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.

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 [1,4,5]. 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 [6,7]. Presently, the majority of the empirical evidence demonstrating links between cognition and social relationships comes from studies that compare closely related species [8–11]. 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 [12]. This suggestion is supported by the positive relationship between pair-bonding and relative brain size in birds and non-primate mammalian taxa [13,14]. 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.* [12,15–18]) and with unrelated individuals (*e.g.* [19–21]). Socially bonded individuals support each other in agonistic encounters [22,23], cooperate to acquire rank positions [24], cooperate in infant care, provide protection for young [25], and share resources [26]. Besides affiliative relationships, animals also form dominance relationships that help to reduce the costs associated with aggression [27], 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 [28]. As individual variation in behaviour is the medium via which selection acts on cognition [29], 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 [30]. Thus, to optimize information-gaining processes, individuals must be selective in whom they attend [31]. 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 [32,33] for review) and displays [34] 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 [35] and the exact cognitive abilities involved in assessment of conspecifics have not been fully identified [36], individual variation in attention and perception abilities are likely to contribute to the outcome of competitive interactions and consequently to the establishment and maintenance of social relationships [37,38].

*(b) Individual recognition*

Individual recognition can be used to identify kin, offspring, mates, competitors, and affiliates. The ability to recognize individuals is especially important when there are repeated interactions between individuals, as discriminating and recognising conspecifics benefits both the signaller and the receiver [39]. However, the cognitive requirements behind individual recognition, including how receivers process individual signatures, are not yet fully understood [40,41]. Furthermore, ‘true’ individual recognition, where individually distinctive cues are learned and associated with a specific individual, is not always easy to distinguish from ‘class-level’ recognition, where individual’s cues are matched with information about different groups, *e.g.* kin or non-kin [39]. Intriguingly, the cognitive requirements behind the ability to classify individuals may have influenced how the ability to form concepts has evolved [42]. Animals also engage in multi-sensory individual recognition, which is highly interesting from a cognitive perspective, as it requires learning identifying cues from multiple modalities and potentially forming cognitive representations of familiar individuals [41]. To date, the majority of the individual recognition research has focused on competitive social interactions. For example, paper wasps individually recognise nest mates, and this leads to a reduction in aggression. Experimental alteration of facial and abdominal markings leads to increased aggression, which returns to ‘baseline’ levels after nest mates learn these new markings [43]. Although recent modelling studies suggest that recognition ability may influence group structure and dynamics, there is currently a lack of empirical evidence demonstrating that individual differences in recognition shape social relationships [44].

*(c) Learning and memory*

General learning mechanisms, such as associative learning, underpin social interactions in a wide array of species [45]. The ability to learn about conspecifics by observing them allows the observers to gather social information while reducing time [46,47], energy, and potential injury [48] from direct social interactions. Furthermore, efficiently storing and retrieving information regarding conspecifics, *i.e.* memory of conspecifics and social interactions, is likely to influence responses during repeated interactions. For example, species with fission-fusion group dynamics form long-term memories for specific individuals [49,50], and can also categorise their memories of conspecifics based on the quality of their prior relationship with them [51].

The association between social relationships and individual differences in learning and memory has been most extensively examined in correlational studies of social rank and cognitive performance (Table 1; [52–57]). In comparison, relatively few studies on learning ability have focused on aspects of social behaviour besides social rank [58]. Although correlational studies suggest that learning ability may be associated with competitive interactions, the precise nature of these relationships is unclear, as evidence that cognitive differences existed prior to the establishment of dominance is often lacking [59]. For example, the acquisition of dominant status improves spatial learning performance in mice [60], whereas a decrease in rank is associated with a decrease in errors on a reversal learning task in crab-eating macaques, *i.e.* subordinates perform more accurately [61].

However, current evidence is equivocal, as other studies suggest that individual differences in learning ability are not always closely associated with social rank. For example, in studies of black-capped chickadees (*Poecile atricapillus*), social rank was not related to performance in a social learning task [62], while in mountain chickadees (*Poecile gambeli*), spatial learning task performance, but not non-spatial task performance, was related to social rank [63]. Some of the discrepancies between studies may be due to the use of different forms of social rank [27]. For example, competitive rank of starlings, defined as the ability to monopolise food and water, was found to correlate with individual learning performance in three groups, whereas agonistic social rank correlated with learning performance in only one of the three groups [55].

*(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 [64] for detailed references). Inter-specific differences in the speed of learning linear hierarchies is related to social complexity (see [65] 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 [66,67]. 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 [66,68]. 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 [69]. 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 [70]. 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 [71]. 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 [72].

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 [73]. 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 [74–79]. 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 [80], whereas a study in spotted hyenas (*Crocuta crocuta*) found no direct link between inhibitory control and innovative behaviour [81].

*(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 [11,82,83]. 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 [84]. Likewise, carrion crows with stronger inequity aversion are less frequently involved in affiliative behaviours [85].

