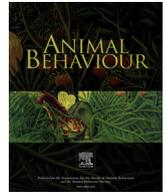




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Social cognition

Robert M. Seyfarth^{a,*}, Dorothy L. Cheney^b^a Department of Psychology, University of Pennsylvania, Philadelphia, PA, U.S.A.^b Department of Biology, University of Pennsylvania, Philadelphia, PA, U.S.A.

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The social intelligence hypothesis argues that competition and cooperation among individuals have shaped the evolution of cognition in animals. What do we mean by social cognition? Here we suggest that the building blocks of social cognition are a suite of skills, ordered roughly according to the cognitive demands they place upon individuals. These skills allow an animal to recognize others by various means; to recognize and remember other animals' relationships; and, perhaps, to attribute mental states to them. Some skills are elementary and virtually ubiquitous in the animal kingdom; others are more limited in their taxonomic distribution. We treat these skills as the targets of selection, and assume that more complex levels of social cognition evolve only when simpler methods are inadequate. As a result, more complex levels of social cognition indicate greater selective pressures in the past. The presence of each skill can be tested directly through field observations and experiments. In addition, the same methods that have been used to compare social cognition across species can also be used to measure individual differences within species and to test the hypothesis that individual differences in social cognition are linked to differences in reproductive success.

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The social intelligence hypothesis, originally proposed by [Chance and Mead \(1953\)](#), [Jolly \(1966\)](#) and [Humphrey \(1976\)](#), argues that selective pressures imposed by the social environment, specifically, competition and cooperation with conspecifics, have played an important role in shaping the evolution of the brain and cognition in animals. But what, exactly, do we mean by 'social cognition'? Here we discuss the mechanisms that underlie social cognition, and how they can be measured and compared across both species and individuals. Our goal is to quantify levels of social cognition, to show how cognitive complexity can be tested among free-ranging animals, and to discuss the potential links between social cognition and fitness.

In her original formulation, [Jolly \(1966\)](#) was struck by the fact that many primates, like the ringtailed lemurs, *Lemur catta*, she studied, exhibit complex societies, differentiated social relationships and extensive social learning 'but lack much capacity to learn about objects' (1966, page 506). She concluded that 'social life preceded, and determined the nature of, primate intelligence' (1966, page 506).

In practice, however, it is difficult to place a strict dividing line between 'social' and 'nonsocial' cognition, for at least two reasons.

First, among group-living animals, many interactions with the nonsocial environment have a social component. Memory of the location and timing of fruiting trees, for example, or the boundaries of a large home range, are formed as a group moves through its habitat, with some individuals leading, others following, and all animals presumably learning from each other as they go. As a result, while laboratory studies may try to separate social and nonsocial performance in their analysis of the factors that have shaped brain evolution (e.g. [Genovesio, Wise, & Passingham, 2014](#)), under natural conditions it is often difficult to do so. Second, as [Bond, Wei, and Kamil \(2010\)](#) noted, the ability to remember nonsocial stimuli (e.g. location of cached food) or social stimuli (e.g. a dominance hierarchy) may be governed by many of the same underlying general mechanisms, making it difficult to distinguish whether skills in modern species have arisen through social or nonsocial pressures. Consistent with this view, measures of cognitive skill in primates are correlated across multiple domains (e.g. behavioural innovation, social learning, tool use and extractive foraging), suggesting that 'social, technical and ecological abilities have coevolved' ([Reader, Hager, & Laland, 2011, page 1017](#); see also [Holekamp, Dantzer, Stricker, Yoshida, & Benson-Amran, 2015, this issue](#)).

We begin, therefore, with a disclaimer: when we talk about social cognition we are not claiming that selection has not acted on individuals' knowledge of other environmental features (for reviews see e.g. [Morand-Ferron, Cole, & Quinn, 2015](#); [Reader et al.](#),

* Correspondence: R. M. Seyfarth, Department of Psychology, University of Pennsylvania, Philadelphia, PA 19104, U.S.A.

E-mail address: seyfarth@psych.upenn.edu (R. M. Seyfarth).

2011; Thornton & Lukas, 2012), nor do we support 'an exclusively social model of primate intelligence' (Reader et al., 2011, page 1017). Instead, we focus on the fact that all group-living animals confront a multitude of social problems, and that some aspects of cognition may have evolved at least in part because selection has favoured individuals who are skilled and motivated to solve them (Cheney & Seyfarth, 2007). Social cognition, moreover, can be quantified and tested experimentally, both across and within species. Our focus on social problems may also help to redress an imbalance: in a recent forum on the evolution of cognition in animals (Rowe & Healey, 2014, plus commentary replies) studies of social cognition are barely mentioned.

We define social cognition as knowledge about conspecifics, and we measure the complexity of social cognition by measuring the complexity of individuals' knowledge of their own and other animals' social interactions and relationships. Our focus is on those aspects of cognition that can be attributed, wholly or in part, to selection acting within the domain of conspecific interactions. It remains an open question whether the social environment presents animals with problems that are formally different or more complex than those presented by other stimuli.

PREVIOUS APPROACHES

Several studies have used experiments to quantify social cognition and test the hypothesis that individuals living in more complex societies should exhibit greater cognitive skills, at least in the social domain. For example, Bond, Kamil, and Balda (2003) compared the performance of highly social pinyon jays, *Gymnorhinus cyanocephalus*, and much less social western scrub-jays, *Aphelocoma californica*, on tests of transitive inference. They found that the pinyon jays' performance was superior to that of the scrub-jays, supporting an association between social complexity and cognitive skill (see also Paz y Miño, Bond, Kamil, & Balda, 2004). Similarly, Hick, Reddon, O'Connor, and Balshine (2014) compared contest behaviour in four species of cichlid fish. Two were pair-breeders, one was group living and highly social, and a fourth was solitary. They found that individuals in highly social species were better at discriminating between familiar and unfamiliar individuals, had shorter contests with fewer aggressive acts and resolved contexts more peacefully than individuals in other species. They concluded that skills in resolving conflicts 'are fundamentally linked to the evolution of complex social systems' (2014, page 47; see also Sandel, MacLean, & Hare, 2011).

