



Acoustic Cooperation: Acoustic Communication Regulates Conflict and Cooperation Within the Family

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Acoustic communication is central to many social interactions between family members. Whilst song and begging calls have been extensively studied, in this review I focus on familial interactions, where acoustic communication plays a critical role but has often been overlooked. I show that considering acoustic information transfer challenges the traditional views on sexual and parent-offspring conflicts. In particular, I first discuss the role of acoustic communication between breeding partners in parental care negotiation and coordination. I consider the potential for vocalisations to signal partners' state, in terms of current satiation or energy levels during parental care provisioning. Secondly, I review the occurrence of parent-embryo acoustic communication and highlight the possibility for acoustic developmental programming to facilitate the matching of offspring phenotype with parental provisioning capacities. I also discuss how acoustic information available to avian embryos from the environment may empower them to direct their development, independently of their parents. Thirdly, I bring together evidence on sib-sib acoustic communication before and after birth, and highlight its function in sibling cooperation for hatching synchronisation and resource partitioning. Overall, this synthesis demonstrates the importance of considering acoustic information to understand the evolution of parental care and cooperation.

Keywords: cooperation, coordination, negotiation, conflict, acoustic communication, prenatal interactions, acoustic developmental programming

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INTRODUCTION

Interactions within the family are regulated by both cooperation and conflict. Whilst parents cooperate with each other to rear offspring, and provide care to their offspring at a cost to themselves, conflict arises between family members over the amount of care to be provided (Trivers, 1972, 1974).

Notably, sexual conflict over parental care, as first formulated by Trivers (1972), occurs when parents share equally the benefit of caring (through increased offspring fitness), but only pay the cost of their own investment in parental care. To maximise its benefit-to-cost ratio, a parent should therefore decrease its own effort and let its partner compensate for the shortfall (Trivers, 1972). Theory generally predicts that, in order for bi-parental care to be evolutionary stable, individuals should only partially compensate for their partner's shortfall (Houston and Davies, 1985; McNamara et al., 1999). Whilst most empirical studies conform to this prediction, many others find full compensation, no change, or instead a decrease in investment as individuals match their partner's effort (reviewed in Hinde, 2006; Harrison et al., 2009). Theory predicts that some

of this variation may arise from partners' disparity in access to information about offspring needs, if the least informed parent cues on its partner, thereby matching its effort (Johnstone and Hinde, 2006; Hinde and Kilner, 2007).

Mariette and Griffith (2012, 2015) further proposed that the coordination of parental care could not only lead to investment matching, but may also improve parental care efficiency. Indeed, even though theoretical models generally assume otherwise (but see Johnstone and Savage, 2019), partners may partly share the cost of parental care when it impairs their continued investment within the current breeding attempt or in following attempts with the same partner (Mariette and Griffith, 2015). If so, optimising provisioning may prevail over exploiting partner's efforts, and it is expected that, by providing a simple reciprocity rule, coordination may facilitate negotiation and decrease the cost of sexual conflict (Johnstone et al., 2014). Accordingly, we showed that wild zebra finch parents (*Taeniopygia guttata*) synchronise provisioning by visiting the nest together during nestling rearing, and that better coordinated pairs produce more fledglings (Mariette and Griffith, 2012). Furthermore, consistent with an efficiency benefit of coordination, partners increased nest visit synchrony when parental workload (brood size) was experimentally increased, and nestling condition increased with parental coordination during foraging (Mariette and Griffith, 2015). Interestingly, we also showed that acoustic communication plays a central role in breeding partners interactions at the nest (Elie et al., 2010), including for the coordination of parental care (Boucaud et al., 2016a, 2017). Likewise, parental care coordination, either by alternating or synchronising nest visits, has been evidenced in several other avian species (e.g., Raihani et al., 2010; Bebbington and Hatchwell, 2016; Koenig and Walters, 2016; Savage et al., 2017; but see Khwaja et al., 2017), including in bi-parental care species with short-term pair bonds (Johnstone et al., 2014; Lejeune et al., 2019) and complex acoustic communication between partners (Gorissen and Eens, 2005). Although the effect on nestling growth is largely unknown (but see Iserbyt et al., 2017; Wojczulanis-Jakubas et al., 2018) and varies with ecological conditions (Lejeune et al., 2019) and foraging behaviour (Mariette and Griffith, 2015), the accumulation of recent studies clearly show that parental care coordination and equitable negotiation are more common than previously assumed.