*(g) Individual variation in cognition and vocal communication*

In several bird and primate species, vocal exchanges can strengthen the pair-bond [86,87], suggesting an important role for vocal learning in establishing relationships. For example, passerine song may allow potential mates to signal their cognitive ability [88]. 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 [89]. 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 [90] but perform worse in spatial learning tasks [91]. 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 [92]. 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 [93]. 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 [94], 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 [95,96], they have yielded inconsistent and inconclusive empirical evidence [97]. Understanding how individual variation in cognition is affected by individual differences in social experiences and relationships requires a within-species approach. 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].

Consistent individual variation in social network position through time and across contexts are informative about social personalities or phenotypes [106–108]. Animals may use information about conspecifics’ personalities when making social decisions, which can in turn affect their social relationships. For example, chacma baboons (*Papio hamadryas ursinus*) keep track of conspecifics’ personality types (*i.e.* nice, aloof, loner) and approach conspecifics with different personalities at different rates [109]. An individual’s network position also determines to whom they are indirectly connected [103]. As indirect network connections (*e.g.* friend of a friend) can affect survival and reproductive success [110,111], it is beneficial for animals to know their conspecifics’ relationships and to adjust their social responses accordingly.

Overall, network connections and position have major consequences for learning, health, survival, and reproductive success [112–114,110]. Individuals who occupy central network positions have more opportunities than non-central individuals for learning from others and tend to acquire novel information faster [115–118]. Thus, social connections can directly influence individual differences in learning performance, by affecting who learns novel information from whom and when they learn it [115–123]. The links between individual differences in network connections (including indirect connections) and learning performance, when animals have opportunities to learn from each other, can be quantified through network-based diffusion analysis (NBDA), which infers social transmission of a behaviour if its spread follows social network connections [124,125].

*(b) Learning and knowledge influence social relationships*

Besides cognitive ability, multiple factors including age, sex, personality, and social status can lead to individual differences in learning [29,55][126], for example, by influencing individuals’ motivation and persistence, or by affecting the opportunities that they have for learning. Consequently, some individuals end up acquiring new information faster or more accurately than others, resulting in variation in knowledge among conspecifics. Such variation in knowledge, regardless of whether it arises due to differences in learning ability or due to other factors that lead to variation in information acquisition, can have important consequences for social relationships, especially if it affects individuals’ success in key behaviours ranging from foraging to predator avoidance.

For instance, individuals who are knowledgeable about novel food resources and who use this information while foraging are likely to become successful foragers. Being socially connected to successful foragers offers multiple benefits including scrounging and food sharing [127–129]. For example, rhesus monkeys (*Macaca mulatta*) and vervet monkeys (*Chlorocebus aethiops*) frequently groom conspecifics who provide food to the group by solving a foraging task [127,130]. One of the social learning strategies used by animals is to copy the successful individuals [131,132]. Because animals preferentially observe and learn from the individuals with whom they share affiliative relationships [133–135], they may end up initiating frequent affiliative interactions towards knowledgeable and successful conspecifics.

Addressing whether individuals’ social relationships change after they learn and use novel information provides a promising approach for determining the consequences of learning and success on social relationships. By integrating social network analysis with a learning experiment, a recent study on free-ranging ring-tailed lemurs has demonstrated that lemurs who successfully learn how to solve a novel foraging task, and solve it frequently while being observed, receive more affiliative interactions after the experiment than they did before, and thus achieve higher social centrality after the experiment [94]. The task in this study was designed to minimize scrounging and food sharing, so that only the solvers obtained the food reward. Consequently, there was a direct correlation between learning how to solve the task and retrieving the food reward successfully. As such, individuals who repeatedly solved the task may have been perceived as successful foragers by others. Ring-tailed lemurs use multiple affiliative relationships to form and reinforce differentiated social bonds [107,136]. These affiliative relationships influence social learning; lemurs with high centrality in the affiliation networks were more likely than others to learn the solution after observing a conspecific [94].

Studies such as the above provide evidence of feedback-based bi-directional links between social relationships and learning [94]. 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

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**Authors' Contributions**  
All authors contributed to drafting and revising the manuscript, and gave approval for the final version to be published.

**Competing Interests**

The authors declare no competing interests.

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**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) |

References

1. Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010 Strong and consistent social bonds enhance the longevity of female baboons. *Curr. Biol.* **20**, 1359–61. (doi:10.1016/j.cub.2010.05.067)

2. Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2009 The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc. Biol. Sci.* **276**, 3099–104. (doi:10.1098/rspb.2009.0681)

3. Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H. & Hammerschmidt, K. 2017 Quantifying social complexity. *Anim. Behav.* **130**, 57–66. (doi:10.1016/j.anbehav.2017.06.003)

4. Schülke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. 2010 Social bonds enhance reproductive success in male macaques. *Curr. Biol.* **20**, 2207–2210. (doi:10.1016/j.cub.2010.10.058)

5. Young, C., Majolo, B., Heistermann, M., Schülke, O. & Ostner, J. 2014 Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proc. Natl. Acad. Sci.* **111**, 18195–18200. (doi:10.1073/pnas.1411450111)

6. Humphrey, N. K. 1976 The social function of intellect. In *Growing Points in Ethology* (eds P. Bateson & R. A. Hinde), pp. 303–321. Cambridge: Cambridge University Press.