In other studies, scientists have varied the complexity of the social environment experienced by immature animals, then tested the effect of this manipulation on adult social skills. Arnold and Taborsky (2010), for instance, raised cichlid fish (*Neolamprologus pulcher*) with either adults or alone. They hypothesized that those reared with adults would experience a more complex social environment, and they found that, in subsequent social tests, these individuals exhibited greater skill and success in their interactions with others as compared with peer-raised individuals (see also Kotschal, Rogell, Maklakov, & Kolm, 2012; Kotschal & Taborsky, 2010). In a study of cowbirds (*Molothrus ater*), White, Gersick, Freed-Brown, and Snyder-Mackler (2010) created two types of flocks that differed in social complexity. In 'dynamic' flocks, birds regularly moved between groups, whereas in 'stable' flocks, membership remained constant throughout the year. When males from the two conditions were placed in new environments with unfamiliar females, the dynamic-condition males had higher reproductive success.

These experiments offer a promising approach to studies of social cognition because they involve direct, experimental tests and focus on specific skills that are potentially linked to reproductive

success. Although they cannot yet reveal whether differences in adult behaviour are due to differences in cognitive skill or some other factor, they permit direct comparisons both across species and across individuals within a species.

However, while experiments that manipulate group size, composition and social experience can readily be conducted on insects, fish and birds, they are difficult if not impossible to conduct on larger, long-lived and free-ranging mammals like hyaenas, dolphins, elephants and nonhuman primates. These species are of particular interest because they have large brains and complex societies. With this limitation in mind, we highlight below some different, complementary methods that lend themselves to field studies of large mammals and focused experimentation. These methods allow direct comparisons of social cognition across species and individuals. They may also allow tests of the hypothesis that individual differences in cognitive skill are linked to differences in reproductive success.

As an organizing framework, we propose that the building blocks of social cognition are a suite of skills, ordered roughly according to the cognitive demands they appear to place upon individuals. These skills allow animals to recognize individuals by various means, remember past interactions, observe others, recognize their social relationships and attribute mental states to them.

We treat these building blocks of social cognition as targets of selection. We assume that they are adaptive because they allow individuals to predict other animals' behaviour and intentions, to succeed in competitive encounters, and to form and maintain beneficial social bonds. We hypothesize that more complex levels of social cognition evolve only when simpler methods are inadequate and that, as a result, more complex levels of social cognition indicate greater selective pressures in the past (Cheney & Seyfarth, 2007; Humphrey, 1976; Wiley, 2013). Some skills are elementary and virtually ubiquitous in the animal kingdom; others are more complex and more limited in their taxonomic distribution. Exactly how the various skills are distributed across species and individuals remains an empirical question.

The building blocks of social cognition can be tested directly through field observation and experiments. We discuss some of these experiments in Part 1. In Part 2 we argue that the same methods can also be used to measure individual differences within a species and to test the hypothesis that individual variation in social cognition is linked to variation in reproductive success. The skills we describe are of broad scientific interest because of their close relation to many of the mental processes that play central roles in neuroscience and cognitive science. Finally, in Part 3 we discuss some avenues for future research.

Our method borrows from that used in the comparative study of animal navigation, where a recent review concludes as follows:

Comparing across a range of species whose navigational competence varies from simple to sophisticated, we note that complex and more phylogenetically recent abilities appear to be synthesized from simple, phylogenetically older ones. Using the observation as a starting point, we organize ... navigational behaviours loosely into a hierarchical framework – the navigation toolbox – which is a collection of processes that can support, either alone or collectively, navigational behaviours of varying complexity. (Wiener et al., 2011)

Our goal is not a complete review of the literature on tests of social cognition. Instead, our aim is to suggest ways in which social cognition can be quantified, tested experimentally on free-ranging animals, and compared across species and individuals, thereby offering tests of the social intelligence hypothesis that complement and extend existing methods.

PART 1: COMPARISON ACROSS SPECIES

Individual Recognition

Behaviour that suggests individual recognition is well documented in many insects, fish, amphibians, reptiles, birds and mammals, and occurs in the visual, olfactory and auditory modalities (reviewed in: Tibbetts & Dale, 2007; Wiley, 2013). As already noted, many species have sensory mechanisms that appear to be specialized for individual recognition, leading observers to conclude that the ability to recognize other conspecifics has been strongly favoured by selection. Receivers that recognize individuals may simply be exploiting the naturally occurring variation in other animals' voices, appearances or secretions. Alternatively, selection may have actively favoured 'identity signals' by signallers (Dale, Lank, & Reeve, 2001) through negatively frequency-dependent selection (Tibbetts & Dale, 2007).

Recognition, however, comes in many different forms, each of which may place different cognitive demands on the individuals involved (Wiley, 2013). Some species, for example, appear to distinguish only broad categories of individuals (male versus female, familiar versus stranger, worker versus reproductive) without discriminating among the individuals within these groups (Tibbetts & Dale, 2007; Wiley, 2013). In other cases, what looks at first like individual recognition may be based on simpler mechanisms. Territorial bullfrogs, for example, may associate (and habituate to) particular calls coming from specific neighbouring areas without necessarily recognizing the singers as specific individuals (Bee & Gerhardt, 2001). Song-type matching in song sparrows (reviewed in Searcy, Akçay, Nowicki, & Beecher, 2014) provides stronger evidence for true individual recognition.

Recognition of individuals may be based on single perceptual cues, like the distinctive facial features of paper wasps, *Polistes fuscatus* (Sheehan & Tibbetts, 2011), or involve the integration of information from different cues within a single modality or from different sensory modalities. Multicue and multimodal integration of identity cues are of interest because they appear to involve increasingly sophisticated levels of memory and cognitive processing.

Individual recognition is most often documented in the auditory mode, through playback experiments. In these studies, however, it is often difficult to escape the impression that animals are engaged in cross-modal or even multimodal processing. A monkey who looks or moves towards the source of the sound when she hears her offspring's call (e.g. Rendall, Rodman, & Emond, 1996) acts as if the sound has created an expectation of what she will see if she moves in that direction (Seyfarth & Cheney, 2009). Humans, of course, do this routinely, integrating information about faces and voices to form the rich, multimodal percept of a person (Campanella & Belin, 2007).

Some of the first evidence that animals might integrate multiple cues from the same modality to form a representation of an individual came from work on hamsters (Johnston & Bullock, 2001). Golden hamsters, *Mesocricetus auratus*, produce at least five different individually distinctive odours. In a typical experiment, a male familiar with females A and B was exposed (and became habituated to) the vaginal secretions of female A. He was then tested with either A's or B's flank secretions. Males tested with A's flank secretions showed little response (across-odour habituation); however, males tested with B's flank secretions responded strongly. The authors concluded that 'when a male was habituated to one odor he was also becoming habituated to the integrated representation of that individual' and was therefore not surprised to encounter a different odour from the same animal. Hamsters, they suggested, have an integrated, multi-odour memory of other

individuals. Direct physical contact with an individual may be necessary for such memories to develop (Johnston & Peng, 2008, page 122).

