained as fixed effects in all final models. Retaining fixed effects in final models minimizes repeated testing and hence concern about the risk of type I errors (e.g., Steel et al., 2013) and increased our ability to interpret model output and effect size calculations in a biologically meaningful way (e.g., Nakagawa and Cuthill, 2007). We adjusted convergence tolerance using the arguments 'allFit' and 'control' to specify the optimizer to 'bobyqa' and increased the number of iterations to 100,000, a practice considered 'gold standard' for ensuring stable model fit (Bates et al., 2019). Model fit was assessed by visually inspecting plots of fitted model residuals to ensure an even spread of residuals, which we found in all cases. We assessed each final model by comparing it against the null model (an identical model except for the removal of the predictor and control variables, with an intercept of 1 specified) using the anova command in R. The final model was only accepted where it was a significantly better fit than the null model (Burnham and Anderson, 2002). To aid model interpretation significant interactions were explored using appropriate planned *post hoc* comparisons.

We checked for evidence of collinearity within models using the function 'vif' (variance inflation factor) in the package 'car,' and extracted effect sizes using the r.squaredGLMM command in the package MuMIn (Barton, 2015). To facilitate future meta-analyses, we report both marginal and conditional effect sizes, r^2m and r^2c, respectively, where r^2m explains variance due to fixed effects and r^2c explains variance due to fixed and random effects (Nakagawa and Cuthill, 2007). We assessed repeatability (R) of behavior by accounting for the degree of variation attributable to bird identity using the rptR package (Stoffel et al., 2017). Repeatability can highlight persistent differences in novelty reactions between individuals (Dingemanse et al., 2003; Nakagawa and Schielzeth, 2010).

Finally, we re-ran all models with a restricted data set ($n = 25$ birds; 100 rows of data) excluding all focal birds that had been tested with an experienced partner bird to control for possible influences of these experienced partners on the focal birds' behavior.

Ethical Note

We conducted all experiments in accordance with published guidelines for the treatment of animals in behavioral research (ASAB/ABS guidelines, ASAB, 2018; ARRIVE guidelines; Kilkenny et al., 2010). Holding and experimental aviaries conformed to Home Office codes of practice (Home Office, 2013) and were carried out in approved facilities within Liverpool John Moores University. All experiments were non-regulated by the Home Office and complied with the ethical and welfare guidelines for animals and the legal requirements of the University (CMH_GE/2016-5) and the United Kingdom.

RESULTS

Responses to the novel environments differed between individual birds: In experiment 1, all birds entered the open habitat and 26 out of 31 birds entered the dense habitat. Birds that did not enter were three black-headed birds and two red-headed birds. In experiment 2, all but one bird (black-headed) entered the open habitat and 27 out of 31 birds the dense habitat. Birds that did not enter were three black-headed birds and one red-headed bird. Overall, six birds (four black-headed and two red-headed) failed to enter a particular habitat (all but one dense) of which two (one red and one black) never entered any dense habitat and one black-headed bird only entered the first open habitat.

Number of Approaches

There was no significant three-way interaction between habitat type, head color and experiment number on number of approaches (model 1). Removal of this term revealed a significant two-way interaction between head color and experiment (GLMM: LRT = 5.848, $P = 0.016$; **Table 1A**). Planned *post hoc* comparisons revealed black headed birds made significantly more approaches prior to entering in experiment 1 than they did in experiment 2 (Wilcoxon signed rank test: $V = 117$, $P = 0.001$; **Figure 2**). All other planned *post hoc* comparisons were non-significant (all Ps > 0.16). There was a main effect of habitat type (LRT = 45.935, df = 1, $P < 0.001$). Birds made more approaches before entering dense habitat (mean = 5.47 ± SE = 0.64) compared to open habitat (2.98 ± SE = 0.30). There was no effect of age (1 year vs. older) on number of approaches. Effect size for number of approaches was larger when random effects were included ($r^2m = 0.22$; $r^2c = 0.65$). Repeatability of number of approaches approached significance ($R = 0.14$, $P = 0.068$). Repeatability of number of approaches was significant for black-headed birds ($R = 0.29$, $P = 0.019$) but not for red-headed birds ($R = 0$, $P = 1$).

When we re-ran the analysis using the restricted dataset the three-way interaction between head color, habitat and experiment was significant (GLMM: $n = 25$; LRT = 5.064, $P = 0.024$; S2) including all associated two-way interactions between head color and experiment ($z = 2.857$, $P = 0.004$), head color and habitat ($z = 1.990$, $P = 0.047$) and habitat and experiment ($z = 2.074$, $P = 0.038$; S2, **Supplementary Table S1**). Planned *post hoc* comparisons revealed that black-headed birds made significantly more approaches in experiment 1 than they did in experiment 2 (Wilcoxon signed-rank test: $V = 54$, $P = 0.008$), that during experiment 1 black headed birds made more approaches to dense habitat than open habitat (Wilcoxon rank sum test: $W = 547$, $P = 0.009$), and they did so significantly more than did red-headed birds (Mann–Whitney test: $U = 140$, $P = 0.051$; S2, **Supplementary Figures S1, S2**). All other planned *post hoc* comparisons were non-significant (all Ps > 0.06). There was no significant effect of age (S2, **Supplementary Table S1**). This largely confirms the findings from the full data set but also reveals some additional effect of head color.

The GLMM to test for social factors (model 2) did not retain any significant variables and the variables did not explain the data any better than the null model (**Table 1B**). The restricted dataset resulted in a significant two-way interaction between head color and partner head color (GLMM: $n = 25$; LRT = 5.820, $P = 0.016$; S2, **Supplementary Table S1**). Planned *post hoc* comparisons revealed that red-headed birds paired with another red-head made significantly fewer approaches than they did when paired with a black-headed bird (Wilcoxon signed rank test: $V = 33$, $P = 0.042$; S2, **Supplementary Figure S2**). All other head color combinations were non-significant (all Ps > 0.235). There was no significant effect of relative age within pairs. Results of the two models remained significant after sequential Bonferroni correction.

Entry Latency

There was a significant three-way interaction between habitat type, head color and experiment on latency to enter the two habitat types (model 1; LMM: $n = 31$; LRT = 5.967, $P = 0.015$; **Table 2A**) including the associated two-way interactions between head color and habitat type ($t = 2.509$, $P = 0.012$, **Table 2A**) and between head color and experiment ($t = 2.603$, $P = 0.009$; **Table 2A**). Planned *post hoc* comparisons revealed the interaction was driven by the significantly longer entry latency of black-headed birds to dense habitat in experiment 1 compared to red-headed birds (Mann–Whitney test: $U = 176$, $P = 0.025$, **Figure 3**). All other planned *post hoc* comparisons were non-significant (all Ps > 0.077). Age did not affect entry latencies.

TABLE 1 | Results of the general linear mixed effects model on the number of approaches before entering the novel open and dense habitats of Gouldian finches addressing **(A)** the effect of ecological variables and color morphs and **(B)** social effects.

	(A) Effects of ecological variables and head color (model 1)					
	Estimate	***SE***	***z*-value**	***P*-value**	**CI (2.5%)**	**CI (97.5%)**
(Intercept)	0.97	0.33	2.91	0.004	0.32	1.62
Key predictor						
Habitat type (open)	0.61	0.09	6.71	<0.001	0.43	0.78
Head color (red)	−0.68	0.37	−1.84	0.066	−1.40	0.05
Controls						
Experiment	−0.47	0.14	−3.40	<0.001	−0.75	−0.20
Age (1-year-old)	0.07	0.21	0.34	0.737	−0.34	0.49
Interactions						
Experiment × head color	0.54	0.21	2.52	0.012	0.12	0.96
	(B) Social effects (model 2)					
	Estimate	***SE***	***z*-value**	***P*-value**	**CI (2.5%)**	**CI (97.5%)**
(Intercept)	1.41	0.33	4.29	<0.001	0.77	2.06
Key predictor						
Head color (red)	0.10	0.19	0.53	0.594	−0.27	0.47
Partner head color	−0.19	0.12	−1.54	0.123	−0.42	0.05
Controls						
Relative age (within pairs)	0.09	0.16	0.58	0.560	−0.22	0.41

Only the final model of each analysis is shown. The reference modality is in parentheses.

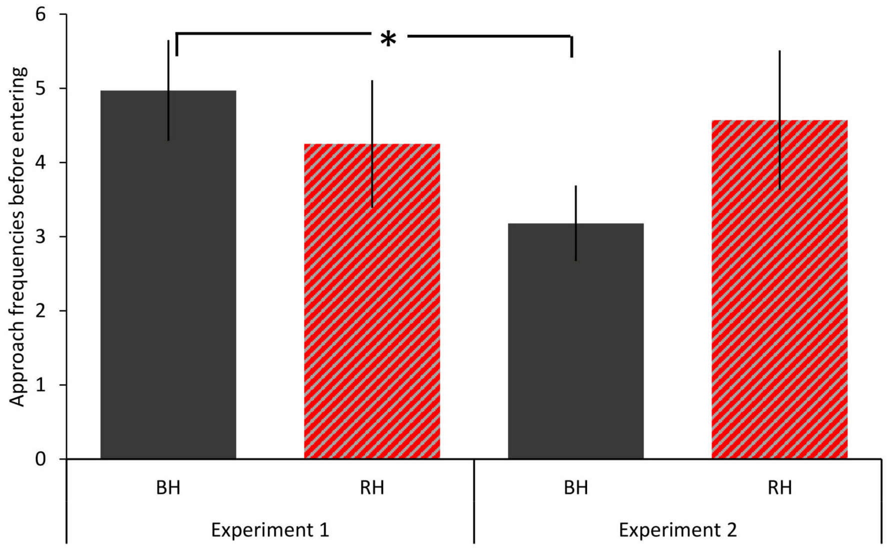

FIGURE 2 | Effects of head color and experiment on number of approaches before entering the novel habitats. In experiment 1, same sex pairs of either same or different head color were tested on their response to enter an artificial open habitat (their preferred habitat type) and an artificial dense habitat. In experiment 2, birds were tested in the opposite head color composition with a new open and dense habitat. Mean and SE of number of approaches to novel habitats in the first and second experiment for each head color. **P* < 0.05. Black bars: black-headed birds (BH), striped red and gray bars: red-headed birds (RH).

TABLE 2 | Results of the linear mixed effects models on the entry latencies of Gouldian finches into open and dense habitats addressing **(A)** the relationship between ecological variables and color morph and **(B)** social effects.

	(A) Effects of ecological variables and color morph (model 1)					
	Estimate	***SE***	***t*-value**	***P*-value**	**CI (2.5%)**	**CI (97.5%)**
(Intercept)	−0.83	0.02	−53.67	<0.001	−0.86	−0.80
Key predictor						
Habitat type (open)	−0.02	0.02	−1.13	0.257	−0.06	0.02
Head color (red)	−0.06	0.02	−2.87	0.004	−0.10	−0.02
Controls						
Experiment	−0.01	0.01	−1.54	0.124	−0.03	0.00
Age (1-year-old)	0.01	0.01	1.59	0.113	−0.00	0.03
Interactions						
Habitat type × experiment	0.01	0.01	0.63	0.528	−0.02	0.03
Habitat type × head color	0.07	0.03	2.51	0.012	0.02	0.12
Experiment × head color	0.03	0.01	2.60	0.009	0.01	0.06
Habitat type × experiment × head color	−0.04	0.02	−2.41	0.016	−0.07	−0.01
	(B) Social effects (model 2)					
	Estimate	***SE***	***z*-value**	***P*-value**	**CI (2.5%)**	**CI (97.5%)**
(Intercept)	−0.85	0.01	−61.16	<0.001	−0.88	−0.82
Key predictor						
Head color (red)	−0.01	0.01	−1.29	0.196	−0.03	0.01
Partner head color	0. 01	0.01	0.95	0.340	−0.01	0.02
Controls						
Relative age (within pairs)	0.0	0.01	0.19	0.854	−0.01	0.02

Only the final model for each analysis is shown. The reference modality is in parentheses.

Effect size for entry latencies was larger when random effects were included ($r^2m = 0.12$; $r^2c = 0.46$). Entry latencies across all birds were repeatable (0.33, $P < 0.001$). Entry latencies across head colors were not repeatable but showed a trend in black-headed birds, ($R = 0.26$, $P = 0.087$) but not in red-headed ones ($R = 0.15$, $P = 0.195$). The restricted data set model

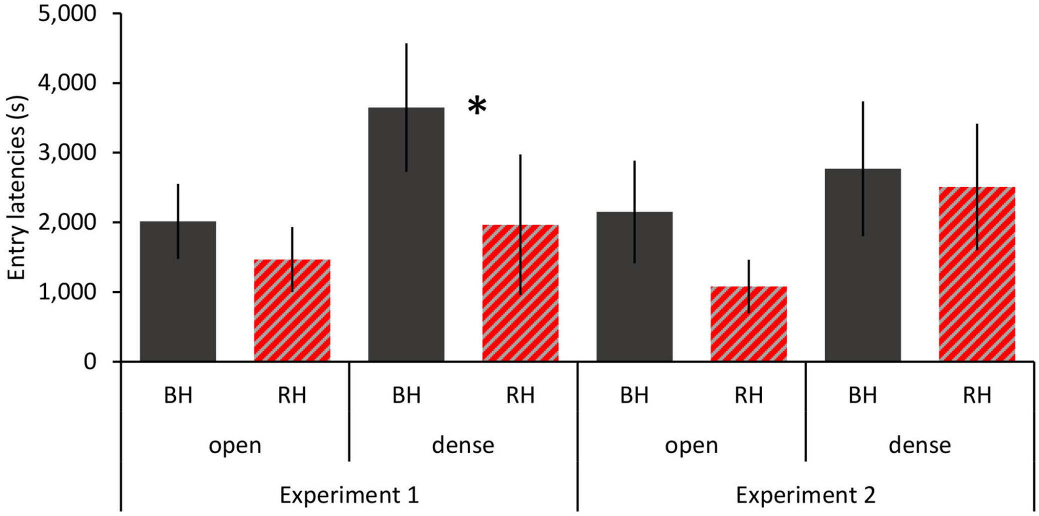

FIGURE 3 | Effects of habitat type, head color and experiment on entry latencies of Gouldian finches to unfamiliar habitats. The experimental setup was the same as in **Figure 2**. Mean and SE for entry latencies into open and dense habitats for experiments 1 and 2 and the two head colors. Cut-off points for entry latencies were 10,800 s (3 h). Black bars: black-headed birds (BH), striped red and gray bars: red-headed birds (RH). $*p < 0.05$.

($n = 25$) confirmed the findings from the full data set model (S2, **Supplementary Table S2**).

The LMM output to test for social effects (model 2) did not retain any significant variables and the variables did not explain the data any better than the null model (**Table 2B**). Similarly, the restricted data set model ($n = 25$) did not retain any significant variables (S2, **Supplementary Table S2**).

DISCUSSION

We investigated novelty responses of the color-polymorphic Gouldian finch toward unfamiliar habitats that deviated to different degrees from their preferred habitat. Decisions to enter unfamiliar habitats differed between open and dense habitats and were affected by head color. All birds showed more approach-avoidance conflict before entering the dense as compared to the open habitat. Additionally, black-headed birds entered the dense habitat later, particularly during the first experiment.

Novelty Responses to Open and Dense Habitats

As an open habitat specialist (Brazill-Boast et al., 2013), we expected Gouldian finches to take longer to enter the dense habitat and show a stronger approach-avoidance conflict for this habitat (hypothesis 1). Nearly all Gouldian finches entered the novel open habitat quickly, on average within half an hour, and demonstrated a low approach-avoidance conflict; both of which indicate low spatial neophobia and high spatial neophilia toward their open habitat preference. This mirrors similar novelty reactions in migratory birds (Mettke-Hofmann et al., 2009) facilitating swift entry into unfamiliar but suitable habitats. These novelty reactions seem to be well suited for the nomadic lifestyle of the Gouldian finch.

The picture changed when confronted with dense habitats, particularly for black-headed birds. Almost a third of the black-headed birds refused to enter one of the dense habitats, their entry latencies in the first experiment nearly doubled compared to the open habitats, and they made more approach attempts before entering. Their behavior suggests considerable avoidance of a habitat type that deviates from their preferred habitat, supporting hypothesis 1. Higher neophobia toward novelty that deviates stronger from what has been experienced before or from innate preferences has been shown in other species (Grünberger and Leisler, 1993; Greenberg and Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2006). Moreover, the dense habitats were more complex than the open ones, potentially hiding more threats (Mettke-Hofmann et al., 2006). The black-headed birds' repeated approaches allowed them to collect information about the novel habitat, thereby reducing uncertainty (Inglis et al., 2001) and subsequently neophobia. In Sardinian warblers, spatially neophobic individuals not only had a higher frequency of approaches to but also spent more time in front of a novel environment supporting the idea of information gathering (Mettke-Hofmann et al., 2009). Overall, black-headed birds seem to be repelled by deviating habitats, which may affect decisions about small-scale as well as large scale movements in fragmented landscapes.

In contrast, red-headed birds showed a lesser response to dense habitats, supporting hypothesis 1 only partly. While they appeared more afraid of the dense than the open habitat (more approach attempts), they also seemed to be motivated to explore this unfamiliar habitat because they showed similar entry latencies as compared to the open habitat. Consequently, unsuitable habitats may be less of a barrier for red-headed than black-headed birds. This is an unexpected finding and clearly rejects hypothesis 2 that predicted black-headed birds to enter unfamiliar habitats faster. In other contexts, red-headed birds were known to be less neophilic than black-headed birds (Mettke-Hofmann, 2012; Williams et al., 2012). The finding contributes to the growing evidence that novelty reactions are context dependent (e.g., Greggor et al., 2016b).

Interestingly, similar opposing novelty responses to changes in the familiar environment and novel spatial environments have been found in resident and migratory warbler species (Mettke-Hofmann et al., 2005, 2009). The black-headed birds' novelty responses resemble a resident response (Mettke-Hofmann et al., 2005) with early approach to and investigation of any change in their familiar environment (Mettke-Hofmann, 2012; Williams et al., 2012) but reduced interest to enter unsuitable novel environments. This is further supported by an increased approach-avoidance conflict to enter unsuitable habitat in experiment 1 as found in the restricted model (note that this was not the case in the model with the full data set). Red-headed birds' novelty responses are like a migrant's response with a low propensity to explore changes in the familiar environment (Mettke-Hofmann, 2012; Williams et al., 2012) but fast entry into unfamiliar environments (Mettke-Hofmann et al., 2009). Consequently, the two morphs may cognitively complement each other in different situations. While black-headed birds thoroughly assess changes in their familiar environment and may be able to find new resources from which red-headed birds can benefit (Williams et al., 2012), red-headed birds are more prone to venture into new and potentially unsuitable habitats facilitating movements across fragmented landscapes. As a gregarious species, individuals of both morphs may benefit from their diverging cognitive strategies and make them better prepared for environmental change, which could improve survival and population persistence. Moreover, since the polymorphism exists across the entire species' distribution, i.e., is not restricted to a mixing zone where the two morphs meet as in many other polymorphic species (e.g., Roulin, 2004; Holderby et al., 2014), individuals may benefit from associating with different morphs. This supports Forsman et al. (2008) who proposed that polymorphic species are better prepared for environmental change due to the existence of different behavioral strategies.

