SYMPOSIUM

Social Complexity as a Driver of Communication and Cognition

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Synopsis Cognition and communication both can be essential for effectively navigating the social environment and thus, social dynamics could select for enhanced abilities for communication and superior cognition. Additionally, social experience can influence both the ability to communicate effectively and performance in cognitive tasks within an individual's lifetime, consistent with phenotypic plasticity in these traits. Historically, research in animal cognition and animal communication has often addressed these traits independently, despite potential commonalities in social function and underlying mechanisms of the brain. Integrating research on animal communication and cognition will provide a more comprehensive understanding of how the social environment may shape behavior and specializations of the brain for sociality through both evolutionary and developmental processes. This selective review of research on the impacts of social dynamics on cognition and communication in animals aims to highlight areas for future research at both the ultimate and proximate levels. In particular, additional work on the effects of the social environment on cognitive performance over an individual's lifetime, and comparative studies of specialized abilities for communication, should be pursued.

Introduction

Group living can buffer individuals from ecological conditions, and cooperative interactions may provide fitness benefits (Coleman and Mellgren 1994; Lima et al. 1999; Soma and Hasegawa 2004; Rieucau and Giraldeau 2009). However, navigating a complex social environment can require superior cognition and effective communication in order to reap those benefits (Humphrey 1976; Cheney et al. 1986; McComb and Semple 2005; Byrne and Bates 2007; Tomasello 2008; Pinker 2010; Taborsky and Oliveira 2012; Seyfarth and Cheney 2014). Cognition, often defined as all mechanisms that permit animals to acquire, process, store, or act upon information from the environment, can be essential for effectively navigating large or complex groups because individuals must remember prior social interactions, anticipate companions' behaviors, and understand the relationships between members of the group (Humphrey 1976; Cheney et al. 1986; Shettleworth 2009; Taborsky and Oliveira 2012). Similarly, communication is essential for mediating social interactions, and

greater sociality has been associated with enhanced ability to communicate and with more complex signaling repertoires in species from primates to birds (Blumstein and Armitage 1997; Jackendoff 1999; McComb and Semple 2005; Freeberg 2006; Pollard and Blumstein 2011; Freeberg et al. 2012; Nowicki and Searcy 2014). Communication requires perception of signals by receivers, who may learn to associate distinct signals with particular contexts, companions, or referents through contextual learning (Janik and Slater 2000; Bradbury and Vehrencamp 1998). Additionally, in the case of vocal communication, signalers may learn to modify their production of signals with social experience, which can permit the encoding of new and more complex social information (Plooj 1979; Jackendoff 1999; Janik and Slater 2000; Freeberg et al. 2012; Nowicki and Searcy 2014). Although communication is essential to many social interactions and also is inherently cognitive because it depends upon sensory-motor integration and can be modified with experience, communication and cognition often have been considered as separate traits in the field of

animal cognition (Shettleworth 2009). Integrating approaches to research and examining cognition and communication as interrelated traits will provide a more comprehensive understanding of how the social environment may shape specializations of behavior and the brain to support social living (Dunbar 2003; Connor 2007; Tomasello 2008; Fitch et al. 2010; Pinker 2010; Seyfarth and Cheney 2014).

Cognition and specialized learning abilities for enhanced communication vary among and within species. Differences in traits among species are generally explained by macroevolutionary change, while variation in traits within species can reflect phenotypic plasticity, as well as ongoing response to selection. This review provides a short overview of current research on the means by which social dynamics shape cognition and communication both through evolutionary processes and through mechanisms of phenotypic plasticity. A key aim of this selective review is to encourage future research on the relationship between social dynamics, cognition, and specialized abilities to communicate from both proximate and ultimate perspectives. I begin with an overview of ideas and of approaches to research from these two fields and end with a case study on one specific form of specialized communication, the modification of the acoustic properties of social calls, to illustrate how integrating theory and methodology may generate new avenues for research.