Subsequent experiments have demonstrated cross-modal individual recognition across the visual and vocal domains in horses (*Equus caballus*: Proops, McComb, & Reby, 2009), meerkats (*Suricata suricatta*: Townsend, Allen, & Manser, 2012) and crows (*Corvus macrorhynchos*: Kondo, Izawa, & Watanabe, 2012). At a neural level, several studies document the integration of auditory and visual information in rhesus macaques, *Macaca mulatta* (Adachi & Hampton, 2012; Ghazanfar, Maier, Hoffman, & Logothetis, 2005; Sliwa, Duhamel, Pascalis, & Wirth, 2011).

Like Wiley (2013, page 179), we assume that 'complex mechanisms for recognition are expected to evolve only when simpler mechanisms [are not] sufficient' to meet the demands of social life (see also Neff & Sherman, 2002; Stoddard, 1996). Many insects distinguish between individuals from different colonies but not among individuals within a colony (e.g. Langen, Tripet, & Nonacs, 2000), presumably because a more detailed level of recognition would require an enormous increase in memory without bringing additional benefits. Mechanisms of recognition can therefore be ranked in order of increasing complexity according to whether they involve discrimination among broad classes, among individuals within these classes, or simultaneous classification at multiple levels.

Mechanisms of recognition can also be ranked in complexity according to whether they involve single features, multiple features within the same modality, or the integration of multimodal features into a single percept. Each level of complexity seems to require increasingly complex levels of neural processing (e.g. Ghazanfar et al., 2005). Because more complex mechanisms are expected to evolve only when simpler mechanisms fail, we can use the sophistication of mechanisms underlying recognition as a measure of the selective pressures facing individuals in different species.

If individual recognition can evolve in any species but does so primarily when the social environment requires it, we should expect to find an absence of individual recognition even in complex societies if circumstances appear to make it unnecessary. Chittka and Niven (2009) argued that this occurs in many insect societies, which are demonstrably complex but lack individual recognition. Social complexity with limited recognition may also be present in an Old World monkey, the Ethiopian gelada, *Theropithecus gelada* (Bergman, 2010; Bergman & Beehner, 2015, this issue). The limited recognition in geladas is striking when contrasted with clear evidence for individual recognition in closely related chacma baboons, *Papio hamadryas ursinus* (e.g. Crockford, Wittig, Seyfarth, & Cheney, 2007). Bergman (2010) speculated that gelada males may not recognize other males by voice either because they are unable to do so (there are simply too many possible candidates) or because they are unmotivated to do so (a leader male in a neighbouring one-male unit does not present a challenge to their own tenure). The presence, or lack, of individual recognition may thus depend not on the overall complexity of a society but on the precise demands of the social environment.

Knowledge of Other Animals' Relationships

In many animal groups, individuals interact in predictably different ways with each of their potential partners. This nonrandom pattern of interactions creates a social environment in which there are statistical regularities, which raises two questions. What do individuals know about these regularities? What do they know about each other's relationships? Such 'third-party' knowledge is of interest because it can only be acquired by recognizing

other individuals, observing them interact, often in many different ways, and making the appropriate deductions. It thus requires animals to adopt a nonegocentric perspective, assessing interactions in which they are not themselves involved. In this respect, knowing about other individuals' relationships is akin to having a Euclidean map of your surroundings, whereas knowing only about your own relationship is more like dead reckoning (Wiener et al., 2011).

Knowledge of other individuals' relationships is also of interest because it may involve the formation of social categories, like 'closely bonded individuals', or the organization of knowledge about relationships in some kind of structure, like the linear transitive order of animals in a dominance hierarchy or the hierarchical tree-structured arrangement of ranked, matrilineal kin groups (see below).

Finally, knowledge of other individuals' relationships is relevant to research on the evolution of cognition because, if selection favours individuals who can recognize other dyads or triads, even moderately large groups present animals with a task that is combinatorially explosive (Seyfarth & Cheney, 2001). In a group of 80 individuals (not unusual for many primates), there are 3160 possible dyads and 82 160 possible triads. Social pressures may therefore create problems in learning and memory that are both quantitatively and qualitatively different from those in other contexts.

Recognition of dominance rank and transitive inference

A linear, transitive dominance rank order in animals could emerge if each individual divided her social companions into two groups, those that ranked above her and those that ranked below (Boyd & Silk, 1983; Wiley, 2013). Alternatively, the same kind of hierarchy could be based on each individual's knowledge of the rank relations among every other individual. Both observation (Silk, 1999) and field playback experiments (Borgeaud, van de Waal, & Bshary, 2013; Cheney, Seyfarth, & Silk, 1995; Kitchen, Cheney, & Seyfarth, 2005) have shown that macaques (*Macaca radiata*), baboons and vervet monkeys (*Chlorocebus aethiops*) recognize the linear rank order among the individuals in their group. Recognition of other individuals' ranks has also been demonstrated in fish (Bshary, Gingsins, & Vail, 2014; Grosenick, Clement, & Fernald, 2007), birds (Massen, Pasukonis, Schmidt, & Bugnyar, 2014; Paz y Miño et al., 2004), spotted hyaenas, *Crocuta crocuta* (Engh, Siebert, Greenberg, & Holekamp, 2005), ringtailed lemurs (MacLean, Merritt, & Brannon, 2008), capuchin monkeys (*Cebus capucinus*: Perry, Barrett, & Manson, 2004) and mangabeys (*Cercocebus atys*: Range & Noe, 2005), suggesting that the ability is widespread throughout the animal kingdom.

In all of these species, rank orders are usually transitive, such that if A dominates B and B dominates C, A always dominates C. In experimental studies of birds and fish, individuals appeared to recognize this transitivity: having seen B dominate C and C dominate D, they treated B as dominant to D without having observed them interact directly (Bond et al., 2003; Bshary et al., 2014; Grosenick et al., 2007; Mikolasch, Kotschal, & Schloegel, 2013; Paz y Miño et al., 2004). Evidence for transitivity is important because it suggests that social knowledge may be organized and structured when stored in memory.