7. Cheney, D. L., Seyfarth, R. M. & Smuts, B. 1986 Social relationships and social cognition in nonhuman primates. *Science (80-. ).* **234**, 1361–1366. (doi:10.1111/acer.12325.Chronic)

8. Amici, F., Aureli, F. & Call, J. 2008 Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Curr. Biol.* **18**, 1415–1419. (doi:10.1016/j.cub.2008.08.020)

9. Bond, A. B., Wei, C. a & Kamil, A. C. 2010 Cognitive representation in transitive inference: a comparison of four corvid species. *Behav. Processes* **85**, 283–292. (doi:10.1016/j.beproc.2010.08.003)

10. Paz-Y-Miño C, G., Bond, A. B., Kamil, A. C. & Balda, R. P. 2004 Pinyon jays use transitive inference to predict social dominance. *Nature* **430**, 778–781. (doi:10.1038/nature02723)

11. Brosnan, S. F. 2013 Justice- and fairness-related behaviors in nonhuman primates. *Proc. Natl. Acad. Sci.* **110**, 10416–10423. (doi:10.1073/pnas.1301194110)

12. Emery, N. J., Seed, A. M., von Bayern, A. M. P. & Clayton, N. S. 2007 Cognitive adaptations of social bonding in birds. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **362**, 489–505. (doi:10.1098/rstb.2006.1991)

13. Shultz, S. & Dunbar, R. I. M. 2010 Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biol. J. Linn. Soc.* **100**, 111–123. (doi:10.1111/j.1095-8312.2010.01427.x)

14. Shultz, S. & Dunbar, R. I. . 2007 The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proc. R. Soc. B Biol. Sci.* **274**, 2429–2436. (doi:10.1098/rspb.2007.0693)

15. Silk, J. B., Rendall, D., Cheney, D. L. & Seyfarth, R. M. 2003 Natal attraction in adult female baboons (Papio cynocephalus ursinus) in the moremi reserve, Botswana. *Ethology* **109**, 627–644. (doi:10.1046/j.1439-0310.2003.00907.x)

16. Silk, J. B., Altmann, J. & Alberts, S. C. 2006 Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. *Behav. Ecol. Sociobiol.* **61**, 183–195. (doi:10.1007/s00265-006-0249-2)

17. Silk, J. B., Alberts, S. C. & Altmann, J. 2006 Social relationships among adult female baboons (Papio cynocephalus) II. Variation in the quality and stability of social bonds. *Behav. Ecol. Sociobiol.* **61**, 197–204. (doi:10.1007/s00265-006-0250-9)

18. Mitani, J. C. 2009 Male chimpanzees form enduring and equitable social bonds. *Anim. Behav.* **77**, 633–640. (doi:10.1016/j.anbehav.2008.11.021)

19. Cameron, E. Z., Setsaas, T. H. & Linklater, W. L. 2009 Social bonds between unrelated females increase reproductive success in feral horses. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 13850–3. (doi:10.1073/pnas.0900639106)

20. Langergraber, K., Mitani, J. & Vigilant, L. 2009 Kinship and social bonds in female chimpanzees (Pan troglodytes). *Am. J. Primatol.* **71**, 840–851. (doi:10.1002/ajp.20711)

21. Kerth, G., Perony, N. & Schweitzer, F. 2011 Bats are able to maintain long-term social relationships despite the high fission-fusion dynamics of their groups. *Proc. R. Soc. B Biol. Sci.* **278**, 2761–2767. (doi:10.1098/rspb.2010.2718)

22. Logan, C. J., Ostojić, L. & Clayton, N. S. 2013 Rook, but not jackdaw, post-conflict third-party affiliation reduces aggression for aggressors. *Ethology* **119**, 427–435. (doi:10.1111/eth.12078)

23. Berghänel, A., Ostner, J., Schröder, U. & Schülke, O. 2011 Social bonds predict future cooperation in male Barbary macaques, Macaca sylvanus. *Anim. Behav.* **81**, 1109–1116. (doi:10.1016/j.anbehav.2011.02.009)

24. Matheson, M. D. & Bernstein, I. S. 2000 Grooming, social bonding, and agonistic aiding in rhesus monkeys. *Am. J. Primatol.* **51**, 177–186. (doi:10.1002/1098-2345(200007)51:3<177::AID-AJP2>3.0.CO;2-K)

25. Hohmann, G., Gerloff, U., Tautz, D. & Fruth, B. 1999 Social bonds and genetic ties: Kinship, association and affiliation in a community of bonobos (Pan paniscus). *Behaviour* **136**, 1219–1235. (doi:10.1163/156853999501739)

26. King, A. J., Clark, F. E. & Cowlishaw, G. 2011 The dining etiquette of desert baboons: the roles of social bonds, kinship, and dominance in co-feeding networks. *Am. J. Primatol.* **73**, 768–774. (doi:10.1002/ajp.20918)

27. Drews, C. 1993 The concept and definition of dominance in animal behaviour. *Behaviour* **125**, 283–313. (doi:10.1163/156853993X00290)