Cognition and social living

Social living has been proposed as a driver of enhanced cognition and its underlying specializations of the brain, because navigating a complex social landscape may require superior learning, memory, and perhaps even abilities such as theory of mind (Cheney et al. 1986; Call 2001; Lefebvre et al. 2004; Byrne and Bates 2007; Dunbar and Shultz 2007; Taborsky and Oliveira 2012). This idea has been formalized as the Social Intelligence and Social Brain Hypotheses, which posit that complex cognition and enlarged "executive brains" (i.e., forebrains) evolved in response to challenges that are associated with sociality (Jolly 1966; Byrne and Whiten 1989; Dunbar and Shultz 2007; but see Barrett et al. 2003, 2007; MacLean et al. 2009, 2013). The main alternative to the Social Intelligence Hypothesis is that non-social factors, such as foraging, have driven the evolution of the brain and so-called "domain general" or global aspects of cognition, which permitted the subsequent emergence of greater sociality (Clutton-Brock and Harvey 1980; Milton 1981; Byrne and Whiten 1989; Holekamp 2007).

Comparative studies of primates largely have supported the Social Intelligence and Social Brain Hypotheses, with species' average group size (a common index of sociality) being positively associated with cognition, innovation, and relative volumes of regions within the "executive" forebrain (Reader and Laland 2002; Lefebvre et al. 2004 though see Reader et al. 2011; MacLean et al. 2014). However, in taxa such as birds, sciurid mammals, toothed whales, and ungulates, aspects of social complexity such as the number of social alliances, social competition among groups, or the number of different social roles within a group may better describe the selective pressures of the social environment and thus be associated with cognition and with volumes of the brain (Kudo and Dunbar 2001; Barrett et al. 2003; Lefebvre et al. 2004; Connor 2007; Emery et al. 2007; Holekamp 2007). It will be important to pursue multiple metrics of social complexity, to fully describe variation in social dynamics and understand the selective pressures exerted by the social environment.

In addition to macroevolutionary processes driving species' differences in cognition and brain structure among taxa, several studies suggest that group size *within species* is positively associated with cognition and neuronal architecture (Maguire et al. 2000; Lipkind et al. 2002; Barnea et al. 2006; Liker and Bokony 2009; Morand-Ferron and Quinn 2011; Kotrschal et al. 2013). Co-variation between cognition and group size within species is not easily addressed by macroevolutionary change but could be explained by group-level properties or phenotypic plasticity. At least four emergent, group-level explanations have been raised to address findings that larger groups solve problems more quickly than do smaller groups. First, members of larger groups benefit from cooperative interactions such as shared vigilance for predators and improved efficiency in foraging (Giraldeau 1984; Coleman and Mellgren 1994; Lima et al. 1999; Soma and Hasegawa 2004; Rieucau and Giraldeau 2009; although for costs of group size see Barnard and Sibly 1981; Giraldeau and Lefebvre 1987; Coolen 2002; Gajdon et al. 2006; Rieucau and Giraldeau 2009; Katsnelson et al. 2011). This benefit could permit greater investment in time and energy devoted to solving problems, although only neophobia and foraging behavior have been shown to be influenced by so-called "shared risk", thus far (Elgar 1989; Coleman and Mellgren 1994; Lima et al. 1999; Soma and Hasegawa 2004). Second, the "pool of competency" hypothesis posits that larger groups may simply be more likely to contain an individual, such as an innovator or producer,

