How does cognition shape social relationships?

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Summary

The requirements of living in social groups, and forming and maintaining social relationships, are hypothesized to be one of the major drivers behind the evolution of cognitive abilities. Most empirical studies investigating the relationships between sociality and cognition compare cognitive performance between species living in systems that differ in social complexity. In this review, we ask whether and how individuals benefit from cognitive skills in their social interactions. Cognitive abilities, such as perception, attention, learning, memory, and inhibitory control aid in forming and maintaining social relationships. We investigate whether there is evidence that individual variation in these abilities influences individual variation in social relationships. We then consider the evolutionary consequences of the interaction between sociality and cognitive ability to address whether bi-directional relationships exist between the two, such that cognition can both shape and be shaped by social interactions and the social environment. In doing so, we suggest that social network analysis is emerging as a powerful tool that can be used to test for directional causal relationships between sociality and cognition. Overall, our review highlights the importance of investigating individual variation in cognition to understand how it shapes the patterns of social relationships.

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1. INTRODUCTION

In group living species, individuals repeatedly interact with conspecifics in different social contexts, leading to long-term relationships that underlie social complexity [1–3]. Such enduring relationships convey significant fitness advantages to individuals [1,4]. It is hypothesised that the formation and the management of these relationships requires animals to learn about conspecifics and adjust their behaviour based on the social environment [5,6]. Presently, the majority of the empirical evidence demonstrating links between cognition and social relationships comes from studies that compare closely related species [7–10]. However, as most of this evidence is correlational, it does not allow us to address the causal directional relationships between sociality and cognition.

In this review, we explore whether intra-specific differences in social relationships are influenced by individual differences in cognition. The 'relationship intelligence' hypothesis suggests that cognitive abilities play an important role in maintaining pair-bonds [11]. This suggestion is supported by the positive relationships between pair-bonding and relative brain size in birds and non-primate mammalian taxa [12,13]. However, cognition can also influence the social relationships that exist beyond pair-bonds. For instance, gregarious animals living in multi-male, multi-female groups, such as primates or corvids, form long-term affiliative relationships with kin (*e.g.* [11,14–17]) and with unrelated individuals (*e.g.* [18–20]). Socially bonded individuals support each other in agonistic encounters [21,22], cooperate to acquire rank positions [23], cooperate in infant care, provide protection for young [24], and share resources [25]. Besides affiliative relationships, animals also form dominance relationships that help to reduce the costs associated with aggression [26], especially when individuals compete over limited resources (*e.g.* food, nesting sites).

Here, we suggest that individual variation in cognition is one of the drivers of individual differences in social relationships across multiple behavioural contexts including affiliative and agonistic relationships. Individual variation in the ability to optimize social behaviour based on environmental information, *sensu* 'social competence', can influence relationships and thus drive social evolution [27]. As individual variation in behaviour is the medium via which selection acts on cognition [28], identifying the cognitive abilities that affect social relationships is essential for understanding how cognitive variation may shape and consequently be shaped by selection.

Therefore, we first focus on identifying the key cognitive abilities that animals use when forming and maintaining social relationships. We review whether we have empirical evidence demonstrating that individual variation in these abilities is linked to individual variation in social relationships (Table 1). We then address whether the links between cognition and social relationships are bi-directional, such that individual variation in cognition both influences and is influenced by individual variation in social relationships. We emphasise that to fully understand the relationship between sociality and cognition, an increased focus on intra-specific studies is necessary. We propose social network analysis as a promising tool to quantify the causal bi-directional relationships between cognition and social relationships.

2. THE ROLE OF COGNITIVE ABILITIES IN SOCIAL RELATIONSHIPS

(a) Perception and attention

Evaluating different sources of information is potentially costly [29]. Thus, to optimize information-gaining processes, individuals must be selective in whom they attend [30]. Selective attention depends on numerous factors including conspecifics' quality (*e.g.* aggressive strength) and the reliability of the information that they provide. For example, phenotypic cues (see [31,32] for review) and displays [33] represent an opponent's fighting prowess. The ability to perceive and attend to such cues may influence individuals' decision to engage in a contest. Although species differ in the assessment strategies they use [34] and the exact cognitive abilities involved in assessment of conspecifics have not been fully identified [35], individual variation in

53 attention and perception abilities are likely to contribute to the outcome of competitive interactions and
54 consequently to the establishment and maintenance of social relationships [36,37].