28. Taborsky, B. & Oliveira, R. F. 2012 Social competence: An evolutionary approach. *Trends Ecol. Evol.* **27**, 679–688. (doi:10.1016/j.tree.2012.09.003)

29. Shettleworth, S. J. 2010 *Cognition, Evolution and Behavior*. Oxford: Oxford University Press.

30. Cheney, D. L. & Seyfarth, R. M. 1988 Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Anim. Behav.* **36**, 477–486. (doi:https://doi.org/10.1016/S0003-3472(88)80018-6)

31. Blumstein, D. T., Verneyre, L. & Daniel, J. C. 2004 Reliability and the adaptive utility of discrimination among alarm callers. *Proc. R. Soc. B Biol. Sci.* **271**, 1851–7. (doi:10.1098/rspb.2004.2808)

32. Arnott, G. & Elwood, R. W. 2009 Assessment of fighting ability in animal contests. *Anim. Behav.* **77**, 991–1004. (doi:10.1016/j.anbehav.2009.02.010)

33. Reichert, M. S. & Quinn, J. L. 2017 Cognition in contests: mechanisms, ecology, and evolution. *Trends Ecol. Evol.* **32**, 773–785. (doi:10.1016/j.tree.2017.07.003)

34. Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979 The logical stag: adaptive aspects of fighting in red deer (Cervus elaphus). *Anim. Behav.* **27**. (doi:https://doi.org/10.1016/0003-3472(79)90141-6)

35. Elwood, R. W. & Arnott, G. 2012 Understanding how animals fight with Lloyd Morgan’s canon. *Anim. Behav.* **84**, 1095–1102. (doi:10.1016/j.anbehav.2012.08.035)

36. Fawcett, T. W. & Mowles, S. L. 2013 Assessments of fighting ability need not be cognitively complex. *Anim. Behav.* **86**, e1–e7. (doi:https://doi.org/10.1016/j.anbehav.2013.05.033)

37. Seyfarth, R. M. & Cheney, D. L. 2013 Affiliation, empathy, and the origins of theory of mind. *Proc. Natl. Acad. Sci.* **110**, 10349–10356. (doi:10.1073/pnas.1301223110)

38. Chaine, A. S., Roth, A. M., Shizuka, D. & Lyon, B. E. 2013 Experimental confirmation that avian plumage traits function as multiple status signals in winter contests. *Anim. Behav.* **86**, 409–415. (doi:10.1016/j.anbehav.2013.05.034)

39. Tibbetts, E. A. & Dale, J. 2007 Individual recognition: it is good to be different. *Trends Ecol. Evol.* **22**, 529–537. (doi:10.1016/j.tree.2007.09.001)

40. Yorzinski, J. L. 2017 The cognitive basis of individual recognition. *Curr. Opin. Behav. Sci.* **16**, 53–57. (doi:10.1016/j.cobeha.2017.03.009)

41. Proops, L., McComb, K. & Reby, D. 2009 Cross-modal individual recognition in domestic horses (Equus caballus). *Proc. Natl. Acad. Sci.* **106**, 947–951. (doi:10.1073/pnas.0809127105)

42. Seyfarth, R. M. & Cheney, D. L. 2015 The evolution of concepts about agents: Or, what do animals recognize when they recognize an individual? In *The Conceptual Mind: New Directions in the Study of Concepts.* (eds E. Margolis & S. Laurence), pp. 57–76. Cambridge: MIT Press.

43. Tibbetts, E. A. 2002 Visual signals of individual identity in the wasp Polistes fuscatus. *Proc. R. Soc. B Biol. Sci.* **269**, 1423–1428. (doi:10.1098/rspb.2002.2031)

44. Rios, V. P. & Kraenkel, R. A. 2017 Do I know you? How individual recognition affects group formation and structure. *PLoS One* **12**, 1–13. (doi:10.1371/journal.pone.0170737)

45. Leadbeater, E. & Dawson, E. H. 2017 A social insect perspective on the evolution of social learning mechanisms. *Proc. Natl. Acad. Sci.* **114**, 7838–7845. (doi:10.1073/pnas.1620744114)

46. Giraldeau, L.-A. 1997 The ecology of information use. In *Behavioral Ecology. An Evolutionary Approach*, pp. 42–68. Oxford: Blackwell Science.

47. Galef, B. G. & Giraldeau, L. A. 2001 Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Anim. Behav.* **61**, 3–15. (doi:10.1006/anbe.2000.1557)

48. Johnstone, R. A. 2001 Eavesdropping and animal conflict. *Proc. Natl. Acad. Sci.* **98**, 9177–9180. (doi:10.1073/pnas.161058798)

49. Bruck, J. N. 2013 Decades-long social memory in bottlenose dolphins. *Proc. R. Soc. B Biol. Sci.* **280**.

50. Keenan, S., Mathevon, N., Stevens, J. M., Guéry, J. P., Zuberbühler, K. & Levréro, F. 2016 Enduring voice recognition in bonobos. *Sci. Rep.* **6**, 22046. (doi:10.1038/srep22046)