who is able to solve the problem, as has been found in house sparrows and great tits (Hong and Page 2004; Liker and Bokony 2009; Morand-Ferron and Quinn 2011). Third, individuals may have genetic or fixed cognitive capacities and may choose to join groups of different sizes based on those existing traits, with the result that members of larger groups are better problem-solvers. There is evidence of such fixed cognitive ability and social strategy in house sparrows and great tits (Cole et al. 2011; Katsnelson et al. 2011). Fourth, group members may engage in making cooperative decisions; pooling information from a greater number of individuals has been shown to improve performance in solving problems in swarms of honeybees and schools of fish (Conradt and Roper 2005; Melis et al. 2006; Seed et al. 2008; Couzin 2009). Of the existing studies on cognitive performance in groups of varying size, findings are largely consistent with cooperative decision-making and the pool of competency hypothesis (Melis et al. 2006; Seed et al. 2008; Liker and Bokony 2009; Morand-Ferron and Quinn 2011). However, very small and very large groups may face factors that could impair their problem-solving efficiency, such as effects of competition or greater prevalence of scrounger tactics (Giraldeau and Lefebvre 1987; Coolen 2002; Rieucau and Giraldeau 2009), so this topic deserves further research.

In addition to evolutionary and group-level explanations for associations between cognition and group size within species, developmental processes and flexibility in cognition during adulthood, i.e., change in individuals' cognitive performance as a result of experience after reaching adulthood (Wada and Sewall 2014) could contribute to individual differences in cognitive performance. Either of these two forms of phenotypic plasticity in cognition could then explain observed patterns between group size and problem-solving within species, if living in larger groups provides experiences that enhance cognition. The magnitude of flexibility in problem-solving in adulthood is somewhat unknown in animals and may be limited (Bunnell and Perkins 1980; Boogert et al. 2006; Cole et al. 2011; Cole and Quinn 2012; Buchanan et al. 2013; Sewall et al. 2013a; Bókony et al. 2014). However, cognitive development has been shown to be sensitive to ecological (van Praag et al. 2000; Bredy et al. 2003; Ladage et al. 2009; Kotrschal and Taborsky 2010) and social conditions (Liu et al. 2000; Croney and Newberry 2007; Buchanan et al. 2013) ranging from environmental enrichment to maternal care, consistent with a critical period early in life when cognition is plastic and can be influenced by the social, as well as by the

ecological environment. Living in large social groups, particularly during early development, could improve problem-solving by providing opportunities that exercise cognition (Galef and Giraldeau 2001; Barnea et al. 2006; Liker and Bokony 2009; Shettleworth 2009; Morand-Ferron and Quinn 2011; Taborsky and Oliveira 2012). Mechanisms of neural plasticity underlying cognition, including long-term potentiation, the synthesis and release of neuromodulators, N-methyl-D-aspartate (NMDA) receptor-binding, synaptogenesis, and neurogenesis, can be enhanced by enriching social experiences such as receiving maternal care, forming social bonds, and experiencing social challenges (Liu et al. 2000; Lipkind et al. 2002; Barnea et al. 2006; Sørensen et al. 2007; Huang and Hessler 2008; Sallet et al. 2011; Maruska et al. 2012; Sewall et al. 2013b; Lindsey and Tropepe 2014). Thus, the social environment impacts the neural mechanisms underlying cognition, thereby providing a conduit by which social experience could shape cognition through mechanisms of phenotypic plasticity. Relatively few studies have addressed both cognitive and neural outcomes of social experience in animals (Liu et al. 2000; Gómez 2005; Lupien et al. 2009; Fox et al. 2010; Hackman et al. 2010). Future work should focus on the potential contributions of the social environment to brain function and cognition by manipulating a range of social dynamics within the scope that may naturally occur for a species and testing cognitive performance in a series of tasks so as to detect any change in cognition over time. Further, to distinguish between developmental plasticity and adults' flexibility, the magnitude of change in cognitive performance in adults and juveniles experiencing similar social environments should be compared.

