The Puzzle of Leadership: The Interplay between Individual Traits and Coordination Mechanisms

Kasper F. Hlebowicz [1, 3*], **Jerome Buhl** [2], **Stephan T. Leu** [1]

[1]School of Animal and Veterinary Sciences, The University of Adelaide, Roseworthy SA 5371, Australia

[2]School of Agriculture, Food and Wine, The University of Adelaide, Urrbrae SA 5064, Australia

[3]Wildlife Ecology and Conservation, Wageningen University, Wageningen 6708 PB, the Netherlands

*** Correspondence:**

Kasper Hlebowicz

kasper.hlebowicz@wur.nl

Keywords: leadership1, sociality2, collective behaviour3, collective decision making4, movement ecology5, among-individual variation6

Abstract

In social systems, movement of individual group members scales up to spatiotemporal dynamics of the group. However, the level of influence on group movement dynamics can be variable among group members. The influence of an individual is often referred to as their leadership potential. However, despite the common occurrence of leader-follower patterns across various taxa, little is known whether leadership relates to certain traits of the leader or whether it emerges from the behavioural coordination of leader and followers. Furthermore, leadership can also emerge as a by-product of group coordination mechanisms. This review highlights the variability of leadership across individuals, social groups, and populations emphasizing the need for an interdisciplinary research approach. By combining theory, observations, and novel technologies, we can explore the relationships between social responsiveness, movement characteristics, and coordination processes, advancing our understanding of leadership's ecological and evolutionary implications.

Introduction

Social species exist across all major taxa, and, within groups, coordination processes emerge as an outcome of interactions among individual group members. These processes include for instance collective movement, behavioural synchronisation and social information transmission, which have been shown to affect individual fitness (Fryxell and Berdahl, 2018). Importantly, the level of influence that an individual has within a group can vary among its members (Delgado et al., 2018). But we have a limited understanding of the *proximate* mechanisms and *ultimate* consequences of this variable influence. A dichotomous approach, that classifies individuals into leaders or followers has provided some important insights on leader-follower dynamics. An important question is whether leadership is an *intrinsic* trait that is selected for and hence that evolves. Or whether leadership is an *emergent* trait arising from certain group properties and across varying environmental scenarios. Often, we observe that a few individuals ("followers") follow an animal that moved away from the group or location. This can cascade through the whole group causing everyone to move. If a particular individual consistently initiates group movement and successfully recruits other group members, we call it a "leader" (Krause et al., 2000). A broader definition states that leaders consistently influence, either directly or hierarchically, the behaviour of conspecifics (Strandburg-Peshkin et al., 2018). Leaders often show increased travel speed and directionality as well as a characteristic frontal or peripheral position within the group (Gueron et al., 1996; Couzin et al., 2005; Conradt and List, 2009; Bode et al., 2012; Pettit et al., 2015). Furthermore, empirical studies indicate that leader-follower dynamics are often influenced both by cues of the social and ecological environment (Strandburg-Peshkin et al., 2017; Stutz et al., 2018). However, whether leadership itself or these traits have any fitness benefits and hence are favoured by natural selection remains unclear (Pettit et al., 2015; Strandburg-Peshkin et al., 2018). In this review, we aim to explore the literature on social evolution and leadership and point out knowledge gaps within the field. Addressing those gaps would improve our understanding of the *proximate* and *ultimate* properties of leadership in a social context.

Social behaviour evolved independently in several different taxa (Krause and Ruxton, 2002; Ward and Webster, 2016), with parental care representing an early stage of sociality (Clutton-Brock and Scott, 1991). Sociality offers advantages such as increased protection from predation (Clutton-Brock and Scott, 1991; Couzin et al., 2002; Ebensperger et al., 2014), and enhanced foraging success in heterogeneous environments (Hamilton, 1964; Rubenstein, 2011). Furthermore, harsh environmental conditions have been found to favour the evolution of social behaviour, particularly cooperative behaviour, such as in helper systems. Helpers significantly contribute to the reproductive success of the usually related breeding pair which otherwise would be hard to achieve in such conditions (Rubenstein, 2011; Ebensperger et al., 2014). Nonetheless, other selection pressures aside from kinship have been identified to drive the evolution of sociality (Hamilton, 1964).

An important challenge of group living is to maintain group cohesion. To maintain it, animals combine environmental stimuli and monitor the movement of other group members (Kappeler, 2019). Several behavioural rules have been identified to facilitate group cohesion and within-group synchronisation (Couzin et al., 2002; Couzin and Krause, 2003; Sumpter et al., 2008; Klamser et al., 2021). In some cases, the behavioural rules can be very simple and only involve very minimal sensory and cognitive processes (Camazine et al., 2001; Sumpter, 2010). Overall, these rules relate to the attraction, alignment and/or repulsion with one another (Sumpter, 2010), but even the variability in individual speed itself can have an impact on the synchronisation dynamics (Klamser et al., 2021). Furthermore, these rules can be modulated based on individuals' internal state, such as satiation level (Hansen et al., 2015b), perceived risk of predation (Krause and Godin, 1995), and phenotypic assortment (Couzin et al., 2002). Animals also reach consensus through simple quorum rules which strongly correlate with group size (Sumpter et al., 2008). However, how these behavioural rules are modulated by different environmental contexts remains an open question. Valuable insights can be gained by examining social systems that depend on regular and frequent interactions among individuals in diverse environmental settings, where individuals frequently encounter each other (Freeberg et al., 2012). For instance, investigating social groups with fission-fusion societies, characterized by frequent changes in group size and spatiotemporal cohesion, can greatly contribute to achieving this research objective (Sueur et al., 2011; Silk et al., 2014).

Collective decision making

Group living species benefit from using social information and social learning (Conradt and Roper, 2003; Dunbar and Shultz, 2007; Ward and Webster, 2016). Social information is acquired through observing or communicating with informed or experienced conspecifics (Lesmerises et al., 2018). It can be acquired more quickly than personal information which is acquired through exploring and interacting with the environment (Sigaud et al., 2017). However, social information can be unreliable if it does not represent the actual environmental conditions. Therefore, using social information can either be cheaper or more costly than personal information depending on the level of reliability (Guttal and Couzin, 2010). In situations where the acquisition of personal information and socially transferred information cannot occur simultaneously, relying solely on socially acquired information can occasionally result in sub-optimal behaviours (Giraldeau et al., 2002; Couzin, 2009; Donaldson et al., 2012). For example, birds may choose a night roost site based on an informational cascade, disregarding the survival benefits of communal roosting. Similarly, individuals may ignore their personal preferences in mate choice due to maladaptive copying behaviour, or they may mistakenly employ socially transmitted information in the context of false rapid escape behaviours (Giraldeau et al., 2002). In addition, the efficient transfer of social information among individuals of the same species typically relies on the stability and cohesiveness of a group (Krause and Ruxton, 2002). Consequently, group members should coordinate their movements in both space and time to increase the likelihood of interactions within the group, thereby enhancing social transmission.

Such behavioural coordination is particularly crucial in the context of fission-fusion societies (Aureli et al., 2008), which are characterized by frequent changes in group size and composition, with individuals frequently joining and leaving the group. This dynamic nature often leads to an assumption that fission-fusion societies are less stable and less cohesive compared to other types of social systems. However, it is precisely because of this dynamic nature that the coordination of movement and timing becomes essential between the fissioned individuals to maintain the social relationships within the group (Lerch et al., 2021). As the group members continually join and leave the group, the ability to effectively transmit social information is paramount (Sueur et al., 2011). Mechanisms driving behavioural coordination increase the likelihood of intragroup interactions, allowing for the exchange and transmission of valuable social information between subgroups (Fryxell and Berdahl, 2018). Therefore, in fission-fusion societies, spatiotemporal movement coordination between all group members becomes critical for enhancing social transmission.

Nevertheless, in dynamic and unpredictable natural environments, the transmission of socially acquired maladaptive information can result in fitness loss for group members, particularly if the initial assessment of environmental quality was flawed (Sigaud et al., 2017) or if it hinders the learning of optimal behavioural patterns when acquired from misinformed individuals (Laland and Williams, 1998). This phenomenon, known as "ecological traps," occurs when animals select habitats that appear to be of high quality based on cues but are actually of poor quality (Schlaepfer et al., 2002). For instance, a population of plains bison (*Bison bison bison*) ventured out from a protected area to forage on agricultural land that had higher-quality resources compared to natural meadows. However, this resulted in increased mortality (due to hunting) and no discernible increase in reproduction (Sigaud et al., 2017). Interestingly, researchers found that naïve bison were more likely to forage on the cultivated land when accompanied by at least one informed individual, potentially acting as a leader, thus indicating the maladaptive transmission of information (Sigaud et al., 2017). A similar sub-optimal interaction between social learning and the use of anthropogenic food sources was observed in a study on bottlenose dolphins (*Tursiops aduncus*). Pods led by misinformed individuals that fed on bycatch experienced a higher risk of mortality due to collisions with boats (Donaldson et al., 2012).

