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Grand challenges in foraging behavior and predator-prey interactions: next generation ethology in the Anthropocene

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Everything is eventually eaten by something else; for most organisms, the crowning achievement of their existence is to reproduce before that happens, and (if they are lucky) perhaps have already died relatively peacefully before the eating commences. The interaction between species that are trying to consume and avoid consumption represents a fundamental force in evolution, as the outcome of that interaction shapes the genetic reproductive success of both parties. Ethologists broadly study these interactions under the umbrella of foraging and antipredator behaviors, depending on which party is the focus of the study; but natural selection makes no taxonomic distinctions, and so the processes of herbivory and parasitism would be additional examples of this consumptive species interaction that is shaped over evolutionary time. Nevertheless, for researchers who focus on the expression of behavioral phenotypes in animals, those behaviors related to finding food and avoiding becoming food often play a central role in developing an integrative understanding of an ecological community as a whole (Werner and Peacor, 2003; Nakazawa, 2017; Schmitz, 2017).

Because species interactions related to consumption structure natural communities, in many ways the challenges facing this field are a reflection of the broader challenges facing all of us who attempt to understand the evolution of behavior in natural systems. These challenges are numerous, and so by necessity I will narrow my focus to two in particular: (1) the need to understand the impact of unprecedented environmental changes induced by human development; and (2) the decline of descriptive and observational scientific research focused on organisms and the expression of their behavior in nature (i.e., the decline of natural history). Although these challenges are indeed grand, I believe the technological revolution currently underway in computational power and monitoring devices can go a long way in addressing both.

Species interactions and environmental change

Humans are having an impact on the environment that many consider to be on par with the handful of past geological events that led to mass extinction and a fundamental reordering of biodiversity across the globe (Waters et al., 2016). Because humans are releasing massive amounts of carbon dioxide into the atmosphere, which is also increasing the acidity of oceans, the resultant impact is truly global, affecting all species and ecosystems (Warren et al., 2011; Grimm et al., 2013; Spalding and Hull, 2021). Ethologists (and other types of evolutionary biologists) fully recognize that most species now exist within an environment that is undergoing rapid change (Guiden et al., 2019). Sih et al. (Sih et al., 2011) coined the term HIREC (human-induced rapid environmental changes) to characterize this problem and emphasize its prominence in animal behavior research. No biological discipline can afford to ignore HIREC, but ethology is on the front line of this battle. Perhaps the most fundamental question regarding our ability to predict or protect the future of a species is behavioral: is its behavior flexible enough to cope with change? The plasticity of behavior is what will allow a species to persist (or even thrive) in the face HIREC (Wong and Candolin, 2015; Beever et al., 2017).

Much of the research on behavioral plasticity and HIREC focuses on individual species responding directly to an impact, but ethologists focusing on foraging and antipredator behaviors must also consider the problem from a community perspective: environmental changes that directly impact one species also pull on the linkages that species has to others in the community, and therefore will have a series of rippling effects that move through the whole ecosystem (Nagelkerken and Munday, 2016). Ecologists cannot afford to ignore the behavioral details that mediate those responses, as the extent and type of behavioral variability will determine how natural populations respond (Creel et al., 2019). Studies of behaviorally-mediated trophic cascade at the landscape scale often rely on broad patterns of species distributions and demographics, without adequate characterization how processes and patterns are linked (Peacor et al., 2022); others have also called for the increased use of emerging monitoring technologies to better understand risk-sensitive behaviors (Prugh et al., 2019).

One of the most devastating forms of HIREC related to the ethology of predation is the introduction of species into novel habitats (Bellard et al., 2016). Invasive predators can disrupt entire ecosystems when native species lack appropriate antipredator behaviors (Cox and Lima, 2006; Sih et al., 2010). Prominent examples include the invasion of Guam by brown treesnakes (Anton et al., 2020), the spread of lionfish in the Caribbean (Anton et al., 2020), and the damage done by rats introduced to oceanic islands across the globe (Harper and Bunbury, 2015). Predicting the impact of invasive predators, or the timescale at which impacted species may adjust to the invasion, requires a detailed understanding of the expression and development of antipredator behaviors (Carthey and Blumstein, 2018), work that has a long tradition within the field of ethology (Tinbergen et al., 1967; Curio, 1976).