55

56 *(b) Individual recognition*

57 Individual recognition can be used to identify kin, offspring, mates, competitors, and affiliates. The ability to
58 recognize individuals is especially important when there are repeated interactions between individuals, as
59 discriminating and recognising conspecifics benefits both the signaller and the receiver [38]. However, the
60 cognitive requirements behind individual recognition, including how receivers process individual signatures,
61 are not yet fully understood [39,40]. Furthermore, 'true' individual recognition, where individually distinctive
62 cues are learned and associated with a specific individual, is not always easy to distinguish from 'class-level'
63 recognition, where individual's cues are matched with information about different groups, *e.g.* kin or non-kin
64 [38]. Intriguingly, the cognitive requirements behind the ability to classify individuals may have influenced
65 how the ability to form concepts has evolved [41]. Animals also engage in multi-sensory individual
66 recognition, which is highly interesting from a cognitive perspective, as it requires learning identifying cues
67 from multiple modalities and potentially forming cognitive representations of familiar individuals [40]. To
68 date, the majority of the individual recognition research has focused on competitive social interactions. For
69 example, paper wasps individually recognise nest mates, and this leads to a reduction in aggression.
70 Experimental alteration of facial and abdominal markings leads to increased aggression, which returns to
71 'baseline' levels after nest mates learn these new markings [42]. Although recent modelling studies suggest
72 that recognition ability may influence group structure and dynamics, there is currently a lack of empirical
73 evidence demonstrating that individual differences in recognition shape social relationships [43].

74

75 *(c) Learning and memory*

76 General learning mechanisms, such as associative learning, underpin social interactions in a wide array of
77 species [44]. The ability to learn about conspecifics by observing them allows the observers to gather social
78 information while reducing time [45,46], energy, and potential injury [47] from direct social interactions.
79 Furthermore, efficiently storing and retrieving information regarding conspecifics, *i.e.* memory of conspecifics
80 and social interactions, is likely to influence responses during repeated interactions. For example, species with
81 fission-fusion group dynamics form long-term memories for specific individuals [48,49], and can also
82 categorise their memories of conspecifics based on the quality of their prior relationship with them [50].
83
84 The association between social relationships and individual differences in learning and memory has been
85 most extensively examined in correlational studies of social rank and cognitive performance (Table 1; [51–56]).
86 In comparison, relatively few studies on learning ability have focused on aspects of social behaviour besides
87 social rank [57]. Although correlational studies suggest that learning ability may be associated with
88 competitive interactions, the precise nature of these relationships is unclear, as evidence that cognitive
89 differences existed prior to the establishment of dominance is often lacking [58]. For example, the acquisition
90 of dominant status improves spatial learning performance in mice [59], whereas a decrease in rank is
91 associated with a decrease in errors on a reversal learning task in crab-eating macaques, *i.e.* subordinates
92 perform more accurately [60].
93
94 However, current evidence is equivocal, as other studies suggest that individual differences in learning ability
95 are not always closely associated with social rank. For example, in studies of black-capped chickadees (*Poecile*
96 *atricapillus*), social rank was not related to performance in a social learning task [61], while in mountain
97 chickadees (*Poecile gambeli*), spatial learning task performance, but not non-spatial task performance, was
98 related to social rank [62]. Some of the discrepancies between studies may be due to the use of different forms
99 of social rank [26]. For example, competitive rank of starlings, defined as the ability to monopolise food and
100 water, was found to correlate with individual learning performance in three groups, whereas agonistic social
101 rank correlated with learning performance in only one of the three groups [54].

(d) Transitive inference

Through observing interacting conspecifics, individuals can infer relationships between individuals they have not seen interacting directly. This transitive inference (TI) ability has been demonstrated in multiple species (see [63] for detailed references). Inter-specific differences in the speed of learning linear hierarchies is related to social complexity (see [64] for review). TI also allows individuals to infer their own position in a social hierarchy without directly interacting with conspecifics. For example, primates infer dominance relationships between conspecifics based on their vocalisations [65,66]. Simple associative learning models have been proposed to account for this ability, which suggest that TI is based on the comparison between association strengths of the two stimuli being compared [65,67]. Regardless of the specific cognitive abilities involved, to date, there have been no studies of intra-specific differences in TI ability. Thus, we do not yet know how individual variation in transitive inference ability may influence social interactions.

