

Sociability as a personality trait in animals: methods, causes and consequences

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ABSTRACT

Within animal populations there is variation among individuals in their tendency to be social, where more sociable individuals associate more with other individuals. Consistent inter-individual variation in ‘sociability’ is considered one of the major axes of personality variation in animals along with aggressiveness, activity, exploration and boldness. Not only is variation in sociability important in terms of animal personalities, but it holds particular significance for, and can be informed by, two other topics of major interest: social networks and collective behaviour. Further, knowledge of what generates inter-individual variation in social behaviour also holds applied implications, such as understanding disorders of social behaviour in humans. In turn, research using non-human animals in the genetics, neuroscience and physiology of these disorders can inform our understanding of sociability. For the first time, this review brings together insights across these areas of research, across animal taxa from primates to invertebrates, and across studies from both the laboratory and field. We show there are mixed results in whether and how sociability correlates with other major behavioural traits. Whether and in what direction these correlations are observed may differ with individual traits such as sex and body condition, as well as ecological conditions. A large body of evidence provides the proximate mechanisms for why individuals vary in their social tendency. Evidence exists for the importance of genes and their expression, chemical messengers, social interactions and the environment in determining an individual’s social tendency, although the specifics vary with species and other variables such as age, and interactions amongst these proximate factors. Less well understood is how evolution can maintain consistent variation in social tendencies within populations. Shifts in the benefits and costs of social tendencies over time, as well as the social niche hypothesis, are currently the best supported theories for how variation in sociability can evolve and be maintained in populations. Increased exposure to infectious diseases is the best documented cost of a greater social tendency, and benefits include greater access to socially transmitted information. We also highlight that direct evidence for more sociable individuals being safer from predators is lacking. Variation in sociability is likely to have broad ecological consequences, but beyond its importance in the spread of infectious diseases, direct evidence is limited to a few examples related to dispersal and invasive species biology. Overall, our knowledge of inter-individual variation in sociability is highly skewed towards the proximate mechanisms. Our review also demonstrates, however, that considering research from social networks and collective behaviour greatly enriches our understanding of sociability, highlighting the need for greater integration of these approaches into future animal personality research to address the imbalance in our understanding of sociability as a personality trait.

Key words: behavioural syndromes, behavioural types, collective behaviour, division of labour, personality variation, repeatability, social networks, social structure, sociality, temperament

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I. INTRODUCTION

Individuals within animal populations often vary consistently in their behaviour over time or contexts, even after considering differences in sex, age, size and other factors known to affect behaviour (Réale *et al.*, 2007). This variation in ‘personality’ or ‘temperament’ has become of major interest in the field of animal behaviour, with studies exploring what the mechanistic drivers are of this variation (Stamps & Groothuis, 2010; Jeanson & Weidenmüller, 2014), how this variation is evolutionarily stable (Stamps, 2007; Bergmüller & Taborsky, 2010), and the wider evolutionary and ecological consequences of this variation (Sih, Bell & Johnson, 2004; Dall *et al.*, 2012). In humans, the Five-Factor Model describes the axes of variation in personality traits; researchers have suggested that parallel terminology could be applied to animals (Gosling & John, 1999), namely aggressiveness, activity, exploration, boldness and sociability (Réale *et al.*, 2007). Probably reflecting the importance of social interactions in our own species, two of the five traits in the human Five-Factor Model (extraversion and agreeableness) relate to social behaviour (the others being conscientiousness, neuroticism and openness; McCrae & John, 1992). And while it is still an open question as to whether we should expect non-human animals to have similar axes of personality variation as humans, the fact remains that sociability is clearly a fundamental personality trait in an extensive array of species.

Here, we define sociability as an individual’s tendency or propensity to associate with other individuals, where the association is not driven by reproduction or aggression (thus excluding associations between mates and agonistic interactions). Although this working definition is frequently used and is expected to apply broadly across different species and habitats, it does not differentiate between the reasons why an individual would associate with another, which may be (for example) to reduce predation risk, remove ectoparasites, increase foraging success, or to save energy (Krause & Ruxton, 2002). Nevertheless, as a personality trait, sociability is expected to be stable over time relative to variation between individuals (Réale *et al.*, 2007). Importantly, an individual’s sociability should affect their behaviour across multiple contexts, where more sociable individuals are more

attracted to others and observed more frequently with others, in larger groups and/or at closer distances. Consistent individual variation in sociability has been documented in a wide variety of non-human species including unicellular organisms such as the slime mould *Physarum polycephalum* (Vogel *et al.*, 2015), gregarious insects (Planas-Sitjà *et al.*, 2015), animals with fluid social systems, i.e. those with high fission–fusion (Aplin *et al.*, 2015; Bevan *et al.*, 2018), and mammals with stable social groups (Brent *et al.*, 2013; Blaszczyk, 2017).

Although it is proposed as one of the fundamental personality traits and observed in a wide range of species, sociability has not been researched as extensively within the field of animal behaviour as traits such as boldness or aggressiveness (Smith & Blumstein, 2008; Moiron, Laskowski & Niemelä, 2020), as highlighted by the limited examples of sociability in the seminal review by Réale *et al.* (2007). However, whether individuals differ in their social tendency is also a key question in the study of social networks (Sih, Hanser & McHugh, 2009; Krause *et al.*, 2015) and collective behaviour (Nagy *et al.*, 2013; MacGregor, Herbert-Read & Ioannou, 2020), which have similarly risen to be major themes in animal behaviour research in the past two decades alongside animal personality. In particular, animal social network research has advanced rapidly due to the increased availability of individual tracking systems and computational power and techniques for analysing large-scale network data (Krause *et al.*, 2015). This line of research relies on considering individuals’ social behaviour in terms of their connections within their social networks (i.e. their social network positions) and often considers these differences as social phenotypes. A deeper understanding of sociability can thus be informed by integrating research across these areas.

Here we present a wide-reaching synthesis of the current understanding of sociability as a personality trait. With recent advances in animal personality, social network and collective behaviour research, there is increasing overlap and convergence in questions relating to how individual social tendency is measured, how it relates to other traits, its mechanistic causes, and how variation among individuals is maintained over evolutionary time and with what consequences. Research in the genetics and neuroendocrinology of social behaviour can further inform the proximate mechanisms for consistent inter-individual variation in social

tendency. The time is thus ripe for a comprehensive evaluation of the state of the field to determine what we know and where future research should focus on. By bringing together knowledge from across multiple areas of research, our intention is to encourage cross-fertilisation of concepts and approaches, driving new research forward. As well as those working on animal personality variation, researchers working in social networks and collective behaviour have much to gain from such an integrated approach through understanding the proximate and ultimate causes of why individuals vary in their social network position or behaviour during collective movement and decision making.