Here, I further show how multiple other aspects of cooperation have been overlooked, by failing to consider the communication between family members, and the information it conveys. For example, there is some evidence in birds that skin or bill colour signals individual condition, which parents may cue on to adjust their reproductive investment relative to their partner's current provisioning capacity or offspring needs (e.g., foot colour in blue-footed boobies: Velando et al., 2006; Dentressangle et al., 2008; nestling mouth coloration: Ewen et al., 2008). However, even though visual and chemical signals are used, acoustic signals are likely to play a particularly prominent role in avian family communication. Indeed, acoustic signals can readily indicate individuals' immediate state and perhaps their short-term intentions. In addition, interactive acoustic communication, whereby individuals adjust their vocalisations in

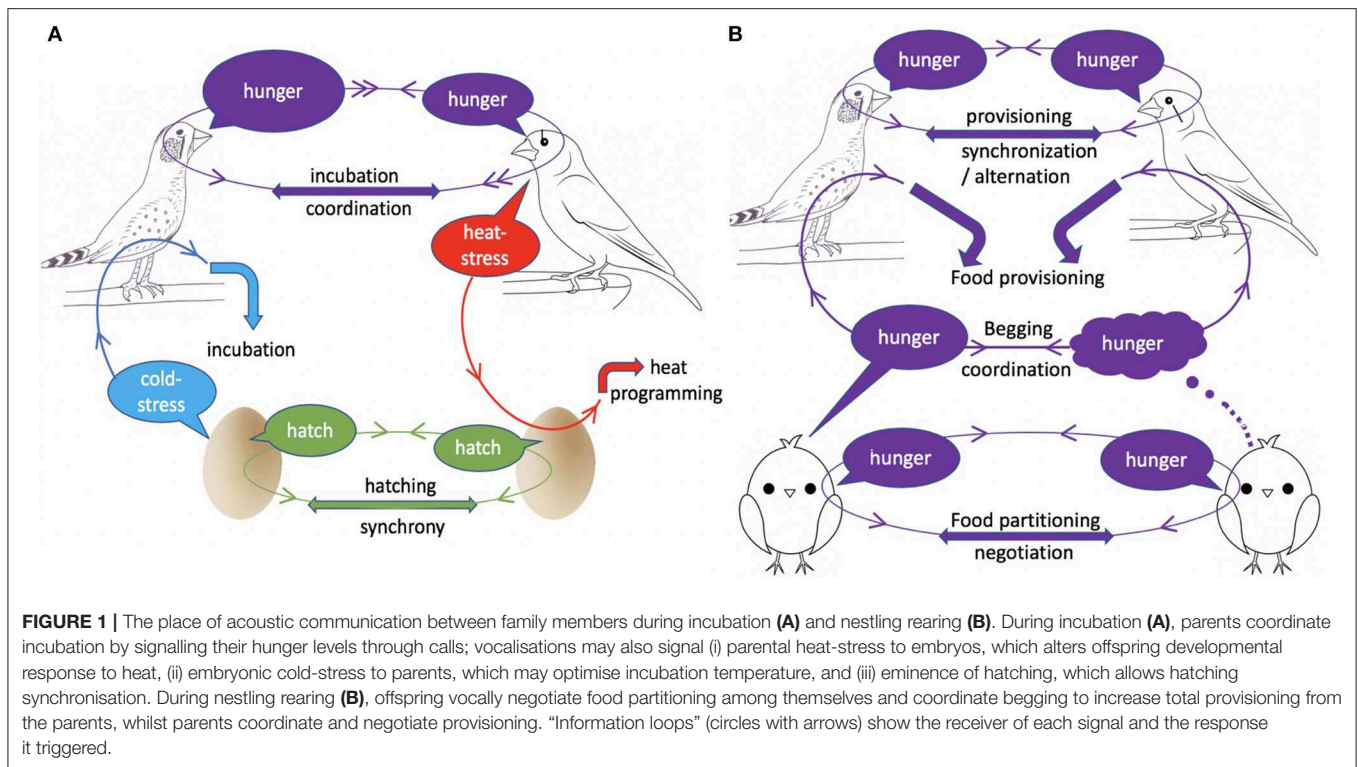
response to others' signalling, is especially well-suited for real-time negotiation (e.g., Ducouret et al., 2019). Lastly, unlike other senses, the acoustic (or vibratory) channel allows a sophisticated level of communication and negotiation to occur prenatally, in parent-embryo and embryo-embryo interactions (Mariette and Buchanan, 2019b; Noguera and Velando, 2019).