(e) Inhibitory control

Inhibitory control is the ability to inhibit a prepotent response [68]. Inhibition often involves an inter-temporal component, such as choosing between a present reward and a more valuable reward in future. Individual differences in inhibitory control have major consequences for formation and maintenance of social relationships, and influence, in at least two ways, whether animals respond appropriately in social interactions [69]. First, during the formation of social relationships, inhibitory control allows individuals to reject undesirable social partners in order to find a more desirable partner in future [70]. Second, when maintaining relationships, it allows individuals to withhold inappropriate social behaviours, such as behaving aggressively when competing over food with a social partner, or initiating aggressive interactions towards higher-ranking individuals [71].

Inhibitory control is also one of the cognitive prerequisites of cooperation, as it affects the decision to engage in a costly interaction in order to receive a future benefit [72]. Comparative studies in species with differentiated relationships demonstrate pronounced levels of individual variation in self-control, that is, overcoming impulsivity or the ability to delay gratification [73–78]. Whether these individual differences also link to the ability to form and maintain social relationships is unknown. However, a recent study in chimpanzees describes a relationship between inhibitory control and overall intelligence [79], whereas a study in spotted hyenas (*Crocuta crocuta*) found no direct link between inhibitory control and innovative behaviour [80].

(f) Inequity aversion

Many species that frequently engage in cooperative behaviours and form strong affiliative relationships are sensitive to disadvantageous inequity, which happens when individuals receive a less preferred reward compared to an experimental partner [10,81,82]. Because individuals need to be able to recognize each other's investment and payoffs in order to successfully cooperate, inequity aversion is considered another crucial prerequisite of cooperation. In addition, responses to inequity can be affected by social relationships. For example, chimpanzees respond stronger to inequity when tested with individuals they were housed with for a short-term, compared to individuals with which they had already established social relationships [83]. Likewise, carrion crows with stronger inequity aversion are less frequently involved in affiliative behaviours [84].

(g) Individual variation in cognition and vocal communication

In several bird and primate species, vocal exchanges can strengthen the pair-bond [85,86], suggesting an important role for vocal learning in establishing relationships. For example, passerine song may allow

potential mates to signal their cognitive ability [87]. In zebra finches (*Taeniopygia guttata*), song complexity is positively correlated with learning proficiency, and males with more song phrase elements require fewer learning trials to solve a novel foraging task [88]. However, studies of the relationship between song repertoire and cognitive performance in song sparrows provide a more complicated picture. Initial investigations reveal that males with larger song repertoires are faster to solve a detour-reaching task [89] but perform worse in spatial learning tasks [90]. By contrast, recent evidence suggests that song complexity is associated with better performance in colour reversal and spatial learning, but worse performance in novel foraging and detour-reaching tasks [91]. These conflicting findings are perhaps unsurprising, as cognition is not a unitary trait; to date, only a few nonhuman cognitive test batteries have revealed positive correlations between cognitive abilities [92]. Until the link between vocal display and individual differences in cognitive abilities is clarified, the question of how cognitive variation influences bonds established through vocal display remains open.

3. BI-DIRECTIONAL RELATIONSHIPS BETWEEN SOCIALITY AND COGNITION

In the previous section, we addressed whether individual differences in cognitive abilities such as attention, learning, and memory influence social relationships. The majority of the current evidence on this topic comes from correlational studies, which cannot determine whether individual differences in cognition drive social relationships, or whether social relationships drive individual differences in cognition. Distinguishing between these causal relationships is essential for understanding the evolution of sociality and cognition. This is because there are likely to be bi-directional relationships between the two [93], leading to feedback-based dynamics such that individuals' social connections and experiences influence their cognitive abilities and performance in addition to being influenced by them. Below, we discuss the existing evidence for bi-directionality between social relationships and cognitive performance, and examine how social network analysis can be used to test for directional causal relationships.