We take a narrative approach in our review for a number of reasons. By drawing on a diverse body of literature that extends beyond animal personality research, there is the risk that differences in terminology across disciplines would bias the quantitative results from a systematic- or meta-analysis, leading to spurious conclusions seemingly based on rigorous data (Westgate & Lindenmayer, 2017). In addition to studies we were aware of, and those that they cite and are cited by, we did conduct extensive searches on *Web of Science* to ensure coverage of the literature, using search terms such as ‘sociability AND oxytocin’. From the search results, we selected studies for inclusion in the review as illustrative examples of trends to include, and with the aim where possible of covering a wide range of taxonomic groups using a wide range of methodological approaches. Finally, the multiple aspects of sociability that we cover would require multiple systematic- or meta-analyses; these approaches are typically used instead to target a small number of related hypotheses based on a set of studies that are relatively straightforward to identify for inclusion (see, for example, Smith & Blumstein, 2008; Bell, Hankison & Laskowski, 2009; Royauté *et al.*, 2018; Moiron *et al.*, 2020).

II. MEASURING INDIVIDUAL SOCIAL TENDENCIES

There are wide-ranging methods that have been used to quantify individual variation in sociability. Within the field of animal personality, the typical approach to measuring any personality trait is to test focal individuals without allowing free interactions with other individuals as these social interactions can affect the expression of personality variation (Bevan *et al.*, 2018; Planas-Sitjà & Deneubourg, 2018; although see Szopa-Comley *et al.*, 2020). The simulations used by Ioannou *et al.* (2019) illustrate why: individuals that had social attraction to others would often follow non-social individuals, giving the appearance that these non-social individuals were more sociable than they really were. This can make measuring traits such as sociability or aggression problematic as, by definition, they require a behavioural response towards another individual. As a result, a diverse range of assays have been devised to quantify sociability, which vary in their ecological validity, standardisation and control.

Most common in studies explicitly interested in individual variation in sociability is to use a single or multiple conspecific(s) as a stimulus constrained (for example behind a transparent barrier) to one location in an arena in which a focal test individual can move. The proportion of time spent within a threshold distance of the social stimulus, or the average distance from it, can be used as a measure of social tendency. Further control and standardisation over the stimulus can be achieved by using non-live social stimuli such as mirrors (Cattelan *et al.*, 2017), video playbacks (Snijders, Naguib & van Oers, 2016), conspecific models (Halloy *et al.*, 2007) or conspecific olfactory cues (Skinner & Miller, 2020). However, these methods often reduce social cues to a single sensory modality, and care is required to provide the adequate cues needed for the test individual to respond socially to the stimulus. Even with knowledge from the literature regarding what cues are likely to be important in social interactions for that species, the extent of careful design and testing needed often justifies these studies being published in their own right (Landgraf *et al.*, 2016; Cattelan *et al.*, 2017; Jägers *et al.*, 2021).

Studies of social networks and collective behaviour take a different approach to quantifying individual social tendencies, and can allow assessment under more natural conditions. A population or group of freely interacting individuals, either in the wild or in the laboratory, can be monitored to quantify different aspects of their individual social behaviour. Investigating individual differences in collective behaviour usually involves measuring fine-scale behaviours related to social interactions, such as how close an individual is to its nearest neighbour, the tendency to follow others, and the alignment of orientation with near neighbour(s) (Nagy *et al.*, 2010; Jolles *et al.*, 2017; Torquet *et al.*, 2018; Dhellemmes *et al.*, 2020). As with studies using a social stimulus, by repeatedly observing or testing the same individual with the same or other group-mates over multiple days researchers can quantify individual variation in sociability.

Repeated observations of a population over time can be used to build social networks based on some measure of social interaction, for example grooming (Brent *et al.*, 2013), the distance between the individuals (Jeanson, 2012) or being in the same group (Firth & Sheldon, 2016). From these individual-by-individual matrices of dyadic scores, metrics for sociability known as ‘social network positions’ for each individual can then be calculated. These individual-level measures can be calculated as simple metrics quantifying individuals’ own direct interactions, for example their ‘degree’ (the number of unique individuals they are connected to). More complex metrics can also be calculated, quantifying individuals’ indirect interactions (‘friends-of-friends’) and wider position within the network such as their ‘betweenness’ (the number of shortest paths between individuals that pass through the focal individual). The consistency of individuals’ social network positions over time has been used to provide evidence of within-population variation in sociability in rhesus macaques *Macaca mulatta* (Brent *et al.*, 2013), female eastern grey kangaroos *Macropus giganteus* (Best, Blomberg & Goldizen, 2015),

great tits *Parus major* (Firth *et al.*, 2017), catsharks *Scyliorhinus canicula* (Jacoby *et al.*, 2014), vervet monkeys *Chlorocebus pygerythrus* (Błaszczuk, 2017), yellow-bellied marmots *Marmota flaviventris* (Blumstein, Petelle & Wey, 2013), forked fungus beetles *Bolitotherus cornutus* (Formica *et al.*, 2017) and guppies *Poecilia reticulata* (Krause *et al.*, 2017).

In general, when using any of these approaches to measure sociability there is a trade-off between standardisation and ecological realism. Any laboratory study, whether conducted with focal individuals or freely interacting groups, will be subject to some level of confounding effects caused by the artificial environment. Testing a focal individual with stimulus conspecifics can measure how attracted they are, or how willing or tolerant they are to being in close proximity, to others. Such studies provide the highest level of control and standardisation in terms of the social environment the focal individual will experience. However, these types of methods may not allow individuals to express their full range of complex social behaviours. By contrast, measuring social behaviour in freely interacting individuals allows the social tendency of multiple individuals to be measured simultaneously, and allows individuals to interact using their full range of sensory modalities. These may be important considerations for species that become stressed or otherwise show atypical behaviour when removed from their group and/or environment. Measuring social behaviour in freely interacting individuals will also often have the advantage of data collection on specific social behaviours, such as grooming (Błaszczuk, 2017), and the consideration of context (Nagy *et al.*, 2013), which can help infer the functional reason why an individual would be associating with another. For example, many species of birds huddle while roosting to minimise heat loss in cold conditions (Gilbert *et al.*, 2010); inter-individual differences in the tendency to huddle will reflect variation in energetic needs rather than minimising predation risk or gaining information during foraging.