Surprisingly however, with the notable exception of nestling begging calls, the importance of acoustic communication for cooperation within the family has received very little attention. Here, I highlight the role of acoustic communication between breeding partners in parental care coordination. I then point to the multiple ways in which acoustic communication may alter parent-offspring cooperation and co-adaptation, before and after birth. Lastly, I discuss the role of begging calls and other offspring vocalisations in sib-sib interactions, including prenatally.

VOCAL NEGOTIATION BETWEEN BREEDING PARTNERS

The hypothesis that acoustic communication allows partners to negotiate their relative efforts in real-time was first proposed by Boucaud et al. (2016a) (**Figure 1**). In this study on captive zebra finches, where both partners incubate, we experimentally delayed the return to the nest of the male partner during incubation, and recorded vocal interactions at the nest. As predicted, partners' acoustic interactions were altered by the male delay. More strikingly however, the time the female subsequently stayed off the nest was predicted by her partner's calling rate when he returned, rather than by how long she had been incubating for. Likewise, the female's calling rate when her belated mate returned was the best predictor of the duration of her next incubation bout (Boucaud et al., 2016a). This suggests the male also cued on its partner's vocal behaviour rather than on the female's recent investment, although the reciprocal experiment (delaying female's return) would be interesting to carry. Overall, it therefore appears that individuals signal their need to be off the nest by calling more during nest reliefs, and that the partner respond to this signal by coming back early to relieve its partner. Acoustic communication may thus inform individuals on their partner's state, and hence on the cost of a prolonged incubation bout in that particular moment. Having access to such information, partners may not simply match their investment (i.e., time spent incubating), but instead match the cost of that parental care investment (e.g., as in Griffioen et al., 2019). If so, focussing research on the matching of investments rather than on their costs may misrepresent individuals' investment decisions, and importantly underestimate the level of cooperation within pairs (see also, asymmetries in "recovery rate" in Johnstone and Savage, 2019).

In follow up studies, Boucaud, Vignal, and collaborators further demonstrated that females may signal their immediate needs to their partner by vocalizing from inside the nest when the male arrives in the vicinity (Boucaud et al., 2016c, 2017). In wild zebra finches, female calling rate and her calls' acoustic structure on her mate arrival predicted whether or not the male relieved the female for incubation (Boucaud et al., 2017). Likewise, in wild



great tits (*Parus major*), with female-only incubation, female's vocalisations, and the pair's vocal interactions differed depending on whether or not the male entered the nest to feed the female (Gorissen and Eens, 2005; Boucaud et al., 2016c). Moreover, when great tit females were experimentally supplemented with food, they altered their vocalisations, uttered before and after the male entered the nest (Boucaud et al., 2016b). This suggests that female vocalisations may honestly signal her needs, and that the male potentially receives information on female's state even from outside the nest. What would appear as a male-only decision (whether or not to relieve/feed the female) when acoustic information is ignored, may in fact be a negotiated decision, incorporating the female's needs. These studies again reveal a higher level of cooperation between partners than is generally assumed, including in species with short-term pair-bonds.

ACOUSTIC COMMUNICATION BETWEEN PARENTS AND NESTLINGS

By far the most studied aspect of acoustic communication within the family is offspring begging calls and their importance for parent-offspring negotiation and conflict mitigation (reviewed in Kilner and Johnstone, 1997; Royle et al., 2002; Kilner and Hinde, 2012). Parent-offspring conflict arises because offspring's provisioning rate optimum is expected to be higher than that of their parents, who trade-off current with future

reproductive investment, as well as offspring quality with quantity (Trivers, 1974; Stearns, 1992; Kilner and Hinde, 2012). Yet, the costs of begging on the offspring maintain begging as an honest signal of needs, that parents may cue on (Kilner and Johnstone, 1997; Kilner, 2001). Moreover, begging sensitivity to maternal hormones provides a mechanism for mothers to control their offspring's begging display (Eising et al., 2001), potentially allowing the co-adaptation of begging display and parental provisioning capacity (Hinde et al., 2009, 2010). It is clear from this large body of work that considering information transfer through acoustic signals can drastically alter our understanding of conflict and cooperation within the family.