On the other side of the predator-prey relationship, the ethology of foraging or hunting is similarly prominent in the biodiversity crisis. A recent meta-analysis of the proximate causes of species declines and extinctions in response to climate change found that altered species interactions associated with decreased ability to find food was the single most frequently cited mechanism underlying species declines (Cahill et al., 2013). Plasticity in foraging or feeding behaviors may be crucial for adapting to changing biotic and abiotic conditions (Tuomainen and Candolin, 2011). Recent prominent examples include the unexpected flexibility in forage use that allowed a population of pikas (*Ochotomys princeps*) to persist well outside their typical climatic niche (Varner and Dearing, 2014), the shift in foraging mode that permitted peacock groupers (*Cephalopholis argus*) to persist in the face of habitat degradation, and a switch to foraging in near-shore benthic habitats by black guillemots (*Cepphus grylle mandtii*) coping with decreased sea ice (Divoky et al., 2021).

The decline of ethological research in nature

A second crisis of a different nature has the potential to greatly exacerbate the first. Research focused on organisms in nature is in decline. For decades, natural historians have been sounding the alarm regarding the increasing difficulty in funding basic descriptive research (Wilcove and Eisner, 2000; Greene, 2005; Tewksbury et al., 2014). The rise of molecular and genetic tools in biology has revolutionized our understanding of biological systems, but has also resulted in a reductionism that increasingly prioritizes the testing of hypotheses far above the accumulation of quantitative observations (Farris, 2020; Yanai and Lercher, 2020). Natural history is a somewhat loosely defined field, but most practitioners consider it to be primarily descriptive; natural historians try to accumulate detailed and quantitative data on natural systems, often while trying to minimize pre-conceived notions about how those systems should work (Herman, 2002; Schmidly, 2005; Barrows et al., 2016). Although such observations are a fundamental component of the scientific process, they are too frequently not treated as such by reviewers and editors of scientific papers. Perhaps one of the most common general types of feedback given in the peer review process is to adopt a hypothesis-testing framework, even when the work in question may be explicitly descriptive, as if the data, discussions, and conclusions would not be meaningful if they were uncovered as part of the process of observing and quantifying natural systems without a preconceived hypothesis in mind.

Of course, hypothesis testing and laboratory studies will always occupy a central place in scientific research, as testing hypotheses is universally regarded as the crux of the scientific method. But experimental work cannot substitute for the descriptive studies, opportunistic observations, and detailed accounts of natural history that lay the foundation for testable questions (Tewksbury et al., 2014; Betts et al., 2021). Both descriptive and experimental studies are necessary and complementary components of discovery. Observations of organisms in their natural environment provide the raw material that can be refined into hypotheses and tested. Not investing in such research is the equivalent of a mining company ignoring the need to find new deposits and just focusing on refining what they have already discovered—an obviously unsustainable plan.

Next generation natural history

Like most major challenges in science, these issues cannot be solved by any single approach, but instead must be addressed by bringing to bear a series of complementary, interacting solutions. For one prominent part of the solution, I would point to the emergence of a number of new technologies that have many field biologists fundamentally rethinking the nature of natural history research (Krishtalka and Humphrey, 2000; Peay, 2014; Bakker et al., 2020; Tosa et al., 2021). Experienced natural historians have always used whatever useful tools may be at hand to aid in the process of observing details of nature (binoculars, cameras, notepads, thermometers, etc.). In recent years, the list of tools and their complexity has grown, and practitioners of ethology now have a powerful array of advanced technological devices that can help them record details of an organism and its environment in ways that previous generations could only dream of (Couzin and Heins, 2023). Tosa et al. (Tosa et al., 2021) refer to this as "Next Generation Natural History" (NGNH) and provide a detailed summary of how such approaches are revolutionizing our understanding of organisms and nature.