Data collection from freely interacting groups can be more difficult and require long periods of observation (Blumstein *et al.*, 2018) or technology such as video tracking (Jolles *et al.*, 2017; MacGregor *et al.*, 2020) or tagging individuals (Nagy *et al.*, 2013; Firth *et al.*, 2018), and can be limited in how much control experimenters have over the experiences of the animals. Within freely associating groups, an individual may appear highly sociable because it is attractive to (or tolerated by) others, rather than having a high social tendency itself (Ioannou *et al.*, 2019). This can be resolved by using more nuanced measures of social tendency than simply the proximity between individuals, for example based on the tendency to follow changes in direction made by others (Nagy *et al.*, 2013); these measures tend to be more species and context specific than proximity, however. The study by Jolles *et al.* (2017) does however confirm that, at least in three-spined sticklebacks (*Gasterosteus aculeatus*), the sociability of focal individuals tested with a stimulus group of conspecifics does predict nearest-neighbour distance in shoals of freely interacting individuals, suggesting consistency between the two approaches.

Although there is a wide range of methodologies available to quantify sociability from across animal personality, social network and collective behaviour research, much more research is needed to have a better understanding of what these methods are measuring. For example, some approaches may be capturing a general measure of an individual's sociability that applies across contexts, while others may be context specific. Additionally, more artificial and controlled methods may be dependent on the sensory modalities available for focal individuals to interact with social stimuli. A better understanding of the methods used has the potential for better informed comparisons across studies. Currently, it is unknown to what extent contrasting results between studies can be accounted for by how sociability is measured, and this is likely to hinder further research in this field.

III. RELATIONSHIP TO OTHER PERSONALITY TRAITS

The correlation between different behaviours among individuals is referred to as a behavioural syndrome (Sih *et al.*, 2004). Such correlations between behaviours can arise due to some constraint on behaviour, for example, if they are mechanistically controlled by the same genes or hormonal pathways. Alternatively, or in addition, syndromes could be a result of correlational selection (Sih *et al.*, 2004; Lacasse & Aubin-Horth, 2014). Understanding how common such syndromes are, in terms of which behaviours are correlated and whether these correlations change across populations, can thus give insight into the processes generating these relationships. Across the literature, there is evidence that sociability can be associated with the other major axes of personality variation in animals: aggressiveness, activity, exploration and boldness. We now review the evidence for whether and how tightly correlated sociability is to these other behavioural traits.

Highly aggressive individuals are expected to be less sociable in terms of tolerating the presence of conspecifics and so in freely interacting groups, aggressive individuals may be avoided by others, a result found in groups of water striders *Aquarius remigis* (Sih & Watters, 2005). Aggressiveness was also found to be negatively correlated to sociability in juvenile three-spined sticklebacks (*G. aculeatus*), but only in individuals from one of two populations (Lacasse & Aubin-Horth, 2014). There were, however, no individuals in either population that were both highly aggressive and sociable, suggesting a potential conflict between the expression of high sociability and high aggressiveness at an individual level.

There are also mixed results regarding the correlation between exploration (movement in a novel environment) and sociability, and between activity (movement in a familiar environment) and sociability. Positive correlations between sociability and activity and/or exploration might be expected if this higher activity/exploration leads to greater encounter rates with other individuals. For example, activity was positively correlated

with sociability in yellow-bellied marmots (*M. flaviventris*) (Petelle, Martin & Blumstein, 2015), and exploration positively correlated with sociability in birds (Aplin *et al.*, 2013). Similarly, positive correlations between all three traits (sociability, activity and exploration) were found in the delicate skink (*Lampropholis delicata*) (Michelangeli, Chapple & Wong, 2016). By contrast, Thys *et al.* (2017) found no correlation between exploration and sociability in male starlings (*Sturnus vulgaris*), Michelangeli *et al.* (2020) found an exploration–sociability positive correlation but only in male mosquitofish *Gambusia affinis*, and Rödel *et al.* (2015) found a negative correlation in rabbits (*Oryctolagus cuniculus*). Dhellemmes *et al.* (2020) also found a negative correlation between sociability and exploration in juvenile lemon sharks (*Negaprion brevirostris*) but only in a population that experienced high predation pressure; the syndrome was absent in a population that experienced overall lower predation threat. They suggest that such a negative correlation may represent different strategies whereby individuals can specialise in resource exploitation (high exploration) or safety in numbers (high sociability).

Boldness is the tendency to take risks (Réale *et al.*, 2007). As predation risk is believed to be a major driver for the evolution of group living, and close proximity to others reduces risk *via* a number of mechanisms (Krause & Ruxton, 2002), it would be expected that if bolder individuals have a lower perception of risk, they would also be less sociable. This negative correlation is supported by studies in eastern grey kangaroos *M. giganteus* (Best *et al.*, 2015), sheep *Ovis aries* (Michelena *et al.*, 2010), great tits *P. major* (Snijders *et al.*, 2016) and garter snakes *Thamnophis sirtalis sirtalis* (Skinner & Miller, 2020). In a similar vein, shy guppies (*P. reticulata*) had more network connections which were stronger than those of bold fish (Croft *et al.*, 2009), but other work with the same species found no relationship (Irving & Brown, 2013) and in male guppies, there is instead evidence of a positive correlation between sociability and boldness (Irving & Brown, 2013). Varma *et al.* (2020) also documented a positive correlation between boldness and sociability in the fish Deccan mahseer (*Tor khudree*). Contrasting trends are also seen across studies that used different populations of three-spined sticklebacks (*G. aculeatus*), with some finding the expected negative correlation between boldness and sociability (Ward *et al.*, 2004), but others finding no relationship (Jolles *et al.*, 2017; Bevan *et al.*, 2018). An explanation for these different results is that the relationship between boldness and sociability may be dependent on state, whereby individuals in better body condition might be able to be both bolder and more sociable than individuals in poorer condition (Öst, Seltmann & Jaatinen, 2015).

Across these studies, it is clear that the relationships between sociability and the other major personality traits are not consistent, with differences not only among species but also among populations within species and within populations based on differences such as sex or body condition. As behavioural syndromes are thought to arise as a result of either correlational selection on multiple behaviours or from physiological allocation trade-offs (Lacasse & Aubin-Horth, 2014), differences among species, populations and sexes in correlational selection or trade-offs may explain the differences found in the

literature. There is also evidence that sociability affects the expression of other personality traits, even when these traits are not directly correlated to sociability. In three-spined sticklebacks (*G. aculeatus*), the frequently observed correlation between boldness and leadership was only observed in less-social fish, presumably because more sociable individuals were more sensitive to, and affected by, the behaviour of their companion (Bevan *et al.*, 2018).