Red-headed birds are usually more aggressive (Pryke and Griffith, 2006; Pryke, 2007; Williams et al., 2012) and their higher willingness to move into new habitats may help them find populations with fewer red-headed birds. This corresponds to similar findings in Great tits (*Parus major*). More aggressive individuals explored novel environments faster than less aggressive individuals (Verbeek et al., 1996). Fast explorers also dispersed further than slow explorers (Dingemanse et al., 2003). The former had also more problems coping with defeat (Verbeek et al., 1999) and their higher propensity to emigrate allowed them to settle into populations where they were subjected to less social stress (Dingemanse et al., 2003). In the Gouldian finch, red-headed birds are also more prone to social stress than black-headed birds when densities of red-headed birds increase (Pryke et al., 2007). In bluebirds, the more aggressive Western bluebird (*Sialia mexicana*) is the more successful colonizer as compared to the Mountain bluebird (*Sialia currucoides*; Duckworth and Badyaev, 2007) indicating that a combination of aggression and movement seem to be beneficial. Indeed, Duckworth and Kruuk (2009) showed that aggression and dispersal were genetically correlated in the Western bluebird. Besides a potential role of aggressiveness, our study shows that the willingness to enter and explore unfamiliar environments is another important component to initiate movement into the unknown.

Individual responses were in part repeatable across the two experiments, indicating that some individuals consistently refuse to interact with unsuitable habitats. Repeatability was higher and more often significant in black-headed than red-headed birds. Spatial novelty responses may be part of a larger personality syndrome characterizing an individual's strategy to cope with environmental challenges. Novelty responses to changes in the familiar environment in this species have been identified as being part of personality traits linked to their head color (Mettke-Hofmann, 2012; Williams et al., 2012). As the black morph accounts for about 70% of the population (Brush and Seifried, 1968) this could negatively affect decision making on the group level to move into unfamiliar habitats, particularly unsuitable ones, ultimately affecting movement patterns and gene flow.

Many of the differences linked to head color only occurred during the first experiment when the situation was entirely new. Most differences disappeared when presented with new environments a second time. This indicates that birds became more familiar with the general procedure and may have generalized from one experiment (and one habitat type) to the other. The ability to generalize to similar but unsuitable habitats may facilitate faster engagement with similar but unfamiliar and unsuitable habitats. Again, this would suit a nomadic lifestyle.

Social Effects on Novelty Responses

Morph composition did not affect the number of approaches in the full data set that included the experienced partner bird data but was significant in the restricted data set. As the experienced partner birds had experienced the situation before, they may have responded differently which could have affected the focal bird's responses. The restricted data set indicates that whenever a pairing included a black-headed bird, the number of approaches before entering increased. This rejects hypothesis 3 that predicted mixed pairs would have shorter entry latencies and potentially fewer approach attempts. Black-headed focal birds or focal birds of any head color partnered with a black-headed bird reacted more cautiously than pure red-headed pairs. This means that black-headed birds induce more hesitation and avoidance in other black-headed birds as well as red-headed birds. This shows that Gouldian finches pay attention to responses of others, particularly black-headed birds, resulting in social conformity (Frost et al., 2007; Magnhagen and Bunnefeld, 2009; Hellstroem et al., 2011). Conformity has also been found in Gouldian finches with respect to risky situations when risk-prone birds became slower when paired with a risk-averse partner and risk-averse birds became faster with a risk-prone partner (King et al., 2015). The only exception to this was when black-headed birds were tested with red-headed birds; black-headed birds did not conform to red-headed birds (King et al., 2015). Interestingly, in our experiment red-headed birds did not affect responses in other birds either. Nonetheless, the effect of black-headed birds on others may improve group cohesion as has been found in species with mixed personalities (Aplin et al., 2014). An effect of group composition with respect to head color was only found in the restricted data set and only for the number of approach attempts. More research with a larger data set is needed to substantiate these findings.

It is currently unclear whether the increased cautiousness in black-headed birds would translate into delayed entry latencies in black-headed dominated groups as they occur in the wild (Brush and Seifried, 1968), but is worth further investigation. Currently, habitat fragmentation does not pose a major barrier for Gouldian finches as there is no evidence of genetic differentiation between populations (Bolton et al., 2016). Nonetheless, fragmentation may affect behaviors during more stationary periods such as breeding. For example, the distance birds flew for extra-pair copulations in Hooded warblers (*Wilsonia citrina*) was restricted by habitat fragmentation, with excursions not exceeding 500 m in fragmented habitats, despite otherwise moving up to 2.5 km (Norris and Stutchburry, 2001) indicating that perception of habitat suitability rather than physical abilities affected movement decisions. If habitat fragmentation restricts decisions about foraging movements in Gouldian finches during breeding or molting before they become nomadic during the wet season (Bolton et al., 2016), then this can negatively affect breeding success and individual condition, particularly in the black-headed morph. Indeed, Gouldian finches living in areas with extreme fire regimes and therefore low availability of suitable seeds at the end of the dry season have lower body condition and higher stress levels than populations with less severe fire regimes (Legge et al., 2015). Unfortunately, the study did not distinguish between red-headed and black-headed birds. The current study would predict that black-headed birds are more affected by food shortage in fragmented habitats as they may be less willing to move into unsuitable habitats than red-headed birds. Over the long-term, this could change morph numbers. Moreover, the higher willingness of red-headed birds to cross unsuitable habitats may have consequences for dispersal as red-headed birds may disperse further than black-headed ones. Again gene flow would be affected and maintained by the more dispersing morph as has been found in several woodland bird species where the more dispersive sex maintained genetic connectivity across fragmented landscapes (Amos et al., 2014). Likewise, novelty responses may affect site faithfulness. While Gouldian finches are nomadic during the non-breeding season, the cognitively more resident-like black-headed birds may decide to return to known sites for breeding, whereas the red-headed birds that cognitively resemble a more migratory type may be more willing to settle in new areas. However, current conservation oriented research with the Gouldian finch (e.g., Brazill-Boast et al., 2011a,b, 2013; Legge et al., 2015; Maute et al., 2015; Weier et al., 2016) rarely considers morph-specific differences in responses.

CONCLUSION

The current study contributes to the growing evidence that morphs differ in their decision-making and may follow different cognitive strategies when encountering unfamiliar situations. While black-headed morphs invest in local exploration and information gathering, which helps them to update information and keep track of newly emerging resources in their familiar environment, red-headed morphs are better cognitively equipped for movements as they have a high motivation to enter unsuitable habitats and which may allow them exploiting a larger area despite habitat fragmentation. Therefore, the two morphs may cognitively complement each other in different novel situations providing an advantage in rapidly changing environments. Interestingly, whenever black-headed birds were involved in pairings, focal birds showed more cautious spatial behavior, which may help group cohesion. More research is needed regarding the effect of the existing morph ratios on novelty responses as the majority of birds in the wild are black-headed, which may facilitate local exploration and adaptation but hinder larger scale movements in fragmented landscapes.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

The animal study was reviewed and approved by Liverpool John Moores Ethical Team (CMH_GE/2016-5).

AUTHOR CONTRIBUTIONS

GE conducted all experiments, transcribed all data, did initial analyses, and provided the general part of the Methods section. EB analyzed the data for the manuscript and wrote the Methods and Results section. AG contributed to the experimental design and initial analyses and gave important intellectual feedback on the manuscript. CM-H came up with the design, advised on data collection and analyses, and wrote the Abstract, Introduction, and Discussion. All authors contributed to manuscript revision, read and approved the submitted version.

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General Cognitive Ability Predicts Survival-Readiness in Genetically Heterogeneous Laboratory Mice

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Although genetically heterogeneous laboratory mice express individual differences in general cognitive ability (c.f., "intelligence"), it is unknown whether these differences are translated into behaviors that would promote survival. Here, genetically heterogeneous laboratory CD-1 mice were administered a series of cognitive tests from which their aggregate general cognitive ability was estimated. Subsequently, all animals were tested on nine (unlearned) tasks designed to assess behaviors that could contribute to survival in the wild. These tests included nest building (in the home and a novel environment), exploration, several indices of food finding, retrieval, and preference, and predator avoidance. Like general cognitive ability, a principal component analysis of these measures of survival-related behaviors (survival-readiness) yielded a general factor that accounted for ∼25% of the variance of mice across all of the tasks. An aggregate metric of general cognitive ability predicted an aggregate metric of general survival-readiness (r = 0.64), suggesting that more intelligent animals would be more suited for survival in natural environments. The nature of the pattern of correlations between general cognitive ability and performance on individual tests of survival-readiness (where tests conducted in previously unexplored contexts were more closely related to general cognitive ability) suggests the possibility that heightened attention (which is taxed in a novel environment) may be the common mediator of both of these classes of abilities, although other potential mediators are discussed. In total, these results suggest that performance on tasks that are explicitly intended to assess the likelihood of survival can be impacted by cognitive abilities.

Keywords: intelligence, survival, fitness, nest building, hoarding, foraging, mice

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INTRODUCTION

In response to the question "how do we know that our [IQ] tests are 'good' measures of intelligence?," Wechsler (1944) wrote:

> "The only honest answer we can make is that our own experience has shown them to be so. If this seems to be a very tenuous answer we need only remind the reader that it has been practical experience which has given (or denied) final validity to every intelligence test. Regrettable as it may seem, empirical judgements, here as elsewhere, play the role of ultimate arbiter."

To an empiricist, Wechsler's comment might seem to lack quantitative substance, instead relying on anecdotal observations to support the utility of the intelligence test. However, to the extent that IQ tests should predict functionally important life outcomes, the decades since Wechsler's statement have filled in the empirical gaps. It is now well-established that IQ tests predict a range of measures of academic success, such as grades, years of education, and performance on other standardized tests (such as the SAT or GRE; for review, see Gottfredson, 1998). A skeptic might be concerned that these correlations are to be expected, since all of these outcomes are dependent (to varying degrees) on test-taking abilities. Thus it is much more impressive that IQ test performance predicts outcomes that are not dependent on formal test-taking abilities, such as rank and performance ratings obtained in military service (Gottfredson, 2003), job performance ratings and satisfaction (Schmidt and Hunter, 1998), income and life-long earnings (Murray, 1998), and even such distantly related outcomes as the inverse relationship between IQ and racist beliefs (Dhont and Hodson, 2014), obesity (Richards et al., 2009), clinical depression (Gale et al., 2009), the likelihood of developing cancer, and even death by automobile accident (Leon et al., 2009). Given these observations, it is not surprising that IQ is directly related to longevity (Wilson et al., 2009). This list of outcomes predicted by performance on the IQ test has been necessarily truncated, but the predictive validity of IQ tests have been discussed more extensively elsewhere (e.g., Gottfredson, 1998, 2003).

Like humans, it is now established that variations in general cognitive performance can be detected across individuals in a variety of animal species including mice (Galsworthy et al., 2002; Matzel et al., 2003; Sauce et al., 2018), rats (Anderson, 1993; Locurto and Scanlon, 1998), birds (Shaw et al., 2015; but see Sorato et al., 2018), dogs (Arden and Adams, 2016), and several non-human primates (Herndon et al., 1997; Banerjee et al., 2009; Herrmann et al., 2010; Beran and Hopkins, 2018; Eisenreich and Hayden, 2018; Damerius et al., 2019). Notably, while the literature on human intelligence is replete with examples of the relationship between IQ test performance and real-life outcomes, very few such demonstrations have been reported in non-human animals. The paucity of predictive validation of these studies of animal "general intelligence" has been noted by Burkart et al. (2016) and Locurto (2017), who wrote that "an important, even critical limitation of such studies is that they lack something that is commonplace in studies of human *g* [general intelligence] – namely, what is called predictive validity," and this paucity of evidence compromises any assessment or conclusions about the nature of general intelligence in non-human species.

To the extent that it validates the utility of an intelligence test, the absence of data related to the predictive capacity of tests of non-human animal (hereafter "animal") intelligence is certainly problematic. It is notable though that some limited data suggests that at least specific cognitive abilities predict outcomes that would have apparent survival value. For instance, mice with characteristically high intelligence (assessed as aggregate performance across a battery of cognitive tests) exhibit more effective foraging for food (Wass et al., 2012) and better avoidance of contact with aversive stimulation (Matzel et al., 2006), and mice that are more intelligent exhibit more exploratory behaviors in what is determined to be a "safe" environment (a behavior that would promote better contact with critical environmental contingencies; Light et al., 2011). Likewise, tests of general intelligence in cotton-top tamarin monkeys have included measures that have clear implications for effective social interactions (Banerjee et al., 2009). In the wild (where more direct evidence of survival skills can sometimes be obtained), similar relationships have been observed. For instance, male New Zealand robins with superior spatial memory have greater breeding success and provide an increased proportion of larger prey items to offspring (Shaw et al., 2019). Similarly, Cole et al. administered problem solving tests to great tits (*Parus major*), and successful problem solvers produced larger broods of chicks and were more efficient foragers for food (Cole et al., 2012; also see Ashton et al., 2018). Cauchard et al. (2017) demonstrated that the link between cognitive abilities and brood size was causal in nature, i.e., while birds of higher cognitive abilities tended to maintain larger broods, direct manipulation of brood size did not in itself promote increases in cognitive ability. Other than reproductive behaviors, cognitive abilities sometimes predict other survival-related skills. For instance, the performance of mountain chickadees in a spatial learning task was predictive of the likelihood of surviving the birds' first winter (Sonnenberg et al., 2019), and longevity was predicted by spatial learning in male African striped mice, while in females of the species, performance on the same spatial task predicted the speed of their response to predators (Maille and Schradin, 2016).

Despite the seeming relationship between specific cognitive skills and survival, in other instances, specific cognitive abilities have not always predicted important functional outcomes such as song repertoire in birds that are dependent on these songs for reproductive success (MacKinlay and Shaw, 2019), and performance on a problem solving task did not predict mating success in male spotted bowerbirds (Isden et al., 2013). In one instance, pheasants that learned a reversal task more quickly were found to be *less* likely to survive in the wild (Madden et al., 2018). Thus consistent with Locurto's (2017) concern, the assessment of the predictive validity of tests of animal intelligence has been non-systematic and has yielded inconclusive results. In part, this may be a reflection of the limited nature of the cognitive tests that have previously been used to assess these relationships. Other than in monkeys, studies of the relationship between survival-related behaviors and cognitive abilities have tended to be limited to the assessment of animals' performance on single domain-specific abilities, e.g., spatial memory. (For a review of these and other relevant issues, see Orr, 2009; Thornton et al., 2014; Shaw et al., 2015).

A difficulty for the assessment of the predictive validity of tests of animal intelligence is that the administration of well-controlled and sensitive cognitive test batteries are facilitated by their administration to animals that are maintained in captivity, and this has been common in tests of mice, rats, dogs, and primates (although some exceptions have been reported in birds; e.g., Shaw et al., 2015). However, these captive (or protected) animals will not typically face the same demands on survival that would present themselves to wild animals, thus mitigating the study of ethologically-relevant survival-related outcomes. Moreover, many of the outcomes predicted by human intelligence tests are a product of the impact of intelligence on the integration and evaluation of available evidence and relevant information, e.g., the better diet selection (and less obesity/Type II diabetes) exhibited by more intelligent individuals is most certainly the product of more acquired awareness of dietary risks in addition to the better development of plans for mitigating those risks (for discussion, see Mackintosh, 1998). These same outcomes would not reasonably be anticipated in captive (or laboratory) animals, where things like diet availability are intentionally controlled (and a history of differential experiences cannot be drawn upon by the animals).

The present study represented our preliminary effort to assess the "functional" consequences of variations in mouse intelligence while still maintaining the laboratory conditions necessary to administer a controlled assessment of general cognitive abilities. Tests of survival-readiness were chosen that did not explicitly depend on prior experience and which had previously been suggested to have survival benefits (and/or which could reasonably be expected to impact the likelihood of survival in the wild, e.g., Deacon, 2006a,b). To this end, 56 genetically heterogeneous CD-1 mice were raised (under homogeneous conditions) in captivity and administered a diverse battery of cognitive tests (designed to characterize general cognitive ability) as young adults. Subsequently, these animals were administered a series of tests to assess unlearned skills related to survival, e.g., nest building in home and novel environments, foraging efficiency, exploration and food source discovery, food preference, and predator avoidance. Since these survival skills were nominally unlearned (a reasonable expectation in laboratory-reared animals), performance on these tests would provide an index of the extent to which general cognitive ability predicted functional (and survival-related) skills.

MATERIALS AND METHODS

Subjects

A total of 56 CD-1 outbred male mice from Harlan Laboratories (Indianapolis, IN, United States) were used. Animals were housed individually in standard shoebox home cages in a temperature-controlled colony room using a standard 12 h light-dark cycle. These animals are well-suited for studies of individual differences as the CD-1 mouse genome displays patterns of linkage disequilibrium and heterogeneity similar to wild-caught mice (Aldinger et al., 2009). In this, our first attempt to assess survival-related behaviors, we focused on only male animals as we have extensive previous experience in the assessment of general cognitive abilities in these animals. Animals arrived in the laboratory at approximately 8–10 weeks of age and were given *ad libitum* access to food and water except during testing that required food deprivation, when animals were given 120 min access to food starting on the day prior to testing, then each day following data collection. Prior to the start of testing (which began at approximately 12–14 weeks of age), animals were handled (i.e., held by an experimenter while walking throughout the laboratory test rooms) for 60 s/day for 7 days to minimize any stress that arises from handling. All procedures were conducted with approval with the Institutional Care and Use Committee (IACUC) at Rutgers University.

Procedures

Two phases of testing were administered to all animals. The first phase of testing was designed to assess general cognitive ability and was comprized of three distinct cognitive tasks (that yielded seven measures of cognitive performance) that depended on different underlying processes. Performance measures (indicative of rate of learning or problem resolution) from these tests were entered into a principal component analysis, to (1) determine the degree to which a general factor influenced performance across all cognitive tests, and (2) to generate factor scores for each animal. A factor score is essentially an average z-score of each animal's performance across all cognitive tests (where the individual tests are weighted according to their loading on the general factor). Thus these factor scores represent each animal's general cognitive performance relative to all of the animals that contributed to this sample.

Upon completion of the cognitive assessment, all animals were then subjected to a series of tests intended to assess performance on tasks with clear implications for animals' survival.

Cognitive Tests (Seven Dependent Measures)

The battery of cognitive tests employed here to assess general cognitive ability is somewhat different in nature than batteries that have been previously used in our laboratory, and notably, the performance in all of the cognitive tests in the current battery was motivated by food deprivation (whereas in prior batteries, several different motivational states were represented). It should be noted, however, that the current battery was compared to prior batteries and it was determined that the amount of cognitive variance accounted for by the present battery of tests was comparable in magnitude and structure to what has previously been reported (Crawford et al., 2020).

The sequence and nature of the cognitive tests are illustrated in **Table 1**.

The first three cognitive tests (that yielded six dependent measures) were conducted in a single piece of apparatus constructed as a convertible hybrid-style straight alley/Lashley maze. An illustration of this maze is provided in **Figure 1**. The tests administered in this maze included a simple discrimination task, egocentric navigation in a Lashley maze, a reversal of path direction in the Lashley maze, and two simple object-permanence puzzles.

Puzzle Solving in a Straight Alley (Yielding One Measure of Cognitive Performance)

Mice were placed in the start box of the maze for 5 s, after which the exit door was opened and the mice were free to traverse the alley. When mice reached the goal area of the maze, access to the alley was blocked to enclose them in the goal area. The goal area contained a single platform with a food dish holding one piece of accessible food and one piece of inaccessible food. Time taken by the mouse to retrieve the food was recorded. This was

TABLE 1 | Cognitive tests were administered in three apparatus over a 17 day period.