Group cohesion and behavioural synchronisation

The mechanisms that govern behavioural synchronization among group members, promoting their proximity and maintaining sensory communication range, are crucial for the evolution and persistence of group living (Michelena et al., 2005; Gautrais et al., 2007; Michelena et al., 2008; King and Cowlishaw, 2009; O'Bryan et al., 2019). Animals within a group tend to coordinate their movements in both space and time, ensuring the cohesion of the group for varying durations (Michelena et al., 2008; Nathan et al., 2008; Ginelli et al., 2015; Westley et al., 2018). Group cohesion can be achieved through allelomimetic interactions (Camazine et al., 2001; Gautrais et al., 2007), wherein individuals are more likely to adopt the behaviour of their neighbouring group members. Furthermore, context-specific group cohesion may be attained through a balancing effect, considering the trade-off between increasing the distance to reduce scramble competition while remaining in proximity to enhance anti-predator benefits (Ginelli et al., 2015).

Synchronization among group members can be achieved through simple interaction rules, including attraction, short-range repulsion, alignment, and behavioural amplification among neighbouring individuals (Couzin, 2009; Sumpter, 2010; Delgado et al., 2018). These interaction rules can be further influenced by past experiences, the local environment, and social cues (King and Cowlishaw, 2009; Michelena et al., 2009). To enhance the effectiveness of behavioural synchronization, individuals are likely to select specific interaction partners based on their identity and shared history and adjust their actions accordingly (Gascuel et al., 2021). In this way, moving group members respond to local changes in the movement and position of their neighbours, leading to "interaction neighbourhoods" resulting in coordinated movement among conspecifics in close proximity (Rosenthal et al., 2015; Herbert-Read, 2016; Jiang et al., 2017; Gascuel et al., 2021). Therefore, group cohesion relies on the spatiotemporal synchrony of activities among group members, rather than being dependent on a particular type of behaviour (Gautrais et al., 2007; King and Cowlishaw, 2009).

When the costs associated with maintaining cohesion outweigh the benefits, behavioural asynchrony among group members can increase. In fission-fusion societies, this may lead to a fission event, reducing the costs of cohesion (Gautrais et al., 2007; Aureli et al., 2008; Sueur et al., 2011; Silk et al., 2014; Senior et al., 2016). In more stable societies, this process helps regulate optimal group size (Markham et al., 2015).

Within-group heterogeneity

Sociality, although ubiquitous, is not a uniform trait. Instead, taxon-specific life history traits (Arnold and Owens, 1998; Griesser and Suzuki, 2016; Griesser et al., 2017; Shell and Rehan, 2018; Beery, 2019; Kappeler, 2019) in interaction with ecological conditions influence the evolution and maintenance of sociality leading to a spectrum of sociability. The evolutionary mechanisms shaping sociality lead to species-specific differences in the fundamental aspects of group living, including variations in social unit size, composition, and spatiotemporal stability. On one end of the spectrum, sociality may confer advantages to species in harsh environmental conditions, favouring the formation of stable social groups. On the other end, species with weaker social systems may benefit from social behaviours to counter demographic challenges but form temporary and less stable associations. It is important to note that this example is not meant to imply a fixed order within the spectrum, as the dynamics can vary. It is worth considering that the reverse could also be true. It is conceivable that fission-fusion societies, which exhibit flexibility in adjusting group size and other aspects of sociability, may be better adapted to harsh and unpredictable conditions (Silk et al., 2014). This flexibility might allow them to maximize the benefits of sociality in a given context, highlighting the importance of considering different strategies along the sociability spectrum in relation to environmental conditions and specific circumstances.

Group size is variable and suggested as a key factor that determines many facets of social living, ranging from maintaining group cohesion (Michelena et al., 2008) to influencing group demography (Grueter et al., 2012). Variation in group size may also alter social preferences among group members (Michelena et al., 2009), their travelling speed (Jang et al., 2019; Klamser et al., 2021) and spatiotemporal patterns (Boissy and Dumont, 2002; Michelena et al., 2010). Moreover, group size may be of principal importance for the transfer of social information and the evolution of collective decision-making (Conradt and Roper, 2003; 2009). If all group members have the same access to noisy environmental information but respond to it in slightly different ways, the average behavioural response is more accurate (Couzin, 2009). Thus, with increasing group size selection should lead to better decisions, known as the many-wrongs hypothesis (Simons, 2004; Sumpter, 2006).

However, not all group members have access to the same information, for example, due to its spatiotemporal occurrence or individuals' varying internal states (King and Cowlishaw, 2007). Such within-group heterogeneities can alter group decision-making leading to the evolution of mechanisms that resolve within-group conflict such as quorum responses (Conradt and List, 2009; Papageorgiou and Farine, 2020) or voting (Ramos et al., 2015). Once a critical number of group members show a certain behavioural response, for instance, leave a foraging patch, then all group members join and show the same behaviour (Sumpter and Pratt, 2009; Ward et al., 2012; Marshall et al., 2019).

Nonetheless, if individuals differ consistently in the expression of movement patterns, e.g., due to varying aspects of foraging behaviour (activity, risk-taking, physiological drivers, specific social roles in foraging groups), or preferences for social and/or habitat features, we would expect assortativity among conspecifics based on those traits or preferences (Toscano et al., 2016). Moreover, it is hypothesised that intraspecific variation in personality, movement and space-use preferences can impact population dynamics and promote coexistence by influencing intra- and inter-specific interactions (Milles et al., 2020). For instance, repeatability in among-individual variation in movement speed across a foraging gradient indicates how the distribution of fast- and slow-moving caribous, in different habitats, may alter group dynamics (Webber et al., 2020). Crucially, a recent meta-analysis of 200 home range estimates, movement metrics and habitat uses across all main animal taxa, indicated generalizability and high repeatability of among-individual variation in movement behaviour (Stuber et al., 2022).

Among-individual heterogeneity in movement can also influence other aspects of spatiotemporal group dynamics by affecting individually-expressed boldness resulting in variation in spatial distribution (Michelena et al., 2008; Michelena et al., 2010; Briard et al., 2021), exploratory behaviour (Michelangeli et al., 2020), foraging (Patrick et al., 2017), learning (Pettit et al., 2015), anti-predator response (Brodin et al., 2019), social structure (Bonnell et al., 2017), social affinity (Briard et al., 2015) and social ranking (Sasaki et al., 2018).

Leader-follower relationship

In social systems characterized by quorum decision-making, all individuals have equal influence on the group. However, leadership can still emerge in many other social systems, even though it may not be a prerequisite for group coordination processes (Couzin et al., 2005). In these systems, certain individuals consistently exhibit marked differences in their influence on the group (Krause et al., 2000; Conradt and Roper, 2005; Couzin et al., 2005; Conradt and List, 2009; Pillot et al., 2010; King and Sueur, 2011; Nakayama et al., 2013; Briard et al., 2015; Sasaki et al., 2018). For example, individuals with disproportionate influence, known as leaders, can recruit and influence other group members to follow their lead (King, 2010). Leadership offers several benefits, such as reducing free-riding behaviour and coordination errors within a group (Frank, 2003; Hooper et al., 2010). Additionally, leaders facilitate the initiation of group activities.

Leader-follower dynamics can be more complex when individuals vary in the propensity and plasticity to lead or follow conspecifics (Harcourt et al., 2009), with followers being less likely to co-opt leadership roles (Nakayama et al., 2013). For example, in guineafowl (*Acryllium vulturinum*), when dominant leaders monopolize resources, some subordinate individuals choose to move away. Once the number of subordinates that move away reaches a critical threshold, it triggers group movement, compelling the dominant leader to abandon the monopolized food patch and catch up with the departing group (Papageorgiou and Farine, 2020). This behavioural flexibility aligns with the conditional strategies hypothesis (Tomkins and Hazel, 2007). Depending on specific environmental and/or social cues, it can be more advantageous to act as a leader in certain situations, while in others, it may be more beneficial to be a follower. This example highlights the complex interplay between resource acquisition, group dynamics, and individual decisions, which may involve a nuanced understanding of the leader-follower relationship and its fluidity.