It is important to note here that another major consideration is that, in non-human animals, it is still unclear which behaviours are expressions of which personality traits. Other authors (Carter *et al.*, 2013) have already highlighted extensive ‘jingle-jangle’ fallacies (Block, 1995) in animal personality research whereby different researchers either use different behaviours as measures of the same trait (e.g. boldness), or the same behaviour as measures of different traits. Correlations among different behaviours might result from these behaviours being manifestations of the same underlying personality trait, rather than different personality traits being correlated. Similarly, the lack of a relationship between two behaviours putatively expected both to be measures of the same trait, for example, may instead be because these are expressions of different, uncorrelated personality traits. While properly identifying the axes of personality variation in non-human animals is no small task, in doing so we will improve our ability to make predictions about which behavioural correlations are expected or not.

IV. THE PROXIMATE CAUSES: HERITABILITY, GENES AND GENE EXPRESSION, AND CHEMICAL MESSENGERS

There has been considerable effort to understand the proximate mechanisms of variation in social tendencies. Part of this is because changes in sociability are often associated with clinical disorders in humans such as autism, driving research on the genetic, physiological and neurological underpinnings of variation in sociability. This provides insights into what causes variable social tendencies in non-human animals as primates, rats, mice and zebrafish are frequently used as model systems (Buffington *et al.*, 2016; Kondrakiewicz *et al.*, 2019; Brenner *et al.*, 2020). As such, we have a better picture of the mechanisms that determine consistent inter-individual differences in sociability in non-human animals compared to the mechanisms that determine differences in exploration, activity, boldness or aggression. Variation in genes, hormone levels, and social and environmental influences during early and later life have all been shown to be important in generating consistent individual differences in sociability.

There are multiple lines of evidence that variation in personality traits is underpinned by genetic differences (Dochtermann, Schwab & Sih, 2014). Heritability for sociability has been shown for rhesus macaques *M. mulatta* (Brent *et al.*, 2013), red deer *Cervus elaphus* (Albery *et al.*, 2021b),

yellow-bellied marmots *M. flaviventer* (Lea *et al.*, 2010), bonobos *Pan paniscus* (Staes *et al.*, 2016) and mice (Knoll, Jiang & Levitt, 2018). Further, inter-specific sociability may also have a heritable basis, such as in dogs *Canis familiaris* in their interaction with humans (Persson *et al.*, 2015). A study by Dimitriadou, Croft & Darden (2019) demonstrates that consistent differences in sociability (as measured by leadership tendency) can be selectively bred. Importantly, environmental context can shape the expression of genes leading to differences in heritability estimates between environments. For example, populations of sticklebacks that have an evolutionary history with predators show higher heritability of personality traits than predator-naïve populations; however direct exposure to predation early in life can also increase the expression of additive genetic variance even in naïve populations (Dingemanse *et al.*, 2009).

The study of Dingemanse *et al.* (2009) highlights how variation in individual behaviour can be the result of the effects of many genes and interactions between these and the environment. Even so, genes involved in a few specific pathways have been clearly identified as affecting variation in social tendency among individuals (Persson *et al.*, 2016). These are often the genes that encode receptors of the two neuropeptides oxytocin and arginine vasopressin, both of which are closely linked to social behaviour (Carter *et al.*, 2008). Oxytocin receptor genes are important in explaining consistent differences in sociability in dogs (Kis *et al.*, 2014) and mice (Sala *et al.*, 2013), but not in chimpanzees *Pan troglodytes*, where variation in sociability is instead associated with the vasopressin receptor gene (Staes *et al.*, 2015). Sociability has also been shown to be linked to variation in the expression of genes involved in stress hormones such as cortisol, and monoamine neurotransmitters such as serotonin and dopamine (Shou *et al.*, 2019; Abbey-Lee *et al.*, 2019; Bond *et al.*, 2020). In the bee *Lasioglossum albipes*, several candidate genes associated with social variation and linked to neurotransmission were identified (Kocher *et al.*, 2018). In particular, the solitary and social forms of *L. albipes* have different levels of brain expression of syntaxin 1a, a gene involved in synaptic release. Interestingly, changes in the expression of this gene, which is largely conserved across taxa, have been associated with social behaviour in other species, including humans (Nakamura *et al.*, 2008).

Consistent with the link between the expression of these genes and social tendency, levels of circulating chemical messengers, such as hormones, neurotransmitters and neuropeptides, play a key role in explaining variation in sociability. This has been shown through direct correlations between chemical messenger levels and behaviour, and through experimental manipulations of chemical messenger levels. For example, in rats, inhaling vasopressin increases sociability (Ramos *et al.*, 2014) and giving them oxytocin in early adolescence increases social tendencies into adulthood (Bowen *et al.*, 2011). Prairie voles *Microtus ochrogaster* have emerged as a model system for investigating social bonding and this system has demonstrated the key role of oxytocin in promoting mother–offspring bonding and pair formation, and in

influencing mate choice and social recognition; all processes that should be expected to affect an individual's sociability (Carter *et al.*, 2008; Ross & Young, 2009). Hewlett *et al.* (2018) demonstrated a positive effect of dopamine on the time spent interacting with nestmates in the honey bee *Apis mellifera*, but less of an effect of serotonin. In rhesus macaques (*M. mulatta*), indicators of serotonin were positively correlated with sociability (Mehlman *et al.*, 1995). Hormonal differences can influence sensitivity to social signals: variation in serotonin levels in the ant *Pheidole dentata* modulates the responsiveness of workers to trail pheromones laid by scouts to recruit nestmates to food sources (Muscedere *et al.*, 2012). Stress hormones such as cortisol and corticosterone have also been shown to alter social tendencies (Berger *et al.*, 2019); however, other studies have found a lack of a relationship between stress hormones and social tendency (Capitanio, Mendoza & Bentson, 2004). Overall, while various chemical messengers and the expression of genes that regulate them are a major proximate mechanism in determining inter-individual variation in social tendencies, there may be differences among species in the specifics of these mechanisms, or complexity in how these hormones and neurotransmitters have their effects, for example through gene-by-environment interactions. Together, these may explain the contrasting results seen in the literature.

V. THE PROXIMATE CAUSES: EXTERNAL INFLUENCES

The study of parental effects investigates how the experiences of mothers (and fathers) can alter offspring phenotypes. Generally, these effects are expected to act by modulating patterns of gene expression, chemical messenger production and sensitivity, and/or other proximate mechanisms in their offspring to affect behavioural change. These parental effects can occur throughout development from pre-birth until offspring independence.