Cognitive tests				
Days 1 and 2: Acclimation **Day 3:** Training (Trials 1–5) and puzzle solving (Trial 6) **Days 4 and 5:** Simple discrimination (Trials 1–12)		**Day 6:** Egocentric navigation (Trials 1–6) Trial 6: Object permanence puzzle **Day 7:** Egocentric navigation (Trials 7–12) **Day 8:** Egocentric refresher trials (Trials 13 and 14) Egocentric reversal trials, disengagement approaches (Trials 15–18)		**Day 9:** One acclimation trial (Trial 1) and one training trial (Trial 2) **Days 10–13:** Two training trials per day (Trials 3–10)
Straight alley (puzzle solving/simple discrimination)	Two day break	Lashley maze (egocentric navigation/object permanence/puzzle/egocentric reversal/disengagement approaches)	Two day break	Decision tree maze (inductive reasoning)

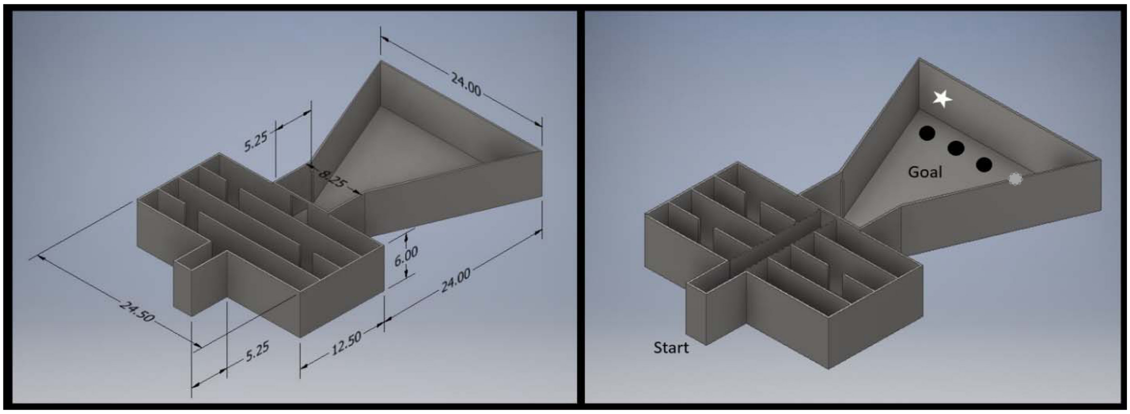

FIGURE 1 | The straight alley and Lashley maze configurations of a single test chamber. The left panel illustrates the maze configuration, and the right illustrates the straight alley configuration. The start box is located near the left side of the maze, and the goal location is near the right. Depending on the task, either 1, 2, or 4 food cups were present at the goal location. In some tasks, discriminative cues were mounted on the wall behind the goal cups (illustrated by the star over Position 1). The apparatus was constructed of black Plexiglas and measurements are in cm.

repeated for a total of five trials with a 6–10 min ITI for each animal. The first five trials in this maze were merely intended to establish directed approach to the food cup and an expectation that food would be located there. Trial 6 served as the critical measure of cognitive performance and proceeded as previous trials, with the exception of an added hexagonal lid (a plastic weigh boat) placed on top of the food cup. Of interest were the number of failures ("errors") to remove the lid in order to collect the food reward. An error was scored if an animal placed at least two paws on platform and withdrew from the platform *or* if the animal made contact with the lid and failed to remove it. This trial was considered complete when the animal removed the lid and retrieved the food reward.

Simple Discrimination in Straight Alley (One Measure of Cognitive Performance)

Mice were again placed in the start box of the straight alley for 5 s and then released. On these trials, the goal box contained four platforms, each with one food cup on it. Each cup was baited with inaccessible food, while the cup marked by a discriminative cue also contained accessible food. During Trial 1, one cup (in position #3, counted from left to right) was covered with a hexagonal lid and baited with accessible food. This trial proceeded as previous trials in the straight alley, counting errors as previously described. Trials 2–12 had four cups in the goal area, all covered with hexagonal lids. One of the four cups were marked by a white star (35 mm diameter) on the wall behind and 20 mm above the food cup. This star served as the discriminative cue and marked the location of accessible food. Position of the target cup was randomly selected for each of these trials and standardized for all animals. Lid errors were recorded as previously described, and errors were also counted any time that the mouse made contact with a non-target lid. Errors could occur multiple times at a single lid provided that the animal stepped off the platform after making initial error (i.e., attempts at same lid without leaving the platform count as a single error). Average number of errors on Trials 6–11 served as each animal's index of performance.

Lashley Maze (Yielding Four Measures of Cognitive Performance)

For this portion of testing the straight alley maze was converted to its Lashley maze configuration. A single platform with an uncovered food cup baited with reinforcer was placed in the center back of the goal area. This phase of training took place over

3 days in total, with 2 days of acquisition testing (Trials 1–12) followed by 1 day of testing (Trials 13–18) in which the learned response requirements were reversed.

For Trials 1–6 (Day 1), animals were placed in the start box, released, and allowed to traverse maze until it entered the arena and food was retrieved. Errors were recorded for the following actions: (1) back-tracking (complete reversal involving movement), (2) missed turn, i.e., passing a door without entering, or (3) wrong direction of turn (i.e., exiting a door and turning in the wrong direction). Errors were not compounded, i.e., if an animal missed a door (error), then back-tracked to return to that door, the back-track was "necessary," and thus was not scored as an error. Likewise, if an animal made a wrong turn (error), it must back-track to return to the proper course and thus back-tracking was not an error. Errors could only occur if an animal was moving toward the goal, i.e., if the animal made an error that leads back through several doors before correcting and moving toward the goal, only the first error in the series was counted. Once the animal again progressed toward the goal, errors were again counted. Trials 7–12 (Day 2) followed this same procedure. A 20 min ITI intervened between each trial. The average number of errors committed on Trials 3–5 (Day 1) served as each animal's index of acquisition. Trials 3–5 were used for this analysis as we have previously found that performance on these trials effectively capture differences between slow and faster learners (A complete description and rationale for our scoring methods can be found in Kolata et al., 2008).

On Trial 6 only, the food cup was covered by a blue ping-pong ball constituting a "puzzle" to be solved in order to obtain food. We recorded errors to enter the arena (as on all trials), then errors committed in solving the puzzle. An error was scored if an animal placed at least two paws on platform and withdrew from the platform or made contact with the ball and failed to remove it. Thus, errors were recorded if an animal approached a cup or made contact with the lid without retrieving the food. The trial was completed (and no error scored) if an animal successfully removed the ball to retrieve the food reward. Trials 7–12 were identical to Trials 1–5.

At the start of Day 3 in the Lashley maze, two "refresher" trials were administered (Trials 13–14) that followed the same procedure as the first 12 acquisition trials. The subsequent four trials (Trial 15–18) required that the animal reverse its previously learned path in order to obtain the food reward. A baited food cup was placed in what was previously the start box. Animals began the trial placed in the center of the goal area facing an empty food cup in the location of the previously baited cup. Two types of errors were recorded: (1) Approach errors were recorded every time the animal approached the old (now empty) food cup. This was constituted any time that an animal placed at least two paws on the platform and withdrew or when its nose crossed the plane of the cup wall (in cases where the animal did not step on to the platform). (2) Maze errors were recorded as the animal traversed the maze toward the new goal location (in what was previously the start box). These errors were scored as they were during forward Lashley maze training, although in this instance, the correct route was reversed. Animals were allowed to find and consume the food, and then removed to begin their inter-trial interval.

Decision Tree Maze (One Measure of Cognitive Performance)

Upon completion of testing in the Lashley maze, an additional cognitive test was administered in a distinct piece of apparatus (a decision tree). The Decision Tree maze is a "tree" shaped maze constructed from black Plexiglass with a start box and series of bifurcating arms at seven symmetric locations, "nodes," after an initial split dividing the maze in two symmetrical halves (see Wass et al., 2012, for an illustration of the maze). Before the initial division in the maze sits an alley that originates from a starting box with a removable door where mice begin the test. At each of the 14 nodes within the maze (located at splits and at the end of arms), a small hole (3 mm wide × 3 mm deep) was drilled to hold a recessed 14 mg Noyes pellet that serves as the food reward, a random selection of which were baited on any given trial. This test involves mice navigating the branch-like structured maze to inspect each node for food. The object of this test is for mice learn the overall structure of the maze and formulate the optimally efficient path through which it can search each potential food deposit while using the lowest amount of time and energy possible. Mice with high general intelligence will explore the maze in efficient paths (i.e., cross the same node only en route to an unexplored node) while mice with lower intelligence will often take meandering paths and make many errors (unnecessarily crossing a node) in exploring the maze. This maze has previously been shown to load heavily (0.49) on a factor analysis describing a general intelligence factor, and the efficiency with which an animal searches the maze has been said to be emblematic of inductive reasoning (Wass et al., 2012).

Animals were food deprived for approximately 16 h before testing began. Testing in this maze lasted 5 days, with animals being tested in two trials per day for a total of 10 trials. On Trial 1, mice were placed in the start box for 10 s before opening the gate to the maze. On this trial, all 14 nodes were baited with food. The path taken by the animal was recorded until all food pellets were retrieved, and then the mice remained in the maze for 12 min to allow further exploration. Mice were then removed and placed back in its home cage in the testing room for the 10 min ITI.

Trials 2–10 involved a similar procedure to trial one, with two exceptions. The first exception is that during these trials, only four to eight of the nodes were baited with food. Standard arrangements of the food baiting were used to ensure consistency among animals. The number and location of nodes to be baited during each trial were selected randomly. The second exception from Trial 1 was that these trials were not subjected to the 12 min time requirement. Rather, these trials ended when all available food had been eaten and all nodes had been explored.

The path an animal takes to explore each node in the maze were recorded. On each trial we recorded the "streak," or number of node crossings an animal made before making an unnecessary node crossing. For the present purpose, the average streak length on best two of Trials 7–10 served as the dependent measure of each animal's performance.

Survival-Related Tests (Nine Measures)

Survival-related measures were obtained in the animals' home cages as well as three novel environments. In total, nine measures of survival-readiness were obtained. The sequence and nature of these tasks are illustrated in **Table 2**.

Nest Building in the Home Cage (One Measure)

This procedure is based on one described by Deacon (2006a), who argued that proper nest building (which is performed by both male and female mice) conserves body heat and protects animals from predation, both of which facilitate survival in the wild.

Mice in this study had no prior experience with nesting material other than the shredded cob bedding that lined their home cages. Approximately 60 min prior to the onset of the dark cycle, a 3 *g* compressed cotton pad (Oasis Shred-a-Bed) was placed against the front wall of the animals' home cages. Even with no prior experience, mice characteristically shred these pads and use the material to construct nests. The pad remained in the home cage throughout the ensuing dark cycle. 2 h after the onset of the light cycle, the quality of the nest was recorded using the 5-point scale recommended by Deacon (2006a), where a score of 1 is assigned to an animal that has not noticeably touched the pad (more than 90% intact), and a score of 5 is assigned to an animal that has constructed a near-perfect nest with more than 90% of the pad shredded, and the nest forming a crater occupying 25% or less of the cage floor, with at least 50% of the walls higher than the prone mouse' body height. Intermediate scores (i.e., between two whole numbers) were used when a nest was judged to be intermediate between any two points on the rating scale.

Exploration and Food Retrieval in a Burrowing Box (Two Measures)

Two adjoining white Plexiglas boxes (20 cm l × 13 cm w × 10 cm h) were connected by a 2.5 cm diameter ×10 cm long tube that emerged through the floor of each box on either side of the adjoining wall. The wall that divided the two boxes was perforated to facilitate the transmission of odors between the two sides of the box. Testing in this box was performed on two consecutive days. On Day 1, each mouse was placed in one box and allowed to freely explore throughout a 12 min session. The dependent measure obtained was the latency for the animal to first cross the tube and enter to other box (recorded when all four paws made contact with the floor of the box). This measure was essentially an index of exploratory tendencies in a novel environment. Upon completion of Day 1 testing, each animal began a 20 h period of food deprivation. Day 2 of testing was similar to Day 1 with two exceptions. First, the tube that connected the two boxes was filled with shredded cob bedding. Second, the side of the box opposite to the start side had in it one gram of standard lab chow. The mouse was started in the empty side of the box, and of interest was the latency to burrow through the occluded connecting tube and retrieve a piece of food in the opposite box. This trial had no time constraint and was ended when the mouse retrieved the piece of food.

TABLE 2 | Survival-readiness tests were administered in four sets of apparatus over a 14 day period.

Survival readiness tests						
Day 1: Overnight nest building		**Day 2:** Acclimation/exploration measurement **Day 3:** Food retrieval		**Day 4:** Two-h nest building **Day 5:** Latency to find food Amount of food hoarded in 20 min **Day 6:** Food size preference		**Day 7:** Acclimation to social box Exploration measure **Day 8:** Predator avoidance
Home cage (nest building)	Two day break	Burrow box (exploration/food retrieval)	Two day break	Hoarding box (nest building/latency to find food/food size preference)	Two day break	Social box (exploration/predator avoidance)

Food Retrieval and Nesting in a Novel Hoarding Box (Four Measures)

Given access to a food supply outside of the home environment, mice will typically retrieve that food and return it to their nesting area. Moreover, when given a choice, mice tend to reject less attractive food in favor of more attractive food. These species-typical behaviors are said to have obvious survival value (Deacon, 2006b). To assess these behaviors in laboratory mice, Deacon (2006b) developed a procedure in which mice are introduced to and housed in a novel environment, and are given access to a tunnel (that protrudes from the nest area) that terminates in a batch of familiar food. In Deacon's description of this task, the mice were mildly food deprived and allowed approximately 12 h to engage in food retrieval, after which was recorded the amount of food (from a 100 *g* source) that was returned to the home box. In a preliminary attempt to employ this procedure, we observed that all mice returned all food by the end of the 12 h interval. Consequently, we made several modifications to the procedure and also collected several other measures related to hoarding and survival in a novel environment. First, we assessed nest building shortly after introduction to the novel box. (This procedure was identical to the procedure used in the home box except that the quality of the nest was assessed 2 h after introduction in the novel box, a behavior that would have important survival benefits when an animal is moved from its familiar home nest.) Second, for the first hoarding test animals were not food deprived and two measures were obtained, including the latency to first contact food after given access to the tunnel, and the amount of food retrieved was recorded after 2 h of access. (In preliminary studies we observed significant variability across animals in the amount of food retrieved at this interval). Access to the tunnel was then blocked. 20 h after the initial bout of hoarding, the mice were again given access to the tunnel and again allowed to retrieve food. However, in this instance the animals had access to 16 food pellets, eight of which were 500 mg, and eight of which were 100 mg of interest was any observed preference for the large pellet among the first eight pellets returned to the home cage.

Apparatus was similar to that described by Deacon (2006b). A test box (30 × 13× 15 cm) was constructed of white Plexiglas with a clear lid covered in orange acetate (which darkened the interior of the box). The floor of the box was lined with shredded cob bedding. A 50 cm long ×5 cm diameter wire mesh (6 mm grid size) tunnel extended from the end of the home box and terminated in an 10 cm long black Plexiglas tube with a sealed end (serving as a food cup). Access to the tunnel could be blocked with a black rubber stopper.

On Day 1 (approximately 4 h after the start of the light cycle), each mouse was transferred from its home cage to the test apparatus (where it would remain for three consecutive days). The home cage bedding was transferred to the test apparatus along with 400 ml of additional fresh bedding and a Shred-a-Bed nest pad. The test box contained the animal's regular food (four pellets) and a water spout. Four pieces of novel food (Hartz Small Animal Diet for Guinea Pigs; two 100 mg pellets, and two 500 mg pellets, designated "small" and "large" test pellets) were also present. (This food type would be used in a later test and was provided at this time to mitigate any neophobic responses). Entrance to wire tunnel was blocked. 2 h after introduction of a mouse to the test box, nest quality was scored in the manner described above.

On Day 2, 100 *g* of the animals' standard diet (pellet size 1.5–3.0 *g*) was placed in food cup at end of the wire tunnel. Mid-way through the light cycle, the rubber plug was removed allowing the animal access to the tunnel. The latency for each animal to traverse the tunnel to reach the food was then recorded. 2 h later, the tunnel was again blocked and food pellets that remained in the tunnel were weighed; this weight was subtracted from the original 100 *g* to yield a measure of successfully hoarded food pellets (i.e., the pellets that had been returned to the nest area). After this test, all food was removed from the nest box. Each animal was then provided one large (500 mg) and one small (100 mg) test food pellet (Hartz Small Animal Diet).

On Day 3 (18 h after removal of food from the home test box) two columns of 8 test food pellets were placed in the food cup at the end of the wire tunnel. The rows of the two columns alternated between small and large pellets. The rubber plug was then removed from the wire tunnel allowing each mouse access, and the size of the first eight pellets retrieved was recorded. For purposes of scoring, each large pellet was worth 1 point, whereas small pellets were worth 0 points, yielding a maximum score of "8" for each animal.

Predator Avoidance in a Social Box (Two Measures)

In their natural environments, mice are the target of predation by rats. Even without prior experience with the predator, mice will avoid areas marked by the odor of rats (Papes et al., 2010). This native defensive tendency was assessed here where mice could approach or withdraw from a live rat. A mouse was placed in the center chamber of a 3-chamber box, in which the mouse could freely move between the chambers. One of the chambers that adjoined the center contained a rat restrained in a wire tube, while the opposite chamber adjoining the center contained a cotton wad similar in size to that of the rat inside a wire tube. Two behaviors were of interest. First, we recorded the latency to first exit the center chamber when both adjoining chambers were empty (Day 1), and second (on Day 2), we recorded the difference in time spent in the chamber containing the rat relative to the chamber containing the cotton wad.

This test was conducted on two successive days, the first of which was intended to acclimate the mouse to the test chambers and to obtain a measure of exploration in a novel environment. Each mouse (in its home cage) was placed in the testing room under dim light for 10 min prior to testing. The predator avoidance box was a 60 × 40 × 24 cm clear Plexiglas box divided into three 20 × 40 × 24 cm sections. A small door (15 cm square) allowed access from the center chamber into each of the adjoining chambers. Each of the chambers that adjoined the center contained a wire mesh container (6 mm grid, 18 cm diameter ×22 cm high). These containers were empty on the acclimation day. Each mouse was placed in the center chamber and allowed to explore the box freely for 10 min. We recorded the latency (in sec) for the animal to leave the center chamber and enter either of the two adjoining chambers (the mouse was considered to have entered a new chamber when all four paws were on its floor). At the conclusion of the 10 min of acclimation, the mouse was returned to its home cage.

On Day 2, the box was arranged as during Day 1, with the addition of a live Sprague-Dawley (Crl:SD) male rat in the wire mesh container in one of the side chambers, and a rat-sized white cotton bundle in the container in the opposite side chamber. The mouse was again placed in the center chamber and allowed to explore the box for 10 min. Of interest was the time spent in the chamber with the cotton wad minus the time spent in the chamber with the rat. A score approaching 10 min would reflect maximum avoidance of the rat. After the 10 min test the mouse was returned to its home cage.

Statistical Analyses

All statistical analyses were completed using IBM Statistics Version 25. The dependent measures from each of the cognitive tasks were entered into a principal component analysis to obtain an estimate of the influence of a general cognitive factor and to compute factors scores which reflect the aggregate (general) cognitive performance of each mouse relative to the other mice in this sample. Next, the performance measures of survival-readiness were entered into a principal component analysis to determine the existence of a "general survival-readiness factor" and to compute factor scores on this dimension (indicative of an animal's relative survival-readiness). The degree of correlation between general survival-readiness and general cognitive ability could then be assessed. We also examined the correlations between general cognitive factor scores and each measure of survival-readiness to determine which, if any, of those individual behaviors were predicted by general cognitive ability.

In some instances, better performance on a task was indicated by a lower score (e.g., fewer errors), whereas in other instances, better performance on a task was indicated by a higher score (e.g., more food retrieved). This complicates the interpretation of correlations, as although better performance on one task might predict better performance on a second task, in one instance this would be reflected in a negative correlation whereas in another instance this would be reflected in a positive correlation. To simplify the presentation (for instance, the correlation matrix presented in **Table 3**), in all cases, correlations are presented such that positive values mean better performance on one value predicts better performance on the other. This was accomplished by inverting raw values in some instances.