51. Boeckle, M. & Bugnyar, T. 2012 Long-term memory for affiliates in ravens. *Curr. Biol.* **22**, 801–806. (doi:10.1016/j.cub.2012.03.023)

52. Molnár, C., Pongrácz, P., Faragó, T., Dóka, A. & Miklósi, Á. 2009 Dogs discriminate between barks: The effect of context and identity of the caller. *Behav. Processes* **82**, 198–201. (doi:10.1016/j.beproc.2009.06.011)

53. Kar, F., Whiting, M. J. & Noble, D. W. A. 2017 Dominance and social information use in a lizard. *Anim. Cogn.* **20**, 1–8. (doi:http://doi.org/10.1007/s10071-017-1101-y)

54. Keynan, O., Ridley, A. R. & Lotem, A. 2016 Task-dependent differences in learning by subordinate and dominant wild Arabian babblers. *Ethology* **122**, 399–410. (doi:10.1111/eth.12488)

55. Boogert, N. J., Reader, S. M. & Laland, K. N. 2006 The relation between social rank, neophobia and individual learning in starlings. *Anim. Behav.* **72**, 1229–1239. (doi:10.1016/j.anbehav.2006.02.021)

56. Nicol, C. J. & Pope, S. J. 1999 The effects of demonstrator social status and prior foraging success on social learning in laying hens. *Anim. Behav.* **57**, 163–171. (doi:10.1006/anbe.1998.0920)

57. Langley, E. J. G., van Horik, J. O., Whiteside, M. A. & Madden, J. R. 2018 Group social rank is associated with performance on a spatial learning task. *R. Soc. Open Sci.* **5**, 171475. (doi:DOI: 10.1098/rsos.171475)

58. Nawroth, C., Prentice, P. M. & McElligott, A. G. 2017 Individual personality differences in goats predict their performance in visual learning and non-associative cognitive tasks. *Behav. Processes* **134**, 43–53. (doi:10.1016/j.beproc.2016.08.001)

59. Chichinadze, K., Chichinadze, N., Gachechiladze, L., Lazarashvili, A. & Nikolaishvili, M. 2014 Physical predictors, behavioural/emotional attributes and neurochemical determinants of dominant behaviour. *Biol. Rev.* **89**, 1005–1020.

60. Barnard, C. J. & Luo, N. 2002 Acquisition of dominance status affects maze learning in mice. *Behav. Processes* **60**, 53–59. (doi:10.1016/S0376-6357(02)00121-3)

61. Bunnell, B. N., Gore, W. T. & Perkins, M. N. 1980 Performance correlates of social behavior and organization: Social rank and reversal learning in crab-eating macaques (M. fascicularis). *Primates* **21**, 376–388. (doi:10.1007/BF02390467)

62. Seok An, Y., Kriengwatana, B., Newman, A. E., MacDougall-Shackleton, E. A. & MacDougall-Shackleton, S. A. 2011 Social rank, neophobia and observational learning in black-capped chickadees. *Behaviour* **148**, 55–69. (doi:10.1163/000579510X545829)

63. Pravosudov, V. V., Mendoza, S. P. & Clayton, N. S. 2003 The relationship between dominance, corticosterone, memory, and food caching in mountain chickadees (Poecile gambeli). *Horm. Behav.* **44**, 93–102. (doi:10.1016/S0018-506X(03)00119-3)

64. Mikolasch, S., Kotrschal, K. & Schloegl, C. 2013 Transitive inference in jackdaws (Corvus monedula). *Behav. Processes* **92**, 113–117. (doi:10.1016/j.beproc.2012.10.017)

65. Vasconcelos, M. 2008 Transitive inference in non-human animals: An empirical and theoretical analysis. *Behav. Processes* **78**, 313–334. (doi:http://doi.org/10.1016/j.beproc.2008.02.017)

66. Cheney, D. L. & Seyfarth, R. M. 1999 Recognition of other individuals’ social relationships by female baboons. *Anim. Behav.* **58**, 67–75. (doi:10.1006/anbe.1999.1131)

67. Slocombe, K. E., Kaller, T., Call, J. & Zuberbühler, K. 2010 Chimpanzees extract social information from agonistic screams. *PLoS One* **5**, 3–8. (doi:10.1371/Citation)

68. Wynne, C. D. L. 1995 Reinforcement accounts for transitive inference performance. *Anim. Learn. Behav.* **23**, 207–217. (doi:10.3758/BF03199936)

69. MacLean, E. L. et al. 2014 The evolution of self-control. *Proc. Natl. Acad. Sci.* **111**, E2140–E2148. (doi:10.1073/pnas.1323533111)

70. Amici, F., Call, J., Watzek, J., Brosnan, S. & Aureli, F. 2018 Social inhibition and behavioural flexibility when the context changes: a comparison across six primate species. *Sci. Rep.* **8**, 3067. (doi:10.1038/s41598-018-21496-6)

71. Fawcett, T. W., McNamara, J. M. & Houston, A. I. 2012 When is it adaptive to be patient? A general framework for evaluating delayed rewards. *Behav. Processes* **89**, 128–36. (doi:10.1016/j.beproc.2011.08.015)