The impacts of prenatal stress on offspring phenotypes have been particularly well studied. Prenatal stress can alter gene expression leading to long-term impacts on the social behaviour of offspring, helping to explain why individuals consistently vary in their sociability (Jawaid & Mansuy, 2019). Prenatal stress is typically associated with reduced sociability, as demonstrated in rats (Takahashi, Haglin & Kalin, 1992) and rhesus macaques *M. mulatta* (Clarke & Schneider, 1993). Even in egg-laying species, there is evidence that maternal stress can be transmitted to the offspring. Gravid female sticklebacks that were exposed to predator cues produced embryos with altered gene expression compared to eggs of non-stressed mothers (Mommer & Bell, 2014), resulting in offspring that showed tighter shoaling (social) behaviour, presumably as an anti-predator defence.

After birth, experience during and after the period of parental care may also play a role in generating variation among individuals in their social tendency. Separation from the mother during critical stages of development is associated

with reduced sociability in pig-tailed macaques *Macaca nemestrina* (Caine, Earle & Reite, 1983), but in female mice is associated with enhanced social behaviour that corresponds with altered gene expression (Ryabushkina, Reshetnikov & Bondar, 2020). A lack of social interactions directly after weaning in rats had a negative effect on social activity that extended into adulthood, but this effect was not seen with isolation later in life, suggesting that certain periods during development can be critical in determining social tendencies (Hol et al., 1999). These trends are not constrained to mammals with complex social systems; in the mite *Phytoseiulus persimilis* and in the spider *Agelena labyrinthica*, individuals reared in isolation were less sociable than controls (Chiara, Ramon Portugal & Jeanson, 2019). Periods of isolation during adulthood can also alter social tendencies (Munson, Michelangeli & Sih, 2021). Other, non-social, experiences can impact differences in sociability too, including exercise and enrichment (Aujnarain et al., 2018), exposure to pollutants (Farhat et al., 2017) and unpredictable chronic mild stress (van Boxelaere et al., 2017). A recent extensive study by Winandy et al. (2021), using a fully crossed design with common lizards (*Zootoca vivipara*), demonstrated that a focal individual's attraction to conspecifics is dependent on the focal individual's previous experience with predators, their mother's experience with predators during gestation, as well as the stimulus conspecific's previous experience with predators. This highlights the need to consider multiple sources of experience in explaining variation among individuals in sociability.

VI. THE PROXIMATE CAUSES: FEEDBACKS

Although variation in genes and/or environment are generally considered to be the main driving factors generating variation in behaviours such as sociability, there is a growing body of work in clonal or isogenic animals that suggest more complex factors may be at play. These studies show that significant individual variation in behaviour, including social behaviours, still emerges even in genetically identical animals raised under highly standardised, near-identical environmental conditions (Vogt et al., 2008; Freund et al., 2013; Bierbach, Laskowski & Wolf, 2017). This suggests that epigenetic variation, micro-environmental variation (i.e. variation that cannot be controlled under experimental settings) and/or developmental noise may play a larger role in generating variation in individual behaviour than previously thought (Vogt, 2015). Regardless of what first generates variation among individuals, there are likely feedback loops occurring between this variation and internal proximate mechanisms, and in the case of positive feedback loops can drive divergence in behaviour among individuals (Sih et al., 2015; MacGregor, Cottage & Ioannou, 2021). For example, recent research suggests that individuals' microbiota, influenced by the environment, could affect social behaviour in a wide range of taxa (Sherwin et al., 2019).

Higher levels of sociability can then in turn increase transmission of microbiota, creating a feedback loop.

Variation in the social environment at any point in an animal's life may play an especially important role in generating feedback loops, ultimately leading to divergence in consistent individual behaviour. This idea has been formalised as the social niche specialisation hypothesis (Bergmüller & Taborsky, 2010; Montiglio, Ferrari & Reale, 2013), which draws on ecological niche theory and relies on the assumption that individuals, by choosing divergent behavioural strategies that reduce conflict, increase their own fitness. Early evidence for differentiation within groups came from the emergence of stable producer and scrounger roles during group foraging (Barnard & Sibly, 1981; Colin & Desor, 1986; Krafft, Colin & Peignot, 1994). In cooperatively breeding cichlids *Neolamprologus pulcher*, juvenile fish who remain at the nest site to help raise related siblings specialise in their social roles with some individuals showing helping behaviour and others showing submissive behaviour (Fischer et al., 2017). Social interactions, even without conflict, can drive divergence in individual's behaviour, with less social 'leaders' and more social 'followers' emerging from initially homogeneous groups in models (Rands et al., 2003) or random group compositions in laboratory experiments (Ioannou, Ramnarine & Torney, 2017). However, whether the social interactions in these studies had a lasting effect on consistent inter-individual variation in behaviour outside of the group context was not investigated. A study by Torquet et al. (2018) documented the divergence of social tendencies in a large experimental population of mice, which was associated with different neuronal activity in the dopamine system in the mid-brain. This variation occurred despite the fact that there was low genetic diversity among individuals. Modifying the social environment led to a rapid change in both behaviour and the dopamine neuron firing pattern, suggesting that differentiation is highly plastic. Direct experimental evidence for social niche specialisation is thus currently suggestive rather than direct, and in some species, the social environment may not be a primary factor altering personality variation (Laskowski & Bell, 2014; Bierbach et al., 2017; Munson et al., 2021).

Division of labour in animal groups may, however, be a common example of social niche specialisation and reflects the existence of individuals within groups that divide the workload and specialise on different tasks (Beshers & Fewell, 2001; Jeanson & Weidenmüller, 2014). Task specialisation can emerge spontaneously even in forced associations of normally solitary individuals. For instance, one individual specialised in digging and the other in guarding the nest entrance within pairs of the solitary halictine bee, *Lasioglossum (Ctenonomia) NDA-1*. The degree of behavioural specialisation in the artificial pairs was greater than expected due to random variation, suggesting that the division of labour is an emerging phenomenon generated in part by social dynamics (Holbrook et al., 2009). In fact, these pairs of solitary bees showed a higher level of specialisation than those of communal (i.e. social) bees because their lower social tolerance led individuals to be spatially separated and to encounter different tasks (Jeanson, Kukuk & Fewell, 2005). A particular

strength of research in the collective behaviour of social insect colonies is that distinct inter-individual behavioural interactions can be observed and then associated with outcomes. For example, agonistic interactions directed towards part of the worker caste can contribute to the allocation of tasks, as in the ant *Acromyrmex versicolor* where garbage workers receive more aggressive interactions than nestmates not engaged in waste management (Hart & Ratnieks, 2001). Given the wide diversity among species in their social organisation and the extensive literature on what drives division of labour within colonies (Jeanson & Weidenmüller, 2014), social insects have great potential as a model for how consistent individual variation in sociability can arise from social interactions.