Recognition of others' associates

Many animals adjust their behaviour as a result of having observed interactions in which they are not themselves involved. If a female Japanese quail, *Coturnix japonica*, observes a particular male mating with another female, this experience increases her subsequent willingness to mate both with that male and with other males that share his physical features. By contrast, if a male quail has observed a particular female mating with another male, this

experience decreases his subsequent willingness to mate with that female (reviewed in Galef & White, 2000). In socially monogamous chickadees (*Poecile atricapillus*), females that hear their mate apparently lose an aggressive encounter against a neighbouring male engage in significantly more extrapair matings than do females that hear their mate apparently win an encounter (Mennill, Ratcliffe, & Boag, 2002). Many other examples of adaptive 'eavesdropping' are reviewed in McGregor (2005). Experiments on cichlid fish (*Astatotilapia burtoni*) indicate that, when a female observes an aggressive encounter involving her chosen mate, the outcome produces changes in her brain even before she engages in any behavioural interaction with him. Brain areas associated with reproduction are activated if her mate wins; areas associated with anxiety are activated if he loses (Desjardins, Klausner, & Fernald, 2010; Fernald, 2015, this issue; reviewed in Weitekamp & Hofmann, 2014).

There is evidence from both observations and field playback experiments that nonhuman primates recognize other individuals' social relationships (e.g. Bachmann & Kummer, 1980; Cheney & Seyfarth, 1980, 1999). For example, after receiving aggression from a higher-ranking female, adult female baboons treat the threat-grunt of a close relative of their opponent as a vocal alliance indicative of possible renewed aggression, and they avoid both the original opponent and her relative (Wittig, Crockford, Seyfarth, & Cheney, 2007). They show little reaction, however, to the threat-grunt of a female unrelated to the opponent. Conversely, if subjects hear the 'reconciliatory' grunt of a close relative of their opponent, they are more likely both to approach their former opponent and to tolerate the opponent's approaches. No such reconciliatory effect occurs if subjects hear the grunt of a female unrelated to the opponent (Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007). Recognition of other individuals' relationships extends even to very transient relationships, such as sexual consortships, as demonstrated by experiments conducted by Crockford et al. (2007).

Similarly, in playback experiments on free-ranging chimpanzees, *Pan troglodytes*, Wittig, Crockford, Langergraber, and Zuberbühler (2014) showed that males were more likely to avoid the aggressive barks of a former opponent's close associate than the aggressive barks of a nonassociate. The recognition of other individuals' close associates may be particularly important for chimpanzees, which can improve their dominance rank, and hence reproductive success, by forming coalitions with other males. Over a 14-year period at the Gombe Stream Reserve in Tanzania, the males that gained the greatest reproductive benefits from coalitionary behaviour were those that had as coalition partners individuals 'who themselves did not form coalitions with each other' (Gilby et al., 2013, page 373). These data suggest that individuals used their knowledge of other animals' relationships when choosing their coalition partners.

Simultaneous recognition across two or more dimensions

Individual recognition and the recognition of others' relationships appear to be widespread among animals. But animal societies are multidimensional: at any one time an individual can be classified according to its identity, dominance rank, close associates, reproductive state, or even the rank, associations and reproductive state of its current mating partner. Do animals recognize these multiple associations?

To test whether adult female baboons classify other females simultaneously according to both matrilineal kinship and dominance rank, Bergman, Beehner, Cheney, and Seyfarth (2003) played sequences of calls mimicking within- and between-matriline rank reversals to subjects in matched trials. Dominance ranks among female baboons are typically very stable. When rare rank reversals do occur, however, their repercussions may differ according to

whether they occur within or between matriline. Rank reversals within a matriline (e.g. between sisters) typically affect only the two individuals involved. However, a rank reversal between matrilines can result in all the members of one matriline rising in rank above all members of the other (Cheney & Seyfarth, 2007; Engh et al., 2006b).

In one trial, subjects heard an apparent rank reversal involving two members of the same matriline: for example, female B3 giving threat-grunts while female B2 screamed. In another trial, the same subject heard an apparent rank reversal involving the members of two different matrilines: for example, female C1 giving threat-grunts while female B3 screamed. As a control, the subject heard a fight sequence that was consistent with the female dominance hierarchy. To control for the rank distance separating the subject and the individual whose calls were being played, each subject heard a rank reversal (either within- or between-family) that involved the matriline one step above her own (cf. Penn, Holyoak, & Povinelli, 2008). Within this constraint, the rank distance separating apparent opponents within- and between-families was systematically varied. Between-family rank reversals elicited a consistently stronger response than did within-family rank reversals (Bergman et al., 2003). Subjects acted as if they classified individuals simultaneously according to both kinship and rank. The classification of individuals simultaneously according to these two criteria has also been documented in observations of Japanese macaques, *Macaca fuscata* (Schino, Tiddi, & Polizzi di Sorrentino, 2006).

These results are difficult to explain without assuming that, when listening to others' vocalizations, a baboon encodes information not just about the caller's identity but also about her dominance rank and family membership, among many other attributes. And when a listener hears the sound of two individuals interacting, she encodes information about the nature of this interaction, responding strongly if it violates the listener's current knowledge of the animals' social relationship. Just as we cannot hear a word without thinking about its meaning, so a baboon cannot hear vocalizations without thinking about the animals who are calling, their ranks, their close associates and history of interaction. These features are bound together in much the same way that auditory and visual cues are bound together in a cross-modal, cognitive percept. Individual recognition thus constitutes a form of 'object perception' (Bregmann, 1990; Miller & Cohen, 2010), in which a variety of disparate stimuli are linked together to form a coherent object. As a result, perception of one attribute (for example, a voice) reflexively creates a rich variety of expectations in the perceiver's mind of, for instance, what she will see when she looks towards the sound, whom the caller is likely to dominate and who is likely to support her in an aggressive interaction. Under these conditions, individual recognition involves more than just the recognition of an individual; it includes the recognition of that individual's place in its society (for an argument that such behaviour involves the formation of social categories, see Seyfarth & Cheney, 2013b, 2014).

To summarize, some form of recognition of other animals' relationships has not yet been documented in insects but appears to be widespread among fish, birds, hyaenas and nonhuman primates. Many animals are skilled observers of other animals' behaviour. They appear to recognize who is dominant to whom, and who mates, grooms or interacts with whom in a particular way. However, while the classification of other animals' interactions along a single dimension is widespread, studies of baboons and macaques provide the only evidence to date that animals recognize other individuals' relations along two or more dimensions simultaneously. Whether this skill is unique to primates, unique to species with particular sorts of social organization, or widespread and

independent of both taxonomy and social organization, remains to be tested (see below).