72. Strayer, F. F. & Strayer, J. 1976 An ethological analysis of social agonism and dominance relations among preschool children. *Child Dev.* **47**, 980–989. (doi:doi:10.2307/1128434)

73. Stevens, J. R. & Hauser, M. D. 2004 Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn. Sci.* **8**, 60–65. (doi:10.1016/j.tics.2003.12.003)

74. Hillemann, F., Bugnyar, T., Kotrschal, K. & Wascher, C. A. F. 2014 Waiting for better, not for more: corvids respond to quality in two delay maintenance tasks. *Anim. Behav.* **90**, 1–10. (doi:10.1016/j.anbehav.2014.01.007)

75. Auersperg, A. M. I., Laumer, I. B. & Bugnyar, T. 2013 Goffin cockatoos wait for qualitative and quantitative gains but prefer ‘better’ to ‘more’. *Biol. Lett.* **9**, 20121092–20121092. (doi:10.1098/rsbl.2012.1092)

76. Anderson, J. R., Kuroshima, H. & Fujita, K. 2010 Delay of gratification in capuchin monkeys (Cebus apella) and squirrel monkeys (Saimiri sciureus). *J. Comp. Psychol.* **124**, 205–10. (doi:10.1037/a0018240)

77. Beran, M. J. & Evans, T. a 2009 Delay of gratification by chimpanzees (Pan troglodytes) in working and waiting situations. *Behav. Processes* **80**, 177–181. (doi:10.1016/j.beproc.2008.11.008)

78. Bramlett, J. L., Perdue, B. M., Evans, T. a & Beran, M. J. 2012 Capuchin monkeys (Cebus apella) let lesser rewards pass them by to get better rewards. *Anim. Cogn.* **15**, 963–969. (doi:10.1007/s10071-012-0522-x)

79. Leonardi, R. J., Vick, S. J. & Dufour, V. 2012 Waiting for more: The performance of domestic dogs (Canis familiaris) on exchange tasks. *Anim. Cogn.* **15**, 107–120. (doi:10.1007/s10071-011-0437-y)

80. Beran, M. J. & Hopkins, W. D. 2018 Self-control in chimpanzees relates to general intelligence. *Curr. Biol.* **0**, 1–6. (doi:10.1016/j.cub.2017.12.043)

81. Johnson-Ulrich, L., Johnson-Ulrich, Z. & Holekamp, K. 2018 Proactive behavior, but not inhibitory control, predicts repeated innovation by spotted hyenas tested with a multi-access box. *Anim. Cogn.* (doi:10.1007/s10071-018-1174-2)

82. Range, F., Horn, L., Viranyi, Z. & Huber, L. 2009 The absence of reward induces inequity aversion in dogs. *Proc. Natl. Acad. Sci.* **106**, 340–345. (doi:10.1073/pnas.0810957105)

83. Wascher, C. A. F. & Bugnyar, T. 2013 Behavioral responses to inequity in reward distribution and working effort in crows and ravens. *PLoS One* **8**, e56885. doi:10.1371/journal.pone.0056885.

84. Brosnan, S. F., Schiff, H. C. & Waal, F. B. M. De 2005 Tolerance for inequity may increase with social closeness in chimpanzees. *Proc. R. Soc. B Biol. Sci.* **272**, 253–258. (doi:10.1098/rspb.2004.2947)

85. Wascher, C. A. F. 2015 Individual performance in socio-cognitive tasks predicts social behaviour in carrion crows. *Behaviour* **152**, 615–634. (doi:10.1163/1568539X-00003245)

86. Geissmann, T. 1999 Duet songs of the siamang, Hylobates syndactylus: Ii. Testing the pair-bonding hypothesis during a partner exchange. *Behaviour* **136**, 1005–1039. (doi:10.1163/156853999501694)

87. Baldassarre, D. T. et al. 2016 The couple that sings together stays together: duetting, aggression and extrapair paternity in a promiscuous bird species. *Biol. Lett.* **12**, 1–4. (doi:10.1098/rsbl.2015.1025)

88. Boogert, N. J., Fawcett, T. W. & Lefebvre, L. 2011 Mate choice for cognitive traits: A review of the evidence in nonhuman vertebrates. *Behav. Ecol.* **22**, 447–459. (doi:10.1093/beheco/arq173)

89. Boogert, N. J., Giraldeau, L.-A. & Lefebvre, L. 2008 Song complexity correlates with learning ability in zebra finch males. *Anim. Behav.* **76**, 1735–1741. (doi:10.1016/j.anbehav.2008.08.009)

90. Boogert, N. J., Anderson, R. C., Peters, S., Searcy, W. a. & Nowicki, S. 2011 Song repertoire size in male song sparrows correlates with detour reaching, but not with other cognitive measures. *Anim. Behav.* **81**, 1209–1216. (doi:10.1016/j.anbehav.2011.03.004)