RESULTS

Fifty-six male mice contributed to this analysis. All 56 contributed data on all cognitive tests. For tests of survival-readiness, one animal was removed from the study due to illness, yielding ns = 55 on all tests except "Hoarded weight," where due to a procedural error, data from eight animals was lost, yielding an $n = 47$ on that test. Principal component analyses require that all subjects contribute to all dependent variables. Consequently, the principal component analysis of cognitive abilities was based on an $n = 56$, whereas the analysis of survival abilities was based on an $n = 47$. In one instance, we compared aggregate performance on the cognitive tests (based on factor scores) to aggregate performance on survival-readiness tests (see **Figure 2**, described below). For this purpose, only the 47 animals that were represented in both sets of tests were included in the analysis.

TABLE 3 | Principal component analysis of seven cognitive tests ($n = 56$).

	General factor
Straight alley lid puzzle errors	0.35
Straight alley discrimination errors	0.35
Lashley maze acquisition errors	0.64
Lashley maze lid puzzle errors	0.51
Lashley maze reversal errors	0.72
Lashley maze approach errors	0.65
Decision tree streak length	0.40
Variance explained	29.08%
Eigenvalue	2.03

Data for this analysis was entered such that in all tasks, lower values represented better performance (requiring in several instances that raw values were inverted).

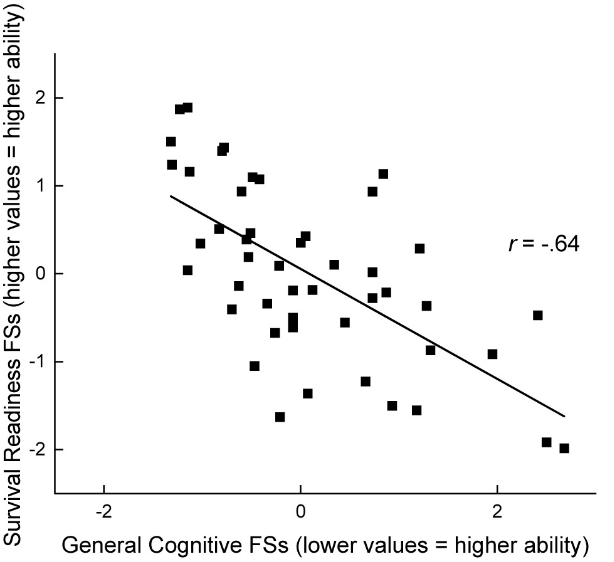

FIGURE 2 | Factor scores for general cognitive ability and general survival-readiness are compared. A correlation was observed indicating that better overall cognitive ability predicted better overall performance on tests of survival skills ($n = 47$).

General Cognitive Ability

Table 3 presents the results of the principal component analysis of all seven cognitive measures.

As evident from **Table 3**, the performance on all cognitive tests loaded moderately to strongly on a principal factor, indicative of a common influence on performance across all tests. This general factor accounted for ∼29% of the variance in performance across all tasks. This degree of variance is comparable to that observed using batteries of tests that were very dissimilar to the one used here (e.g., Kolata et al., 2008; Sauce et al., 2018). This is notable since in the present battery, all of the cognitive tests were motivated by food rewards, which could make it difficult to distinguish between a general *cognitive* factor and a general *motivational* factor. However, the results obtained from other test batteries were based on tasks that depended on at least three different motivational systems. Thus it is reasonable to conclude that the present results are a reflection more of cognitive ability rather than a common motivational state.

General Survival-Readiness

Table 4 presents the results of the principal component analysis of all nine measures of survival-related behaviors.

As evident from **Table 4**, the performance on many measures of survival-readiness loaded moderately to strongly on a single factor that accounted for ∼25% of the variance in performance across all tests. This suggests the existence of a "general survival-readiness" ability that would influence an individual's capacity for survival. Notably though, three of the measures loaded negligibly or in the opposite direction on this factor, indicating a less than universal influence on these survival-related behaviors.

The Relationship Between General Cognitive Ability and General Survival-Readiness

Forty-seven animals contributed scores on all of the cognitive tests and all of the survival-readiness tests. Of particular interest was the relationship between general cognitive abilities and general survival-readiness. To understand this relationship, we assessed the correlation between factor scores obtained on the cognitive test battery and factor scores derived from tests of survival-related behaviors, yielding r (46) = -0.64, $p < 0.01$. This correlation indicates that higher cognitive abilities (reflected in lower values of performance, e.g., fewer errors, and thus lower factor scores) predicts better performance in tests of survival-readiness (reflected in higher values of performance, e.g., a higher quality nest, thus higher factor scores). The relationship of these two variables is illustrated in **Figure 2**.

To demonstrate the consistency of animals across tasks in the cognitive battery and the survival-readiness battery, as well as the relationship of these two trait, in **Figure 3** we illustrate the relative performances of two animals, one of which (#29) was one of the best performers in the cognitive battery, and one of which (#61) was the worst performer in the cognitive battery. These designations were based on factor scores extracted from performance on the battery of cognitive tests. These scores ranged from -1.83 [best general cognitive performance] to +2.67 [worst general cognitive performance]. Subject #29 received a factor score of -1.31, and Subject #61 received the factor score of +2.67. The subject that performed best on the cognitive battery (factor score of -1.83) could not be used for this analysis as it did not contribute one score on the survival-readiness battery of tests). Subjects #29 and 61 were assigned a rank based on its performance relative to all other animals on each of the cognitive tasks and each of the survival-readiness tasks. These ranks are illustrated in **Figure 3**. As this figure illustrates, Subject #29 performed near above the median (near the top of the distribution) on each of the cognitive tests, and also performed above the median on each of the survival-readiness tests. Subject #61 performed below the median on all of the cognitive tests, and also tended to perform poorly on most of the survival-readiness tests.

TABLE 4 | Principal component analysis of nine survival-related tests (eight animals did not contribute a score on the amount of food hoarded, resulting in 47 animals that contributed scores to all tests).

	General factor
Exploratory latency in burrow box	–0.31
Food retrieval in burrow box	0.33
Nest quality in home environment	–0.03
Nest quality in novel environment	0.82
Latency to find food in hoard box	0.27
Amount of food hoarded in 20 min	0.64
Preference for larger food	0.86
Exploration in social box	0.01
Predator avoidance in social box	0.35
Variance explained	24.96%
Eigenvalue	2.24

In some instances, higher raw values reflected better performance, and in other instances, lower raw values reflected better performance. Thus to simplify the presentation, values were in some instances inverted such that for all variables, higher reported values represented better performance.

General Cognitive Ability and Performance on Individual Tests of Survival-Readiness

Finally, we examined the relationship between general cognitive ability and performance on individual tests of survival-related behaviors, as well the relationship between the various measures of survival-readiness. A matrix of correlations of all relevant variables (i.e., general cognitive factor scores and all measures of performance on tests of survival-readiness) is presented in **Table 5**.

The correlation matrix presented in **Table 5** is a mixed set of results. Most correlations were positive (suggesting a common influence on general cognitive ability and all measures of survival-readiness), although several negative correlations were observed and most correlations were not significant (and weak). However, general cognitive ability did significantly predict several measures of survival-readiness, including nest building in a novel environment, the amount of food hoarded in a 20 min interval, the degree of preference for larger portions of food, and predator avoidance. Notably, most of the strong correlations between cognition and measures of survival-readiness were observed in those cases where survival-related behaviors were assessed in an environment that was unfamiliar to the mouse. This suggests the possibility that distractions that arise in a new environment (but which are minimal in a familiar environment) are more easily overcome in animals with higher cognitive abilities. This and other possibilities are considered more fully below.

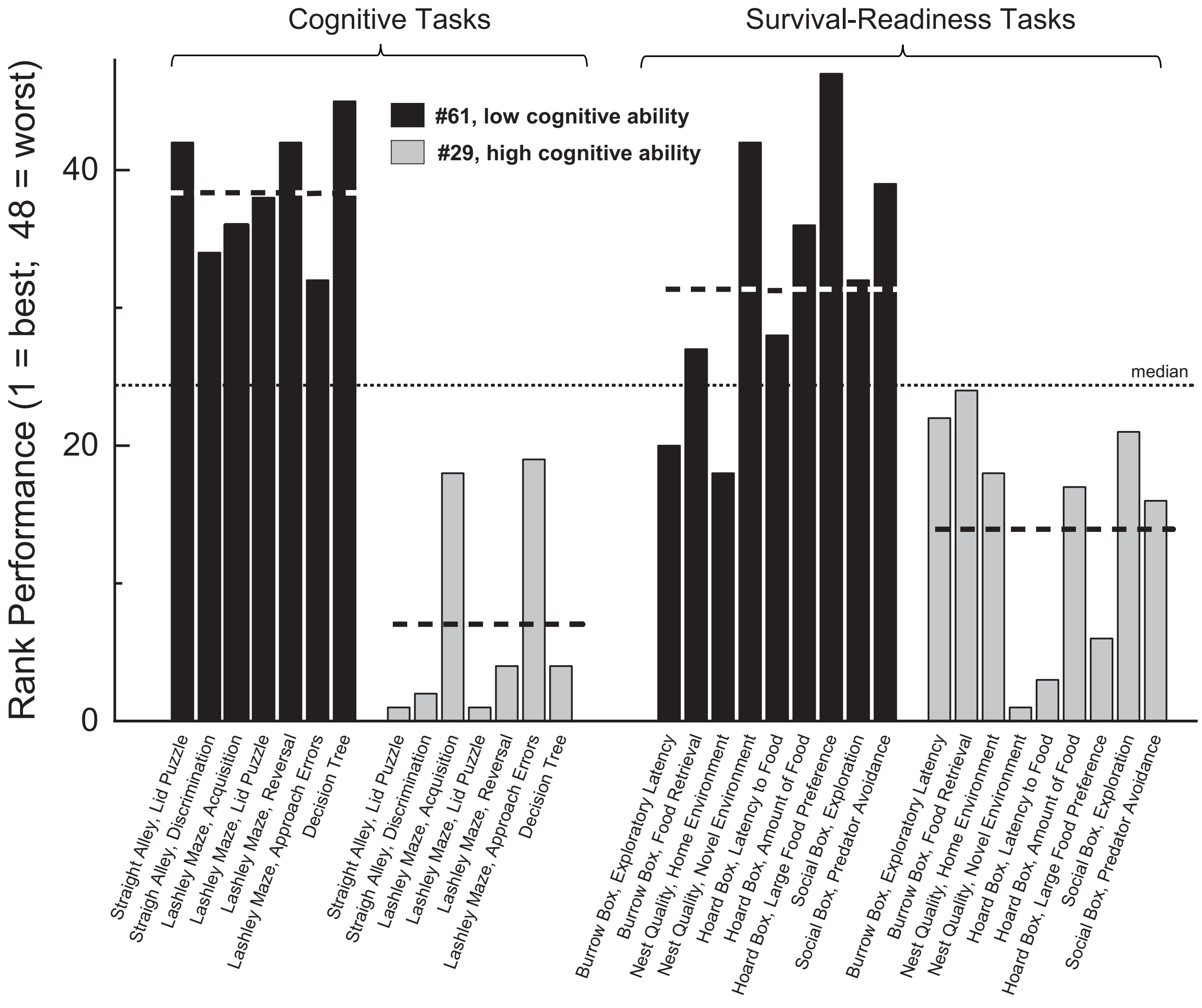

FIGURE 3 | Subject #29 (high general cognitive abilities, as determined by factor scores obtained from the PCA of cognitive tasks) and Subject #61 (low general cognitive abilities) were ranked relative to other animals in this sample (*n* = 47) on each cognitive (left sets of bars) and survival-readiness task (right sets of bars). The heavy dashed line represents each animal's mean rank on that set of tasks, and the light dashed line is the expected median for the sample of 47 animals. Subject #29 performed well above the median on each of the cognitive tasks, and also performed well on each of the survival readiness tasks. Subject #61 performed around the median or poorly on each class of tests.

GENERAL DISCUSSION

It had been noted by several authors (e.g., Burkart et al., 2016; Locurto, 2017) that measures of "intelligence" in non-human animals have suffered from the lack of independent verification of the impact of those measures on outcomes that were independent of the intelligence test itself. While some exceptions were noted above, this criticism was certainly true of laboratory assessments performed on mice, is thus it is an important concern to address. An impediment to such an analysis arises when working with laboratory mice, from which is difficult (or impossible) to assess obvious practical outcomes of variations in intelligence, e.g., the relationship of intelligence to survival in the wild (which could be expected to be impacted by variations in cognitive abilities). Here we took an intermediate approach, i.e., intelligence was assessed in laboratory mice, and then these same mice were assessed for performance on unlearned behaviors that could be reasonably expected to impact survival in the wild.

In the present study, genetically heterogeneous laboratory mice were assessed on a battery of cognitive tests (where individual's aggregate performance served as an index of "intelligence") and were then assessed on a number of tasks relevant to nest building (in familiar and unfamiliar environments), exploration in novel/familiar environments, food discovery, efficiency of food retrieval and preference, and predator avoidance. Better performance on these tasks might promote survival-readiness under more natural (non-laboratory) conditions. Several key observations arose from this analysis.

TABLE 5 | A correlation matrix of cognitive factor scores (indicative of general cognitive ability) and all measures of survival-related behaviors.

	Cognitive FSs	Explore latency (burrow)	Food latency (burrow)	Nest in home	Nest in novel box	Food latency (tunnel)	Hoarded weight	Food size preference	Exploration latency (social)
Exploration latency	−0.16								
Food latency (burrow)	0.15	0.03							
Nest in home	0.10	0.28*	0.09						
Nest in novel box	0.42**	−0.16	0.18	−0.08					
Food latency (tunnel)	0.10	0.20	0.02	0.08	0.16				
Hoarded weight	0.36*	0.00	0.10	0.06	0.43**	0.18			
Food size preference	0.57**	0.41**	0.16	0.10	0.55**	0.00	0.43**		
Explore latency (social)	0.04	−0.02	0.07	0.03	0.04	−0.19	0.20	0.15	
Predator avoidance	0.28*	−0.03	0.13	0.07	0.13	0.20	0.01	0.21	0.27*

In all cases, correlations are reported such that a positive correlation indicates that better performance on one measure predicts better performance on the other measure. (This was done to simplify the presentation where in some instances, better performance was reflected in lower raw values whereas in other instances, better performance was reflected in higher raw values). The ns for all comparisons are either 55 or 56 except for measures of "Hoarded weight," where data from eight animals was lost, yielding an $n = 47$. *$p < 0.05$ (uncorrected). **$p < 0.01$ (uncorrected).

First (and as in many previous reports, e.g., Matzel et al., 2006, 2008; Kolata et al., 2007, 2008), a single factor was found to contribute to performance on all cognitive tests. Similarly (and second), a general "survival-readiness" trait was also identified, i.e., a single source of variance was found to exert an influence on some measures of unlearned survival-related skills, accounting for 24.96% of the variance among individuals across nine different tasks. Thirdly, and of principal relevance to our intentions here, general cognitive abilities were strongly predictive of general survival-readiness (r = -0.64). This latter observation suggests that animals with higher cognitive abilities (all other things equal) would indeed exhibit a higher likelihood of survival in the wild.

The analysis of the relationship between general cognitive ability and specific survival-related tasks is not entirely straightforward. For instance, nest building in the home cage was unrelated to general cognitive ability (r = 0.10), while nest building in a novel environment was significantly predicted by an individual's general cognitive ability (r = 0.42). Although many differences characterize these different tasks, a distinguishing feature is that general cognitive ability appears to have a stronger influence on tests of survival-readiness when those later tests are administered in unfamiliar settings. We have previously suggested that attentional abilities may be a principal determinant of variations in mouse intelligence (Kolata et al., 2005, 2007; Sauce et al., 2014; for review, see Matzel and Kolata, 2010; Matzel and Sauce, 2017), a relationship that may also exist among humans (Engle, 2002, 2018; Cowan et al., 2005, 2006; Shipstead and Engle, 2013). Lapses in attention (which could be exacerbated in unfamiliar environments with new distractions) might explain the relationship between general cognitive ability (and its dependence on attention) and survival skills.

In addition to variations in general cognitive ability, other "general" influences might account for the relationship between performance on the cognitive battery and survival readiness. Notably, it is conceivable that variations in stress reactivity or anxiety might contribute to general cognitive performance and thus might underly the relationship to survival readiness. However, our prior work suggests that this is unlikely. In a series of papers, general influences such as stress reactivity, exploratory tendencies, and anxiety have been dissociated from the principal factor in three ways. First, nominal measures of fear/anxiety/stress do not load (or load weakly) on the principal factor that captures general cognitive performance (Matzel et al., 2006). Second, pharmacological reductions in anxiety or stress reactivity do not promote increases in general cognitive performance or change the pattern of loadings on the general cognitive factor (where the cognitive tasks are differentially dependent on fear-motivated responses; Grossman et al., 2007). Lastly, Light et al. (2008) found that behavioral interventions that reduce fear/stress/anxiety do not change the pattern of loading on the principal factor that represents general cognitive performance. These results have led us to favor the interpretation that the general factor that describes performance across our batteries of cognitive tests is reflective of a general influence on *cognitive* abilities.

The potential relationship between attention and survival-readiness might be best described with an anecdotal description of mouse behavior. We have consistently observed that mice that are classified as expressing low general cognitive abilities seem to have difficulty maintaining directed behavior (an observation that is consistent with empirical evidence, e.g., Kolata et al., 2007; Matzel et al., 2008; Light et al., 2010). For example, in a straight alley (a very simple test of learned behavior in which a mouse runs in a straight line to a food reward), dull mice often appear to lose focus, e.g., in the course of a run they may stop and rear or engage in bouts of grooming. Thus even on such a simple task, a dull mice will exhibit more between-trial variability, and "worst" performance might best distinguish between high and low intelligence individuals (a tendency that has been repeatedly observed and quantified in humans' performance on many cognitive tasks; Juhel, 1993; Coyle, 2003). Relatedly, it is possible that in a new environment, an animal could be more distractible (and thus less directed) than would be the case in a familiar environment. This suggests the possibility that distractions inherent to a new environment (but which are absent from a familiar environment) are more easily overcome in animals with higher cognitive abilities. In total, the possibility that attentional variation is the common factor that mediates the relationship between intelligence and expression of survival skills seems both plausible and parsimonious with the range of available data.