Beside offspring vocalisations, parents are also known to communicate vocally with their nestlings, particularly using alarm or food calls (Madden et al., 2005; Magrath et al., 2007 and references therein). These parental vocalisations have been hypothesised to reduce detection of nests by predators cueing on loud nestling begging calls. Specifically, parental alarm calls for nest predators are found to suppress begging (Madden et al., 2005; Platzen and Magrath, 2005), whereas in some species, parents produce food calls when arriving at the nest, which generally indicates to nestlings that it is safe to beg (Madden et al., 2005; Magrath et al., 2007). Indeed, whilst fledglings may blackmail parents by begging in dangerous locations (Thompson et al., 2013), we may expect parents and nestlings to cooperate more closely, as both equally benefit from avoiding detection by predators when nestlings are not yet mobile.

PARENT-EMBRYO ACOUSTIC COMMUNICATION

Occurrence of Prenatal Acoustic Communication

Prenatal acoustic and vibratory communication is widespread across taxa ranging from insects to humans (Gottlieb, 1965; Grier et al., 1967; DeCasper and Fifer, 1980; Endo et al., 2019). In birds and humans in particular, late-stage embryos have been found to perceive, respond and even learn acoustic signals from their parents and the external environment (Gottlieb, 1965; Grier et al., 1967; Partanen et al., 2013). A large part of the field have focused on the cognitive effects of prenatal acoustic experience, including its role in imprinting and individual recognition (Gottlieb, 1965; Grier et al., 1967; Lickliter and Lewkowicz, 1995), as well as in vocal learning (Mampe et al., 2009; Colombelli-Négrel et al., 2012). A few studies however, have revealed functions of prenatal acoustic communication – namely for developmental programming and embryonic thermoregulation – that warrant further investigation in the context of intra-familial cooperation.

Acoustic Developmental Programming

Extensive research in birds and mammals have demonstrated the importance of maternal hormones in programming offspring development (Schwabl, 1996; Mousseau and Fox, 1998; Groothuis et al., 2005). However, it is not clear how much avian mothers may control the transfer of hormones to their eggs (Groothuis et al., 2019); and post-natal environments, such as climatic conditions or predation risk, may not always be predictable at laying when hormones are deposited into the eggs. Recently, we proposed that prenatal acoustic communication, which mostly occurs late in the incubation period, may provide an alternative mechanism for adaptive developmental programming (Mariette and Buchanan, 2016).

We discovered that adult zebra finch produce a peculiar call at high ambient temperatures, particularly in the late stage of incubation (Mariette and Buchanan, 2016, 2019a). Using playback to embryos in artificial incubators, we demonstrated that this call alone adaptively alters nestlings growth in a temperature-dependent manner (**Figure 1**). Individuals exposed prenatally to heat calls rather than control calls were lighter in hot nests throughout the nestling period, but then produced more fledglings as adults, consistently across breeding seasons (Mariette and Buchanan, 2016). However, whilst embryonic programming by parental heat calls is adaptive, we later demonstrated that heat calls are not exclusively uttered for embryos. Instead, heat calls are also spontaneously produced (albeit less often) outside the late incubation period, when adults are in roost nests (without eggs) in the wild, or on a perch in a heated chamber in the lab (Mariette et al., 2018). Importantly nonetheless, the temperature threshold triggering calling is highly repeatable within individual, and predicted by body mass, which suggests heat-calls provide an honest signal of parental heat-stress to embryos (Mariette et al., 2018). Whether heat-calling is associated with a particular thermoregulatory behaviour of the parent remains to be established. Nevertheless, it is possible that embryonic eavesdropping on parental

heat-stress could benefit both parents and offspring, if it prepares offspring to withstand long periods of fasting during heat events, when their heat-stressed parents have to interrupt provisioning.

Very recently, a second study, in another avian order and environmental context, also provided evidence that embryos eavesdrop on external sounds to channel their development (Mariette and Buchanan, 2019b; Noguera and Velando, 2019). They demonstrated that prenatal exposure to parental alarm calls in yellow-legged gulls shaped the development of embryos and hatchlings, compared to individuals exposed to silence (Noguera and Velando, 2019). Remarkably, prenatal sound altered a wide range of traits, including early skeletal growth, physiology (corticosterone levels), molecular traits (mitochondrial DNA) and behaviour (prenatal vibration and call rates, crouching behaviour). Whether this programming can be considered as parent-offspring cooperation remains to be established, by first testing whether the observed effects are specific to alarm calls, and bring a fitness advantage in a high predation environment (Mariette and Buchanan, 2019b). Fascinatingly however, that same study showed that embryos may cooperate with each other and coordinate their developmental trajectories, by exchanging information, most likely through the changes in vibration or call rates (Noguera and Velando, 2019).