91. Sewall, K. B., Soha, J. A., Peters, S. & Nowicki, S. 2013 Potential trade-off between vocal ornamentation and spatial ability in a songbird. *Biol. Lett.* **9**, 20130344. (doi:DOI: 10.1098/rsbl.2013.0344)

92. Anderson, R. C., Searcy, W. A., Peters, S., Hughes, M., DuBois, A. L. & Nowicki, S. 2017 Song learning and cognitive ability are not consistently related in a songbird. *Anim. Cogn.* **20**, 309–320. (doi:10.1007/s10071-016-1053-7)

93. Shaw, R. C. & Schmelz, M. 2017 Cognitive test batteries in animal cognition research: evaluating the past, present and future of comparative psychometrics. *Anim. Cogn.* **20**, 1003–1018. (doi:10.1007/s10071-017-1135-1)

94. Kulahci, I. G., Ghazanfar, A. A. & Rubenstein, D. I. 2018. Knowledgeable lemurs become more central in social networks. *Curr. Biol.* **28**, 1306-1310 (doi: <https://doi.org/10.1016/j.cub.2018.02.079>).

95. Jolly, A. 1966 Lemur social behavior and primate intelligence. *Science (80-. ).* **153**, 501–506. (doi:DOI: 10.1126/science.153.3735.501)

96. Byrne, R. W. & Whiten, A. 1988 *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkey, Apes and Humans*. Oxford, UK: Clarendon Press.

97. Holekamp, K. E. 2007 Questioning the social intelligence hypothesis. *Trends Cogn. Sci.* **11**, 65–9. (doi:10.1016/j.tics.2006.11.003)

98. White, D. J., Gersick, A. S. & Snyder-Mackler, N. 2012 Social networks and the development of social skills in cowbirds. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 1892–1900. (doi:10.1098/rstb.2011.0223)

99. Ashton, B. J., Ridley, A. R., Edwards, E. K. & Thornton, A. 2018 Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature* (doi:10.1038/nature25503)

100. Pinter-Wollman, N. et al. 2014 The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behav. Ecol.* **25**, 242–255. (doi:10.1093/beheco/art047)

101. Krause, J., James, R., Franks, D. W. & Croft, D. P. 2014 *Animal Social Networks*. Oxford, UK: Oxford University Press.

102. Wey, T., Blumstein, D. T., Shen, W. & Jordán, F. 2008 Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* **75**, 333–344. (doi:10.1016/j.anbehav.2007.06.020)

103. Croft, D. P., James, R. & Krause, J. 2008 *Exploring Animal Social Networks*. Princeton, New Jersey: Princeton University Press.

104. Wassermann, S. & Faust, K. 1994 *Social Networks Analysis*. Cambridge, UK: Cambridge University Press.

105. Lusseau, D. & Newman, M. E. J. 2004 Identifying the role that animals play in their social networks. *Proc. R. Soc. B Biol. Sci.* **271**, S477–S481. (doi:10.1098/rsbl.2004.0225)

106. Aplin, L. M. et al. 2015 Consistent individual differences in the social phenotypes of wild great tits, Parus major. *Anim. Behav.* **108**, 117–127. (doi:10.1016/j.anbehav.2015.07.016)

107. Kulahci, I. G., Ghazanfar, A. A. & Rubenstein, D. I. 2018 Consistent individual variation across interaction networks indicates social personalities in lemurs. *Anim. Behav.* **136**, 217–226. (doi:10.1016/j.anbehav.2017.11.012)

108. Wilson, A. D. M., Krause, S., Dingemanse, N. J. & Krause, J. 2013 Network position: a key component in the characterization of social personality types. *Behav. Ecol. Sociobiol.* **67**, 163–173. (doi:10.1007/s00265-012-1428-y)

109. Seyfarth, R. M., Silk, J. B. & Cheney, D. L. 2012 Variation in personality and fitness in wild female baboons. *Proc. Natl. Acad. Sci.* **109**, 16980–16985. (doi:10.1073/pnas.1210780109/-/DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1210780109)

110. Cheney, D. L., Silk, J. B. & Seyfarth, R. M. 2016 Network connections, dyadic bonds and fitness in wild female baboons. *R. Soc. Open Sci.* **3**, 160255. (doi:10.1098/rsos.160255)

111. Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J. & Pusey, A. E. 2013 Fitness benefits of coalitionary aggression in male chimpanzees. *Behav. Ecol. Sociobiol.* **67**, 373–381. (doi:10.1007/s00265-012-1457-6)

112. Duboscq, J., Romano, V., Sueur, C. & Macintosh, A. J. J. 2016 Network centrality and seasonality interact to predict lice load in a social primate. *Sci. Rep.* **6**, 1–13. (doi:10.1038/srep22095)

113. Godfrey, S. S., Bull, C. M., James, R. & Murray, K. 2009 Network structure and parasite transmission in a group living lizard, the gidgee skink, Egernia stokesii. *Behav. Ecol. Sociobiol.* **63**, 1045–1056. (doi:doi: 10.1007/s00265-009-0730-9)

114. Stanton, M. A. & Mann, J. 2012 Early social networks predict survival in wild bottlenose dolphins. *PLoS One* **7**, 1–6. (doi:10.1371/journal.pone.0047508)