Of the nine tests of survival-readiness used here, three of those tests (the latency to cross sides in the burrowing box, the latency to traverse a tunnel in the hoarding box, and the latency to leave the center compartment in the social box) were thought to be primarily dependent on the propensity for exploration (which of course can be influenced by stress, fear, or anxiety; Matzel et al., 2006; Grossman et al., 2007). While other tests of survival-readiness used here had obvious survival benefits, the relationship of exploration to survival is more complex. Exploration (or "novelty seeking") could be beneficial under some circumstances, but could be detrimental in others (necessitating a balance between "too little" and "too much"). In this regard, we have reported that variations in "exploration" may in fact be a consequence of differences in rate of learning, such that more competent animals evaluate their environment more quickly and are thus more likely to engage in exploration when conditions have been deemed appropriate (Light et al., 2008, 2011). This interpretation is consistent with our regular observation that exploration covaries with general cognitive ability (e.g., Matzel et al., 2003). In this regard, it is quite surprising that none of the measures of exploration employed here were related to general cognitive performance and did not load appreciably on the principal component analysis of survival-related behaviors. One possible explanation of this result is consistent with previous data of Light et al. (2011) who reported that the relationship of exploration and general cognitive ability is diminished as animals spend more time in a novel environment, i.e., after the environment becomes familiar. In the present study, animals had extensive experience in environments (during tests of cognitive abilities) similar to those utilized for later tests of exploration, and thus their novelty might have been minimized. Regardless of the explanation, the results obtained here suggest that the relationship between cognitive abilities and exploration might be less universal than we had previously believed. Importantly, we note that previous research suggests general cognitive abilities of individuals may be differentially impacted by socialization paradigms present in natural environments (e.g., Fitchett et al., 2005; Chida et al., 2006). One of us has previously reported that predisposition to submission within a social hierarchy predicts superior cognitive performance (Matzel et al., 2017). One possible explanation for this result was that survival-readiness strategies reliant on cognitive abilities may have evolved to facilitate the survival of those not predisposed to benefit from strategies that favor dominant physical or social abilities. As such, the social environment of an animal likely plays an integral role in its survival strategy. Based on the results reported in the present study it is possible, for example, that an animal with a predisposition for high cognitive ability reared in an environment free of socially dominant peers may enjoy a high degree of survival-readiness (perhaps even enhanced by socialization, given the relationship between socialization and improved cognitive ability; see Voiker et al., 2005; Chida et al., 2006), while that same animal reared with exposure to social submission may experience decreased survival-readiness (given that social submission can impair cognitive performance; see Fitchett et al., 2005; Colas-Zelin et al., 2012).

In a general sense, it is unlikely that genes common to both survival skills and intelligence could mediate the relationship between these two sets of variables. In any nominal way, it seems unlikely that the same genes could regulate tasks as dissimilar as those that constitute tests of cognition (e.g., the Lashley Maze) and tests of survival skills (e.g., nest building). However, while these different traits are almost surely regulated independently, they may also be regulated in common by networks of genes that could impact processes like attention. While the heritability of mouse intelligence (e.g., Galsworthy et al., 2002, 2005; Sauce et al., 2018; Matzel et al., 2019) suggests a strong genetic influence on the expression of this trait, the heritability of survival skills in mice is presently unknown (but is currently under investigation in our laboratory).

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by Rutgers IACUC.

AUTHOR CONTRIBUTIONS

LM and DC performed data analyses and wrote the manuscript. LM, DC, HP, MP, MM, and AT maintained animals and collected data. All authors contributed to the article and approved the submitted version.

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The Role of Cognition in Social Information Use for Breeding Site Selection: Experimental Evidence in a Wild Passerine Population

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In spatio-temporally variable environments, individuals are known to use information for making optimal decisions regarding where and when to breed. Optimal decision making can be complex when relying on multiple information sources with varying levels of reliability and accessibility. To deal with such complexity, different cognitive abilities such as learning and memory might enable individuals to optimally process and use these information sources. Yet, the link between information use and cognitive ability remains unexplored in natural populations. We investigated whether learning performance on a problem-solving task was related to the use of an experimentally manipulated source of social information for nest site selection in wild collared flycatchers (*Ficedula albicollis*). Collared flycatchers are known to use heterospecific information from their main competitors, the great tits (*Parus major*). Here, we created a local apparent preference by tits for an artificial nest site feature (a geometric symbol attached to nest boxes occupied by tits) and recorded whether flycatcher pairs chose to settle in nest boxes displaying the same feature as tits (i.e., copied tit apparent preference). Using a problem-solving task requiring opening a door temporarily blocking the nest box entrance, we then measured flycatchers' learning performance during nestling rearing as the number of entrances required to solve the task and enter the nest box twice in a row below a given efficiency threshold. We found that the probability to copy tit preference decreased with decreasing learning performance in females, particularly yearling ones: fast learning females copied tit preference, while slow learning ones rejected it. Male learning performance did not affect copying behavior. Our results showed that learning performance might play an important role in the ability to optimally use information for nest site selection in females: both fast and slow learning females could process this heterospecific information source but used it differently. This could partly explain the link between cognitive abilities and reproductive success reported in previous studies. Whether cognitive abilities may modulate condition-dependent costs of using different information remains to be explored.

Keywords: breeding site choice, collared flycatcher, *Ficedula albicollis*, heterospecific social information, information processing, problem-solving task, trial and error learning

INTRODUCTION

In most environments, habitat quality varies in time and space, generating environmental uncertainty for individuals, with potentially major fitness consequences (e.g., Franklin et al., 2000; Gunnarsson et al., 2005). Strong selective pressures should therefore favor strategies allowing individuals to reduce this uncertainty by obtaining and using reliable information on habitat quality before making decisions (Danchin et al., 2004; Dall et al., 2005). Many different information sources can be available simultaneously to individuals, such as personal information, acquired from direct observation or sampling of the environment (trial and error tactics), and social information, obtained from observing other individuals' location, behaviors, and success (Danchin et al., 2004; Schmidt et al., 2010). These information sources can vary in reliability (i.e., the extent to which they allow individuals to forecast their own success in the habitat) and accessibility (i.e., the cost at which they can be obtained; Doligez and Boulinier, 2008). They may also provide potentially conflicting information contents (e.g., Grüter et al., 2011). Furthermore, reliability, accessibility, and information contents may themselves depend on individual parameters (e.g., prior knowledge; Kivelä et al., 2014) and/or on the environment (e.g., predation risk; Kendal et al., 2004).

Dealing with multiple information sources for decision making may thus be complex and require different information processing mechanisms. First, individuals may have to prioritize information sources depending on their reliability. For example, individuals may favor the use of personal over social information when the reliability of personal information increases (e.g., when the ecological distance with social information provider increases; Seppänen et al., 2007); conversely, they may favor the use of social over personal information when this reliability decreases (e.g., due to increasing time since information acquisition; van Bergen et al., 2004). Among social information sources, information may be more reliable and favored when provided by conspecifics compared to heterospecifics (Jaakkonen et al., 2015). Second, the information to be prioritized also depends on the context-dependent future rewards of the decision to be made, which implies forecasting the consequences of decisions depending on the context. For example, the use of personal vs. social information can depend on the expected risk of predation: social information may be preferred compared to more reliable personal information for foraging patch choice only when using personal information involves loosing visual contact with conspecifics in a group (Kendal et al., 2004). Adjusting the information used depending on the context was also well-demonstrated in cleaner fish *Labroides dimidiatus* that alter their cleaning behavior depending on the client fish (Bshary, 2002) or on the audience, in response to potential future clients (Bshary and Grutter, 2006). Third, information use may require long-term memory when the delay between information gathering and use is long (Doligez and Boulinier, 2008). Individuals may use social information cues such as the presence or success of con- or heterospecifics from the previous year to select a breeding site (Doligez et al., 2002; Boulinier et al., 2008; Forsman et al., 2014). In the foraging context, long-term memory has been shown in food-storing birds that hide food reserves during the summer for the next winter (Clayton and Krebs, 1994) but also in non-food-storing birds such as great tits that remembered foraging strategies learned from conspecifics after more than 9 months (Aplin et al., 2014).

The complex use of multiple information sources in a condition- and context-dependent way for optimal decision-making has now been evidenced in various taxa (e.g., in fish, van Bergen et al., 2004; Bshary and Grutter, 2006; birds, Doligez et al., 2008; Kivelä et al., 2014; Jaakkonen et al., 2015; insects, Grüter and Ratnieks, 2011; Grüter et al., 2011; primates, Carter et al., 2013; Kendal et al., 2015). Yet, the mechanisms underlying individuals' ability to cope with such complex information use are still largely unknown. Cognition, broadly defined as all the sensory, neurological, memory, and decision processes used by individuals when interacting with their environment (Shettleworth, 2010), can be expected to play a major role in the ability to optimally process and use information. Cognitive abilities could in particular allow individuals to (i) identify and select the most reliable and/or less costly information cues (e.g., Aplin, 2019), (ii) store and relevantly update information (e.g., Tello-Ramos et al., 2019), (iii) adjust information meaning depending on external factors and individual phenotype (e.g., Kendal et al., 2004), and (iv) use new information by associating cues to fitness-related environmental features (e.g., Loukola et al., 2020). Yet, which cognitive processes enable individuals to optimally use information remains to be investigated in the wild. Among cognitive abilities, learning, defined as the adjustment of behavior to local physical and social conditions through individual experience (Shettleworth, 2010), should in particular allow individuals to efficiently respond to environmental variability by rapidly incorporating new relevant information sources into decision-making processes. Learning can therefore be expected to take a major part in the ability to cope with complex and/or multiple information sources.

Here, we experimentally investigated whether the use of a social information source for nest site selection was related to learning ability measured during nestling rearing in a natural population of a migratory hole-nesting passerine bird, the collared flycatcher. In collared flycatchers and their sister species, pied flycatchers *Ficedula hypoleuca*, both pair members jointly choose the nest site (Alatalo et al., 1986; Pärt and Qvarnström, 1997). They are well-known to use social information from their main heterospecific resident competitor, the great tit, for making breeding decisions (Seppänen and Forsman, 2007; Forsman et al., 2008) and to gain fitness benefits from this information use (Forsman et al., 2002, 2007). In particular, flycatchers have been experimentally shown to copy great tits' preference for an artificial feature of nesting cavities (e.g., Seppänen and Forsman, 2007; Forsman and Seppänen, 2011; Seppänen et al., 2011). Using the same experimental design, we created an apparent local preference of tits for an artificial nest site feature by attaching geometric symbols on nest boxes occupied by tits. We then recorded whether flycatchers copied this apparent tit preference when choosing their own nest site, i.e., chose a nest box with the same symbol as tits (Seppänen and Forsman, 2007; Seppänen et al., 2011; Morinay et al., 2018). During nestling rearing, we estimated flycatchers' learning performance on a new problem-solving task at the nest by assessing the number of attempts needed to reach a learning threshold when solving the problem over successive trials. If higher cognitive abilities allow individuals to better process and use information, we predict fast learners to be more likely to use social information from tits for nest site selection (i.e., copy the tit apparent preference) than slow or non-learners.

MATERIALS AND METHODS

Study Species and Population Monitoring

The study was conducted in a natural population of a small hole-nesting passerine bird, the collared flycatcher, breeding on the island of Gotland (Baltic Sea, Sweden, 57°03′ N, 18°18′ E), between April and June from 2012 to 2015. In the study forest patches, collared flycatchers, and titmice (great tits and blue tits *Cyanistes caeruleus*) breed in sympatry and readily settle in nest boxes provided in excess (Doligez et al., 1999). This allowed us to monitor flycatcher's timing and success of breeding throughout the season, by recording settlement date, laying, and hatching dates, clutch size and fledgling success. Collared flycatchers are migratory and have been shown to use resident titmice as information sources to adjust their own breeding decisions upon arrival on the breeding grounds (Seppänen and Forsman, 2007; Forsman et al., 2008). In particular, flycatchers have been found to use great tits' presence (Kivelä et al., 2014), density (Forsman et al., 2008), phenology (Samplonius and Both, 2017), clutch size (Loukola et al., 2013), and song features (Morinay et al., 2020a) for breeding site selection (along with conspecific social information). The reproductive benefits obtained by using social information from tits may result from settling in higher quality habitat/site as assessed from tit cues or from enhanced access to food resources during nestling rearing and/or social protection from nest predators when settling close to tits (Forsman et al., 2002, 2007). As part of the long-term monitoring of the population, flycatchers breeding in nest boxes were captured (females during incubation and males during nestling provisioning, since both parents feed young), identified (ringed with individually numbered rings if previously unringed) and aged (yearling vs. older based on plumage criteria; Svensson, 1992). Collared flycatchers show plumage sexual dimorphism (males are black and white while females are brown), allowing us to easily sex parents from a distance.

Social Information Use Experiment

The experiment was conducted in 12–17 forest patches (depending on year), containing 29–106 nest boxes each. At the beginning of the breeding season, when tits started settling in nest boxes (i.e., from early April onwards), we chose for each forest patch one (white) geometric symbol between two symbols, either a triangle or a circle, and we attached this symbol around the nest box hole of all boxes occupied by tits in this forest patch. This created a local apparent preference of tits for this artificial nest box feature in the patch. We then randomly attached either a triangle or circle on each unoccupied nest box in the experimental patches so that new-coming birds were provided nest boxes with each of the two symbols in equal proportion in each patch.

When flycatchers arrived on the breeding grounds, on average 2 weeks after tit settlement (i.e., late-April to mid-May), we monitored their nest box choice in terms of the symbol present on the box chosen. We thus recorded whether flycatchers settled in a box with the same symbol than tits in the patch (i.e., they copied local tit apparent preference) or with the other symbol (i.e., they rejected tit apparent preference). To do so, we visited all previously unoccupied nest boxes every second day to detect new settlement of flycatcher or tit pairs (based on nest material used: dry grass for flycatchers and moss with fur or feathers for tits). If a new tit pair settled and the symbol on the box was opposite to the symbol associated with tit nests in the patch, we changed the symbol to match the local apparent tit preference. If a new flycatcher pair settled, we recorded the symbol on the chosen box and removed it to avoid possible information transfer to conspecifics about the pair's choice. We then adjusted the number of each symbol on the remaining unoccupied boxes to keep providing later arriving flycatchers available boxes with each of the two symbols in equal proportion. Keeping an equal proportion was however not always feasible (e.g., for an odd number of empty nest boxes). We thus controlled for the possible resulting deviation by including in our models the ratio of the number of empty boxes with the apparently preferred symbol over the total number of empty boxes −0.5 (i.e., equal proportion) as a covariate (for more details, see Morinay et al., 2018). This experimental design allowed us to disconnect copying behavior (resulting from natural selection for an advantageous information use strategy) from direct fitness benefits of information use because symbols were here associated at random on available nest boxes, i.e., independently from actual box or territory quality. Thus, we investigated here the mere ability of individuals to use heterospecific social information independently from other fitness-related factors.

The symbol associated with tit nests in a given patch was alternated in space, i.e., between patches, and in time, i.e., between years. This allowed us to control for (i) the possible innate preference of hole-nesting birds for a natural circular shape and (ii) the local information gathered in the preceding year by philopatric individuals (i.e., birds that returned to breed in the same forest patch as the preceding year). Furthermore, great tit early reproductive investment (as measured by clutch/brood size on the day of flycatcher settlement) has previously been shown to affect the probability for flycatchers to copy tit apparent preference (Forsman and Seppänen, 2011; Forsman et al., 2012; Morinay et al., 2020b). Flycatchers indeed gather information on tit reproductive investment by directly prospecting tit nests upon their arrival from migration (Forsman and Thomson, 2008; Forsman et al., 2018). This information supposedly reflects tit quality (early breeders for which clutches are complete and/or individuals with overall large clutches being higher quality individuals) and thus the rewards flycatchers may expect when copying their decisions. Accordingly, flycatchers were more likely to copy (respectively, reject) tit apparent preference when local average early reproductive investment of tits in the patch was high (respectively, low) on the day of choice

(Forsman and Seppänen, 2011; Seppänen et al., 2011; Loukola et al., 2013; Morinay et al., 2020b). Therefore, we recorded the average great tit clutch/brood size in the forest patch on the settlement day of each flycatcher pair and controlled for this variable in the models testing for the use of social information (here symbol choice) by flycatchers.

Problem-Solving Task and Learning Performance

We measured the individual learning performance of the flycatchers settled in the experimental patches using a problem-solving task (**Figure 1**) presented at the nest for 1 h during the peak of nestling provisioning, i.e., when nestlings were 6 days old, between 06:00 AM and 04:00 PM. The task featured a door blocking the entrance of the nest box. The participation to the test was therefore motivated here by the access to the young. To access the nestlings, parents had to open the door by perching on one of the three levers attached below the door (**Figure 1**): only one lever opened the door, either the right or the left one, and the position of the opening lever was randomized among pairs to control for a possible innate preference for one side. Once a parent had entered, the door then closed automatically behind it, allowing us to measure separately each parent's performance in opening the door over successive trials. The parent could afterwards easily get out by pushing the door open from the inside. To limit flycatchers' neophobic response toward the task, we attached on the nest box a fake task with no door and unmoving levers on the evening before the day of the test to let the birds habituate to the device. The 1-h tests were video recorded using a camouflaged camera placed 6–8 m away from the nest box. They were conducted only if nestlings were sufficiently satiated, as measured by begging intensity at the beginning of the test, to avoid starvation if parents were not able to solve the task. If nestlings were strongly begging, the task was not set up and the experimenter came back later during the day or on the next day to check nestling satiation and try again if conditions were more favorable; if this was not the case, no test was conducted and the nest was left out of the study.

Video recordings were analyzed after the field season, blindly with respect to the nest site choice of the flycatcher pair (i.e., whether it copied or rejected tit apparent preference). For each parent, we extracted from the video recording (i) time (in s.) elapsed between the beginning of the test and the first time the individual contacted the task, to control for possible neophobia toward the task despite habituation to the fake task. We also recorded (ii) total time spent on the task (in s.) between the first contact with the task and the first entrance, or until the end of the test for those individuals that never succeeded in entering the nest box during the 1-h test, to control for the level of motivation to solve the task. Finally, for individuals that succeeded in entering, we extracted (iii) the number of times the birds perched on each lever between the first contact with the task and the first entrance, and between subsequent entrances when applicable. Individuals that did not participate to the test (i.e., contacted the task <10 s or <5 times) and those that did not solve the task (i.e., did not enter) were discarded from the analyses.

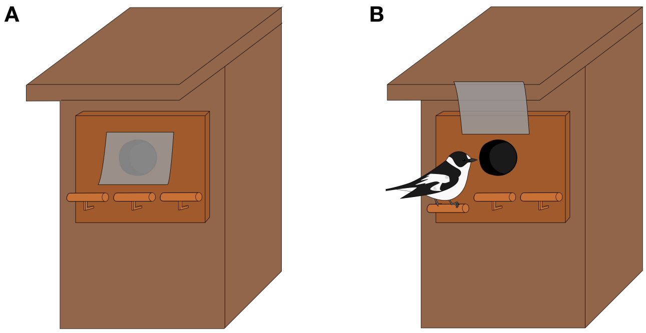

FIGURE 1 | Problem-solving task at the nest used to measure flycatchers' learning ability. **(A)** The entrance hole is closed by a plastic door but **(B)** can be opened by the parent (here a male) to enter and feed the nestlings by perching on one of the levers, here the left one. The position of the opening lever, either left or right, was randomized between pairs. See text for the measure of learning performance extracted from the problem-solving test.