Sociality as a driver of communication

Just as with cognition, social living can shape specialized abilities to communicate through mechanisms both of phenotypic plasticity and of evolution. The importance of the developmental environment, and thus phenotypic plasticity, to species-typical communication is well-documented (Catchpole and Slater 1995; Janik and Slater 2000; Smith et al. 2000; Marler and Slabbekoorn 2004). Specifically, many animals need social contact and experience to develop species-typical responses to communicative signals within a species' repertoire, which they acquire through "contextual" learning. Contextual learning occurs when a receiver learns to associate a signal with a context or referent as a

result of experience with other individuals' signals and responses (Janik and Slater 2000). For example, vervet monkeys must learn to associate different variants of alarm calls (meaning leopard, eagle, or snake) with these particular classes of predator and to both produce the correct variant upon contacting a predator and to respond appropriately (run into the trees, look up for an eagle, or look down for a snake) when hearing a particular variant of an alarm call (Seyfarth et al. 1980; Seyfarth and Cheney 1986). Learning to use the correct signal in response to a referent and to act appropriately upon hearing a variant of a signal are both forms of contextual learning (Janik and Slater 2000). Additionally, some mammals and birds are capable of "vocal learning", defined as the ability to modify their vocalizations based on auditory input and social feedback (Janik and Slater 2000). Vocal learning is generally identified by imitation, which results when one individual modifies its vocalizations to mimic another animals' signal, or when multiple individuals converge on signals with similar acoustic properties (Janik and Slater 2000; Tyack 2008). For example, young male songbirds produce songs (after a period of memorization and practice) that are very similar to those of adult tutors, which reflects imitation. In contrast, in mated pairs of some birds, both the male and female modify the acoustic properties of their calls over time to achieve a call with a shared structure, which reflects convergence (Tyack 2008).

While the importance of developmental plasticity (i.e., learning) to communication is well established, the potential for social dynamics to select for enhanced abilities to communicate over evolutionary time is somewhat less well studied. Rather, much of the thinking about the evolution of specialized abilities to communicate comes from studies of the learning of songs (hereafter song learning) by birds, which is shaped by sexual selection and is not taxonomically widespread (Nowicki and Searcy 2014). In contrast to song, social dynamics are argued to have driven the evolution of learned communication in other animals, including humans (Fitch et al. 2010; Pinker 2010; Freeberg et al. 2012; Seyfarth and Cheney 2014; although see Fitch 2005; Burling 2007; Puts et al. 2007; Miller 2000). A class of vocal signals, termed "calls", may provide insight into the role of social dynamics in the evolution of specialized learning abilities underlying communication because calls are used to mediate social interactions in diverse taxa (Marler 2004; Kondo and Watanabe 2009). While bird song is used in attracting mates and defending territories, calls mediate social interactions ranging from alerting companions

to the presence of predators, to coordinating foraging efforts (Marler 2004). One sub-category of calls, known as "contact" calls, is particularly taxonomically widespread. Contact calls are produced by animals when reuniting or coordinating behaviors with companions and they therefore mediate social recognition and many social interactions (Kondo and Watanabe 2009; Sewall 2012). Importantly, several species of mammals and birds show specialized learning abilities that may enhance their capacity to mediate social interactions using contact calls. Specifically, some species, such as baboons, jays, and parrots are known to use companions' distinctive "signature" contact calls for individual recognition by associating each unique signature call with the signaler (Cheney et al. 1995; Wanker et al. 1998; Hopp et al. 2001; Seyfarth and Cheney 2014). Thus, distinctive signature contact calls, coupled with enhanced contextual learning, can mediate individual recognition. Another specialized form of learning is found in species that are able to modify the acoustic properties of their contact calls to imitate or converge on calls that share similarities with companions (hereafter call-production learning; Tyack 2008; Sewall 2012). Thus, contact calls provide a taxonomically widespread system for considering the evolutionary factors shaping specialized abilities to communicate. Sociality has the potential to drive the evolution both of improved contextual learning and of call-production learning, which in turn permit the encoding of more complex social interaction (Blumstein and Armitage 1997; Jackendoff 1999; Wilkinson 2003; McComb and Semple 2005; Tyack 2008; Pollard and Blumstein 2011; Freeberg et al. 2012; Sewall 2012; Seyfarth and Cheney 2014).