Contrasts between leaders and followers

Social attraction and responsiveness vary among conspecifics (Ward et al., 2004; Kurvers et al., 2009; Michelena et al., 2010; Briard et al., 2015; Jolles et al., 2015; Sih et al., 2018; Sumpter et al., 2018). Socially responsive individuals prioritise social interactions and proximity to others and are often followers. Whereas leaders are characterised by decreased social responsiveness, preferentially choosing environmental cues and their preferences over maintaining cohesiveness of the social group (Lamprecht, 1996; Wolf et al., 2008; Johnstone and Manica, 2011; Pettit et al., 2015). A mix of followers and leaders within a single population is hypothesised to be maintained through negative frequency-dependent selection, as the benefits of social responsiveness might be high for some individuals, but not for all of them at the same time (Wolf et al., 2008; Wolf and McNamara, 2013). In particular, when group size and/or population density increase, individuals are more likely to encounter conspecifics, which negatively affects individuals with lower sociability, such as leaders. Importantly, theoretical models indicate that even in large groups, only a small proportion of leaders is needed to achieve high accuracy of coordination (Couzin et al., 2005). Hence, the frequency-dependent coexistence of leader-follower strategies remains evolutionarily stable even in large groups (Guttal and Couzin, 2010). Perhaps, a socially responsive cohort that pays attention to socially transmitted cues within a heterogenous group can act as a social glue preserving cohesiveness, while a socially unresponsive cohort determines group movement and influences decision-making (Harcourt et al., 2009; Pettit et al., 2015).

The value of leadership in social systems is not solely determined by the resources a leader possesses or can obtain, but rather by the likelihood of making resources available to others (Lamprecht, 1996). When an individual seeks a resource and subsequently increases its critical distance from conspecifics, it can become a leader if others choose to follow (Lamprecht, 1996). However, natural selection acts on the individual, thus there must be a net benefit for leaders themselves. Yet, this perspective holds if leadership is an *inherent* individual trait, as natural selection would then favour specific leadership traits. In contrast, if leadership *emerges* solely as an outcome of coordination processes among group members, it becomes less clear how net fitness gains are distinctly different between individuals. The emergence of leadership through coordination processes blurs the line between individual fitness benefits and the overall benefits of group coordination. In this view, the value of leadership is intertwined with the benefits gained by followers, indicating that leadership is not solely driven by individual fitness gains, but rather by the cumulative advantages of collective behaviours. For instance, in a scenario where knowledgeable individuals lead naïve individuals to known food patches (Merkle et al., 2015), leadership is beneficial for the leaders as they access first and forage more than followers, while simultaneously benefit from the dilution effect (Hamilton, 1971). At the same time, following is beneficial for naïve individuals, as they discover food patches faster than if they had to forage on their own. However, it is important to note that leadership can also be driven by other factors, such as variation in exploratory propensities among individuals (Wolf and McNamara, 2013). In this view, leaders being characterized by lower sociability and a higher propensity to forage farther away from conspecifics, increase their chances of discovering new food patches, regardless of their initial knowledge state. Followers, on the other hand, by being more socially responsive, move towards departing individuals to maintain group cohesion and consequently benefit from the newly discovered food patches. This highlights the complexity of leader-follower dynamics and suggests that leadership can have multiple underlying mechanisms and benefits for both leaders and followers. For example, Rands and colleagues (2003) introduced a state-dependent game-theoretical model that demonstrated the emergence of leaders in foraging dyads when individuals have different energetic requirements, allowing them to coordinate their foraging activities (Rands et al., 2003; Rands et al., 2006; Rands et al., 2008). Empirically, this effect has been observed in food-deprived fish occupying front positions in shoals more frequently and influencing the movement preferences of others (Krause, 1993; Hansen et al., 2015b). Additionally, lactating zebras, due to their elevated nutritional needs, initiate group movement more frequently, showcasing the dynamic relationship between individual needs and the emergence of leadership within the group (Fischhoff et al., 2007).

Behavioural coordination, such as the dilution effect (Hamilton, 1971) and shared vigilance (Krause and Ruxton, 2002), benefits all members of a group, including leaders and followers. However, the magnitude of these benefits can be modulated by the spatial position of individuals within the group. For example, the dilution effect, which reduces individual predation risk through group size, provides greater benefits to individuals positioned more centrally within the group, while those occupying frontal and peripheral positions face increased mortality risk (Bumann et al., 1997). It is noteworthy that leaders often occupy these frontal and peripheral positions, potentially diminishing their net benefit from the dilution effect compared to other group members positioned more inward. This spatial distribution of risk highlights an intriguing aspect of leadership dynamics. Leaders, driven by their own goals, may deliberately sway the group towards their selfish objectives using various strategies such as vocalizations, explicit motions, or coercion (Garland et al., 2018). In doing so, leaders can exploit the benefits of behavioural coordination, such as the dilution effect and shared vigilance, to their advantage. By encouraging followers to adopt their actions, leaders increase the likelihood of achieving their goals while potentially gaining personal advantages. This scenario underscores how leaders may benefit when others in the group, particularly followers, adopt or co-opt their behaviours.

Leadership dynamics encompass a range of complexities, involving both costs and benefits for individuals taking on leadership roles depending on ecological and social conditions. While leadership may impose unequal costs on individuals assuming the leadership role (Gillet et al., 2011), theoretical models suggest that the maintenance of followership can be driven by voluntary propensity to follow, rather than coercive dominance and exploitation, if leadership enhances group productivity (Hooper et al., 2010; Powers and Lehmann, 2014). It is crucial to consider both within-group and between-group effects to fully grasp the net benefits of leader-follower dynamics. Within-group analysis might suggest that followers receive greater benefits compared to leaders (Koykka and Wild, 2015). However, when we incorporate between-group effects, a more nuanced perspective emerges. Leaders can benefit from the presence of followers during inter-group conflicts and competition with leaders from other groups (Gavrilets and Fortunato, 2014). Indeed, empirical observations from a range of species engaged in between-group conflicts align with this prediction demonstrating unequal energetic expenditures of high-rank individuals. This was observed in chimpanzees during territorial border patrols (Amsler, 2010), and in blue monkeys when defending communal feeding territories (Cords, 2007). These findings highlight the role of individuals likely occupying leadership roles in resource defence. Furthermore, studies on grey wolf packs demonstrate how older and more aggressive males assess opponents from competing groups and adjust their behaviour based on relative pack size. The more a grey wolf pack outnumbers their opponent, the more likely an individual will participate in an aggressive in-between group interaction (Cassidy et al., 2017). As such, the net benefits of leader-follower interactions may extend beyond the immediate group dynamics and encompass the broader context of group competition and self-interest. Therefore, understanding leader-follower dynamics requires a comprehensive examination of both within-group and between-group effects. By considering the impact on group productivity, and the potential costs and benefits for leaders and followers, we can develop a clearer and more comprehensive understanding of the complexities and nuances underlying leadership dynamics.

However, gregarious species are often engaged in a producer-scrounger game, where individuals employ different foraging strategies. The scrounging tactic tends to spread within these populations (Dumke et al., 2016). Drawing parallels to leader-follower dynamics, leaders can be likened to producers, while followers can be likened to scroungers. The decision to lead or follow is influenced by the perceived payoffs associated with each strategy, and individuals rely on social learning rules to make these decisions. In this context, individuals that forage effectively alone without relying on social information act as producers/leaders and likely benefit other group members (Morand-Ferron and Giraldeau, 2010). While theoretical insights shed light on these dynamics, the generalizability of these findings is limited due to a current lack of empirical data. Therefore, further research is needed to better understand the similarities between producer-scrounger and leader-follower patterns.

Leadership in socially stratified systems

In gregarious species, we often observe a social stratification and the development of hierarchies which reduces instances of free-riding and aggression within the group (Issa and Edwards, 2006). The most dominant individuals are characterised by the tendency to monopolise resources and occupy the best and safest relative positions witing the group (Ward and Webster, 2016). Even though leadership can be correlated with high dominance status (Squires and Daws, 1975; Robbins, 1995; Peterson et al., 2002; King et al., 2008; Sueur and Petit, 2010; Krueger et al., 2014; Tokuyama and Furuichi, 2017; Ramos et al., 2018; Papageorgiou and Farine, 2020), the effect of social hierarchy is hard to evaluate because it is intertwined with other factors, such as age (Tokuyama and Furuichi, 2017; Ramos et al., 2018), sex (Squires and Daws, 1975), degree of kinship (Sueur and Petit, 2010) or reproductive status (Robbins, 1995; Peterson et al., 2002; King et al., 2008; Krueger et al., 2014). Moreover, in some systems with dominance-driven leadership, the most dominant individual was not the sole leader, but instead, leadership was distributed among several high-ranking group members (Peterson et al., 2002; King et al., 2008; Papageorgiou and Farine, 2020). Dominance also plays an important role in within- and between-group interactions and conflict mediation (Smith et al., 2016). However, dominant individuals may simply induce followership by acting more independently and being less socially responsive (King et al., 2009) or individuals that are strongly connected and occupy important positions within their social network may have a disproportionate influence on their group (King, 2010; Briard et al., 2015; Tokuyama and Furuichi, 2017; Strandburg-Peshkin et al., 2018).