Theory of Mind

In children, the ability to recognize another individual's mental state develops gradually. As early as 6 months of age, children recognize that speech and gaze have referential content and they begin to learn the meaning of words (Bergelson & Swingley, 2012). Children aged 6–12 months act as if they understand that gaze and attention are a reflection of underlying knowledge and motivation (e.g. Baldwin, 1993; Tomasello, Carpenter, Call, Behne, & Moll, 2005). By roughly 18 months they begin to understand peoples' likes and dislikes (Repacholi & Gopnik, 1997), and by roughly 2 years of age they begin to distinguish between ignorance and knowledge in others (e.g. O'Neill, 1996).

These increasing levels of complexity provide a useful point of comparison for studies of animals. Without pretending to review this enormous literature (reviewed in: Call & Tomasello, 2008; Cheney & Seyfarth, 2007; Heyes, 2014; Seyfarth & Cheney, 2013b), three broad conclusions seem apparent. First, many animals appear to attend to cues like gaze direction when assessing others' likely behaviour (e.g. Bugnyar, 2011; Flombaum & Santos, 2005; Goossens, Dekleva, Reader, Sterck, & Bolhuis, 2008; Hare, Call, Agnetta, & Tomasello, 2000; Schloegl, Kotrschal, & Bugnyar, 2007; Schmitt, Pankau, & Fischer, 2012). These cues allow animals to infer, for example, whether a vocalization is being directed towards them or towards some other individual. Such inferences would seem to be adaptive, because it would be costly for animals to respond to every call they heard as if it were directed at them. As already noted, both baboons and chimpanzees appear to rely on both their knowledge of others' relationships and their memory of recent interactions when deciding whether or not to respond to a call. In playback experiments, Engh, Hoffmeier, Cheney, and Seyfarth (2006) found that a female baboon responded to another female's threat-grunt only if she had recently been threatened by that female. If she had recently groomed with that individual, or if she heard another female's threat-grunt she ignored the call (see also Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010, for experiments showing similar results). Although experiments of this sort have so far been conducted only on nonhuman primates, it is certainly possible that similar tests would reveal comparable abilities in many other species (see also Burkhardt, Kupferberg, Glasauer, & van Schaik, 2012).

Despite heroic efforts, there is still little conclusive evidence that animals recognize the relation between seeing and knowing. This arises in part because the results of most experiments are also consistent with the simpler explanation that animals are sensitive to the presence of rivals or the direction of their gaze. Several experiments with captive chimpanzees have attempted to control for these confounds (e.g. Kaminski, Call, & Tomasello, 2008; MacLean & Hare, 2012). These studies suggest that chimpanzees may have a rudimentary understanding of the relation between seeing and knowing, but the performance of subjects across trials is much less consistent than that of humans.

Two recent field experiments on chimpanzees illustrate both the promise and the difficulty of testing whether animals recognize knowledge or ignorance in others. The experiments are particularly important because they ask both whether chimpanzees recognize the difference between a knowledgeable and an ignorant companion and whether they make use of this information by selectively informing ignorant individuals more than knowledgeable ones. In separate studies, Crockford, Wittig, Mundry, and Zuberbühler (2012) and Schel, Townsend, Machanda, Zuberbühler, and Slocombe (2013) placed a snake model in the path of a lone chimpanzee and then

observed whether this now knowledgeable individual gave alarm calls (or more alarm calls) to recent arrivals who were unlikely to know about the snake's presence. Both studies found evidence that callers gave more alarm calls to recent arrivals than to individuals who, as measured by their continued presence and own calling behaviour, were likely knowledgeable. Moreover, their calling behaviour exhibited many of the goal-directed features of intentional communication (e.g. Dennett, 1983). However, the possibility that the decline in the rate of calling over time may have been due to habituation could not be ruled out entirely. Both studies also found that informed individuals were more likely to warn new arrivals if they were closely bonded to them (Crockford et al., 2012; Schel et al., 2013). As a result, it remains possible that callers may have been responding to the new arrivals' identity rather than their perception of the arrivals' ignorance. Once again, this complicates the interpretation of results, at least as they apply to tests of a theory of mind.

Summary: Comparisons across Species

Just as we can measure the increasing complexity of mechanisms that underlie skills in navigation (Wiener et al., 2011), or the complexity of the mechanisms that underlie songbirds' responses to complex song (ten Cate, 2014), or children's linguistic knowledge at different ages (e.g. Swingley, 2009), so we can compare different species by assessing how many of the building blocks of social cognition are required to explain their behaviour.

Because 'social intelligence' is not a single trait but a collection of abilities, some more complex than others, tests of the relation between social intelligence and some measure of brain size or societal complexity are likely to yield different results depending on which building block is being tested. If the measure is individual recognition at the simplest level, or the recognition of other animals' relationships along a single dimension like dominance rank, then there is no clear relation between social intelligence and either brain size or societal complexity because these building blocks are so widely distributed across taxa.

By contrast, if we use more complex, less widely distributed building blocks to measure social intelligence (e.g. cross-modal individual recognition, the recognition of other animals' relationships along two or more dimensions, the recognition of other animals' intentions, or the recognition of other individuals' knowledge or ignorance), then we may find more support for hypotheses that posit a positive link between social intelligence, brain size or societal complexity because these building blocks have so far been found only in nonhuman primates, particularly chimpanzees. Several authors have argued that the chimpanzees' fission–fusion organization places unique demands on individuals' cognitive abilities (Aureli et al., 2008).

PART 2: INDIVIDUAL DIFFERENCES

For years, the working hypothesis in studies of social cognition has been that natural selection has favoured individuals who have the skill and motivation both to cooperate and compete effectively with group-mates, to recognize and monitor other individuals' relationships and to predict other individuals' likely behaviour. Indeed, studies of animal cognition make the implicit assumption that cognitive skills are adaptive. In fact, however, there is little direct evidence that cognitive skills vary among individuals, or that variation in these skills is correlated with variation in fitness. The lack of focus on individual differences may have arisen because most studies have involved cross-species comparisons, which test hypotheses about the evolution of cognition with a broad brush, often glossing over individual variation in the search for species norms (Rowe & Healey, 2014; Thornton & Lukas, 2012). A more

rigorous procedure examines individual variation within a species and tests the hypothesis that individuals with greater cognitive skills have higher reproductive success than others.

For example, male satin bowerbirds, *Ptilonorhynchus violaceus*, construct bowers to attract females. Males decorate their bowers with colourful objects but remove any red objects from the immediate area (Borgia & Keagy, 2006). Keagy, Savard, and Borgia (2009) presented males with two problems: either they had to remove a transparent barrier to gain access to red objects that could then be removed, or they had to cover a red object that could not be removed because it was fixed to the ground. Males that solved the problems more quickly had higher mating success (for further analysis using six different cognitive tasks, see Keagy, Savard, & Borgia, 2011; for similar tests on great tits, *Parus major*, see Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Cole, Cram, & Quinn, 2011, 2012). Thornton and Lukas (2012) and Rowe and Healey (2014) discuss the limitations of this 'problem solving' approach.