VII. THE MAINTENANCE OF VARIATION IN SOCIABILITY AND ITS COSTS AND BENEFITS

Although the previous section reviews the mechanisms by which individuals differ in their social tendency, if and why this variation is maintained by evolutionary selection is a more difficult question to answer and is less well understood (Fisher & McAdam, 2017; Snyder-Mackler *et al.*, 2020). From studies comparing species, populations and individuals that differ in sociability, there is extensive evidence that being social can increase fitness. Here, we discuss the potential adaptive processes that can maintain variation in social tendency within populations, rather than individuals within a population tending toward a single level of sociability that is optimal at a given time and context.

Through considering individuals' sociability as their social centrality, recent social network studies have often found sociability to be positively associated with key life-history traits such as survival, growth and reproduction. Female baboons (*Papio cynocephalus*) with strong social bonds benefit from increased survival, both in terms of their own lifespan and also in terms of their offspring's survival (Silk, Alberts & Altmann, 2003). Similarly, individuals' positions within the social network have been linked to reproductive output for rhesus macaques *M. mulatta* (Brent *et al.*, 2013), long-tailed manakins *Chiroxiphia linearis* (McDonald, 2007), degus *Octodon degus* (Wey *et al.*, 2013) and brown-headed cowbirds *Molothrus ater* (Kohn, 2017). By contrast, high levels of sociability may be limited by stabilising selection where an intermediate degree of sociability is favoured. In prairie voles (*M. ochrogaster*), individuals with an intermediate number of social connections had significantly higher mating and reproductive success, and for males, a higher body mass (Sabol *et al.*, 2020). Finally, some work has actually found negative associations between sociability and fitness, for example in marmots, where strong social relationships within certain demographic groups were related to lower survival (Yang, Maldonado-Chaparro & Blumstein, 2017; Blumstein *et al.*, 2018) and reduced reproductive success (Wey & Blumstein, 2012).

While these studies demonstrate that social tendencies within a population can be favoured by natural selection, they do not explain why variation in sociability among individuals is maintained over time. Individual variation in sociability may be a by-product of variation in the proximate causes discussed above, without this variation necessarily being adaptive. If selection for a single, optimal level of sociability is not strong enough, the cost of minimising this variation in proximate causes is not outweighed by the benefits. However, consistent differences in sociability may be selected for directly. The social niche specialisation hypothesis discussed in Section VI provides one such mechanism for this: individuals gain by adopting different behaviours from others in their group, so that the success of a strategy is negatively frequency dependent (Bergmüller & Taborsky, 2010).

The social niche hypothesis is linked to the concept of state-behaviour feedbacks (Sih *et al.*, 2015). State-behaviour feedbacks acknowledge that while intrinsic state variables, such as physiology, hunger or information, affect an individual's behaviour, the consequences of these behavioural decisions can impact the individual's state, resulting in feedbacks. For example, in the context of explaining variation in sociability, social interactions can affect the metabolism of hormones (e.g. Benítez *et al.*, 2018) such as oxytocin, and in turn, these chemicals can affect the frequency of subsequent social interactions (as discussed in Section IV). Consistent differences in social tendencies among individuals can emerge or be strengthened from positive state-behaviour feedbacks. A simple scenario may be when some individuals within a population experience isolation from social contact, which tends to reduce social tendency (Chiara *et al.*, 2019; although see Munson *et al.*, 2021), and could further increase the time spent alone.

The pace-of-life syndrome (POLS) hypothesis as an explanation for personality variation (Réale *et al.*, 2010; Dammhahn *et al.*, 2018) has been investigated more widely than the social niche hypothesis, likely because it can be applied to non-social, as well as social, animals (Montiglio *et al.*, 2018; Royauté *et al.*, 2018). POLS predicts that individual behavioural variation is maintained in a population as a result of life-history trade-offs: individuals with a slow pace-of-life maximise future reproductive success through minimising risk, whereas individuals with a faster pace-of-life are willing to incur greater risk to increase current reproductive success. With the emphasis on the foraging-predation risk trade-off (Stamps, 2007), this hypothesis has been used to explain inter-individual variation in exploration, activity, boldness and aggression (Royauté *et al.*, 2018). It remains unclear however if POLS could directly explain consistent differences in sociability, i.e. whether individuals with a faster or slower pace-of-life should be expected to be more or less sociable. In a rare example that investigated the link between sociability and reproductive investment, Kim & Velando (2016) showed that more sociable juvenile male three-spined sticklebacks (*G. aculeatus*) had reduced sexual signalling (red colouration) during reproduction as adults, although there was no association between sociability and fecundity in females. Further research as to whether and how individual

variation in sociability could be incorporated within the POLS hypothesis is clearly needed.

The fluctuating environments hypothesis is a simple but potentially ubiquitous explanation for the persistence of personality variation in general, and there is better empirical support for this hypothesis in explaining individual variation in sociability as compared to POLS. Variability in selection pressure across time and/or space means there is no single optimal behavioural phenotype (Boon, Réale & Boutin, 2007). For example, bolder behaviour may be advantageous when resources are scarce and predation risk is low, and shyer behaviour favoured when predation risk is high and resources abundant; in variable environments, a range of risk-taking tendencies can be maintained. Indeed, a recent meta-analysis found that individual behaviour significantly predicted individual survival, but not necessarily in the same direction highlighting that a single behavioural strategy is not always optimal (Moiron *et al.*, 2020). The fluctuating environments hypothesis assumes that individuals cannot optimally adjust their behaviour to match changing selection pressures through time, which is a reasonable assumption given the high cost of being able to accurately estimate and adjust to the optimal behaviour at any given time depending on the prevailing conditions.