Most animal social networks are non-random and individuals are connected with a different number of conspecifics or their ties are of different strength. Hence, we may expect that individuals also differ in their importance within the social network (Wey et al., 2008). An advantage of studying leadership from a social network perspective is its direct insight into inter- and intra-individual variability in social responsiveness underlying leader-follower dynamics. Some advances have been made in this area, with theoretical research indicating the importance of centralised leadership positions within the social network (Krause et al., 2007; Bode et al., 2011; Bode et al., 2012; Clemson and Evans, 2012; Sueur et al., 2012; Strandburg-Peshkin et al., 2018). However, empirical studies are lacking which would greatly improve our limited understanding of the role of leaders in the network (Briard et al., 2015; Lerch et al., 2021).

The puzzle of leadership

Researchers are successively broadening the list of individual characteristics associated with leadership, such as more directional and faster movement (Gueron et al., 1996; Couzin et al., 2005; Conradt and List, 2009; Sasaki et al., 2018), elevated nutritional requirements (Fischhoff et al., 2007; Hansen et al., 2015b; a), age (Tokuyama and Furuichi, 2017; Allen et al., 2020), learning abilities (Pettit et al., 2015), personal knowledge (Pillot et al., 2010; Mueller et al., 2013; Berdahl et al., 2018; Allen et al., 2020), social responsiveness (Briard et al., 2015) and a high degree of kinship with followers (Sueur and Petit, 2010; Ramos et al., 2018). Despite this suite of identified characteristics, a question that remains open is whether these traits led to the evolution of leadership or vice versa. One argument proposes that leaders may have evolved dominance as a means to secure an unequal proportion of resources (Koykka and Wild, 2015). In this view, dominance and the associated traits may have emerged as a strategy for leaders to gain an advantage in resource acquisition. However, it is important to note that the relationship between these traits and leadership is complex and multifaceted. It is possible that a combination of factors, including genetic predispositions, environmental conditions, and social dynamics, have shaped the evolution of leadership and its associated traits. Further research is needed to unravel the causal relationships and understand the evolutionary origins of leadership in different species.

A noteworthy challenge when studying leader-follower relationships is the need to simultaneously monitor many potential decision-makers in a group, as leadership might be distributed among several individuals, rather than being monopolised by a single individual (Bourjade and Sueur, 2010; Taylor et al., 2011; Bourjade et al., 2015; Ramos et al., 2015; Ramos et al., 2018; Sasaki et al., 2018). Hence, to examine whether and how group members influence each other, particularly in initiating movement, it is paramount to monitor whether the speed or direction of a focal individual is adopted by its neighbours across the entire group (Ramseyer et al., 2009; Nagy et al., 2010; Herbert-Read, 2016).

A significant challenge awaiting to be addressed is whether leadership is *inherent* or *emergent* (Garland et al., 2018; Strandburg-Peshkin et al., 2018). In other words, whether it is linked with certain semi-persistent individual traits such as size, sex, personality, or social status? Or whether leadership emerges as a consequence of group coordination combined with variation in travel velocity and spatial position within the group? This topic is even more complex, as these two scenarios are not necessarily mutually exclusive. It seems plausible that movement initiation and successful recruitment might be driven by the interaction of leader characteristics (Ramseyer et al., 2009) and allelomimetic processes (Taylor et al., 2011), thus carefully designed experiments are needed to disentangle these phenomena. Additionally, exploration of how individual traits interact with group coordination processes can provide insights into the evolutionary origins and the relative importance of intrinsic traits and social dynamics in shaping leadership.

Another question is the consistency of leadership. Does the same individual or group of individuals repeatedly assume leadership roles, or does leadership change between movement events? Examining the repeatability and/or context-dependence of leadership can deepen our understanding of social dynamics and help to identify patterns of stability and variability of leader-follower relationship. The consistency of leadership may also depend on socio-ecological factors and potentially have a heritable component. Exploring the influence of these factors on leadership can provide insights into its adaptive value and contribute to our understanding of the evolutionary processes shaping social systems.

Furthermore, investigating how leadership differs between species, populations, and different social groups within the context of social responsiveness across the sociability spectrum can provide valuable insights. Understanding leader-follower relationships in groups with varying levels of social complexity can shed light on the implications of the sociability spectrum for movement coordination, decision-making, and social organization.

Lastly, we should explore how we can leverage leadership dynamics to improve agricultural and/or nature conservation practices and enhance animal welfare. Understanding how to utilise leader-follower relationships can optimize agricultural practices, inform conservation strategies, contribute to animal welfare and bridge the gap between scientific research and practical applications, benefiting both human and animal well-being.

Concluding Remarks

In conclusion, leadership plays a crucial role in the functioning of complex animal social systems. However, it is important to acknowledge that the nature of leadership can vary significantly depending on the specific context in which it occurs. For instance, the characteristics and mechanisms associated with leadership may differ between species, populations, and even within different social groups of the same species. To further advance our understanding of leader-follower dynamics, we propose a more interdisciplinary approach. For example, social network analysis, as discussed by Makagon et al. (2012), can contribute valuable tools for investigating social interactions in applied ethology. Moreover, the assimilation of novel technologies offers exciting opportunities to study spatiotemporal dynamics simultaneously among all group members. High fidelity and resolution biologgers, as well as unmanned aerial vehicles (drones), as highlighted by Hughey et al. (2018), enable us to capture at the same time detailed information about all individual movements, group coordination, and collective behaviours in the wild. By leveraging these advanced technologies, we can gain a more comprehensive understanding of how leader-follower dynamics manifest across species in different socio-ecological contexts. To address key questions concerning the fitness costs and benefits of leadership and its generality across social systems and species, it is essential to integrate theory, behavioural observations, and well-designed experiments. By combining these approaches, we can explore the causal relationships between inter- and intra-individual heterogeneity in social responsiveness, movement characteristics, and coordination processes. This integrative approach holds great promise for advancing our knowledge of leadership dynamics and its ecological and evolutionary implications.

Author Contributions

KF Hlebowicz: conceptualisation, investigation, writing - original draft, writing - review & editing; J Buhl, and ST Leu: conceptualisation, writing - review & editing, supervision. All authors contributed to the article and approved the submitted version.

Funding

KF Hlebowicz was supported by an Australian Government Research Training Program Scholarship from the University of Adelaide. ST Leu was supported by an Australian Research Council DECRA Fellowship [DE170101132].

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Allen, C.R.B., Brent, L.J.N., Motsentwa, T., Weiss, M.N., and Croft, D.P. (2020). Importance of old bulls: leaders and followers in collective movements of all-male groups in African savannah elephants (*Loxodonta africana*). *Scientific Reports* 10(1): 13996. doi: https://doi.org/10.1038/s41598-020-70682-y.

Amsler, S.J. (2010). Energetic costs of territorial boundary patrols by wild chimpanzees. *American Journal of Primatology* 72(2)**,** 93-103. doi: https://doi.org/10.1002/ajp.20757.

Arnold, K.E., and Owens, I.P.F. (1998). Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society B-Biological Sciences* 265(1398)**,** 739-745. doi: https://doi.org/10.1098/rspb.1998.0355.

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., et al. (2008). Fission-Fusion Dynamics New Research Frameworks. *Current Anthropology* 49(4)**,** 627-654. doi: https://doi.org/10.1086/586708.

Beery, A.K. (2019). Frank Beach Award winner: Neuroendocrinology of group living. *Hormones and Behavior* 107**,** 67-75. doi: https://doi.org/10.1016/j.yhbeh.2018.11.002.

Berdahl, A.M., Kao, A.B., Flack, A., Westley, P.A.H., Codling, E.A., Couzin, I.D., et al. (2018). Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Philosophical Transactions of the Royal Society B-Biological Sciences* 373(1746): 20170009. doi: https://doi.org/10.1098/rstb.2017.0009.

Bode, N.W.F., Franks, D.W., and Wood, A.J. (2012). Leading from the front? Social networks in navigating groups. *Behavioral Ecology and Sociobiology* 66(6)**,** 835-843. doi: https://doi.org/10.1007/s00265-012-1331-6.

Bode, N.W.F., Wood, A.J., and Franks, D.W. (2011). The impact of social networks on animal collective motion. *Animal Behaviour* 82(1)**,** 29-38. doi: https://doi.org/10.1016/j.anbehav.2011.04.011.

Boissy, A., and Dumont, B. (2002). Interactions between social and feeding motivations on the grazing behaviour of herbivores: sheep more easily split into subgroups with familiar peers. *Applied Animal Behaviour Science* 79(3)**,** 233-245. doi: https://doi.org/10.1016/S0168-1591(02)00152-1.