(a) Social relationships affect cognitive performance

Individual variation in social relationships will determine the overall group structure and composition, which can then affect cognitive variation. Although numerous comparative studies have addressed the role of social environment on cognition [94,95], they have yielded inconsistent and inconclusive empirical evidence [96]. Understanding how individual variation in cognition is affected by individual differences in social experiences and relationships requires a within-species approach [97]. However, as our above discussion highlights, such studies are surprisingly rare, especially in the wild. In particular, experimental manipulations of group composition, size, and social relationships [98], and repeated tests throughout individuals' development [99], can be highly informative for addressing how social environment influences cognition. For example, group size predicts individual variation in cognitive performance in Australian magpies, and this variation emerges during early life [99]. Overall, there is immense potential for intra-specific studies that investigate the role that social relationships and social environment play on individual variation in cognition.

Analysing social relationships as social network connections provides a unique opportunity for robustly addressing the causal links between sociality and cognitive performance, especially under conditions where animals have the opportunity to learn novel information and behaviours from each other. Social network analysis is a powerful framework for quantifying individual variation in social relationships at multiple levels (i.e. individual, dyad, group) to understand the causes and the consequences of social differences [100][101–103]. Variation in social relationships leads to variation in network connections, which then determine individuals' position in the network. Some individuals occupy central network positions, either because they have diverse or frequent connections, or because they connect the otherwise unconnected group members [104,105].

208 Consistent individual variation in social network position through time and across contexts are informative
209 about social personalities or phenotypes [106–108]. Animals may use information about conspecifics'
210 personalities when making social decisions, which can in turn affect their social relationships. For example,
211 chacma baboons (*Papio hamadryas ursinus*) keep track of conspecifics' personality types (*i.e.* nice, aloof, loner)
212 and approach conspecifics with different personalities at different rates [109]. An individual's network
213 position also determines to whom they are indirectly connected [103]. As indirect network connections (*e.g.*
214 friend of a friend) can affect survival and reproductive success [110,111], it is beneficial for animals to know
215 their conspecifics' relationships and to adjust their social responses accordingly.
216
217 Overall, network connections and position have major consequences for learning, health, survival, and
218 reproductive success [110,112–114]. Individuals who occupy central network positions have more
219 opportunities than non-central individuals for learning from others and tend to acquire novel information
220 faster [115–118]. Thus, social connections can directly influence individual differences in learning
221 performance, by affecting who learns novel information from whom and when they learn it [115–123]. The
222 links between individual differences in network connections (including indirect connections) and learning
223 performance, when animals have opportunities to learn from each other, can be quantified through network-
224 based diffusion analysis (NBDA), which infers social transmission of a behaviour if its spread follows social
225 network connections [124,125].
226
227
228 *(b) Learning and knowledge influence social relationships*
229
230 Besides cognitive ability, multiple factors including age, sex, personality, and social status can lead to
231 individual differences in learning [28,54,126,127], for example, by influencing individuals' motivation and
232 persistence, or by affecting the opportunities that they have for learning. Consequently, some individuals end
233 up acquiring new information faster or more accurately than others, resulting in variation in knowledge
234 among conspecifics. Such variation in knowledge, regardless of whether it arises due to differences in learning
235 ability or due to other factors that lead to variation in information acquisition, can have important
236 consequences for social relationships, especially if it affects individuals' success in key behaviours ranging
237 from foraging to predator avoidance.
238
239 For instance, individuals who are knowledgeable about novel food resources and who use this information
240 while foraging are likely to become successful foragers. Being socially connected to successful foragers offers
241 multiple benefits including scrounging and food sharing [128–130]. For example, rhesus monkeys (*Macaca
242 mulatta*) and vervet monkeys (*Chlorocebus aethiops*) frequently groom conspecifics who provide food to the
243 group by solving a foraging task [128,131]. One of the social learning strategies used by animals is to copy the
244 successful individuals [132,133]. Because animals preferentially observe and learn from the individuals with
245 whom they share affiliative relationships [134–136], they may end up initiating frequent affiliative interactions
246 towards knowledgeable and successful conspecifics.
247
248 Addressing whether individuals' social relationships change after they learn and use novel information
249 provides a promising approach for determining the consequences of learning and success on social
250 relationships. By integrating social network analysis with a learning experiment, a recent study on free-
251 ranging ring-tailed lemurs has demonstrated that lemurs who successfully learn how to solve a novel foraging
252 task, and solve it frequently while being observed, receive more affiliative interactions after the experiment
253 than they did before, and thus achieve higher social centrality after the experiment [93]. The task in this study
254 was designed to minimize scrounging and food sharing, so that only the solvers obtained the food reward.
255 Consequently, there was a direct correlation between learning how to solve the task and retrieving the food
256 reward successfully. As such, individuals who repeatedly solved the task may have been perceived as
257 successful foragers by others. Ring-tailed lemurs use multiple affiliative relationships to form and reinforce
258 differentiated social bonds [107,137]. These affiliative relationships influence social learning; lemurs with high
259 centrality in the affiliation networks were more likely than others to learn the solution after observing a
260 conspecific [93].