These recent findings clearly show that acoustic signals and cues provide an alternative source of information to embryos, beyond endocrine and nutritional maternal effects. Whilst parents may exploit this information channel (as suggested in zebra finches by the intensification of heat-calling in late incubation compared to other breeding stages or roost nests: (Mariette et al., 2018; Mariette and Buchanan, 2019a), audition can potentially also allow embryos to by-pass parental control by collecting information directly from the environment. Acoustic eavesdropping, similarly to embryonic metabolism of maternal hormones (Groothuis et al., 2019), may therefore empower embryos to control their own developmental trajectory (Mariette et al., 2018). This challenges the traditional views of embryos as a passive agent during their development, and may lead to either parent-offspring conflict or cooperation, depending on the degree to which offspring's interests align with those of their parents.

Vocal Thermoregulation: Honest Signal of Embryonic Thermal Needs?

Sub-optimal incubation temperatures are known to delay hatching and increase embryonic mortality, but also have negative carry-over effects on nestling growth, immune functions and metabolism (Ardia et al., 2010; Nord and Nilsson, 2011; Martin et al., 2013). Therefore, whilst incubation is costly to the parent (Nord and Williams, 2015), it may pay to invest sufficiently in incubation to produce fast-growing nestlings. Accordingly, the majority of avian studies suggest that parents work at the maximum of their capacity during incubation (Chalfoun and Martin, 2007; Ardia et al., 2009; Nord and Williams, 2015; but see Bulla et al., 2014). On the other hand however, experimentally increased parental effort during incubation (by reducing nest temperature) negatively impacts the parents' subsequent investment in nestling provisioning,

thereby impairing offspring growth (Ardia et al., 2010). Overall, therefore, because parents have to trade-off the energy they may save during incubation against the additional cost of raising low-efficiency nestlings, and offspring have to trade-off the level of care they receive before vs. after hatching, the optimal incubation temperature for parents and offspring may closely align (Evans et al., 1995). However, since the costs and benefits of parental incubation varies with nest temperature (e.g., Ardia et al., 2009, 2010), we may expect embryos to signal their thermal needs to the incubating parent. In a series of experiments in the 1990s, Evans showed that avian embryos do so using acoustic signals. In a number of precocial and altricial species, embryos increase calling rate when their temperature deviates from the optimal incubation temperature (Evans, 1990; Evans et al., 1995; Bugden and Evans, 1997) (**Figure 1**). Evans demonstrated that if parents respond to calls by resuming incubation, embryonic vocalisations can effectively maintain optimal incubation temperature (Evans, 1990; Evans et al., 1995). This likely represents a case of parent-offspring cooperation for optimal incubation investment.

ACOUSTIC COOPERATION BETWEEN SIBLINGS

Vocally Synchronised Hatching

Embryonic vibrations, clicks and calls have long been known to alter hatching time in order to synchronise hatching within clutches (Vince, 1964). In particular, early studies in birds and a more recent one in reptile have shown that late eggs accelerate hatching when exposed to calls or clicks from more developed siblings (Vince, 1964; Woolf et al., 1976; Schwagmeyer et al., 1991; Vergne and Mathevon, 2008) (**Figure 1**). Most strikingly, a recent study in yellow-legged gulls, where unmanipulated embryos were in physical contact with clutchmates independently exposed to alarm calls or silence, found that prenatal communication between siblings altered not only hatching time, but also a suite of behavioural and physiological traits (Noguera and Velando, 2019; see above). Whether vocally synchronised hatching represents a case of sibling cooperation may depend on the study system. On the one hand, late embryos are understood to accelerate hatching to avoid poor incubation conditions, and associated mortality risk, after hatching of the first eggs (Evans et al., 1995). Early embryos, on the other hand, likely benefit from synchronous hatching through a predation dilution effect, at least in precocial species (Vergne and Mathevon, 2008). However, by eroding the disparity in competitiveness between older and younger siblings, synchronous hatching, particularly in altricial species, increases sibling competition over food, to the detriment of older siblings, and the benefit of the younger ones (Roulin and Dreiss, 2012). Overall therefore, embryos in precocial species may cooperate to synchronise hatching, whereas in altricial species, synchronous hatching may be mostly driven by the benefits to the younger siblings.