Group size could exert selection for enhanced contextual learning of contact calls when individuals produce distinctive, signature contact calls, and live in large, stable social groups, because larger groups will have greater diversity in calls (Cheney et al. 1995; Hopp et al. 2001; Aubin and Jouventin 2002; McComb and Semple 2005; Pollard and Blumstein 2011; Seyfarth and Cheney 2014). The ability to recognize companions within such large social groups and to associate them with past experiences may provide fitness advantages, thus generating selection for superior contextual learning of companions' signature contact calls (Pollard and Blumstein 2011; Taborsky and Oliveira 2012; Seyfarth and Cheney 2014). In contrast to large, stable groups selecting for enhanced contextual learning, fluid social dynamics may select for vocal learning throughout life because vocal learning has the potential to generate new signals and thus encode changing social

relationships (Jackendoff 1999; Tyack 2008; Freeberg et al. 2012; Sewall 2012; Nowicki and Searcy 2014). Collectively, just as sociality is proposed to drive the evolution of cognitive specialization (Jolly 1966; Byrne and Whiten 1989), it may also contribute to the origin and maintenance of specialized abilities to communicate, including contextual and vocal learning (Dunbar 2003; McComb and Semple 2005; Fitch et al. 2010; Pinker 2010; Seyfarth and Cheney 2014). Considering specialized learning abilities underlying communication as aspects of cognitive specialization that may be selected for by the social environment will broaden our understanding of the mechanisms that support sociality. To illustrate the strength of integrating theory and research approaches from the fields of animal cognition and communication, I address the potential for social dynamics to select for one specialized form of communication learning: call-production learning.

Sociality and call-production learning

Although not commonly studied or reported, the learning of contact-call production is taxonomically widespread among birds and mammals (Fig. 1, Table 1). Contact-call production learning has been described for several species of finches, tits, parrots, primates, bats, whales, elephants, and seals (Mundinger 1979; Mammen and Nowicki 1981; Farabaugh et al. 1994; Boughman 1998; Sugiura 1998; Snowdon and Elowson 1999; Baker 2000; Janik 2000, 2014; Poole et al. 2005; Tyack 2008; Salinas-Melgoza and Wright 2012; Knörnschild 2014; Reichmuth and Casey 2014; Stoeger and Manger 2014). Additionally, there is evidence of experience-dependent plasticity in the acoustic structure of calls in goitered gazelles and goats, although vocal modification in bovines may be of lesser magnitude than in other taxa (Briefer and McElligott 2012; Volodin et al. 2014; Table 1).

Across taxa, contract-call production learning has been proposed to serve several specific functions, but a unifying theme is that it permits the formation of new social associations within fission–fusion groups (Tyack 2008; Sewall 2012). For example, the "Password" or "Badge" hypothesis posits that learned contact calls signal group-membership in large social groups of birds and bats that reunite to share roosts, or collectively defend food resources (Feekes 1982; Wilkinson and Boughman 1998). Similarly, imitated calls are thought to reflect affiliation and social coalitions in social groups and mated pairs of primates, birds, bats, elephants, and whales (Mundinger 1979; Snowdon and Elowson 1999; Janik

2000; Poole et al. 2005; Tyack 2008; Lemasson et al. 2011; Sewall 2012). Additionally, call dialects, which are calls with acoustic structures shared by all members of a population, have been argued to signal local knowledge in whales, birds, and seals (Mammen and Nowicki 1981; Rendell and Whitehead 2003; Tyack 2008; Sewall 2009; Deecke et al. 2010; Reichmuth and Casey 2014). Not all of these hypotheses are mutually exclusive because each applies to a different level of social organization (Tyack 2008; Sewall 2012). However, all of these proposed functions support an overarching argument that the learning of calls is a specialization for navigating temporally changeable social bonds. An initial review of the empirical reports of call-production learning across families and subfamilies suggest that there is a reliable association between fluid social dynamics and call-production learning (Table 1, Fig. 1). One key exception is that one suborder of bats (Yinpterochiroptera) often reunite at shared roosts, but have not yet been reported to imitate companions' calls, although future research should address this (Knörnschild 2014).