Changes in population density can be one such source of selection pressure which could maintain variation in social tendencies. Higher levels of sociability have been found to have both positive and negative fitness effects on growth, reproduction and survival depending on population density. At low density, growth was higher in more sociable individuals in the lizard *Zootoca vivipara* (Le Galliard, Paquet & Mugabo, 2015), and in the lizard *Lacerta vivipara*, more sociable females reproduced better in low-density conditions (Cote, Dreiss & Clobert, 2008). In terms of survival however, asocial *L. vivipara* individuals survived better in low-density populations (Cote *et al.*, 2008). In a similar sense, rare events may also provide variable selection pressures on sociability. Social network positions have been found to be related to survival following catastrophic events in feral horses (*Equus caballus*) (Nuñez, Adelman & Rubenstein, 2015), providing evidence that higher social tendency may be linked to fitness under some scenarios but not others.

Variation in ecological conditions alters selection pressure through shifting the balance between the costs and benefits that directly and causally link sociability to fitness. Understanding these costs and benefits involves dissecting the effect on fitness of how sociability affects key tasks such as finding food or avoiding predation and disease. Living in groups is a common adaptation across taxa and there is extensive evidence that group living helps animals to avoid predation, find food or mates, and gain aero- or hydrodynamic benefits when moving (Krause & Ruxton, 2002; Ioannou, 2021), although there are potential costs (Côté & Poulin, 1995; Bauer *et al.*, 2015; MacGregor *et al.*, 2020). The balance between these trade-offs, dependent on ecological conditions (predation, food availability, disease prevalence, etc.) as well as social factors such as social structure, social organisation and mating

system (Kappeler & van Schaik, 2002), then determines the average social tendency of populations or species.

While some of these benefits and costs have been explicitly linked to the sociability of individuals within populations, such as the risk of disease (Drewe, 2010; see below), others such as the risk of predation are less well supported. A reduced risk of predation is the benefit of group living that has the most widespread support, but there is little evidence demonstrating that more sociable individuals within a population are at lesser risk from predation. In groups of freely interacting fish, less-sociable individuals are more likely to be found on the spatial periphery or at the front of groups (Jolles *et al.*, 2017), and predators disproportionately target prey on the periphery (Duffield & Ioannou, 2017) and in the front (Ioannou *et al.*, 2019), making it likely that more sociable individuals are less likely to be predated upon. However, the only study we are aware of that explicitly tested the survival of individuals with varying sociability scores demonstrated that less-sociable mosquitofish (*G. affinis*) were more, not less, likely to survive encounters with predators than more sociable individuals, even when they were tested in small groups (Brodin *et al.*, 2019). Similarly, studies of social networks in marmots *M. flaviventris* have shown that more sociable individuals live shorter lives, where predation is a likely cause of mortality (Blumstein *et al.*, 2018), as well as higher mortality during hibernation over winter (Yang *et al.*, 2017), but that more sociable young females have an increased likelihood of survival over the summer (Montero *et al.*, 2020). Exposure to predators may be the result of an indirect effect, as it has been shown that less-sociable Iberian wall lizards (*Podarcis hispanica*) are less likely to use refuges with cues of conspecifics, reducing their overall refuge use and exposing them more frequently to predators (Rodríguez-Prieto, Martín & Fernández-Juricic, 2010).

Access to food has been shown to vary depending on individuals' sociability. Less-sociable individual sticklebacks (*G. aculeatus*), which tended to swim faster and be at the front of groups, were more likely to discover foraging patches (Jolles *et al.*, 2017). By contrast, more sociable guppies (*P. reticulata*) reached and acquired more food resources than less-social ones (Snijders *et al.*, 2018). An intuitive explanation for this result is that more sociable individuals use more information from others ('social' or 'public' information) rather than private information that they gain directly from their non-social environment. Webster & Laland (2015) however found no evidence that sociability was related to public information use in ninespine sticklebacks (*Pungitius pungitius*). Less-direct evidence comes from a study of three-spined sticklebacks (*G. aculeatus*): sticklebacks that were more aligned in the direction of travel with their neighbours, a measure of sociability within moving animal groups, were more reliant on social information (MacGregor *et al.*, 2020).

A long-recognised cost of being social is the increased risk of encountering a socially transmitted infectious disease or parasite. Studies analysing disease transmission through social networks confirm that high sociability can increase transmission by increasing the frequency of interactions with other individuals, but that the specific dynamics of

transmission may differ among diseases and ecological settings (Silk & Fefferman, 2021; Albery *et al.*, 2021a). Indeed, such studies have demonstrated that the transmission of contagious diseases appears to be related to network architecture (Kappeler, Cremer & Nunn, 2015; Silk *et al.*, 2019). For instance, the density of social interactions within nests of the bumble bee *Bombus impatiens* largely influences the spread of the pathogen *Crithidia bombi* (Otterstatter & Thomson, 2007). In giraffe (*Giraffe camelopardalis*) societies, *Escherichia coli* transmission has been shown to correlate strongly with the social network (VanderWaal *et al.*, 2014). It may thus be expected that individuals with high social centrality, in the centre of the network, may suffer costs of increased risk of transmission, which is supported by studies of Gidgee skinks (*Egernia stokesii*) infected by ticks and blood parasites (Godfrey *et al.*, 2009) and brushtail possums (*Trichosurus vulpecula*) infected with *Mycobacterium bovis* (Corner, Pfeiffer & Morris, 2003). Collective strategies can however be deployed to reduce contamination within groups and provide ‘social immunity’. For example, colonies of the ant *Lasius niger* infected with the fungus *Metarhizium brunneum* show significant changes in the structure of their social interaction networks by reducing connectivity between workers and thus attenuating disease transmission (Stroeymeyt *et al.*, 2018).

Although social networks have the potential to transmit harmful elements (i.e. disease), beneficial socially transmitted elements also exist. Beneficial microbes can be socially transmitted between hosts (Sarkar *et al.*, 2020); in red-bellied lemurs *Eulemur rubriventer*, the transmission of potentially beneficial gut microbiota increased with higher levels of sociability, with the potential to enhance immunity (Raulo *et al.*, 2018; although see Probeste *et al.*, 2019). Access to social information is a well-supported benefit of social interactions, and can explain why more sociable individuals can be more successful foragers (Snijders *et al.*, 2018). Social network experiments have shown that social connections between individuals causally predict the pathways of how information diffuses within natural populations, such as in great tits *P. major* (Aplin *et al.*, 2012, 2015; Firth, Sheldon & Farine, 2016).