Post-hatch Vocal Negotiation and Cooperation Between Siblings

Since Trivers' landmark model (Trivers, 1974), sib-sib interactions post-hatch have been mostly viewed as competitive interactions over parental resources, either through scramble competition between evenly competitive siblings, or through a dominance hierarchy generally following birth order (Mock and Parker, 1997; Roulin and Dreiss, 2012). Nonetheless, following theoretical predictions (Johnstone and Roulin, 2003), there is emerging evidence of negotiation and cooperation among siblings, notably through acoustic communication (Roulin and Dreiss, 2012) (**Figure 1**). Most remarkably, in the barn owl (*Tyto alba*), a series of original experiments by Dreiss, Roulin, and collaborators has revealed the vocal negotiation occurring between siblings, before parents bring a single indivisible prey back to the nest (Roulin and Dreiss, 2012). They have shown that owlets challenge each other vocally in an interactive process by adjusting their calls to those of their siblings, either intensifying or reducing begging calls depending on their level of need (Roulin et al., 2009) and their opponents' vocalisations (Ducouret et al., 2019). The most vocal chick in parent's absence is more likely to get the next prey from the parents (Roulin et al., 2009), whilst others refrain from begging to the parents (Dreiss et al., 2010). Interestingly, negotiation rules are dynamic, as individuals become more cooperative with age, being more likely to withdraw from a vocal contest with an hungry sibling (Dreiss et al., 2017). Beside the barn owl, parent-absent vocalisations have also been found to increase with hunger levels and predict nestling begging to parents in both spotted starlings (*Sturnus vulgaris*) and barn swallows (*Hirundo rustica*, Bulmer et al., 2008; Romano et al., 2013, 2015), which suggests that sib-sib vocal negotiation may be more widespread than currently acknowledged.

In addition, beside negotiation for food partitioning among siblings, theory predicts that siblings may also cooperate to obtain more resources overall for the brood (Johnstone, 2004) (**Figure 1**). In both birds and mammals, siblings have been found to coordinate their begging calls, which then increased parental provisioning (Mathevon and Charrier, 2004; Bell, 2007; Madden et al., 2009; Blanc et al., 2010). For example in meerkat, playback of alternating begging calls triggers more provisioning than when calls of the same two individuals overlap (Madden et al., 2009). In addition, the coordination of begging calls within brood or litter may reduce the per-capita cost of begging, as siblings decrease begging call rate when their siblings' calling rate is high (Mathevon and Charrier, 2004; Bell, 2007; Madden et al., 2009).

CONCLUSION AND PERSPECTIVES

Even though negotiation has been identified as a key process for the evolution of cooperation and parental care (McNamara et al., 1999, 2003; Johnstone and Hinde, 2006), we know surprisingly little on how negotiation operates, particularly on a behavioural time scale. The evidence brought together here strongly suggests that acoustic communication is likely to play a central role in family negotiation and cooperation.

Interestingly, the evidence above on vocal negotiation between incubating partners, temperature-dependent calls in both parents or embryos, and vocal cooperation between siblings pre and post-natally, consistently demonstrates that considering acoustic communication often reveals previously unsuspected cooperative interactions where conflict had instead been considered as the driving force. This likely stems from the capacity of acoustic signals to convey large amount of information, notably on individual's hunger or thermal state in both parents and offspring. Access to this information can drastically alter investment decisions, by allowing the optimisations of costs and benefits to family members. A theoretical approach will be highly valuable in predicting the impact of prenatal and postnatal acoustic communication on the evolution of cooperation and parental care.

In addition, more empirical studies are clearly needed on a range of species to understand the generality of the patterns highlighted here. Beside their ubiquity in many taxa, acoustic signals are particularly amenable to fine experimental research using playbacks and continuous recordings, including automatic

interactive playbacks (Ducouret et al., 2019) and playbacks targeting specific individuals (e.g., Hinde and Kilner, 2007). Integrating acoustic communication to the study of cooperation is therefore a highly promising field of research.

AUTHOR CONTRIBUTIONS

MM conceived the manuscript, reviewed published literature, and wrote the manuscript.

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Conflict of Interest: The author declares 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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