Although call-learning and fluid social dynamics may be closely associated across taxa at present, the cognitive and neural machinery underlying vocal learning may have had a different evolutionary origin and later been co-opted for call-production learning (Nowicki and Searcy 2014). Specifically, vocal learning by birds may have originated in song learning and been shaped by sexual selection, while vocal learning by toothed whales and bats may have originated from echolocation calls and been selected by ecological conditions (Nottebohm 1972; Knörnschild et al. 2010; Knörnschild 2014; Nowicki and Searcy 2014; Table 1). That is, social selection may not have been the original evolutionary driver of vocal learning in the species that now demonstrate call-production learning. However, several taxa present inconsistencies with the hypothesis that the evolution of either song learning or echolocation preceded that of call-production learning. First, both hummingbirds and baleen whales learn their songs, yet have not been reported to modify the acoustic properties of their calls. Species of baleen whales and hummingbirds often are reported to be solitary, and thus there may not be selective pressure to learn call-production in these taxa, which lends support for the hypothesis that call-production learning is, in fact, shaped by social dynamics (Winn et al. 1981; Baptista and Schuchmann 1990; Rendell and Whitehead 2003). Reciprocally, the learning of calls is well-documented in parrots, yet song is relatively uncommon across these species, providing a lineage in which the evolution of call-
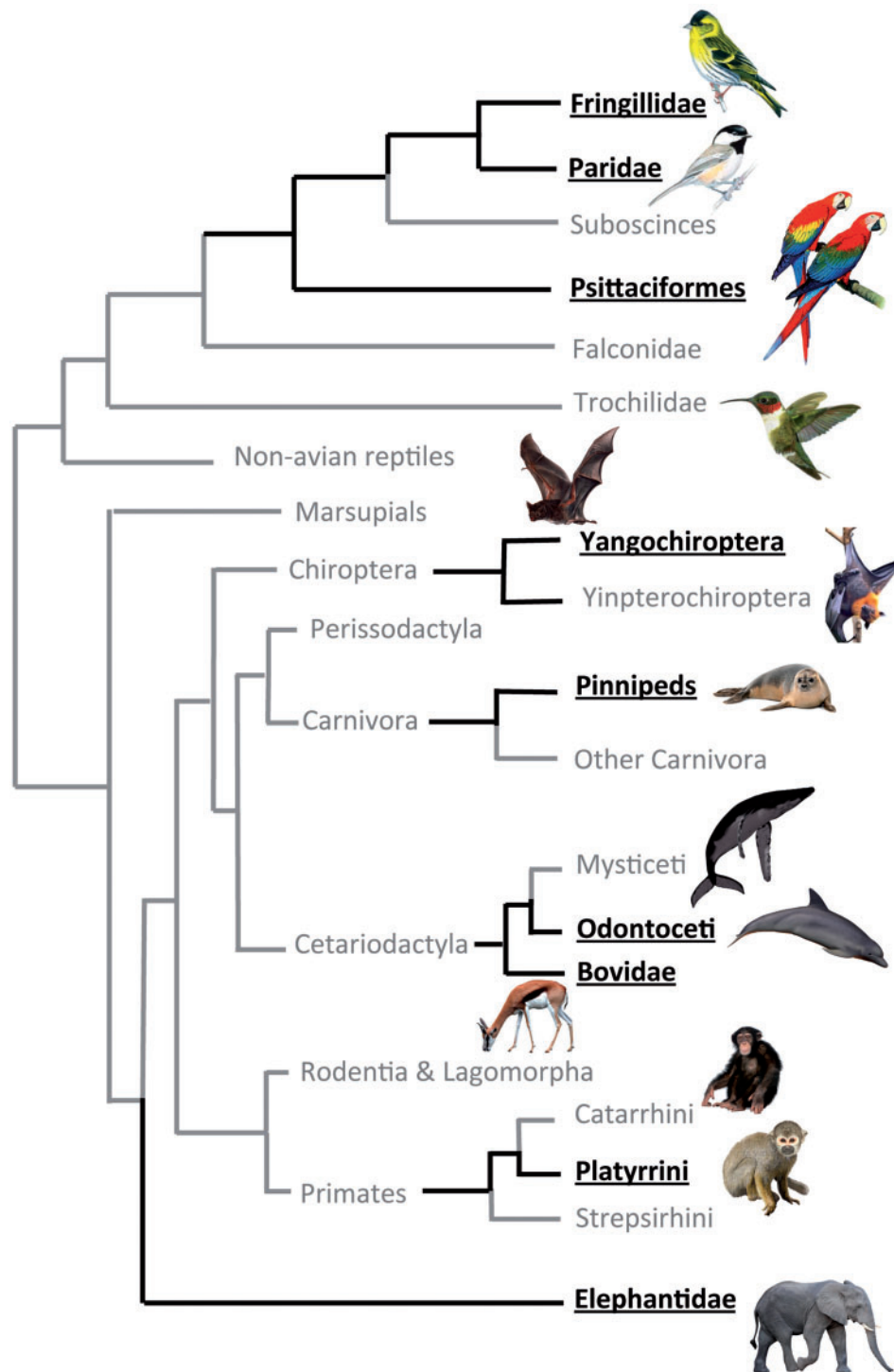
Fig. 1 The association between fluid social dynamics and the learning of call-production is visually illustrated using existing phylogenies from birds and mammals (Hackett et al. 2008; Meredith et al. 2011). Lineages for which there is evidence of learned modification of the acoustic properties of calls are indicated by black underlining and bold text; lineages that show fluid social dynamics are indicated by black lines in the cladogram. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