Studies such as the above provide evidence of feedback-based bi-directional links between social relationships and learning [93]. Such links mean that on one hand, individual differences in social relationships influence cognitive performance when social learning is favoured, while on the other hand, individual differences in knowledge and success can have long-lasting effects on social relationships. Future studies utilizing a similar approach are now needed to confirm the presence of bi-directional relationships in other species with different social systems and social structures.

4. CONCLUSION

Our review illustrates the necessity to investigate individual variation in cognitive performance to understand how cognition shapes patterns of social relationships and vice versa. Studies on intra-specific variation in cognition and sociality are essential for determining whether forming and maintaining social relationships has shaped the evolution of cognition, as hypothesized by the 'relationship intelligence hypothesis'. Our understanding of the relationships between sociality and cognition will benefit from an increased focus on intra-specific studies, for which network analysis provides a promising tool with which the causal bi-directional relationships between cognition and social relationships can be quantified.

Additional Information

Table 1. Empirical studies investigating cognitive abilities relating to different social contexts and whether studies are conducted with a species, considering individual variation in cognition.

Species	Cognitive Ability	Social Context	Individual Variation	Reference
Golden-crowned sparrows (*Zonotrichia atricapilla*)	perception and attention	dominance rank	yes	Chaine et al. (2013)
Paper wasps (*Polistes fuscatus*)	individual recognition	reduction in aggression	no	Tibbetts (2002)
Bottlenose dolphins (*Tursiops truncates*)	learning and memory	memory of group members	no	Bruck (2013)
Bonobos (*Pan paniscus)*	learning and memory	memory of group members	no	Keenan et al. (2016)
Common ravens (*Corvus corax*)	learning and memory	memory of social relationships	no	Boeckle et al. (2012)
Dogs (*Canis familiaris*)	learning and memory	dominance rank	yes	Molnár et al. (2009)
Eastern water skinks (*Eulamprus quoyii*)	learning and memory	dominance rank	yes	Kar et al. (2017)
Arabian babblers (*Turdoides squamiceps*)	learning and memory	dominance rank	yes	Keynan et al. (2016)
European starlings (*Sturnus vulgaris*)	learning and memory	dominance rank	yes	Boogert et al. (2006)
Domestic hens (*Gallus gallus domesticus*)	learning and memory	dominance rank	yes	Nicol & Pope (1999)
Pheasants (*Phasianus colchicus*)	learning and memory	dominance rank	yes	Langley et al. (2018)
Mice (*Mus musculus*)	learning and memory	dominance rank	yes	Barnard & Luo (2002)
Crab-eating macaques (*Macaca fascicularis*)	learning and memory	dominance rank	yes	Bunnell et al. (1980)
Goats (*Capra hircus*)	learning and memory	sociability	yes	Nawroth et al. (2017)
Song sparrows (*Melospiza melodia*)	learning and memory	song complexity	yes	Sewall et al. (2013); Anderson et al. (2017)

Ring-tailed lemurs (*Lemur catta*)	learning and memory	engagement in affiliative behaviour	yes	Kulahci et al. (2018)
Baboons (*Papio cynocephalus ursinus*)	transitive inference	recognition of social relationships	no	Cheney & Seyfarth (1999)
Chimpanzees (*Pan troglodytes*)	transitive inference	recognition of social relationships	no	Slocombe et al. (2010)
Chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus)*, orang-utans (*Pongo pygmaeus*), and spider monkeys (*Cebus apella*)	inhibitory control	fission –fusion dynamics	no	Amici et al. (2008)
Chimpanzees (*Pan troglodytes*)	inequity aversion	quality of social relationships	yes	Brosnan et al. (2005)
Carrion crows (*Corvus corone corone*)	inequity aversion	engagement in affiliative behaviour	yes	Wascher (2015)
Australian magpies (*Cracticus tibicen dorsalis*)	general cognitive performance	group size	yes	Ashton et al. (2018)

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