VIII. WIDER ECOLOGICAL CONSEQUENCES

Consistent individual variation in behaviour can have widespread ecological impacts (Sih *et al.*, 2004). A mix of individuals with different behavioural tendencies that vary in their response to changing ecological conditions can make population sizes more stable due to a greater diversity of responses, such as the different responses to population density in lizards depending on their sociability (Cote *et al.*, 2008). Similarly, animals' positions within their social networks have a wide variety of consequences for wildlife management and conservation (as reviewed recently by Snijders *et al.*, 2017), including how natural populations respond to loss/harvesting/poaching of individuals (Firth *et al.*, 2017; Arlinghaus *et al.*, 2017), responses to anthropogenically driven

disturbances to social systems (Ansmann *et al.*, 2012) or outcomes of relocation/reintroduction programs (Franks *et al.*, 2020). Individuals having consistent social network positions also suggests that over timescales longer than the initial spread of diseases, more sociable individuals will be more likely to be exposed repeatedly. Transmission would be expected to slow if individuals acquire immunity (Nunn *et al.*, 2006), and be faster if earlier infections compromise immune responses in defence against later infections by the same or different pathogens (Kotob *et al.*, 2016).

As sociability determines an individual's tolerance of being in proximity to others, it can affect an individual's tendency to disperse, with dispersal being a fundamentally important ecological process. Population density and sociability in the common lizard (*L. vivipara*) interact to determine dispersal of individuals, with more sociable individuals dispersing from low-density populations (Cote & Clobert, 2007). In mosquitofish (*G. affinis*), less-sociable individuals disperse further than more sociable ones (Cote *et al.*, 2010). After dispersing, sociability also affects individuals' success during settlement into the new population. In female bank voles (*Myodes glareolus*), more sociable immigrant individuals were more likely to survive in low-density populations, but less likely to breed than less-sociable ones (Rémy *et al.*, 2014).

As a consequence of inter-individual variation in social tendencies on dispersal, sociability may be important in invasive species biology. Invading a new habitat involves dispersing and spreading, initial establishment, and eventual growth to a large enough population size that can cause negative effects on ecological communities (Sol & Weis, 2019). Fogarty, Cote & Sih (2011) modelled the spread of invasive species taking into account personality variation. Initially the founder populations at the invasion front will be biased towards asocial individuals, but as these reproduce and/or are joined by more individuals dispersing from the source population, density will increase, facilitating the further dispersal of asocial individuals and establishing populations of more sociable ones. Thus, a source population with a mix of both social and asocial individuals would be the most successful invaders (Fogarty *et al.*, 2011). Consistent with this modelling, populations of the invasive round goby (*Neogobius melanostomus*) in recently invaded areas have been shown to be less social than resident populations (Thorlacius & Brodin, 2018).

IX. CONCLUSIONS

- (1) The literature from animal personalities, social networks and collective behaviour highlights the importance of, and growing interest in, sociability as a major axis of personality variation in animals. While this research spans taxa and species from those with simple fission–fusion social behaviour where associations between individuals are anonymous to those with highly organised and stable group memberships,

consistent inter-individual variation in social tendencies is widespread.

- (2) Our review demonstrates that some aspects of sociability have attracted substantial research effort, but even in these areas, while it is clear that sociability can be associated with other personality traits and that the proximate drivers of sociability vary from genetic differences to differences in experience, the specifics often vary among studies. In comparison to other major personality traits such as boldness (Smith & Blumstein, 2008; Moiron *et al.*, 2020), the evolutionary explanations and ecological consequences of individual variation in sociability are understudied. A major goal of future research could be to develop a robust theoretical–conceptual framework for how and why we expect variation in individual sociability to change according to species' ecologies, for example, their social structure, mating systems or foraging tactics (Kappeler & van Schaik, 2002; Aplin *et al.*, 2013; Yuen *et al.*, 2015). There is likely to be a strong, but currently unresearched, link between consistent differences in sociability and social systems. In populations where some individuals form strong and stable relationships, at least these individuals will have a consistently high social tendency to maintain these relationships. We may expect wider inter-individual differences in social tendency in species with stable group compositions where social niches and other feedbacks can develop, such as those common in social insects, primates and some species of fish and birds (Kappeler & van Schaik, 2002; Fischer *et al.*, 2017). Species that show variation in social systems within populations, such as the striped mouse (*Rhabdomys pumilio*), have great potential as models for the interaction between sociability and social systems (Yuen *et al.*, 2015).
- (3) Differences among studies may also be related to the many methodological differences in how sociability is measured. Across research in animal personality variation, social networks and collective behaviour, there is a wide range of approaches to quantifying sociability. There is unlikely to be a single 'best' method to measure sociability given the diversity in how animals interact socially, and given the breadth of biological and ecological questions related to this topic. For example, the sensory modalities used to interact will vary widely among species (Cattelan *et al.*, 2017; Winandy *et al.*, 2021). Additionally, the range of metrics that can be used to define an individual's social network position (Krause *et al.*, 2015), which depend on the identities of who individuals interact with, suggests that the typical approach in personality variation (and collective behaviour) research of simply measuring the proximity to other individuals regardless of their identity may be too unrefined and loses some of the nuances of social behaviour.
- (4) Even when using the same methodology, some studies show that trends differ between populations and sexes

even within the same species (e.g. Öst *et al.*, 2015; Dhellemmes *et al.*, 2020). A potential reason for such inconsistency, which also applies to social networks based upon the proximity of individuals to one another or sharing of group membership, is that there can be different reasons for why an individual associates closely with another. For example, circulating stress hormones may correlate with social tendency when predation risk is high, but may not when individuals are motivated to associate closely to gain information about foraging opportunities. Without knowing what the motivations are for social associations, variable results among and within studies may remain the rule rather than the exception. Ingenious experimental design may be able to estimate or manipulate motivation in a social context, and demonstrate how motivation affects the correlation of sociability with other personality traits, sociability's proximate causes, or the fitness and ecological consequences of sociability.

- (5) Beyond interest from behavioural biologists, much of the research in this area uses animals as models for understanding the mechanisms behind variation in social behaviour in humans (Buffington *et al.*, 2016; Kondrakiewicz *et al.*, 2019; Brenner *et al.*, 2020). Additionally, many social species are important to humans for food (Ginelli *et al.*, 2015), as pests (Bazazi *et al.*, 2010; Thorlacius & Brodin, 2018) or because their populations are threatened (VanderWaal *et al.*, 2014; Varma *et al.*, 2020). Consistent variation in social tendency towards other species is also an important line of research, given the close association between our species and companion animals, particularly dogs (Jakovcovic, Mustaca & Bentosela, 2012; Kis *et al.*, 2014; Persson *et al.*, 2015, 2016). It is unknown whether inter-species sociability differs fundamentally from intra-species sociability, and if so, how. A holistic view of sociability within and across species thus has potential to advance progress in applied research, as well as our understanding of inter-individual variation and social behaviour.

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