learning may have preceded that of song learning (T. Wright, personal communication). Second, some species of seals, bovines, new world primates, and elephants are reported to modify their calls with

experience, yet have not been reported to learn to produce songs or use echolocation, ruling out the hypothesis that some other form of vocal learning must pre-exist call-production learning (Masataka

Table 1 Relationships between call learning, social structure, song-learning, and echolocation across lineages

Family/sub-family	Learned call production	Social structure	Sexually selected vocalizations	Echolocation	Sources
Fringillidae (finches)	Yes	Fission–fusion	Learned	No	Mundinger (1979)
Paridae (chickadees and tits)	Yes	Fission–fusion	Learned	No	Mammen and Nowicki (1981)
Corvidae (crows and jays)	No	Stable families/groups	Learned	No	Hopp et al. (2001)
Suboscines	No	Seasonal groups	No	No	Kroodsma and Konishi (1991)
Psittaciformes (parrots)	Yes	Fission–fusion	Rare	No	Baker (2000); Balsby and Bradbury (2009); Farabaugh et al. (1994); Scarl and Bradbury (2009); Wright et al. (2008)
Trochilidae (hummingbirds)	No	Solitary	Learned	No	Baptista and Schuchmann (1990); Petkov and Jarvis (2012)
Chiroptera	Yes				Knörnschild (2014)
Yangochiroptera (microbats)	Yes	Fission–fusion	Learned	Yes	
Yinpterocchiroptera (mega-bats and some microbats)	No	Fission–fusion	No	No	
Pinnipeds (seals, walruses, and sea lions)	Yes	Fission–fusion	Unlearned	No	Reichmuth and Casey (2014)
Other carnivora	No	Stable families/groups	Unlearned	No	
Bovidae (cloven hoofed ruminants)	Yes	Fission–fusion	No	No	Briefer and McElligott (2012); Volodin et al. (2014)
Other ruminants	No	Seasonal groups	No	No	
Odontoceti (toothed whales)	Yes	Fission–fusion pods	No	Yes	Deecke et al. (2010); Janik (2000, 2014); Miller et al. (2004)
Mysticeti (baleen whales)	No	Solitary/stable families	Learned	No	Rendell and Whitehead (2003); Winn et al. (1981)
Hominoidea[a] and Catarrhini (great apes and old world primates)	No	Stable families/groups and fission–fusion groups	Unlearned	No	Crockford et al. (2004); Lemasson et al. (2011); Mitani et al. (1992); Petkov and Jarvis (2012)
Platyrrini (new world primates)	Yes	Very large groups	No	No	Koda et al. (2007); Masataka and Fujita (1989); Petkov and Jarvis (2012); Snowdon and Elowson (1999); Sugiura (1998)
Strepsrihini (prosimians and tarsiers)	No	Stable families/groups and fission–fusion groups	No/unlearned	No	Oda (2002); Petkov and Jarvis (2012); Seyfarth and Cheney (2014)
Elephantidae	Yes	Fission–fusion	No/unlearned	No	Poole et al. (2005); Stoeger and Manger (2014)