Many NGNH approaches are directly applicable to the quantification of behavior, and are likely to be on the front lines of future efforts to understand the details of foraging and antipredator behaviors (Gomez-Marin et al., 2014). Perhaps one of the most promising is the increasing use of animal-borne biologgers to quantify the moment-to-moment details of a behavior, even when an animal is not under direct observation (Brown et al., 2013). Accelerometery loggers as small as 2 grams can store hundreds of values per second, every second, for days at a time. If a large database of validation observations can be accumulated, machine learning models can often determine, with high levels of accuracy, which behavior corresponds to a given acceleration pattern, thereby allowing researchers to accumulate a detailed record of naturalistic behaviors across a variety of individuals and situations (Wang, 2019). This technique could provide unparalleled insight into predatory behaviors, since one of the major limitations in quantifying such behaviors in free ranging animals is that, for many predators, these interactions occur rarely and unpredictably (Viviant et al., 2009; Hanscom et al., 2023). Accelerometry is similarly useful for quantifying rates and types of antipredator behaviors in free ranging animals (Zenone et al., 2020), an approach that will likely be able to inform more dynamic and realistic "landscape of fear" models for balancing risk and reward in natural environments (Palmer et al., 2022). Accelerometry represents just one part of a biologging revolution; sensor devices can include gyroscopes, thermometers, heart or breath rate loggers, depth loggers, and different options for location sensing, memory, and data retrieval (Jeantet et al., 2020; Williams et al., 2020; Papastamatiou et al., 2022; Wild et al., 2023).

Another NGNH approach that is likely to transform ethology is the expanding use of image-based tracking (Dell et al., 2014; Weinstein, 2018). A number of software programs are available that allow researchers to use machine learning programs to automatically identify and track the detailed movements of hundreds or thousands of individual animals or their component parts from digitized video recordings of behavior (Crall et al., 2015; Mathis et al., 2018; Graving et al., 2019; Walter and Couzin, 2021). These approaches have been employed to identify individual animals within large social groups (Ferreira et al., 2020) or categorize species across millions of images (Steenweg et al., 2017; Ahumada et al., 2020). As with many NGNH techniques, these tools do not necessarily do something that was impossible before, but they make it possible to bring massive datasets to bear on questions that previously required weeks or years of effort (Kellenberger et al., 2021).

These examples are not meant to be comprehensive, just illustrative. Additional advances in animal monitoring, tracking, and observation are detailed in a number of other review papers (Peters et al., 2014; Valletta et al., 2017; Farley et al., 2018; Lahoz-Monfort and Magrath, 2021; Tosa et al., 2021; Tuia et al., 2022; Couzin and Heins, 2023). The power of big data accumulated via NGNH represents not just a revitalization of the field of natural history, but also rebalances the emphasis in scientific research between quantitative descriptive research and hypothesis testing. Many NGNH studies are explicitly descriptive, representing not the test of preconceived hypotheses based on past observation, but instead the detailed documentation of how animals interact with their environment. Such studies are vital, as they provide inspiration and fodder for the formulation and testing of key hypotheses. NGNH also represents a primary tool in the arsenal of researchers conducting HIREC studies. Do you suspect that increasing temperatures may be facilitating the spread of an invasive predator and driving the extinction of numerous native species (Hellman et al., 2008)? Accumulating large datasets via animal-borne biologging on how individuals of those species interact (i.e., how their feeding and antipredator behaviors play out under different thermal regimes), could be a key tool for determining if temperature is associated with movement or interaction rates, laying the groundwork for focused experimental tests.

Although it is undoubtedly the case that future research on the ethology of predator-prey interactions will continue to be difficult to fund, and that the very subjects we seek to study will become even more imperiled, our research community can embrace the powerful techniques stemming from the explosion of computational power and our increasing ability to manufacture smaller and more affordable monitoring devices. We should use these developments to inspire and train young students with a love of the natural world and a desire to preserve it. In this way, ethological research can provide some of the most salient solutions to the biodiversity crisis.

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