115. Aplin, L. M., Farine, D. R., Morand-Ferron, J. & Sheldon, B. C. 2012 Social networks predict patch discovery in a wild population of songbirds. *Proc. R. Soc. B Biol. Sci.* **279**, 4199–4205. (doi:10.1098/rspb.2012.1591)

116. Schakner, Z. A., Petelle, M. B., Tennis, M. J., Van der Leeuw, B. K., Stansell, R. T. & Blumstein, D. T. 2017 Social associations between California sea lions influence the use of a novel foraging ground. *R. Soc. Open Sci.* **4**, 160820. (doi:10.1098/rsos.160820)

117. Claidière, N., Messer, E. J. E., Hoppitt, W. & Whiten, A. 2013 Diffusion dynamics of socially learned foraging techniques in squirrel monkeys. *Curr. Biol.* **23**, 1251–1255. (doi:10.1016/j.cub.2013.05.036)

118. Kulahci, I. G., Rubenstein, D. I., Hoppitt, W., Mikus, N. & Schwab, C. 2016 Social networks predict selective observation and information spread in ravens. *R. Soc. Open Sci.* **3**, 160256. (doi:10.1098/rsos.160256)

119. Atton, N., Hoppitt, W., Webster, M. M., Galef, B. G. & Laland, K. N. 2012 Information flow through threespine stickleback networks without social transmission. *Proc. R. Soc. B Biol. Sci.* **279**, 4272–4278. (doi:10.1098/rspb.2012.1462)

120. Jones, T. B., Aplin, L. M., Devost, I. & Morand-Ferron, J. 2017 Individual and ecological determinants of social information transmission in the wild. *Anim. Behav.* **129**, 93–101. (doi:10.1016/j.anbehav.2017.05.011)

121. Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A. & Sheldon, B. C. 2015 Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541. (doi:10.1038/nature13998)

122. Allen, J., Weinrich, M., Hoppitt, W. & Rendell, L. 2013 Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science (80-. ).* **340**, 485–488. (doi:DOI: 10.1126/science.1231976)

123. Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W. & Gruber, T. 2014 Social Network Analysis Shows Direct Evidence for Social Transmission of Tool Use in Wild Chimpanzees. *PLoS Biol.* **12**. (doi:10.1371/journal.pbio.1001960)

124. Franz, M. & Nunn, C. L. 2009 Network-based diffusion analysis: a new method for detecting social learning. *Proc. R. Soc. B Biol. Sci.* **276**, 1829–1836. (doi:10.1098/rspb.2008.1824)

125. Hoppitt, W., Boogert, N. J. & Laland, K. N. 2010 Detecting social transmission in networks. *J. Theor. Biol.* **263**, 544–555. (doi:10.1016/j.jtbi.2010.01.004)

126. Morand-Ferron, J., Cole, E. F. & Quinn, J. L. 2016 Studying the evolutionary ecology of cognition in the wild: A review of practical and conceptual challenges. *Biol. Rev.* **91**, 367–389. (doi:10.1111/brv.12174)

127. Stammbach, E. 1988 Group responses to specially skilled individuals in a Macaca fascicularis. *Behaviour* **107**, 241–266. (doi:DOI: 10.1163/156853988X00368)

128. Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999 Market forces predict grooming reciprocity in female baboons. *Proc. R. Soc. B Biol. Sci.* **266**, 665–670.

129. Fruteau, C., Voelkl, B., van Damme, E. & Noë, R. 2009 Supply and demand determine the market value of food providers in wild vervet monkeys. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 12007–12012. (doi:10.1073/pnas.0812280106)

130. Borgeaud, C. & Bshary, R. 2015 Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts. *Curr. Biol.* **25**, 3011–3016. (doi:10.1016/j.cub.2015.10.016)

131. Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M. & Laland, K. N. 2011 Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends Cogn. Sci.* **15**, 68–76. (doi:10.1016/j.tics.2010.12.002)

132. Hoppitt, W. & Laland, K. N. 2013 *Social learning: an introduction to mechanisms, methods, and models*. Princeton, New Jersey: Princeton University Press.

133. Heyes, C. M. 1993 Imitation, culture and cognition. *Anim. Behav.* **46**, 999–1010. (doi:https://doi.org/10.1006/anbe.1993.1281)

134. Heyes, B. Y. C. M. & Street, G. 1994 Social learning in animals: categories and mechanisms. *Biol. Rev.* **69**, 207–231. (doi:DOI: 10.1111/j.1469-185X.1994.tb01506.x)

135. Dindo, M., Thierry, B. & Whiten, A. 2008 Social diffusion of novel foraging methods in brown capuchin monkeys (Cebus apella). *Proc. R. Soc. B Biol. Sci.* **275**, 187–193. (doi:10.1098/rspb.2007.1318)

136. Kulahci, I. G., Rubenstein, D. I. & Ghazanfar, A. A. 2015 Lemurs groom-at-a-distance through vocal networks. *Anim. Behav.* **110**, 179–186. (doi:10.1016/j.anbehav.2015.09.016)