Note: Selected sources are provided for each lineage.
[a]Only non-human hominids are considered for this review.

and Fujita 1989; Sugiura 1998; Snowdon and Elowson 1999; Poole et al. 2005; Koda et al. 2007; Lemasson et al. 2011; Briefer and McElligott 2012; Petkov and Jarvis 2012; Reichmuth and Casey 2014; Volodin et al. 2014). The species that neither learn their songs nor use echolocation seem to demonstrate less vocal plasticity (Tyack 2008). However, the fact that these animals show some plasticity in the production of calls and have fluid social associations supports the hypothesis that social dynamics can generate sufficiently strong selection pressure to drive the evolution of call-production learning. Future comparative studies should pursue the relationship between the fluidity of social dynamics and call-production learning at a finer taxonomic scale to determine whether social dynamics do, in fact, select for vocal learning.

Collectively, in addition to playing an important role in the development of communication, social dynamics could select for enhanced ability to communicate, in at least two ways. First, large, stable social groups can result in greater diversity of

signature contact calls that encode individual identity when vocal production is not learned, with the result that species that live in larger groups will face selection for enhanced contextual learning (Pollard and Blumstein 2011; Seyfarth and Cheney 2014). Second, fluid social affiliations, such as fission–fusion social systems, are associated with the learning of the production of contact calls across diverse taxa, consistent with complex social dynamics providing selective pressure for vocal learning. Such vocal learning in turn has the potential to encode new social associations (Jackendoff 1999; Freeberg et al. 2012). While the role of sexual selection in shaping specialized abilities to learn that underlie communication has been well studied, considering such specialized learning as part of the continuum of cognitive specializations for sociality is less common in research on animals (although see Seyfarth and Cheney 2014). Applying research approaches from comparative cognition to research on animal communication will increase our understanding of the roles of these traits both as products and as agents of evolutionary change.

Conclusions

Integrating research on sociality, cognition, and communication will provide a more comprehensive understanding of how the social environment may shape behavior and specializations of the brain for social living. Several areas may prove particularly productive for future research. First, macroevolutionary change and group-level effects on cognition have been relatively well studied, but plasticity in cognition as a result of social experiences during an individuals' lifetime is less-frequently examined under naturalistic conditions. Future work in this area should expose animals to a range of social conditions that naturally occur for a species and examine the effects on brain function and cognitive performance. This approach would identify social factors that negatively or positively impact cognition, which is important for understanding the relationship between population density and fitness in wild populations (Greggor et al. 2014). Second, although the development of species-typical communication is well studied, the potential for social dynamics to select for specialized communicative abilities through evolutionary processes is somewhat overlooked, outside of the role of sexual selection in shaping birdsong. Examining the relationships among contextual learning, vocal learning, and social complexity across taxa offers insight into the role of social dynamics in the evolution of enhanced communication. Finally,

studies both of proximate and ultimate causes should consider the relationships among social complexity, cognition, communication, and the brain to better understand the evolutionary processes and underlying mechanisms that explain behavioral specializations for social living.

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