Research on the adaptive correlates of individual differences in cognitive skills has thus far focused primarily on birds, using problem-solving tasks that involve the manipulation of objects (Rowe & Healey, 2014; Thornton & Lukas, 2012). Much less is known about individual differences in cognitive abilities among free-ranging mammals. Although some studies of captive apes have begun to consider individual variation in cognitive tasks (e.g. Hermann & Call, 2012), the artificial conditions under which those subjects live make it impossible to link such variation to fitness. Here we briefly review some results from research of individual differences in measures of social cognition among free-ranging baboons.

Given the salience of a matrilineal dominance hierarchy in baboon groups, one might predict that the primary determinants of female reproductive success would be high dominance rank and the presence of female kin. Instead, a female's reproductive success, as measured by longevity and offspring survival, appears to depend largely on the strength and stability of her bonds with other females. In one long-term study of female baboons conducted in Moremi, Botswana, the best predictors of offspring survival and longevity were two measures of females' bond strength, the composite sociality index (CSI), which measures the strength of a female's social bonds with other females, and the partner stability index (PSI), which measures the stability of a female's top three partners across years (Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012). Similar results were obtained in Amboseli, Kenya, where females with strong social bonds with both females and males experienced greater infant survival (Silk, Alberts, & Altmann, 2003). Females in the Botswana study also experienced lower stress (as measured by faecal glucocorticoid metabolites, fGC) when their grooming network was more focused than when it was more diffuse (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008). High dominance rank had an independent, positive effect on longevity, but this effect was less strong than that of bond strength (Silk et al., 2010b). The relation between offspring survival and bond strength remained even when controlling for the presence of kin: mothers and daughters with strong social bonds experienced greater offspring survival than mothers and daughters with weaker bonds (Silk et al., 2009). Furthermore, females established close bonds with other females even when they had no close kin available in the group.

These observations suggested that some individuals were more motivated or skilled than others at establishing and maintaining social bonds, and that variation in patterns of affiliation that were correlated with fitness might have arisen from variation in consistent individual differences, or 'personalities'. We therefore attempted to determine whether different personalities could be

identified and, if so, whether different personality traits were more or less associated with social bond strength and, ultimately, fitness. We also wondered how personality differences might relate to differences in cognition.

To test these hypotheses, we applied exploratory principal component analysis to the behaviour of 45 female baboons over a 7-year period (Seyfarth, Silk, & Cheney, 2012). We identified three relatively stable personality dimensions, each characterized by a distinct suite of behaviours that were uncorrelated with each other and could not be explained by dominance rank or availability of kin. Females scoring high on the 'Nice' dimension were very friendly to others; those scoring high on the 'Aloof' dimension were less friendly and more aggressive; and those scoring high on the 'Loner' dimension were often alone, relatively unfriendly, but not particularly aggressive (Seyfarth et al., 2012). The baboons themselves seemed to recognize these differences. For example, although they generally approached higher-ranking females at lower rates than they approached lower-ranking females, they approached females with above-average scores on the Nice dimension at higher rates, and females with above-average scores on the Aloof and Loner dimensions at lower rates, than would have been expected from those females' ranks alone (Seyfarth et al., 2012).

Two sorts of data suggested that the different personality dimensions were associated with differences in fitness. First, females' scores on the Nice dimension were significantly positively correlated with both CSI and PSI scores, whereas their scores on the Aloof dimension were significantly positively correlated with PSI but unrelated to CSI. Females' scores on the Loner dimension were unrelated to their PSI scores but significantly negatively correlated with their CSI scores (see Table 2 in Seyfarth et al., 2012). These females also had higher fGC values than would have been predicted from their rank alone (see Figure 3 in Seyfarth et al., 2012).

To test whether variation in personality traits was also associated with variation in females' ability and/or motivation to keep track of, anticipate and react adaptively to social events, we subsequently examined females' responses to three different types of social challenges: the immigration of a high-ranking, potentially infanticidal male, the death of a close female relative and their behaviour during playback experiments (Seyfarth & Cheney, 2013a). We hypothesized that these challenges provided a measure of females' ability to anticipate adversity, to respond adaptively to adversity once it had occurred and to keep track of social interactions that had the potential to influence their own relationships.

Previous analyses had demonstrated that females experience a significant increase in fGC levels following the immigration of a potentially infanticidal male (Beehner, Bergman, Cheney, Seyfarth, & Whiten, 2005; Engh et al., 2006a; Wittig et al., 2008). This increase was particularly acute in lactating females who were at most risk of infanticide, but during some immigration events all females experienced increases in fGC levels. We found that females who scored high on the Nice dimension had the greatest increase in fGC levels in the two weeks following male immigration, whereas females who scored high on the Aloof and Loner dimensions were less responsive, showing more dampened increases than other females (Seyfarth & Cheney, 2013a). None of these differences were significant, however.

Females also experienced elevated fGC levels following the death of a close adult female relative, probably in part because the death resulted in the loss of a regular grooming partner. In a previous study, we had found that, in the 3 months following a relative's death, 'bereaved' females increased their number of female grooming partners. This response may facilitate the repair of females' social networks through the establishment of new bonds.

To examine individual differences in response to this challenge, we compared the number of each 'bereaved' female's different

grooming partners in the 3 months following the death of a close female relative with the mean number of grooming partners for unaffected females in the group during the same period, controlling for reproductive state. Whether or not females had a higher or lower number of partners than unaffected females appeared to be related in part to their personality scores. Females who scored high on the Nice and Aloof dimensions tended to increase their number of grooming partners compared with other females (Seyfarth & Cheney, 2013a). In contrast, females scoring high on the Loner component had fewer grooming partners following the death of a relative than unaffected females, behaving as if they found it difficult to repair the damage to their social network. This occurred despite the fact that females who scored high on the Loner component showed a greater increase in fGC levels than other females following their relative's death, particularly when the relative was a mother or daughter. Again, however, these differences were not significant.

We next combined data from five different playback trials designed to measure subjects' knowledge of other animals' social relationships and their memory of recent interactions. The correlations between subjects' strength of response and their scores on the Aloof, Loner and Nice dimensions were all positive, but only the Nice scores were statistically significant (Seyfarth & Cheney, 2013a). Thus, although most females responded more strongly during test than during control trials, females that scored high on the Nice component were the most responsive.