Bonnell, T.R., Clarke, P.M., Henzi, S.P., and Barrett, L. (2017). Individual-level movement bias leads to the formation of higher-order social structure in a mobile group of baboons. *Royal Society Open Science* 4(7): 170148. doi: https://doi.org/10.1098/rsos.170148.

Bourjade, M., and Sueur, C. (2010). Shared or unshared consensus for collective movement? Towards methodological concerns. *Behavioural Processes* 84(3)**,** 648-652. doi: https://doi.org/10.1016/j.beproc.2010.02.027.

Bourjade, M., Thierry, B., Hausberger, M., and Petit, O. (2015). Is Leadership a Reliable Concept in Animals? An Empirical Study in the Horse. *PLOS ONE* 10(5): e0126344. doi: https://doi.org/10.1371/journal.pone.0126344.

Briard, L., Deneubourg, J.L., and Petit, O. (2021). Group behaviours and individual spatial sorting before departure predict the dynamics of collective movements in horses. *Animal Behaviour* 174**,** 115-125. doi: https://doi.org/10.1016/j.anbehav.2021.01.014.

Briard, L., Dorn, C., and Petit, O. (2015). Personality and Affinities Play a Key Role in the Organisation of Collective Movements in a Group of Domestic Horses. *Ethology* 121(9)**,** 888-902. doi: https://doi.org/10.1111/eth.12402.

Brodin, T., Fogarty, S., Sih, A., and Cote, J. (2019). Personality-dependent survival of the invasive mosquitofish: being social can be deadly. *Aquatic Invasions* 14(3)**,** 465-477. doi: https://doi.org/10.3391/ai.2019.14.3.06.

Bumann, D., Krause, J., and Rubenstein, D. (1997). Mortality risk of spatial positions in animal groups: The danger of being in the front. *Behaviour* 134**,** 1063-1076. doi: https://doi.org/10.1163/156853997x00403.

Camazine, S., Deneubourg, J.-L., Franks, N.R., Sneyd, J., Theraulaz, G.U.Y., and Bonabeau, E. (2001). *Self-Organization in Biological Systems.* Princeton University Press.

Cassidy, K.A., Mech, L.D., MacNulty, D.R., Stahler, D.R., and Smith, D.W. (2017). Sexually dimorphic aggression indicates male gray wolves specialize in pack defense against conspecific groups. *Behavioural Processes* 136**,** 64-72. doi: https://doi.org/10.1016/j.beproc.2017.01.011.

Clemson, T., and Evans, T.S. (2012). The emergence of leadership in social networks. *Physica A: Statistical Mechanics and Its Applications* 391(4)**,** 1434-1444. doi: https://doi.org/10.1016/j.physa.2011.11.011.

Clutton-Brock, T.H., and Scott, D. (1991). *The evolution of parental care.* Princeton, NJ, US: Princeton University Press.

Conradt, L., and List, C. (2009). Group decisions in humans and animals: a survey. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364(1518)**,** 719-742. doi: https://doi.org/10.1098/rstb.2008.0276.

Conradt, L., and Roper, T.J. (2003). Group decision-making in animals. *Nature* 421(6919)**,** 155-158. doi: https://doi.org/10.1038/nature01294.

Conradt, L., and Roper, T.J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution* 20(8)**,** 449-456. doi: https://doi.org/10.1016/j.tree.2005.05.008.

Conradt, L., and Roper, T.J. (2009). Conflicts of interest and the evolution of decision sharing. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364(1518)**,** 807-819. doi: https://doi.org/10.1098/rstb.2008.0257.

Cords, M. (2007). Variable participation in the defense of communal feeding territories by blue monkeys in the Kakamega Forest, Kenya. *Behaviour* 144(12)**,** 1537-1550. doi: https://doi.org/10.1163/156853907782512100.

Couzin, I.D. (2009). Collective cognition in animal groups. *Trends in Cognitive Sciences* 13(1)**,** 36-43. doi: https://doi.org/10.1016/j.tics.2008.10.002.

Couzin, I.D., and Krause, J. (2003). Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior* 32**,** 1-75. doi: https://doi.org/10.1016/S0065-3454(03)01001-5.

Couzin, I.D., Krause, J., Franks, N.R., and Levin, S.A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature* 433(7025)**,** 513-516. doi: https://doi.org/10.1038/nature03236.

Couzin, I.D., Krause, J., James, R., Ruxton, G.D., and Franks, N.R. (2002). Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology* 218(1)**,** 1-11. doi: https://doi.org/10.1006/jtbi.2002.3065.

Delgado, M.D., Miranda, M., Alvarez, S.J., Gurarie, E., Fagan, W.F., Penteriani, V., et al. (2018). The importance of individual variation in the dynamics of animal collective movements. *Philosophical Transactions of the Royal Society B-Biological Sciences* 373(1746): 20170008. doi: https://doi.org/10.1098/rstb.2017.0008.

Donaldson, R., Finn, H., Bejder, L., Lusseau, D., and Calver, M. (2012). The social side of human-wildlife interaction: wildlife can learn harmful behaviours from each other. *Animal Conservation* 15(5)**,** 427-435. doi: https://doi.org/10.1111/j.1469-1795.2012.00548.x.

Dumke, M., Herberstein, M.E., and Schneider, J.M. (2016). Producers and scroungers: feeding-type composition changes with group size in a socially foraging spider. *Proceedings of the Royal Society B-Biological Sciences* 283(1828): 20160114. doi: https://doi.org/10.1098/rspb.2016.0114.

Dunbar, R.I.M., and Shultz, S. (2007). Evolution in the social brain. *Science* 317(5843)**,** 1344-1347. doi: https://doi.org/10.1126/science.1145463.

Ebensperger, L.A., Villegas, A., Abades, S., and Hayes, L.D. (2014). Mean ecological conditions modulate the effects of group living and communal rearing on offspring production and survival. *Behavioral Ecology* 25(4)**,** 862-870. doi: https://doi.org/10.1093/beheco/aru061.

Fischhoff, I.R., Sundaresan, S.R., Cordingley, J., Larkin, H.M., Sellier, M.J., and Rubenstein, D.I. (2007). Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Animal Behaviour* 73**,** 825-831. doi: https://doi.org/10.1016/j.anbehav.2006.10.012.

Frank, S.A. (2003). Repression of Competition and the Evolution of Cooperation. *Evolution* 57(4)**,** 693-705. doi: https://doi.org/10.1111/j.0014-3820.2003.tb00283.x.

Freeberg, T.M., Dunbar, R.I.M., and Ord, T.J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity Introduction. *Philosophical Transactions of the Royal Society B-Biological Sciences* 367(1597)**,** 1785-1801. doi: https://doi.org/10.1098/rstb.2011.0213.

Fryxell, J.M., and Berdahl, A.M. (2018). Fitness trade-offs of group formation and movement by Thomson's gazelles in the Serengeti ecosystem. *Philosophical Transactions of the Royal Society B-Biological Sciences* 373(1746). doi: https://doi.org/10.1098/rstb.2017.0013.

Garland, J., Berdahl, A.M., Sun, J., and Bollt, E.M. (2018). Anatomy of leadership in collective behaviour. *Chaos* 28(7): 075308. doi: https://doi.org/10.1063/1.5024395.

Gascuel, H.M., Peruani, F., and Bon, R. (2021). Identifying interaction neighbours in animal groups. *Animal Behaviour* 174**,** 97-104. doi: https://doi.org/10.1016/j.anbehav.2021.01.019.

Gautrais, J., Michelena, P., Sibbald, A., Bon, R., and Deneubourg, J.L. (2007). Allelomimetic synchronization in Merino sheep. *Animal Behaviour* 74**,** 1443-1454. doi: https://doi.org/10.1016/j.anbehav.2007.02.020.

Gavrilets, S., and Fortunato, L. (2014). A solution to the collective action problem in between-group conflict with within-group inequality. *Nature Communications* 5: 3526 (2014). doi: https://doi.org/10.1038/ncomms4526.

Gillet, J., Cartwright, E., and van Vugt, M. (2011). Selfish or servant leadership? Evolutionary predictions on leadership personalities in coordination games. *Personality and Individual Differences* 51(3)**,** 231-236. doi: https://doi.org/10.1016/j.paid.2010.06.003.

Ginelli, F., Peruani, F., Pillot, M.H., Chate, H., Theraulaz, G., and Bon, R. (2015). Intermittent collective dynamics emerge from conflicting imperatives in sheep herds. *Proceedings of the National Academy of Sciences of the United States of America* 112(41)**,** 12729-12734. doi: https://doi.org/10.1073/pnas.1503749112.