We scored learning performance using the number of entrances needed to reach a learning threshold. This threshold was based on the number of times the bird perched on any of the levers before entering the nest box. The number of perches used to define the learning threshold was determined from the learning curve of our sample: the mean number of perches before entering showed a strong decrease from the first to the second entrance and then reached a plateau, with no further main change, from the third entrance (**Figure 2**, **Supplementary Table 1**). This decrease was accompanied by an increase in the proportion of perches on the opening lever, i.e., correct choices (results not shown here). We thus based our learning threshold on 8 perches, that is, the mean number of perches after which we observed the plateau showing that individuals had on average learnt how to enter (**Figure 2**). For each entrance, we assessed whether the individual perched <8 times before entering (but we also tested the robustness of our results to this chosen value by repeating all analyses with a threshold based on 6 or 10 perches instead of 8). Because birds may from time to time enter after perching <8 times by chance, we considered that an individual had actually learnt how to enter only if it entered twice in a row with <8 perches per entrance, defining our learning threshold. Individual learning score was then calculated from the number of entrances needed to reach this learning threshold: individuals that entered with <8 perches per entrance both at their first and second entrances (i.e., fastest learning individuals) were assigned a score of 1; those that entered with <8 perches at their second and third entrances were assigned a score of 2; those that entered with <8 perches at their third and fourth entrances were assigned a score of 3; and those that entered with <8 perches at their fourth and fifth entrances were assigned a score of 4. A low score thus corresponded to a low number of entrances needed to reach the learning threshold, thus to fast learning, i.e., high learning performance. Importantly, once an individual reached the learning threshold, the number of perches before subsequent entrances remained low (e.g., 90–95% of individuals with score 1 perched <8 times before the third

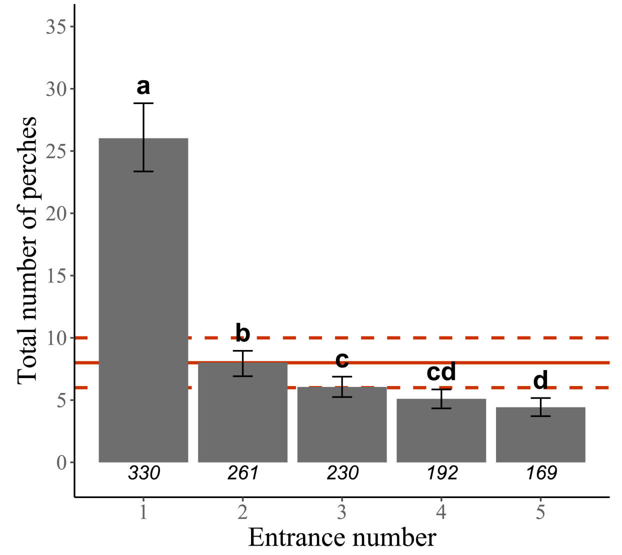

FIGURE 2 | Learning curve showing the decrease in the mean number of perches needed to solve the problem-solving task presented at the nest, i.e., to enter the nest box, over the first five entrances (data restricted to individuals that succeeded in entering the nest box at least once, i.e., solvers, and to the first learning score for individual with repeated scores across years; $N = 330$ individuals). Predicted means and 95% CI are represented. Bars with different letters have non-overlapping 95% CI. The red solid line corresponds to the value used for defining the learning threshold, i.e., 8 perches or less over two successive entrances (see main text), and the red dashed lines correspond to the two other values used to test the robustness of the results, i.e., 6 and 10 perches, respectively. Sample sizes (number of individuals) are given for each entrance number below each bar. See **Supplementary Table 1** for statistics.

to fifth entrances), thus validating our choice of two successive entrances with <8 perches to define the threshold.

To ensure that individuals had the opportunity to learn how to solve the task, we initially included only individuals that entered at least three times (because our learning threshold is based on two entrances in a row). Furthermore, because the total number of entrances over the duration of the test strongly varied among individuals (from 0 to 26 entrances), and because the mean number of perches needed tended to stabilize after the first three entrances (**Figure 2**), we considered only the first five entrances when individuals entered more than five times to standardize our learning score. Individuals that did not enter with <8 perches twice in a row over up to five entrances were assigned a score of 5. Our initial learning score thus ranged from 1 to 5, with $N = 285$ individuals scored out of 395 that succeeded to solve the task: 54 with score 1, 119 with score 2, 39 with score 3, 20 with score 4 and 53 with score 5. We exceptionally attributed a score of 1 for three individuals that entered only twice during the test but with <8 perches on both occasions; the results however did not qualitatively change when these three individuals were excluded (results not detailed here). In a second step, we assumed that individuals that entered only once or twice but without reaching the learning threshold could potentially be very slow learners that did not have time to learn within the test duration and we assigned a score of 6 to them ($N = 110$ individuals). However, because the variability in learning performance for these individuals may be higher than for other score values, we also tested the robustness of our results by repeating all analyses with and without them.

We observed no brood desertion following our learning tests; fledging success (i.e., whether pairs succeeded to fledge at least one young or not), as well as fledgling number and condition (measured as the ratio of body mass over tarsus length) for successful pairs did not differ between pairs that were subjected to our learning test and pairs that were not (**Supplementary Material**). Thus, our learning tests led to no short- or middle-term adverse effects.

Statistical Analyses

We first explored whether learning performance could be affected by variables often found to influence cognitive performance in previous studies (Griffin and Guez, 2014). Using a Generalized Linear Mixed effects Model (GLMM), we tested whether learning score (i.e., ordinal variable, ranging from 1 [fast] to 5 [slow] or 6 [very slow]—see above) depended on individual sex (male vs. female), age (yearling vs. older individuals, a dichotomy capturing most of the relevant variation in experience in this short-lived species) and their interaction, as well as the latency to return to the box and contact the task for the first time and the total time spent on the task before the first entrance, both mean-centered and scaled (fixed effects). We included the pair as a random effect to account for the potential non-independence of the learning scores of both parents within a pair. Very few individuals were scored for learning performance over several years (31 over 330 ringed individuals in total), and it was not possible to include an individual random effect (quantifying repeatability of learning score) in the model due to convergence issues. Therefore, we retained only the first learning score for each individual with repeated scores.

We then tested whether the probability to copy or reject the apparent tit preference (binary variable: choice of the same vs. opposite symbol than present on boxes occupied by tits in the patch) was related to learning score (considered here as a continuous variable, from 1 to 5 or from 1 to 6) using a GLM. Besides individual's learning score, we included in the model (i) individual's age, to control for possible age-related differences in the probability to copy tit preference as found in previous studies (see also Seppänen and Forsman, 2007 for pied flycatchers; Morinay et al., 2018), (ii) average tit clutch/brood size in the forest patch on the day of flycatcher's nest box choice, and (iii) the deviance to the equal proportion of triangles and circles in the patch (see above). We also included the two-way interaction between individual's learning score and age, to control for possible age-specific relation between learning performance and information use, and the two-way interaction between learning score and tit clutch/brood size, to test whether individuals with higher learning ability may be more prone to use several sources of information simultaneously (here, apparent tit preference and tit early reproductive investment). Because individuals may have been tested several years in the symbol choice experiment, we retained only individuals that were naïve to the symbol experiment, i.e., the first nest box choice with respect to symbols. Finally, the copying behavior being a joint decision by both the male and the female within a pair, we initially intended to include male and female learning scores simultaneously in the model. However, there were only a limited number of pairs for which both partners were naïve to the symbol experiment, scored with the learning test for the first time and were aged ($N = 36$ pairs). Therefore, we decided to fit sex-specific models including either male or female age and learning score. Yet, we also explored a model with both sexes together on the restricted subset of pairs, and we observed the same trend as for sex-specific models (**Supplementary Material**). In total, we obtained 232 individuals of known age with both a nest site choice with respect to symbols and a measure of learning performance (130 females and 102 males).

All statistical analyses were performed in R (version 4.0.0, R Core Team, 2020) and we show here posterior means and 95% CI for all estimates. In all models, we initially included year and forest patch as random factors to control for potential spatio-temporal variation in learning performance or copying behavior, but we removed them because (i) the variance associated with year and patch did not differ from zero (lower bound of 95% CI $<10^{-6}$) or (ii) including these random effects led to convergence issues (both year and forest patch passed stationary tests, but year failed to pass half-width tests despite increased iteration number; *heidel.diag* diagnosis function, *CODA* R package; Plummer et al., 2006). Interactions for which 95% CI overlapped zero were also removed (Engqvist, 2005). All models were fitted with the function *MCMCglmm* (R package *MCMCglmm;* Hadfield, 2010). Learning score, considered as an ordered factor, and copying probability were fitted with "threshold" families. We used the default wide Normally distributed priors for fixed terms ($\mu = 0$, $V = 10^{10}$), and expanded priors ($V = 1$, $\upsilon = 1$, $\alpha.\mu = 0$, $\alpha.V = 1{,}000$) for random terms. We fixed the residual variance to 1 in all models (Hadfield, 2010). We parameterized all models to obtain an effective sample size >2,000 and autocorrelation levels <0.1. We used 3×10^6 iterations, a burn-in of 3×10^5 and a thinning interval of 800 for models fitting learning score, and 10^5 iterations, a burn-in of 10^4 and a thinning-interval of 20 for models fitting copying probability. Convergence was assessed visually and by running Gelman and Rubin's convergence diagnosis tests on three MCMC chains with different starting points (*gelman.diag* function, package *CODA*, Plummer et al., 2006).

TABLE 1 | Influence of age, sex, latency to perch on the task and time spent perching on the task before the first entrance on the learning score [from 1 (fast learners) to 5 (slow or non-learners)].

	Posterior mean	[95% CI]
Intercept	1.60	[1.07; 2.16]
Fixed effects		
Sex	0.06	[−0.33; 0.47]
Age	0.27	[−0.23; 0.80]
Latency to perch on the task	0.03	[−0.29; 0.32]
Time spent perching on the task	**0.82**	**[0.46; 1.20]**
Random effect		
Pair identity variance	**2.67**	**[0.81; 4.79]**

Estimates for sex and age are given for males and yearlings, respectively (with older females as the reference). The interaction between sex and age did not differ from zero (mean [95% CI] = 0.29 [−0.25; 0.94]) and was thus removed. N = 319 individuals with information on sex, age, and learning score. Effects for which the 95% CI does not overlap zero are shown in bold.

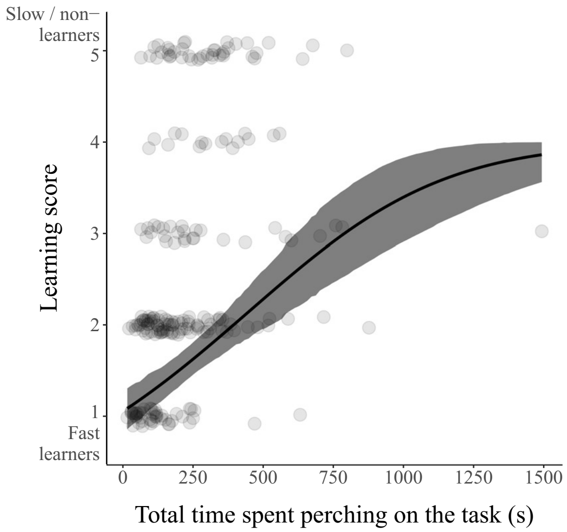

FIGURE 3 | Relation between the total time spent perching on the task before the first entrance and learning score. Low score values indicate fast learning individuals, and high score values slow or non-learning individuals (i.e., learning score increases with decreasing learning performance). Predicted distributions (means and 95% CI) are estimated for the sake of illustration from a model including only time spent perching on the task as a fixed effect. Data points are shown in gray.

RESULTS

Factors Affecting Learning Performance

Learning score depended neither on individual's sex or age, nor on the latency to contact the task (**Table 1**). Learning score, i.e., the number of entrances needed to reach down the learning threshold, however increased (and thus learning performance decreased) with increasing time spent on the task before the first entrance: slow learners (with higher score) took more time to enter for the first time than fast learners (estimate [95% CI]: 0.82 [0.46; 1.20] for individuals with learning scores from 1 to 5, and 0.39 [0.21; 0.58] when also including individuals with a learning score of 6; **Figure 3**, **Supplementary Figure 1**, **Table 1**, **Supplementary Table 2**).

Learning Performance and Social Information Use

Among females, learning score affected the probability to copy apparent tit preference. When we considered a learning threshold based on <8 perches per entrance and included females with score from 1 to 5, the effect of learning score was found to differ between yearling and older females (interaction learning

TABLE 2 | Influence of individual's age and learning score on the probability to copy tit preference.

	Model with female traits *N* = 84		Model with male traits *N* = 71	
	Posterior mean	**[95 % CI]**	**Posterior mean**	**[95 % CI]**
Intercept	2.32	[−1.35; 6.10]	−0.63	[−3.61; 2.30]
Learning score	−0.19	[−0.42; 0.04]	−0.04	[−0.28; 0.20]
Age	1.03	[−0.54; 2.71]	0.19	[−0.51; 0.92]
Tit clutch/brood size	**0.13**	**[0.03; 0.25]**	0.04	[−0.08; 0.15]
Deviance from symbol equal proportion	−5.13	[−12.52; 2.60]	0.78	[−4.55; 7.23]
Learning score × age	**−0.66**	**[−1.41; −0.01]**		

The age estimate corresponds to yearling individuals, with older ones as the reference. Fast-learning individuals need lower number of entrances to reach the learning threshold, i.e., they have low scores, while slow-learning individuals have high scores (see text). N are sample sizes. Effects for which the 95% CI does not overlap zero are shown in bold.

score × age; **Table 2**). Yearling females with lower score, i.e., higher learning performance, were more likely to copy tit apparent preference, while yearling females with higher score, i.e., lower learning performance, were more likely to reject it (**Figure 4**). This relation between learning performance and probability to copy was however not detected in older females alone, despite a similar decreasing trend (mean [95% CI] = −0.19 [−0.42; 0.04]; **Figure 4**). Importantly, when considering a learning threshold based on either 6 or 10 perches, or when including females with a score from 1 to 6 (even for the threshold based on 8 perches), the probability to copy tit preference decreased with increasing learning score, i.e., with decreasing learning performance, with no difference between the two age categories (no interaction between learning score and female age; **Table 3**, **Supplementary Table 3**, **Supplementary Figure 2**, **3**). The decrease with learning score alone was also retained in the model for the learning threshold based on <8 perches per entrance and females with score from 1 to 5 when the interaction with age was removed (**Table 3**). Females with lower score were more likely to copy tit apparent preference (mean [95% CI] copying probability for females with score 1 = 0.65 [0.51; 0.79], i.e., >0.5 = random choice), while females with higher score were more likely to reject it (mean [95% CI] copying probability for females with score 6 = 0.34 [0.22; 0.46], i.e., <0.5; **Supplementary Figure 3**). In addition, for all female models, the probability to copy tit preference also increased with tit clutch/brood size within the patch on the day of female choice (**Table 2**, **Supplementary Table 3**; no interaction with age).

Among males, the probability to copy tit preference did not depend on learning score, alone or in interaction with age, whatever the model considered, i.e., for a learning threshold based on either 6, 8, or 10 perches, and when including or not males with a score of 6 (**Tables 2**, **3**, **Supplementary Table 4**).

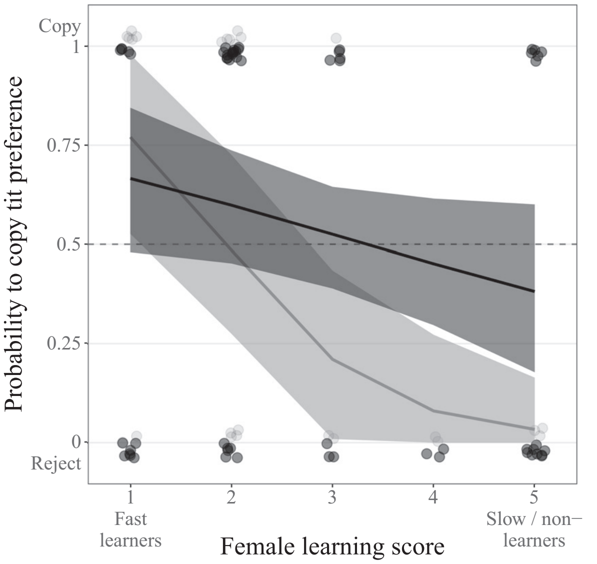

FIGURE 4 | Relation between learning score (from 1 to 5) and the probability to copy apparent tit preference for nest site choice in flycatcher females, depending on female age (light gray: yearlings: *N* = 25, dark gray: older females: *N* = 59). Predicted distributions (mean and 95% CI) are estimated from the model including the interaction between learning score and age, with a mean value set for other continuous predictors (see **Supplementary Table 2**). Data points show actual choices.

DISCUSSION

To make optimal decisions, individuals often have to process multiple, complex, and potentially conflicting information from the environment. Cognitive abilities can therefore be expected to play a crucial role in such information processing. In this study, we used an experimental approach on wild collared flycatchers to test whether variation in learning ability was linked to variation in the use of a source of heterospecific social information (here, apparent tit preference for a nest site feature) for nest site selection. Overall, our results show that females that were faster to learn how to solve a new task at the nest were more likely to copy tit apparent preference while females that were slower to learn were more likely to reject it. This effect seemed more pronounced in yearling females, but because the interaction between learning score and female age was found only when the learning threshold was based on 8 perches before entrance and when females with score 6 were excluded, and in no other case, it did not seem to reflect a strong biological difference. Despite between-pair

TABLE 3 | Summary of the estimates for the learning score effect on the probability to copy tit preference, when alone (i.e., no interaction with age included in the model) depending on the value considered for defining the learning threshold (<6, 8, or 10 perches per entrance, for two successive entrances) and the individuals considered (individuals with scores 1–5 only or individuals with scores 1–6), for (a) females and (b) males.

	Scores 1–5			Scores 1–6		
	N	**Posterior mean**	**[95 % CI]**	**N**	**Posterior mean**	**[95 % CI]**
(a) Model with female traits						
<6 perches	83	***−0.18***	***[−0.38; 0.00]***	130	***−0.12***	***[−0.24; 0.00]***
<8 perches	84	**−0.28**	**[−0.50; −0.09]**	130	**−0.17**	**[−0.29; −0.05]**
<10 perches	85	**−0.35**	**[−0.58; −0.11]**	130	**−0.15**	**[−0.26; −0.04]**
(b) Model with male traits						
<6 perches	71	0.01	[−0.21; 0.23]	102	−0.04	[−0.18; 0.10]
<8 perches	71	−0.04	[−0.28; 0.20]	102	−0.06	[−0.20; 0.07]
<10 perches	71	−0.07	[−0.33; 0.19]	102	−0.07	[−0.19; 0.07]

*N are sample sizes. Cases in which the 95% CI does not overlap zero are shown in bold. For the threshold based on <6 perches per entrance, the upper limit of the 95% CI just reached 0 for females (in italics). Note that for the female model for the learning threshold based on <8 perches per entrance and individuals with scores 1–5, the interaction learning score × age is positive (see **Table 2**) and has here been removed from the final model to document the effect of learning score alone.*

variance in learning performance, we found no relation between learning score and the probability to copy tit preference in males, whether yearling or older. These results suggest that cognitive abilities (in this study learning ability) can at least partly shape information use for decision-making, here in females, providing a new mechanistic explanation for the positive link between cognitive abilities and fitness components (Cauchard et al., 2017; see also Ducatez et al., 2020) that was previously observed in the wild (e.g., Keagy et al., 2011; Cauchard et al., 2013; Smith et al., 2015).

Linking Cognition and Fitness: The Role of Information Processing

To explain the links between cognitive abilities and fitness traits recently reported in wild populations (e.g., reproductive success: Cauchard et al., 2013; Smith et al., 2015; Ashton et al., 2018; survival: Sonnenberg et al., 2019; Wild et al., 2019), it has been hypothesized that individuals with higher cognitive abilities may achieve higher fitness because of a higher ability to optimally exploit their habitat (Cole et al., 2012; Cauchard et al., 2017). This may rely on a better processing and use of information sources about the environment (e.g., prioritize and memorize information but also learn from either personal or social experience), allowing individuals to optimally choose between alternatives (Mery, 2013). This is in line with previous results showing that higher problem-solving ability was associated with increased nestling provisioning rate (Cauchard et al., 2017), which could involve different habitat use strategies (e.g., range of territory use: Cole et al., 2012). Yet, empirical evidence that cognitive abilities influence the use of complex information for decision making in the wild is still extremely scarce. Our results experimentally show that, in the collared flycatcher, learning performance is related to the use of a manipulated source of information for nest site selection, a crucial decision with major impact on reproductive success. The complex use of social information of heterospecific origin (i.e., from potential competitors) for nest site selection has been demonstrated in previous studies on flycatchers based on the same experimental set up: individuals modulate the use of apparent tit preference for nest site choice depending on tit early reproductive investment (Forsman and Seppänen, 2011; Seppänen et al., 2011; Loukola et al., 2013; Morinay et al., 2020b), but also their own previous experience (Morinay et al., 2018, 2020b) and behavioral traits (Morinay et al., 2020b). In our study, we make one step forward by showing that between-individual variation in the context- and condition-dependent use of this social information source may also depend on variation in learning ability.