To summarize, our previous work demonstrated that individual female baboons vary in their tendency to form strong, enduring social relationships with others (as measured by the CSI and PSI), and that these differences could be linked to differences in two measures of fitness (Silk et al., 2010a, 2010b). Subsequent analysis indicated that the same individual differences in behaviour were consistent over time and could be linked to different personality traits (Seyfarth & Cheney, 2012). Consistent with this view, results from three independent measures suggested that the same individuals whose personality traits were correlated with high values of the CSI and PSI, and hence higher fitness, also tended to be more responsive to social challenges and more motivated than others to attend to social interactions within their group. Selection may have favoured certain personality traits because these traits increase the likelihood that an individual will form and maintain those bonds with others that ultimately improve fitness.

At present, we cannot say whether the differences we identify were the result of differences in cognitive ability, differences in the motivation to attend and respond to social challenges, or some combination of these and other factors. It also remains to be determined whether any of the apparent differences between personality dimensions and responsive are robust. Finally, as already noted, all of the observed differences were small (Seyfarth & Cheney, 2013a). As a group, females responded significantly positively to all three of the behavioural challenges in our analyses, so individual differences in response strength were subject to a ceiling effect. The attributes associated with females that scored high on the Nice dimension were not unique to these individuals; rather, such females seemed most consistently to show strong anticipatory and reactive responses to challenges. Clearly, however, this hypothesis remains to be tested.

Summary: Individual Differences

Just as one can measure individual differences in tool use and object manipulation and correlate these with differences in reproductive success (e.g. Thornton & Lukas, 2012), one can measure individual differences in behavioural responses associated with social cognition and relate these to individual differences in

the strength and stability of social bonds, and hence reproductive success. At present, tests of individual differences in social cognition have barely begun. We suggest, however, that the same techniques used to establish species norms in cognition and behaviour, particularly playback experiments, physiological measures of stress and behavioural responses to social challenges, can now be applied to the study of individual differences in cognition and reproductive success.

PART 3: WHERE DO WE GO FROM HERE?

The building blocks of social cognition provide a framework within which animals' knowledge of conspecifics can be quantified, tested and compared across species and individuals. Where are the most striking gaps in our knowledge? Here we offer a few suggestions.

Multimodal and Cross-modal Individual Recognition

The recognition of individuals along a single dimension is so common that, by itself, it is unlikely to provide a useful means of distinguishing among species or individuals. By contrast, the recognition and classification of individuals according to multiple dimensions of the same modality or across different modalities may be much less widespread and may therefore provide a better means of comparing species' social cognitive skills. For example, do wasps that recognize individuals by facial markings (Sheehan & Tibbetts, 2011) also recognize individuals along other sensory dimensions? If so, do they integrate information across modalities to form 'an integrated representation of an individual' (Johnston & Bullock, 2001)? Tests for multimodal and cross-modal individual recognition are widely available (e.g. Proops et al., 2009). They may yield interesting species differences, or they may lead us to conclude that multisensory integration is more widespread than previously imagined (Ghazanfar & Schroeder, 2006).

Recognition and Classification along Multiple Dimensions

Territorial songbirds face a daunting problem in classification. For example, song sparrows, *Melospiza melodia*, must distinguish among the singing of several neighbours, each of which has a repertoire of several different song types and sings each type with some day-to-day variation. Further complicating matters, some songs in neighbour A's repertoire are shared with neighbour B, and an 'intruder' male may mimic the song of a resident when he tries to enter an area. Nevertheless, experiments indicate that song sparrows are capable of impressive feats of recognition and, perhaps, classification. Males recognize other individuals by their songs and rapidly learn to discriminate between song types, while remaining sensitive to the day-to-day variation in a particular type (reviewed in Searcy et al., 2014). Since sparrows apparently do not associate a particular male's song types based on common 'voice' characteristics (Beecher, Campbell, & Burt, 1994), listeners seem to learn each song type and associate it with a particular singer. During learning, when some song types or individuals are unfamiliar, subjects may make mistakes in their attribution of a shared song type (Beecher et al., 1994), but in at least one field study subjects responded strongly to an unfamiliar male's song even when this intruder mimicked the song type of a resident (Wilson & Vehrencamp, 2001).

Faced with the problem of remembering large amounts of data, animals as diverse as rats, pigeons and humans search for a higher-order rule or pattern that makes the task easier (e.g. Macuda & Roberts, 1995). The animals' behaviour suggests that they have organized their knowledge of the environment and stored it in

working memory along two dimensions simultaneously, like food type and spatial location, much as we have argued that baboons organize their knowledge of other individuals according to matrilineal kinship and dominance rank (Bergman et al., 2003). More speculatively, we have suggested that baboons store data in a hierarchical tree structure that essentially involves the formation of a model-based predictive system (e.g. Fitch, 2014). This organization of knowledge would be adaptive because it would allow easy access and rapid response to incoming stimuli: just what an animal needs to make quick decisions about other animals' relationships.

At present, however, evidence for two-dimensional classification comes only from primates. Do song sparrows recognize songs along multiple dimensions simultaneously (caller, song type, shared/unshared, neighbour/stranger)? Do they organize their knowledge hierarchically, recognizing between-individual differences at one level and within-individual differences at another? What about dolphins, hyenas and elephants? We simply do not know. But experimental methods are at hand to test this hypothesis, both in the laboratory and in the field (e.g. Beecher et al., 1994; Bergman et al., 2003; Rendall et al., 1996). Given the ubiquity of tree-structured, hierarchical knowledge in human language and cognition (Fitch, 2014), research on the mechanisms that underlie animals' social classifications would address a fundamental issue in cognitive science and the evolution of cognition.

The Classification of Social Relationships

Although it seems likely that knowledge of other individuals' dominance ranks and close associates is widespread among animals, the classification of other group members simultaneously according to these two different criteria has thus far been documented only in nonhuman primates. Other aspects of animals' knowledge of third-party relationships also remain unexplored. For example, we still do not know whether any animals recognize kinship in any sense other than a close association between two individuals. Do monkeys recognize the difference between mothers and daughters, sisters and close friends, even when all three relationships are associated with the same rates and kinds of behaviour? Would it be adaptive to do so? In one experiment in which a single longtailed macaque, *Macaca fascicularis*, was asked to classify matrilineal sisters, as opposed to other pairs that shared a close bond (Dasser, 1988), the subject did not classify sisters as distinct from mothers and daughters. Clearly, more research is required to address this question.