Giraldeau, L.A., Valone, T.J., and Templeton, J.J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society B-Biological Sciences* 357(1427)**,** 1559-1566. doi: https://doi.org/10.1098/rstb.2002.1065.

Griesser, M., Drobniak, S.M., Nakagawa, S., and Botero, C.A. (2017). Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLOS Biology* 15(6): e2000483. doi: https://doi.org/10.1371/journal.pbio.2000483.

Griesser, M., and Suzuki, T.N. (2016). Occasional cooperative breeding in birds and the robustness of comparative analyses concerning the evolution of cooperative breeding. *Zoological Letters* 2: 7 (2016). doi: https://doi.org/10.1186/s40851-016-0041-8.

Grueter, C.C., Chapais, B., and Zinner, D. (2012). Evolution of Multilevel Social Systems in Nonhuman Primates and Humans. *International Journal of Primatology* 33(5)**,** 1002-1037. doi: https://doi.org/10.1007/s10764-012-9618-z.

Gueron, S., Levin, S.A., and Rubenstein, D.I. (1996). The dynamics of herds: From individuals to aggregations. *Journal of Theoretical Biology* 182(1)**,** 85-98. doi: https://doi.org/10.1006/jtbi.1996.0144.

Guttal, V., and Couzin, I.D. (2010). Social interactions, information use, and the evolution of collective migration. *Proceedings of the National Academy of Sciences of the United States of America* 107(37)**,** 16172-16177. doi: https://doi.org/10.1073/pnas.1006874107.

Hamilton, W.D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7(1)**,** 1-16. doi: https://doi.org/10.1016/0022-5193(64)90038-4.

Hamilton, W.D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology* 31(2)**,** 295-311. doi: https://doi.org/10.1016/0022-5193(71)90189-5.

Hansen, M.J., Schaerf, T.M., and Ward, A.J.W. (2015a). The effect of hunger on the exploratory behaviour of shoals of mosquitofish *Gambusia holbrooki*. *Behaviour* 152(12-13)**,** 1657-1683. doi: https://doi.org/10.1163/1568539x-00003298.

Hansen, M.J., Schaerf, T.M., and Ward, A.J.W. (2015b). The influence of nutritional state on individual and group movement behaviour in shoals of crimson-spotted rainbowfish (*Melanotaenia duboulayi*). *Behavioral Ecology and Sociobiology* 69(10)**,** 1713-1722. doi: https://doi.org/10.1007/s00265-015-1983-0.

Harcourt, J.L., Ang, T.Z., Sweetman, G., Johnstone, R.A., and Manica, A. (2009). Social Feedback and the Emergence of Leaders and Followers. *Current Biology* 19(3)**,** 248-252. doi: https://doi.org/10.1016/j.cub.2008.12.051.

Herbert-Read, J.E. (2016). Understanding how animal groups achieve coordinated movement. *Journal of Experimental Biology* 219(19)**,** 2971-2983. doi: https://doi.org/10.1242/jeb.129411.

Hooper, P.L., Kaplan, H.S., and Boone, J.L. (2010). A theory of leadership in human cooperative groups. *Journal of Theoretical Biology* 265(4)**,** 633-646. doi: https://doi.org/10.1016/j.jtbi.2010.05.034.

Hughey, L.F., Hein, A.M., Strandburg-Peshkin, A., and Jensen, F.H. (2018). Challenges and solutions for studying collective animal behaviour in the wild. *Philosophical Transactions of the Royal Society B-Biological Sciences* 373(1746): 20170005. doi: https://doi.org/10.1098/rstb.2017.0005.

Issa, F.A., and Edwards, D.H. (2006). Ritualized submission and the reduction of aggression in an invertebrate. *Current Biology* 16(22)**,** 2217-2221. doi: https://doi.org/10.1016/j.cub.2006.08.065.

Jang, H., Boesch, C., Mundry, R., Ban, S.D., and Janmaat, K.R.L. (2019). Travel linearity and speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. *Scientific Reports* 9: 11066 (2019). doi: https://doi.org/10.1038/s41598-019-47247-9.

Jiang, L., Giuggioli, L., Perna, A., Escobedo, R., Lecheval, V., Sire, C., et al. (2017). Identifying influential neighbors in animal flocking. *PLOS Computational Biology* 13(11): e1005822. doi: https://doi.org/10.1371/journal.pcbi.1005822.

Johnstone, R.A., and Manica, A. (2011). Evolution of personality differences in leadership. *Proceedings of the National Academy of Sciences of the United States of America* 108(20)**,** 8373-8378. doi: https://doi.org/10.1073/pnas.1102191108.

Jolles, J.W., Fleetwood-Wilson, A., Nakayama, S., Stumpe, M.C., Johnstone, R.A., and Manica, A. (2015). The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks. *Animal Behaviour* 99**,** 147-153. doi: https://doi.org/10.1016/j.anbehav.2014.11.004.

Kappeler, P.M. (2019). A framework for studying social complexity. *Behavioral Ecology and Sociobiology* 73(1): 13 (2019). doi: https://doi.org/10.1007/s00265-018-2601-8.

King, A.J. (2010). Follow me! I'm a leader if you do; I'm a failed initiator if you don't? *Behavioural Processes* 84(3)**,** 671-674. doi: https://doi.org/10.1016/j.beproc.2010.03.006.

King, A.J., and Cowlishaw, G. (2007). When to use social information: the advantage of large group size in individual decision making. *Biology Letters* 3(2)**,** 137-139. doi: https://doi.org/10.1098/rsbl.2007.0017.

King, A.J., and Cowlishaw, G. (2009). All together now: behavioural synchrony in baboons. *Animal Behaviour* 78(6)**,** 1381-1387. doi: https://doi.org/10.1016/j.anbehav.2009.09.009.

King, A.J., Douglas, C.M.S., Huchard, E., Isaac, N.J.B., and Cowlishaw, G. (2008). Dominance and Affiliation Mediate Despotism in a Social Primate. *Current Biology* 18(23)**,** 1833-1838. doi: https://doi.org/10.1016/j.cub.2008.10.048.

King, A.J., Johnson, D.D.P., and Van Vugt, M. (2009). The Origins and Evolution of Leadership. *Current Biology* 19(19)**,** 911-916. doi: https://doi.org/10.1016/j.cub.2009.07.027.

King, A.J., and Sueur, C. (2011). Where Next? Group Coordination and Collective Decision Making by Primates. *International Journal of Primatology* 32(6)**,** 1245-1267. doi: https://doi.org/10.1007/s10764-011-9526-7.

Klamser, P.P., Gomez-Nava, L., Landgraf, T., Jolles, J.W., Bierbach, D., and Romanczuk, P. (2021). Impact of Variable Speed on Collective Movement of Animal Groups. *Frontiers in Physics* 9: 715996. doi: https://doi.org/10.3389/fphy.2021.715996.

Koykka, C., and Wild, G. (2015). The evolution of group dispersal with leaders and followers. *Journal of Theoretical Biology* 371**,** 117-126. doi: https://doi.org/10.1016/j.jtbi.2015.02.008.

Krause, J. (1993). The Relationship between Foraging and Shoal Position in a Mixed Shoal of Roach (*Rutilus rutilus*) and Chub (*Leuciscus cephalus*) - a Field-Study. *Oecologia* 93(3)**,** 356-359. doi: https://doi.org/10.1007/Bf00317878.

Krause, J., Croft, D.P., and James, R. (2007). Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology* 62(1)**,** 15-27. doi: https://doi.org/10.1007/s00265-007-0445-8.

Krause, J., and Godin, J.G.J. (1995). Predator Preferences for Attacking Particular Prey Group Sizes - Consequences for Predator Hunting Success and Prey Predation Risk. *Animal Behaviour* 50**,** 465-473. doi: https://doi.org/10.1006/anbe.1995.0260.

Krause, J., Hoare, D., Krause, S., Hemelrijk, C.K., and Rubenstein, D.I. (2000). Leadership in fish shoals. *Fish and Fisheries* 1(1)**,** 82-89. doi: https://doi.org/10.1111/j.1467-2979.2000.tb00001.x.

Krause, J., and Ruxton, G. (2002). *Living in Groups.* USA: Oxford University Press.

Krueger, K., Flauger, B., Farmer, K., and Hemelrijk, C. (2014). Movement initiation in groups of feral horses. *Behavioural Processes* 103**,** 91-101. doi: https://doi.org/10.1016/j.beproc.2013.10.007.

Kurvers, R.H.J.M., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S.E., Ydenberg, R.C., et al. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour* 78(2)**,** 447-453. doi: https://doi.org/10.1016/j.anbehav.2009.06.002.

Laland, K.N., and Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology* 9(5)**,** 493-499. doi: https://doi.org/10.1093/beheco/9.5.493.