One important but still open question is the nature of the cognitive processes underlying our measure of learning ability and how these processes relate to those underlying social information use for decision-making. Identifying these cognitive processes would allow us to better understand on which cognitive trait(s) selective pressures are acting. Although we did not explore here the detailed cognitive processes involved in learning how to solve our task, the test was based on operant conditioning, i.e., a type of associative learning process in which the strength of a behavioral response is modified by reinforcement (leading to response increase) or punishment (leading to response decrease; Skinner, 1938). Here, reinforcement corresponded to door opening, granting access to nestlings, and the rewarded behavior was perching on the opening lever. Such associative learning process is widespread in the animal kingdom (Dickinson, 2012; Morand-Ferron et al., 2015) and should underlie many behavioral decisions during the breeding season, especially those involving repeated individual actions, such as here the visit of many nest boxes needed to associate the symbol to box occupancy by tits and tit early reproductive investment. Much remains to be done to unravel the key underlying cognitive processes (e.g., associative learning, memory, spatial cognition) that are driving between-individual variation in information use processes in the wild and their fitness consequences.

Influence of Individual Factors on the Link Between Learning and Information Use

The relation observed here between learning performance and the use of heterospecific social cues for nest site choice depended on sex: the probability to copy tit apparent preference decreased with decreasing learning performance (i.e., with increasing number of entrances to reach down the learning threshold) only in females. Male learning performance had no effect on copying behavior here, even though nest site choice is a joint behavior by both pair members (Pärt, 1994; Pärt and Qvarnström, 1997). Previous studies in collared and pied flycatchers suggest that females often use social information collected at large spatial scales for breeding site selection (e.g., local tit phenology at the forest patch scale: Samplonius and Both, 2017; tit song quality at the scale of a group of nest sites: Morinay et al., 2020a). In contrast, males are more prone to use social information obtained at small scales (e.g., nest reproductive success at the territory scale: Pärt and Doligez, 2003). The link between learning performance and probability to copy tit preference in females is in line with this difference, because the social information provided here relies on associating tit occupancy to the symbol attached to the box at a large (patch) spatial scale. Conversely, males secure a territory encompassing several adjacent nest boxes that most often display both symbols, because our experimental protocol avoided large spatial aggregations of same-symbol boxes. Therefore, the strong male philopatry to breeding patches (e.g., Pärt, 1994, 1995; Germain et al., 2017) and the previously observed effects of male age, experience, and aggressiveness on the probability to copy tit preference for nest-site choice (Morinay et al., 2018, 2020b) may be a response to strong male-male competition. Males familiar with their environment may have an easy access to local heterospecific social information, thus requiring no strong learning ability to process this information for choosing a site. Conversely, females are expected to gain advantage in choosing a nest site over larger scales (Greenwood, 1980), possibly favoring the use of more complex quality-related social cues, requiring higher cognitive abilities for processing these cues. Hence, the sex-specific relation observed in the present study between learning performance and use of social information may result from the different selective pressures acting on both sexes for settlement decisions. Alternatively, females with higher learning performance may be more efficient in assessing, and mating with, more competitive (aggressive) males (Qvarnström et al., 2000), which themselves choose nest boxes with the symbol matching tit preference (Morinay et al., 2020b); in this case, the relation between learning performance and use of social information in females would be indirect. Further work is needed to explore the consequences of learning performances of paired individuals on complex social information use for joint nest site selection.

Even though age-dependent use of social information has been repeatedly reported in previous studies on this population (e.g., Doligez et al., 2004; Kivelä et al., 2014; Morinay et al., 2020a), including studies using the same experimental symbol design (Morinay et al., 2018, 2020b), the age difference in the effect of female learning score on the probability to copy tit preference was not strongly supported. Thus, here, differences between yearling and older females in either past experience, current competitive level, or time constraints linked to the timing of arrival from migration did not seem to strongly affect the link between learning performance and information use.

Only fast-learning females could have been expected to succeed in optimally and/or quickly processing available social information, and thus be more prone to copy tit preference. Yet, slow-learning females were not simply choosing a nest site at random with respect to tit apparent preference: they were actually more likely to reject it compared to a random choice. This suggests that, although all females could access this source of information, they may have processed and/or used it differently for subsequent choices depending on their learning ability. One hypothesis is that slow-learning females may be less competitive than fast-learning ones because of a lower ability to exploit the habitat, e.g., because of a lower ability to use other information sources. By rejecting tit preference, slow-learning females would then avoid expected increased competition with dominant great tits. In this case, the decision-making process of both fast and slow learners may lead to an optimal nest site choice with respect to competitive ability (see e.g., Doligez et al., 1999 for another example of age-related opposite use of social information with respect to competitive ability). Tit apparent preference as a source of social information may be accessible to all individuals regardless of their learning ability; but the relation observed between the probability to copy tit preference and learning performance could indirectly result from the impairment of acquiring other information sources in slow-learning individuals.

This study evidences a link between learning performance and the use of (here heterospecific) social information for nest site choice in the wild. Yet, this relationship appears more complex than initially thought, with sex- (and possibly age-) dependent effects potentially reflecting different consequences for subsequent choices. By reporting a clear relationship between learning performance and social information use, our study moves one step forward toward understanding the mechanisms linking cognition and fitness in the wild. This provides support for the role of cognitive abilities in using complex information for decision-making, with major ecological and evolutionary implications.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are openly available in FigShare at http://doi.org/10.6084/m9.figshare.13229081.

ETHICS STATEMENT

Birds were caught, handled, and ringed under a license from the Ringing Centre of the Museum in Stockholm (471:M015 to BD). Behavioral experiments were conducted in accordance with international standards on animal welfare and complied with local and national regulations.

AUTHOR CONTRIBUTIONS

LC and BD designed the study. JM, LC, and BD carried out the field work. LC and PB supervised the data extraction and JM carried out the statistical analyses. JM and BD drafted the manuscript and all authors revised it.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.559690/full#supplementary-material

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Challenges in Linking Cognition and Survival: A Review

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Linking cognitive performance with fitness outcomes, measured using both reproductive and survival metrics, of free-living animals is crucial for understanding the evolution of cognition. Although there is increasing evidence showing a link between cognitive traits and reproductive success metrics, studies specifically exploring the link between cognition and survival are scarce. We first explore which cognitive traits related to survival have been investigated in free-living animals. We also discuss the challenges associated with investigating the links between cognition and survival. We then review studies that specifically consider survival of animals of known cognitive abilities that are either free-living or in captivity and later released into the wild. We found nine studies exploring cognitive traits in wild populations. The relationships between these cognitive traits and survival were equivocal. We found a further nine studies in captive-reared populations trained to predator cues and later released into the wild. Training to recognize predator cues was correlated with increased survival in the majority of studies. Finally, different individual intrinsic characteristics (i.e., age, body condition, personality, sex) showed varied effects between studies. We argue that finding ecologically relevant cognitive traits is crucial for gaining a better understanding of how selection impacts certain cognitive traits, and how these might contribute to an individual's survival. We also suggest possible standardized, easy to implement, cognitive tests that can be used in long-term studies, which would generate large sample sizes, take into account intrinsic characteristics, and provide an opportunity to understand the mechanisms, development and evolution of cognition.

Keywords: cognitive ecology, reproductive success, sample size, survival, fitness

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INTRODUCTION

Cognition refers to the processes by which animals collect, retain and use information from their environment (Shettleworth, 2010). An array of cognitive functions impact an animal's behavior in the wild, including perception, attention, learning, memory, decision-making and executive functions (flexibility, categorization, problem-solving; Cauchoix and Chaine, 2016). Individuals vary in their cognitive abilities, which likely influences how they react to changes in their environment (Mazza et al., 2018). Consequently, individual variation in cognitive ability is a key component of fitness (Morand-Ferron et al., 2015; Pritchard et al., 2016), which is broadly defined as "the capacity of organisms to survive and reproduce in their environment"

(Hua and Bromham, 2018). However, the relationship between cognition and fitness, both survival and reproductive success, is likely to differ between species, and may depend on the physical/social environment and/or life-history traits. Thus, exploring individual variation in cognition, and its relationship with different fitness components, could aid in understanding how and why cognitive abilities have evolved (Boogert et al., 2018).

Several studies have investigated how fitness, estimated using reproductive success metrics, relates to cognition (**Supplementary Appendix 1**). Surprisingly, few studies have focused on the link between survival, another important fitness proxy, and cognition. Reproductive success and survival are inherently linked since individuals with greater survival also increase their chances of having higher lifetime reproductive success. Furthermore, there are many competing demands for resources that may influence the decision making process on whether to promote growth or reproduction, whether to invest in protection and survival, or to find an optimal balance between these competing interests (Abram et al., 2021), all of which likely depend on cognitive processes. In addition, many studies state that cognitive traits (e.g., learning) can impact survival (e.g., Pravosudov and Roth, 2013), yet the majority of these studies do not specifically test whether this is the case. One explanation could be that measuring survival itself is particularly challenging.

In free-living animals, it is often difficult to discern whether an individual has died or has merely dispersed from the area of capture (e.g., Huebner et al., 2018). Indeed, the only definitive assessment of survival is observed mortality, which is often not observed directly in nature, and ultimately leads to missing values in datasets. Calculating survival is therefore more complicated than assessing reproductive success, and likely requires data-intensive capture-mark-recapture, which could be also influenced by individual personality (e.g., neophobia), and modeling that account for the possibility of dispersal. In addition, species-specific life history traits, particularly for survival, make comparative studies difficult. For example, some studies use juvenile survival (e.g., Sonnenberg et al., 2019), whereas others use adult survival (e.g., Maille and Schradin, 2016; Huebner et al., 2018). Nevertheless, survival analyses are used in other ecological studies (e.g., Santos et al., 2015; MacLeod et al., 2018), regardless of these limitations, and using data loggers could help to determine survival (e.g., African striped mice, *Rhabdomys pumilio*, Maille and Schradin, 2016; Vuarin et al., 2019), which begs the question of why studies relating cognition to survival are not more common. While studying the links between cognition and survival is challenging, one approach that could be adopted is to first measure the performance of individuals in one cognitive test over multiple presentations (i.e., time) or use several cognitive tests to evaluate several cognitive functions (Rowe and Healy, 2014). Thereafter, studies could explore how cognitive ability correlates with a particular survival metric such as "survivor or non-survivor" or "days of longevity" (e.g., Huebner et al., 2018). Using several survival measures should be considered since only one measure could be misleading through overestimation or underestimation (Boogert et al., 2018).

Although greater cognitive performance is associated with fitness benefits, increasing evidence of natural within-species variation in cognitive ability indicates that cognition is not cost-free (reviewed in Thornton and Lukas, 2012). For example, in fruit flies (*Drosophila melanogaster*) tested in the laboratory, learning performance was negatively correlated with longevity (Lagasse et al., 2012), physiological response to food restriction (Mery and Kawecki, 2005) and larval competitive ability (Mery and Kawecki, 2003). In addition, whereas some cognitive traits may be positively or negatively associated with fitness, not all cognitive traits may affect fitness depending on their ecological relevance. For example, song repertoire size, an indirect predictor of various reproductive success measures, in male song sparrows (*Melospiza melodia*) is positively correlated with inhibitory control (detour reaching performance) but not with learning performance in a motor or color discrimination task (Boogert et al., 2011).

The different outcomes described above also indicate many challenges in linking cognitive traits and fitness. For example, the relationships between cognitive abilities and survival may vary depending on the study design (e.g., laboratory vs. studies in the wild, sample size, chosen cognitive and survival metrics) and individual characteristics of particular species (Huebner et al., 2018), such as sex (Maille and Schradin, 2016). For example, a positive relationship between learning (aversive conditioning) and survival post-release in the wild occurs in black-tailed prairie dogs (*Cynomys ludovicianus*, Shier and Owings, 2006) but not in greater bilbies (*Macrotis lagopus*, Moseby et al., 2012). This could be a species-specific response, but it could also be due to differences in study design; Shier and Owings (2006) trained prairie dogs with only a single cue, whereas Moseby et al. (2012) trained bilbies with multiple cues. Survival is also age-dependent, generally decreasing with increasing age in several species (Lemaître and Gaillard, 2020). Senescence is a widespread phenomenon that is especially pronounced in cognitive abilities but it may be delayed in species with strong selection on cognitive abilities, such as food-caching species (Heinen et al., 2021). Personality traits also influence cognitive abilities (Sih and Del Giudice, 2012), fitness outcomes (Collins et al., 2019) and add challenges to measuring survival (e.g., neophobia may decrease recapture success and may bias estimates of survival). Currently, links between cognition and survival have generally only been studied in a small number of free-living species, often focusing on a single cognitive trait (Huebner et al., 2018), and not taking into account intrinsic characteristics such as sex, age and personality, making generalizations on the relationship between cognition and survival challenging.

In this review, we provide the methods and results obtained from cognitive studies of (i) different species tested directly in the wild, (ii) free-living species temporarily held and tested in a field laboratory and later returned to the wild, and (iii*)* captive-reared species later reintroduced to the wild. In these studies, individual cognitive traits were measured and related to specific survival metrics as a proxy of fitness. Our aims were to: (1) investigate whether there is a positive, negative or absence of a relationship between cognition and survival in animals in nature or studied in captivity but released into the wild, and (2) discuss the challenges of studying this relationship in a natural environment. Finally, we suggest some experimental approaches to studying cognition in free-living species to enable us to more accurately assess the relationship between cognition and survival.

METHODS

Literature Survey

We first conducted a thorough search of the literature using the ISI Web of Science. We started with 32 broad (e.g., cognition or cognitive trait) and specific (e.g., "working memory" or "spatial learning") keywords (**Figure 1**). Each of these keyword searches was then refined with five additional keywords (survival, mortality, longevity, death and fitness; **Figure 1**). These searches resulted in a total of 277,438 hits. Therefore, we further refined each search by including first the keyword "animal" (**Figure 1**). If this did not reduce the number of hits to a manageable number (e.g., 60), we further refined the search by including each of the following taxonomic groups: mammal, primate, bird, reptile, amphibian, fish, insect and invertebrate (**Figure 1**). This resulted in a total of 6,637 hits. Articles were discarded if they did not reach three criteria (**Figure 1**): (1) studies had to be conducted on animals that were free-living or were wild strains that had been brought into captivity for a short period for testing and then released (e.g., studies conducted on laboratory strains, such as rats, mice and fish, were not considered). (2) Studies had to explicitly evaluate survival (e.g., some studies merely mentioned survival as a potential benefit but did not actually test this). (3) Studies had to explicitly evaluate the relationship between the cognitive trait and survival.

RESULTS

We found nine studies linking cognition and survival in free-living animals (**Table 1**) and nine studies in captive reared animals reintroduced to the wild (**Table 2**). Different cognitive tasks were used in each study as appropriate for the study species. For example, a Barnes maze was used for spatial learning and memory in striped mice (Maille and Schradin, 2016), whereas "spatial arrays" were used for spatial learning and memory in mountain chickadees (*Poecile gambeli*, e.g., Sonnenberg et al., 2019). In addition, tasks were based either on artificial stimuli (e.g., color discrimination learning, lever pulling problem-solving, Madden et al., 2018) or natural stimuli (e.g., attention toward a predator, memory to find a shelter in a predator-mimicking situation, e.g., Ferrari et al., 2014). Finally, different individual intrinsic characteristics (i.e., age, body condition, personality, sex) were included as co-variates that could explain the link between cognition and survival. However, these varied between studies.

Literature Survey: Cognition and Survival in Wild Populations

In the nine studies on the relationship between several cognitive traits (i.e., problem-solving, spatial and reversal learning, spatial memory) and survival in wild populations, four (three on birds, and one on a reptile; **Table 1**) measured the traits *in situ*, and five (two on mammals, one on birds, and two on fish; **Table 1**) measured the traits in a field laboratory before returning the individuals back to the wild. All studies training individuals to predator cues found a 100% positive relationship between training/learning and survival (N = 5; **Table 1**). Studies testing spatial learning and memory found contrasting results ($\text{N}_{\text{positiverelationship}}$ = 2, but one only with males; $\text{N}_{\text{non-significantrelationship}}$ = 2). One study testing attention found a positive relationship only with females. Studies testing problem-solving (N = 2) or reversal spatial learning (N = 2) did not find any significant relationship with survival.

Literature Survey: Cognition and Survival in Captive Reared Populations

We found one study on the common pheasant (*Phasianus colchicus*) that aimed to relate the performance of two cognitive traits (i.e., discriminative, spatial and reversal learning) with survival when these pheasants were later reintroduced to the wild (**Table 2**). The results showed a negative relationship between survival and reversal learning, that is, pheasants that were slow to reverse previously learned associations were more likely to survive, and a positive relationship between discriminative learning and survival in heavy but not light birds (Madden et al., 2018). Eight studies (two on mammals, five on birds, and one on reptiles; **Table 2**) aimed to train captive-bred animals to predator-prey stimuli to increase species reintroduction success later. Five studies found a positive relationship between training and survival, whereas three studies did not find any significant relationship.

DISCUSSION

We found nine studies specifically focusing on the survival of free-living animals of known cognitive abilities and nine studies exploring survival of captive-reared species later reintroduced to the wild. We found that study designs varied widely in sample size, chosen cognitive traits and survival metrics, and in the inclusion of intrinsic characteristics such as sex, age, and personality. It is challenging practically to link cognition and fitness proxies in free-living animals for two reasons. First, it is difficult to find cognitive traits that are aligned with the ecology of the study species, that are biologically relevant, and that are likely to explain survival across species. Second, in some species, it is difficult to distinguish between dispersal and death to be able to evaluate survival, an often overlooked fitness metric.

The first challenge when studying the effects of cognition on survival is finding appropriate cognitive traits to test in relation to fitness proxies. For example, Huebner et al. (2018) suggested that the absence of a relationship between problem-solving and spatial learning performance and survival in gray mouse lemurs (*Microcebus murinus*) shows that survival might not be predicted by the specific cognitive abilities addressed in the study. Some cognitive traits might be under selection in some species compared to others based on the ecology of that

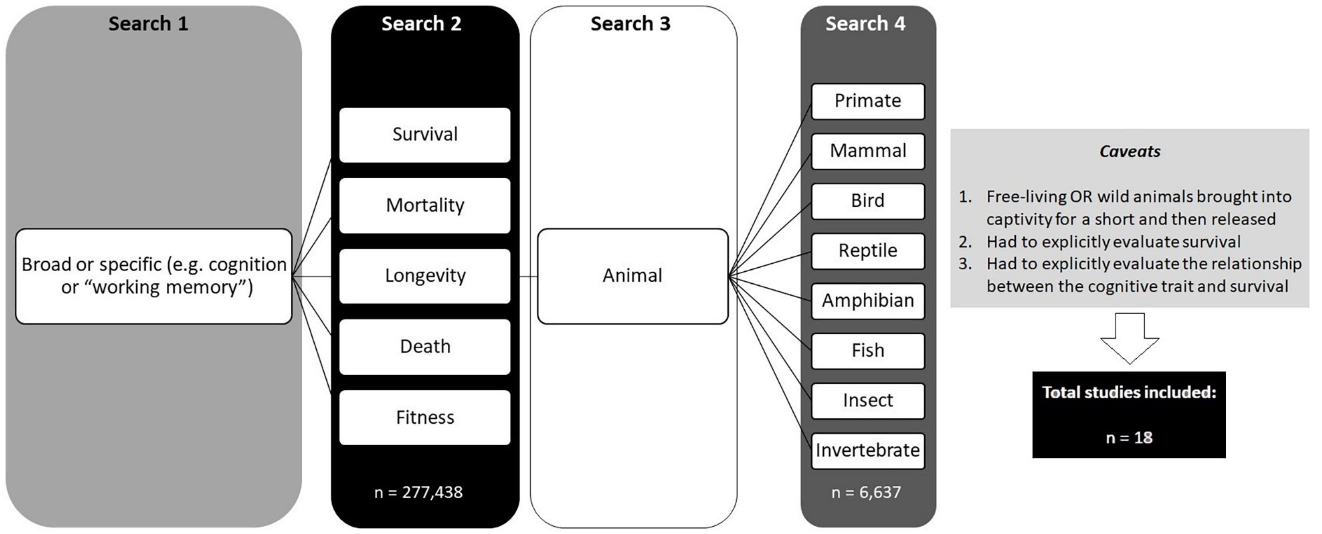

FIGURE 1 | Flow diagram showing the literature search process and the criteria used to include/exclude papers in the review.

species (e.g., memory in food caching birds, Sonnenberg et al., 2019; problem-solving in non-migratory birds, Sol et al., 2016). Thus, one solution is to examine cognitive traits related to a particular hypothesis for an increase or decrease in survival, and hence choose an ecologically relevant cognitive trait to disentangle what selective pressures are acting on it (Boogert et al., 2018). Alternatively, assessing diverse cognitive functions in free-living animals, including perception, learning, memory (short and long-term), attention, decision-making and executive functions (flexibility, categorization, problem-solving), will help us understand whether cognitive performance in a particular context is associated with fitness benefits and/or costs in different species (Cauchoix and Chaine, 2016). For example, attentional processes will impact an animal's behavior in the wild in many different situations, and it has been suggested that attention might explain the relationship between general cognitive ability and survival skills in several species (Matzel et al., 2020). Ultimately, it would be beneficial to find candidate cognitive traits that are likely to explain survival across species.