Similarly, we do not know whether animals recognize that transitive inference accurately predicts the nature and direction of some social relationships, but not others. For example, in species that exhibit stable dominance hierarchies, transitive inference allows an individual to predict the direction of agonistic interactions between two individuals even if she has never observed these individuals interact. Similarly, transitive inference can often be used to predict the presence or absence of a social bond: if a female baboon with a new infant also has a close bond with a particular juvenile, it is probably accurate to predict that the juvenile and the infant will also share a close bond (even, perhaps, to infer that the two are siblings). In other cases, however, transitive inference may be inappropriate. Consider, for example, the friendships that lactating female baboons form with adult males in response to the threat of infanticide (Palombit, Seyfarth, & Cheney, 1997). Such friendships are almost invariably formed with the infants' probable or actual fathers (Moscovice et al., 2010). Several females may simultaneously be involved in a friendship with the same male, but these females are often unrelated to each other and do not themselves share close bonds. More importantly, closely bonded females do not necessarily form

friendships with the same male. A lactating female who forms a friendship with one male might have an adult daughter who forms a friendship with an entirely different individual, an individual, in fact, who might pose an infanticidal risk to her own infant. It remains unclear whether baboons or any other animals recognize that the transitive rule 'If A has a bond with B, and B has a bond with C, then A and C must also have a close bond' is true for some relationships but not for others. It is an interesting question, because the selective application of transitive inference in some contexts but not others would not be predicted by traditional learning paradigms. Nevertheless, the ability to make such subtle distinctions would seem to be adaptive. Phrased in terms of network analysis (Brent, 2015, *this issue*), indirect connections are relevant for understanding some relationships but irrelevant and even incorrect for understanding others.

Adaptive Social Relationships

It is increasingly clear that, in many species of animals, individual fitness is strongly influenced by the ability to form strong and enduring social relationships (reviewed in Seyfarth & Cheney, 2012). As a result, it seems likely that selection has favoured individuals who are motivated to form social bonds and who find interacting with others emotionally rewarding.

Long-term field studies that combine behavioural and hormonal measures suggest how this hypothesis might be tested. For example, Crockford et al. (2013) found that chimpanzees that had recently engaged in a grooming bout with a relative or a closely bonded nonrelative subsequently experienced elevated levels of urinary oxytocin levels. No such increases were detected, however, after the same individuals had engaged in a grooming bout with a group member with whom they did not share a close bond. In other words, chimpanzees did not find the behavioural act of grooming per se to be emotionally rewarding; rather, it was the underlying relationship that made the difference (see also Crockford, Deschner, Ziegler, & Wittig, 2014). Chimpanzees showed even greater increases in levels of urinary oxytocin after food sharing (Wittig, Crockford, Deschner, et al., 2014), while levels of urinary testosterone decreased (Sobolewski, Brown, & Mitani, 2012). Similarly, Weinstein, Bales, Maninger, Hostetler, and Capitanio (2014) found that captive macaques that formed bonds with peers during their first year had higher levels of oxytocin later in life.

Equally intriguing, Sobolewski et al. (2012) found that male chimpanzees experienced a rise in urinary testosterone several hours prior to engaging in a cooperative boundary patrol but not prior to engaging in a cooperative hunt. This raises the possibility that, at some level, chimpanzees are able to anticipate what they will be doing in the future. Whether such anticipation is mediated by relatively simple social cues, like the size and composition of the party, by more complex communicative signals that are exchanged among party members, or by even more explicit forms of planning remain to be determined.

Studies like these, which measure some of the physiological correlates of behaviour, offer an excellent opportunity to test hypotheses about the mechanisms that underlie social bond formation and individuals' apparent preferences for certain partners. They also allow us to 'interview' subjects and ask whether they gain some emotional satisfaction from specific sorts of interaction with particular other individuals. For example, do aggressive interactions followed by reconciliation lead to different physiological changes (e.g. increases in levels of urinary levels of oxytocin or decreases in urinary levels of cortisol) than those that do not? If so, can such changes be detected in both the victim and the aggressor who reconciles? Does the observation of an aggressive event, with

or without reconciliation, affect oxytocin or cortisol levels in bystanders?

Finally, what might changes in animals' physiological states tell us about the emotions they experience when their actions benefit others? Experiments conducted on dogs (McGowan, Rehn, Norling, & Keeling, 2014), pigs (Zebunke, Langbein, Manteuffel, & Puppe, 2011) and cows (Hagen & Broom, 2004) suggest that animals find problem solving to be emotionally rewarding, and that they derive more satisfaction from completing a task to obtain a reward than from simply obtaining the reward without effort. It would be interesting to determine whether such self-monitoring of the consequences of one's own actions also extends to social interactions, particularly in the context of communication. For example, as mentioned previously, the degree to which any animal, even a chimpanzee, is capable of distinguishing between an audience that lacks information and one that does not remains debatable. This debate would be much informed if we could assess whether or not signallers experience different affective states depending on the knowledge states of their audience. Does a chimpanzee who gives an alarm call that warns an ignorant listener about the presence of a predator subsequently exhibit higher levels of oxytocin than one whose alarm call provides redundant information to an already informed listener?

Adaptive Triadic Knowledge

Although most social interactions are dyadic, network analysis has identified some intriguing cases in which an individual's indirect connections, the individual's connections to her partner's partners, are correlated with measures related to fitness (reviewed in Brent, 2015, *this issue*). For example, in the lek mating system of manakins (*Chiroxiphia linearis*), males interact with many other males for up to 8 years before they can potentially rise in rank to form a two-male alpha–beta partnership that allows them opportunities to mate (McDonald, 2007). Over a 10-year period, one measure of a male's interactions with others during his first 6 years, network centrality, significantly predicted whether he would subsequently rise in rank (McDonald, 2007). Do individuals know about each other's centrality? Would a manakin respond differently to signals from an individual with high versus low information centrality? As noted earlier, male chimpanzees appear to monitor both the direct and the indirect connections of other males, since in one study the most successful males were those who formed alliances with those individuals who did not form alliances with others (Gilby et al., 2013, page 373). Given the opportunity, would a male chimpanzee be more likely to respond to recruitment calls from partners who, if he joined them in an alliance, would increase his own betweenness score? Such questions could be addressed through playback experiments.

Clearly, the questions outlined above represent only a small handful of many that will be considered in future research. For the past several decades, studies of social cognition have focused primarily on species norms. Do baboons recognize other individuals' relationships? Do chimpanzees have a theory of mind? By turning our attention to more nuanced questions and integrating experiments on social cognition with studies of the physiological, neural and genetic mechanisms that underlie behaviour, we may begin better to understand how individual variation in social cognition influences individual variation in fitness.

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