Lamprecht, J. (1996). What makes an individual the leader of its group? An evolutionary concept of distance regulation and leadership. *Social Science Information* 35(4)**,** 595-617. doi: https://doi.org/10.1177/053901896035004001.

Lerch, B.A., Abbott, K.C., Archie, E.A., and Alberts, S.C. (2021). Better baboon break-ups: collective decision theory of complex social network fissions. *Proceedings of the Royal Society B-Biological Sciences* 288(1964): 20212060. doi: https://doi.org/10.1098/rspb.2021.2060.

Lesmerises, F., Johnson, C.J., and St-Laurent, M.H. (2018). Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. *Animal Behaviour* 140**,** 39-47. doi: https://doi.org/10.1016/j.anbehav.2018.03.014.

Makagon, M.M., McCowan, B., and Mench, J.A. (2012). How can social network analysis contribute to social behavior research in applied ethology? *Applied Animal Behaviour Science* 138(3-4)**,** 152-161. doi: https://doi.org/10.1016/j.applanim.2012.02.003.

Markham, A.C., Gesquiere, L.R., Alberts, S.C., and Altmann, J. (2015). Optimal group size in a highly social mammal. *Proceedings of the National Academy of Sciences of the United States of America* 112(48)**,** 14882-14887. doi: https://doi.org/10.1073/pnas.1517794112.

Marshall, J.A.R., Kurvers, R.H.J.M., Krause, J., and Wolf, M. (2019). Quorums enable optimal pooling of independent judgements in biological systems. *eLife* 8: e40368. doi: https://doi.org/10.7554/eLife.40368.

Merkle, J.A., Sigaud, M., and Fortin, D. (2015). To follow or not? How animals in fusion-fission societies handle conflicting information during group decision-making. *Ecology Letters* 18(8)**,** 799-806. doi: https://doi.org/10.1111/ele.12457.

Michelangeli, M., Cote, J., Chapple, D.G., Sih, A., Brodin, T., Fogarty, S., et al. (2020). Sex-dependent personality in two invasive species of mosquitofish. *Biological Invasions* 22(4)**,** 1353-1364. doi: https://doi.org/10.1007/s10530-019-02187-3.

Michelena, P., Gautrais, J., Gerard, J.F., Bon, R., and Deneubourg, J.L. (2008). Social cohesion in groups of sheep: Effect of activity level, sex composition and group size. *Applied Animal Behaviour Science* 112(1-2)**,** 81-93. doi: https://doi.org/10.1016/j.applanim.2007.06.020.

Michelena, P., Henric, K., Angibault, J.M., Gautrais, J., Lapeyronie, P., Porter, R.H., et al. (2005). An experimental study of social attraction and spacing between the sexes in sheep. *Journal of Experimental Biology* 208(23)**,** 4419-4426. doi: https://doi.org/10.1242/jeb.01909.

Michelena, P., Jeanson, R., Deneubourg, J.L., and Sibbald, A.M. (2010). Personality and collective decision-making in foraging herbivores. *Proceedings of the Royal Society B-Biological Sciences* 277(1684)**,** 1093-1099. doi: https://doi.org/10.1098/rspb.2009.1926.

Michelena, P., Sibbald, A.M., Erhard, H.W., and McLeod, J.E. (2009). Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behavioral Ecology* 20(1)**,** 145-152. doi: https://doi.org/10.1093/beheco/arn126.

Milles, A., Dammhahn, M., and Grimm, V. (2020). Intraspecific trait variation in personality-related movement behavior promotes coexistence. *Oikos* 129(10)**,** 1441-1454. doi: https://doi.org/10.1111/oik.07431.

Morand-Ferron, J., and Giraldeau, L.A. (2010). Learning behaviorally stable solutions to producer-scrounger games. *Behavioral Ecology* 21(2)**,** 343-348. doi: https://doi.org/10.1093/beheco/arp195.

Mueller, T., O'Hara, R.B., Converse, S.J., Urbanek, R.P., and Fagan, W.F. (2013). Social Learning of Migratory Performance. *Science* 341(6149)**,** 999-1002. doi: https://doi.org/10.1126/science.1237139.

Nagy, M., Akos, Z., Biro, D., and Vicsek, T. (2010). Hierarchical group dynamics in pigeon flocks. *Nature* 464(7290)**,** 890-893. doi: https://doi.org/10.1038/nature08891.

Nakayama, S., Stumpe, M.C., Manica, A., and Johnstone, R.A. (2013). Experience overrides personality differences in the tendency to follow but not in the tendency to lead. *Proceedings of the Royal Society B-Biological Sciences* 280(1769): 20131724. doi: https://doi.org/10.1098/rspb.2013.1724.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., et al. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* 105(49)**,** 19052-19059. doi: https://doi.org/10.1073/pnas.0800375105.

O'Bryan, L.R., Abaid, N., Nakayama, S., Dey, T., King, A.J., Cowlishaw, G., et al. (2019). Contact Calls Facilitate Group Contraction in Free-Ranging Goats (*Capra aegagrus hircus*). *Frontiers in Ecology and Evolution* 7: 00073. doi: https://doi.org/10.3389/fevo.2019.00073.

Papageorgiou, D., and Farine, D.R. (2020). Shared decision-making allows subordinates to lead when dominants monopolize resources. *Science Advances* 6(48): eaba5881. doi: https://doi.org/10.1126/sciadv.aba5881.

Patrick, S.C., Pinaud, D., and Weimerskirch, H. (2017). Boldness predicts an individual's position along an exploration-exploitation foraging trade-off. *Journal of Animal Ecology* 86(5)**,** 1257-1268. doi: https://doi.org/10.1111/1365-2656.12724.

Peterson, R.O., Jacobs, A.K., Drummer, T.D., Mech, L.D., and Smith, D.W. (2002). Leadership behavior in relation to dominance and reproductive status in gray wolves, *Canis lupus*. *Canadian Journal of Zoology* 80(8)**,** 1405-1412. doi: https://doi.org/10.1139/Z02-124.

Pettit, B., Akos, Z., Vicsek, T., and Biro, D. (2015). Speed Determines Leadership and Leadership Determines Learning during Pigeon Flocking. *Current Biology* 25(23)**,** 3132-3137. doi: https://doi.org/10.1016/j.cub.2015.10.044.

Pillot, M.H., Gautrais, J., Gouello, J., Michelena, P., Sibbald, A., and Bon, R. (2010). Moving together: Incidental leaders and naive followers. *Behavioural Processes* 83(3)**,** 235-241. doi: https://doi.org/10.1016/j.beproc.2009.11.006.

Powers, S.T., and Lehmann, L. (2014). An evolutionary model explaining the Neolithic transition from egalitarianism to leadership and despotism. *Proceedings of the Royal Society B-Biological Sciences* 281(1791): 20141349. doi: https://doi.org/10.1098/rspb.2014.1349.

Ramos, A., Manizan, L., Rodriguez, E., Kemp, Y.J.M., and Sueur, C. (2018). How can leadership processes in European bison be used to improve the management of free-roaming herds. *European Journal of Wildlife Research* 64(2): 18 (2018). doi: https://doi.org/10.1007/s10344-018-1175-0.

Ramos, A., Petit, O., Longour, P., Pasquaretta, C., and Sueur, C. (2015). Collective decision making during group movements in European bison, *Bison bonasus*. *Animal Behaviour* 109**,** 149-160. doi: https://doi.org/10.1016/j.anbehav.2015.08.016.

Ramseyer, A., Boissy, A., Thierry, B., and Dumont, B. (2009). Individual and social determinants of spontaneous group movements in cattle and sheep. *Animal* 3(9)**,** 1319-1326. doi: https://doi.org/10.1017/S1751731109004790.

Rands, S.A., Cowlishaw, G., Pettifor, R.A., Rowcliffe, J.M., and Johnstone, R.A. (2003). Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423(6938)**,** 432-434. doi: https://doi.org/10.1038/nature01630.

Rands, S.A., Cowlishaw, G., Pettifor, R.A., Rowcliffe, J.M., and Johnstone, R.A. (2008). The emergence of leaders and followers in foraging pairs when the qualities of individuals differ. *BMC Evolutionary Biology* 8: 51 (2008). doi: https://doi.org/10.1186/1471-2148-8-51.

Rands, S.A., Pettifor, R.A., Rowcliffe, J.M., and Cowlishaw, G. (2006). Social foraging and dominance relationships: the effects of socially mediated interference. *Behavioral Ecology and Sociobiology* 60(4)**,** 572-581. doi: https://doi.org/10.1007/s00265-006-0202-4.

Robbins, M.M. (1995). A Demographic-Analysis of Male Life-History and Social-Structure of Mountain Gorillas. *Behaviour* 132**,** 21-47. doi: https://doi.org/10.1163/156853995x00261.