Some studies merely mentioned, but did not actually test for, survival as a potential benefit, whereas others clearly explore these relationships. For example, the wealth of literature on the cognitive ecology of food-storing in birds that has emerged over the last 30 years suggests that studying spatial memory abilities and associated neural structures in food-hoarding animals that rely on food caching and later retrieval of caches is relevant to understanding overwintering survival (reviewed in Pravosudov and Roth, 2013). Some meta-analysis studies also showed a positive relationship between brain size and innovative propensity as a measure of cognition and survival (Sol et al., 2005, 2007). Nevertheless, only two recent studies in birds empirically tested the relationship between spatial memory abilities and survival *per se* (Tello-Ramos et al., 2018; Sonnenberg et al., 2019). Tello-Ramos et al. (2018) found no significant relationship between survival to the first year and spatial and reversal learning performances, whereas Sonnenberg et al. (2019) found increased survival in individuals performing better in spatial learning and memory tasks. Considering that an array of cognitive abilities could impact an animal's behavior in the wild, it should be noted that some cognitive traits, such as perception or decision-making, and some executive functions (e.g., categorization) have not been studied, either in relation to survival (**Table 1**) or to reproductive success (**Supplementary Appendix 1**).

Studies in cognitive conservation biology (i.e., individuals being aversively conditioned in captivity with olfactory and/or visual stimuli from predators) could be relevant for demonstrating the adaptive value of learned information. Some studies showed a higher proportion of population survival in captive-bred animals trained to recognized predator stimuli (**Table 2**). One study in captivity did not train animals with predator cues but tested two cognitive traits. Madden et al. (2018) related discriminative, spatial and reversal learning performance of captive common pheasants with survival when these pheasants were later reintroduced to the wild; individuals that were slow to reverse previously learned associations (reversal learning task) were more likely to survive to 4 months old (Madden et al., 2018). We included studies on individuals reared in captivity in the results of our review but we should be cautious about the interpretation of fitness consequences of natural variation in learning ability (Morand-Ferron, 2017). Indeed, animals reared in captivity are not confronted with the same environmental challenges compared to their free-living counterparts, particularly if they are retained in captivity from an early age. They are often limited in their food diversity, and/or may be food deprived, forcing participation in a test. In addition, captive animals may be limited by space, again potentially forcing participation, or increasing stress that might impact the results. Consequently, results relating cognition to survival in animals reared in captivity should be treated with caution since they may not reflect true patterns seen in free-living animals.

TABLE 1 | Overview of studies linking cognitive performance and survival in free-living animal populations.

Species	Context	Cognitive traits	Cognitive task	Survival metric	Statistics	Intrinsic characteristics	Sample size	Results	References
Mammals									
African striped mouse (*Rhabdomys pumilio)*	Wild tested in field lab	Spatial memory	Barnes maze (lab)	Survival to breeding season	Logistic regression: Binomial data (survivor or non-survivor)	Litter, sex	*N* = 59		Maille and Schradin, 2016
							30 ♂	+ for ♂	
							29 ♀	- for ♀	
		Attention	Orientation test (lab)				*N* = 59	NS	
							30 ♂		
							29 ♀		
			Moving shadow (field)				*N* = 50		
							20 ♂	NS for ♂	
							30 ♀	+ for ♀	
Gray mouse lemur (*Microcebus murinus*)	Wild tested in field lab	Problem-solving	Food extraction task: lid opening (lab)	# days surviving between birth and date of last capture	Cox proportional hazards models	Age, body condition, sex	*N* = 64	NS	Huebner et al., 2018
		Spatial learning	Plus maze (lab)				*N* = 62	NS	
Birds									
Mountain chickadee (*Poecile gambeli*)	Wild	Spatial learning and memory	Smart feeder and spatial array (field)	Survival in 1st year	Logistic regression: Binomial data (survivor or non-survivor)	Age	*N* = 62	+	Sonnenberg et al., 2019
		Reversal spatial learning and memory						NS	
Mountain chickadee (*Poecile gambeli*)	Wild	Spatial learning and memory	Smart feeder and spatial array (field)	Survival in 1st year vs. adult survival at least 1 year	General linear model (GLM)	Age	*N* = 169	NS	Tello-Ramos et al., 2018
		Reversal spatial learning and memory					*N* = 98	NS	
Great tit (*Parus major*)	Wild tested in field lab	Problem-solving	Lever-pulling task (lab)	Survived winter or the next breeding season	General linear model (GLM): Binomial data (survivor or non-survivor)	Age, body condition, sex	*N* = 698	NS	Cole et al., 2012
Siberian jays (*Perisoreus infaustus*)	Wild	Learning: aversive conditioning	Predator training *via* visual cues (wild)	Survival in 1st year	GLM: Binomial data (survivor or non-survivor)	Age, brood, group size, sex	*N* = 109	+	Griesser and Suzuki, 2017
Fish									
Coral reef damselfish (*Pomacentrus wardi*)	Wild tested in field lab	Learning: aversive conditioning	Predator training *via* visual and chemical (lab)	Survival 70–96 h post-release	Cox's proportional hazard model	Body size	*N* = 52	+	Lonnstedt et al., 2012
Whitetail damselfish (*Pomacentrus chrysurus*)	Wild tested in field lab	Learning: aversive conditioning	Risk training from injured conspecific cues (lab)	Survival to 77 h post-release	Cox's proportional hazard model	-	*N* = 102	+	Ferrari et al., 2014
			Predator training *via* visual and chemical cues (lab)					+	
Reptiles									
Yellow-spotted monitor (*Varanus panoptes*)	Wild	Learning: aversive conditioning	Toxic prey training (field)	# days survived after training	Kaplan–Meier survival analysis	Body size	*N* = 47	+	Ward-Fear et al., 2016

Studies are classified according by taxon (mammals, birds, fishes and reptiles). For each cognitive task, we provide details about whether the study took place in a field laboratory or directly in the field. Survival metrics are provided (# represents number). The relationship between cognitive performance and survival is either positive (+), negative (–) or non-significant (NS). ♂ represents males, ♀ represents females, ↑ represents increased survival.

TABLE 2 | Overview of studies linking cognitive abilities in captive animals and their reintroduction success.

Species	Context	Cognitive traits	Cognitive task	Survival metric	Statistics	Intrinsic characteristics	Sample size	Results	References
				Mammals					
Greater bilby (*Macrotis lagotis*)	Captive, released to wild	Learning: aversive conditioning	Predator training *via* learning multiple cues (field)	Survival 6 months post-release	Fisher test	Body condition, sex	$N = 20$ 7 ♂ 13 ♀	NS ($p = 0.160$)	Moseby et al., 2012
Black-tailed prairie dog (*Cynomys ludovicianus)*	Captive, released to wild	Learning: aversive conditioning	Predator training *via* auditory cues (lab)	Survival 1 year post-release	Multiple logistic regression	Body condition, litter, sex	$N = 18$ 8 ♂ 10 ♀	Trained = ↑ survival ($p = 0.004$)	Shier and Owings, 2006
				Birds					
Blue-fronted Amazon parrot (*Amazona aestiva*)	Captive, released to wild	Learning: aversive conditioning	Predator training *via* visual cues (lab)	Survival to 12 months post-release	Kaplan–Meier survival analysis	Personality, sex	$N = 31$ 17 ♂ 14 ♀	NS ($p = 0.670$)	Lopes et al., 2017
Common pheasant (*Phasianus colchicus*)	Captive, released to wild	Spatial learning and color discrimination	Food-rewarded wells according to location (lab)	Survival to 60 days post-release	GLM: Binomial data (survivor or non-survivor)	Body condition, personality, sex	$N = 154$	+ for heavy birds ($p = 0.060$); − for light birds ($p = 0.018$)	Madden et al., 2018
		Reversal spatial learning and color discrimination						- ($p = 0.036$)	
Greater rhea (*Rhea americana*)	Captive, released to wild	Learning: aversive conditioning	Predator training *via* visual cues (lab)	Survival to 8 months post-release	Chi-square	Sex	$N = 21$ 11 ♂ 10 ♀	NS ($p = 0.280$)	Vera Cortez et al., 2015
Houbara bustards (*Chlamydotis macqueenii*)	Captive, released to wild	Learning: aversive conditioning	Predator training *via* model and live animals (lab)	Survival to the breeding season	Fisher test	NA	$N = 44$	Trained = ↑ survival ($p < 0.05$)	Van Heezik et al., 1999
Little owls (*Athene noctua*)	Captive, released to wild	Learning: aversive conditioning	Predator training *via* visual and auditory cues (lab)	Survival to 6 weeks post-release	NA	NA	$N = 16$	Trained = ↑ survival	Alonso et al., 2011
Red-legged partridges (*Alectoris rufa*)	Captive, released to wild	Social learning	Predator training *via* visual cues (lab)	# days survived after release	Mantel-Cox test	Age, brood, sex	$N = 84$	Trained = ↑ survival ($p < 0.05$)	Gaudioso et al., 2011
				Reptiles					
Velvet gecko, (*Amalosia lesueurii*)	Captive, released to wild	Spatial learning	Find a shelter (lab)	Survival to 9 months post-release	ANOVA	Body size and mass	$N = 64$	Cold-incubated hatchlings = faster learners ($p < 0.001$)	Dayananda and Webb, 2017
					Cormack–Jolly–Seber models			Better learners = ↑ survival (lower AIC)	

One study related problem-solving and spatial learning to survival, and eight studies related learning of predator cues to reintroduction success. ♂ represents males, ♀ represents females, ↑ represents increased survival.

The second challenge when studying the effects of cognition on survival will be to accurately distinguish between dispersal and death, which will permit evaluation of survival in some species. Calculating survival likely requires data-intensive capture-mark-recapture and modeling that account for the possibility of dispersal. Thus, survival could be better estimated in species with no breeding dispersal. For example, food-caching Parids, such as mountain chickadees, are permanent residents that have just one post-natal dispersal movement during their first year of life, enabling the study of test birds for several years (Sonnenberg et al., 2019; Heinen et al., 2021). However, some authors have managed to assess the relationship between cognition and survival in species showing dispersal. For example, Maille and Schradin (2016) found that wild male African striped mice that performed better in a long-term spatial memory task survived for longer. Survival was measured as the number of days alive before the onset of the breeding season and hence before long-distance dispersal. A mouse was considered to have died when it had not been trapped or observed for at least two consecutive months. Survival could also be estimated in individuals where one sex does not disperse. However, this will lead to biased assumptions about how and why cognitive abilities have evolved in a species (Boogert et al., 2018). Furthermore, dispersal and survival are often inter-linked (e.g., an animal that disperses from the natal nest has a higher probably of being predated than one that does not, Clobert et al., 2009). It would be interesting to investigate differences in cognitive abilities between dispersing and non-dispersing species in the same taxonomic group. This could highlight specific cognitive traits that will enhance survival according to the presence/absence of dispersal in phylogenetically closely related species, allowing us to better understand the adaptive value of cognitive traits.

Intrinsic characteristics, such as age, sex and personality, are not always known or considered in studies related to cognition and survival in the wild. These intrinsic characteristics can impact inter-individual variation in cognitive performance and survival. For example, in striped mice, faster attention toward a predator stimulus was positively linked with survival in females but not males, yet male, but not female, survival co-varied positively with better spatial memory of shelter locations (Maille and Schradin, 2016). Survival is also strongly age-dependent (Lemaître and Gaillard, 2020). Therefore, it is important to control for age either during data collection or statistically by taking into account age as a covariate in statistical models. Senescence in specific cognitive traits could also be delayed in species with strong selection on certain cognitive traits, such as in food-caching species, and hence could influence survival outcomes (Heinen et al., 2021). Personality can also influence key behaviors for survival in the wild (e.g., Aplin et al., 2013). Bold animals can adopt risky behaviors toward predators but will also be more willing to explore their environment and increase their chances of finding food or mates (MacPherson et al., 2017). Thus, individual differences in personality might drive individual differences in cognitive abilities, and together they might drive responsiveness to environmental change (Griffin et al., 2015) and ultimately survival. From a practical point of view, personality traits add challenges to accurate survival measurements. For example, neophobia may influence recapture success, and hence may bias estimates of survival. We suggest that studies attempting to link survival or other fitness proxies (such as reproductive success) to cognition should always consider other possible influencing factors, such as sex, age, or personality.

It is also challenging to find the appropriate task to test a particular cognitive trait. For example, individual variation in problem-solving performance could be related to motivational variation rather than cognitive mechanisms *per se* (Van Horik and Madden, 2016). This leads to issues of either capturing animals and testing them in a field laboratory for short-term tests or testing them directly in the field under spontaneous, but less controlled, conditions (e.g., with the possible impact of social learning). Furthermore, assessing the survival of wild animals of known cognitive abilities requires tracking the same individuals in space and over time (Tello-Ramos et al., 2018). The cognitive test should then be standardized between studies and easily applied to be used permanently for long term studies (e.g., Morand-Ferron et al., 2015; Cauchoix et al., 2017). Automated operant devices placed directly in the field could be appropriate for cognitive tests, since animals can participate in a task spontaneously, increasing the probability of generating a large sample size (Morand-Ferron et al., 2016). One could argue that experimental protocols involving novel objects may elicit avoidance in neophobic individuals (Stuber et al., 2013) or those that have better access to other resources (e.g., adults compared to juveniles, Morand-Ferron et al., 2011). However, a longer duration of the experiment could lead to a familiarization to the devices, allowing novelty responses to reduce with time, thereby eliminating personality biases, such as has been observed in great tits (*Parus major,* Morand-Ferron et al., 2015). In addition, the device could be adapted to different species while still assessing the same cognitive response. For example, automated devices have been used in studies of passerine species but are difficult to create and modify. Thus, creating simple, ecologically relevant tasks, such as mimicking a predator shape in order to measure attention, setting a novel object in the field to measure habituation (basis of learning), or documenting the technique and time required for nest building as a measure of problem-solving could also be relevant in studying the evolution of cognition (Keagy et al., 2011).

Standardized and easy to use tests will help to generate sample sizes with better statistical power. Generally, an acceptable statistical power is only associated with very large sample sizes, which are often difficult, if not impossible, to obtain in the wild. The practical challenge will then be to conduct long term studies over several years, such as in Cole et al. (2012). However, to reach a sample size with better statistical power in the wild would likely require several years of study, particularly for species that are rare or cryptic. Conducting studies across years comes with additional potential confounding effects, such as seasonal changes, weather effects (e.g., temperature and humidity changes), unexpected catastrophic events (e.g., bushfires or floods) and human impacts (e.g., deforestation and land degradation).

Some taxa appear to be good study candidates for obtaining adequate sample sizes for linking fitness proxies and cognitive abilities. The few studies conducted on mammals indicate that rodents may be appropriate because of their small body size, short longevity, ease of study and ability to obtain large sample sizes in general (e.g., Maille and Schradin, 2016). Short longevity can add a practical advantage to measuring survival. For example, in striped mice, it is possible to measure several cognitive traits during their 1-year lifespan. Similarly, among birds, most work has been done on short-lived passerines, generating large sample sizes (e.g., Cole et al., 2012). Fish could also be promising candidates for future studies. For example, experimental studies on guppies (*Poecilia reticulata*) showed that individuals with larger brains had improved cognitive abilities (spatial learning tested in a sample of $N = 450$; Kotrschal et al., 2013), and large-brained females had higher survival compared to small-brained females ($N = 794$; Kotrschal et al., 2015), which was related to predation pressure in a wild population ($N = 160$; Kotrschal et al., 2017). Some other model species relating cognition and fitness in the wild are absent in the literature. For example, cephalopods, known for their complex cognitive abilities such as flexible decision-making and future planning (Billard et al., 2020), could be relevant models of study. Some insect species could be candidates for obtaining adequate sample sizes, and linking cognitive performance and fitness (e.g., Raine and Chittka, 2008); however, it may be challenging to study them in the wild and measure their survival. Overall, more studies are needed on survival in a diverse range of free-living animal species of known cognitive abilities. This will allow for comparative studies, highlight potential differences in which cognitive traits are important for survival in some taxa but not in others, and finally will allow us to better understand the factors shaping the evolution of animal cognition.

Because there is no standardized approach to link survival and cognition, the differing results of previous studies could also indicate that the outcome depends on the conditions under which fitness proxy metrics are assessed. Depending on the study species, survival can be evaluated in days from birth to death, in days from birth to dispersal (e.g., Maille and Schradin, 2016), or as seasonal or annual survival vs. death (e.g., Sonnenberg et al., 2019). Madden et al. (2018) determined a threshold for survival at 60 days in common pheasants by using a putative survival curve based on previous observations and according to anthropogenic activity (pheasant shooting). Studies in fish monitored survival from 70 to 96 h post release (Lonnstedt et al., 2012; Ferrari et al., 2014). These different measurements suggest that it is essential to consider a species' characteristics to determine the relevant survival metric to use as a fitness proxy. It is also important to potentially define the baseline longevity of a population and then measure deviations related to cognition to generate continuous data rather than simple binary (yes/no) outcomes and, hence, explore how survival relates to the evolution of cognition.

CONCLUSION

Linking survival and experimental measures of cognitive performance is challenging in free-living species, and clearly more research is needed. Practical challenges for studying wild animals include: (i) proper selection of a cognitive task that will test for ecologically relevant cognitive traits and will be likely to explain the relationship between cognition and survival across species; and (ii) choice of a fitness metric, and if it is possible, consideration of several fitness proxies (e.g., individual survival, clutch size, fledgling number), depending on the species' life history. Moreover, generating large sample sizes to reach an acceptable statistical power, and accounting for individual intrinsic characteristics, such as age, sex and personality, should be considered in cognition studies to partition the direct selection on cognition from other selection pressures. Finding appropriate methods and protocols adapted to wild species will highlight positive, negative or no relationships between cognition and survival, and hence disentangle benefits or costs of cognition. Linking fitness and cognitive ability might explain intra- and/or inter-species variation in a comparative and integrated evolutionary framework.

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All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.729546/full#supplementary-material

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