Rosenthal, S.B., Twomey, C.R., Hartnett, A.T., Wu, H.S., and Couzin, I.D. (2015). Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. *Proceedings of the National Academy of Sciences of the United States of America* 112(15)**,** 4690-4695. doi: https://doi.org/10.1073/pnas.1420068112.

Rubenstein, D.R. (2011). Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proceedings of the National Academy of Sciences of the United States of America* 108**,** 10816-10822. doi: https://doi.org/10.1073/pnas.1100303108.

Sasaki, T., Mann, R.P., Warren, K.N., Herbert, T., Wilson, T., and Biro, D. (2018). Personality and the collective: bold homing pigeons occupy higher leadership ranks in flocks. *Philosophical Transactions of the Royal Society B-Biological Sciences* 373(1746): 20170038. doi: https://doi.org/10.1098/rstb.2017.0038.

Schlaepfer, M.A., Runge, M.C., and Sherman, P.W. (2002). Ecological and evolutionary traps. *Trends in Ecology & Evolution* 17(10)**,** 474-480. doi: https://doi.org/10.1016/S0169-5347(02)02580-6.

Senior, A.M., Lihoreau, M., Charleston, M.A., Buhl, J., Raubenheimer, D., and Simpson, S.J. (2016). Adaptive collective foraging in groups with conflicting nutritional needs. *Royal Society Open Science* 3(4): 150638. doi: https://doi.org/10.1098/rsos.150638.

Shell, W.A., and Rehan, S.M. (2018). Behavioral and genetic mechanisms of social evolution: insights from incipiently and facultatively social bees. *Apidologie* 49(1)**,** 13-30. doi: https://doi.org/10.1007/s13592-017-0527-1.

Sigaud, M., Merkle, J.A., Cherry, S.G., Fryxell, J.M., Berdahl, A., and Fortin, D. (2017). Collective decision-making promotes fitness loss in a fusion-fission society. *Ecology Letters* 20(1)**,** 33-40. doi: https://doi.org/10.1111/ele.12698.

Sih, A., Spiegel, O., Godfrey, S., Leu, S., and Bull, C.M. (2018). Integrating social networks, animal personalities, movement ecology and parasites: a framework with examples from a lizard. *Animal Behaviour* 136**,** 195-205. doi: https://doi.org/10.1016/j.anbehav.2017.09.008.

Silk, M.J., Croft, D.P., Tregenza, T., and Bearhop, S. (2014). The importance of fission-fusion social group dynamics in birds. *Ibis* 156(4)**,** 701-715. doi: https://doi.org/10.1111/ibi.12191.

Simons, A.M. (2004). Many wrongs: the advantage of group navigation. *Trends in Ecology & Evolution* 19(9)**,** 453-455. doi: https://doi.org/10.1016/j.tree.2004.07.001.

Smith, J.E., Gavrilets, S., Mulder, M.B., Hooper, P.L., El Mouden, C., Nettle, D., et al. (2016). Leadership in Mammalian Societies: Emergence, Distribution, Power, and Payoff. *Trends in Ecology & Evolution* 31(1)**,** 54-66. doi: https://doi.org/10.1016/j.tree.2015.09.013.

Squires, V.R., and Daws, G.T. (1975). Leadership and dominance relationships in Merino and Border Leicester sheep. *Applied Animal Ethology* 1(3)**,** 263-274. doi: https://doi.org/10.1016/0304-3762(75)90019-X.

Strandburg-Peshkin, A., Farine, D.R., Crofoot, M.C., and Couzin, I.D. (2017). Habitat and social factors shape individual decisions and emergent group structure during baboon collective movement. *eLife* 6: e19505. doi: https://doi.org/10.7554/eLife.19505.

Strandburg-Peshkin, A., Papageorgiou, D., Crofoot, M.C., and Farine, D.R. (2018). Inferring influence and leadership in moving animal groups. *Philosophical Transactions of the Royal Society B-Biological Sciences* 373(1746): 20170006. doi: https://doi.org/10.1098/rstb.2017.0006.

Stuber, E.F., Carlson, B., and Jesmer, B.R. (2022). Spatial personalities: a meta-analysis of consistent individual differences in spatial behavior. *Behavioral Ecology* 33(3)**,** 477-486. doi: https://doi.org/10.1093/beheco/arab147.

Stutz, R.S., Bergvall, U.A., Leimar, O., Tuomi, J., and Rautio, P. (2018). Cohesiveness reduces foraging efficiency in a social herbivore. *Animal Behaviour* 135**,** 57-68. doi: https://doi.org/10.1016/j.anbehav.2017.11.004.

Sueur, C., Deneubourg, J.L., and Petit, O. (2012). From Social Network (Centralized vs. Decentralized) to Collective Decision-Making (Unshared vs. Shared Consensus). *PLOS ONE* 7(2): e32566. doi: https://doi.org/10.1371/journal.pone.0032566.

Sueur, C., King, A.J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., et al. (2011). Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos* 120(11)**,** 1608-1617. doi: https://doi.org/10.1111/j.1600-0706.2011.19685.x.

Sueur, C., and Petit, O. (2010). Signals use by leaders in *Macaca tonkeana* and *Macaca mulatta*: group-mate recruitment and behaviour monitoring. *Animal Cognition* 13(2)**,** 239-248. doi: https://doi.org/10.1007/s10071-009-0261-9.

Sumpter, D.J. (2006). The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B-Biological Sciences* 361(1465)**,** 5-22. doi: https://doi.org/10.1098/rstb.2005.1733.

Sumpter, D.J.T. (2010). *Collective Animal Behavior.* Princeton University Press.

Sumpter, D.J.T., Krause, J., James, R., Couzin, I.D., and Ward, A.J.W. (2008). Consensus Decision Making by Fish. *Current Biology* 18(22)**,** 1773-1777. doi: https://doi.org/10.1016/j.cub.2008.09.064.

Sumpter, D.J.T., and Pratt, S.C. (2009). Quorum responses and consensus decision making. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364(1518)**,** 743-753. doi: https://doi.org/10.1098/rstb.2008.0204.

Sumpter, D.J.T., Szorkovszky, A., Kotrschal, A., Kolm, N., and Herbert-Read, J.E. (2018). Using activity and sociability to characterize collective motion. *Philosophical Transactions of the Royal Society B-Biological Sciences* 373(1746): 20170015. doi: https://doi.org/10.1098/rstb.2017.0015.

Taylor, D.B., Price, I.R., Brown, W.Y., and Hincha, G.N. (2011). Effects of Merino flock size, paddock complexity and time of day on response to trained leaders. *Small Ruminant Research* 97(1-3)**,** 35-40. doi: https://doi.org/10.1016/j.smallrumres.2011.01.010.

Tokuyama, N., and Furuichi, T. (2017). Leadership of old females in collective departures in wild bonobos (*Pan paniscus*) at Wamba. *Behavioral Ecology and Sociobiology* 71(3): 55 (2017). doi: https://doi.org/10.1007/s00265-017-2277-5.

Tomkins, J.L., and Hazel, W. (2007). The status of the conditional evolutionarily stable strategy. *Trends in Ecology & Evolution* 22(10)**,** 522-528. doi: https://doi.org/10.1016/j.tree.2007.09.002.

Toscano, B.J., Gownaris, N.J., Heerhartz, S.M., and Monaco, C.J. (2016). Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia* 182(1)**,** 55-69. doi: https://doi.org/10.1007/s00442-016-3648-8.

Ward, A., and Webster, M. (2016). *Sociality: The Behaviour of Group-Living Animals.* Springer Cham.

Ward, A.J.W., Krause, J., and Sumpter, D.J.T. (2012). Quorum Decision-Making in Foraging Fish Shoals. *PLOS ONE* 7(3): e32411. doi: https://doi.org/10.1371/journal.pone.0032411.

Ward, A.J.W., Thomas, P., Hart, P.J.B., and Krause, J. (2004). Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology* 55(6)**,** 561-568. doi: https://doi.org/10.1007/s00265-003-0751-8.

Webber, Q.M.R., Laforge, M.P., Bonar, M., Robitaille, A.L., Hart, C., Zabihi-Seissan, S., et al. (2020). The Ecology of Individual Differences Empirically Applied to Space-Use and Movement Tactics. *American Naturalist* 196(1)**,** E1-E15. doi: https://doi.org/10.1086/708721.

Westley, P.A.H., Berdahl, A.M., Torney, C.J., and Biro, D. (2018). Collective movement in ecology: from emerging technologies to conservation and management. *Philosophical Transactions of the Royal Society B-Biological Sciences* 373(1746): 20170004. doi: https://doi.org/10.1098/rstb.2017.0004.

Wey, T., Blumstein, D.T., Shen, W., and Jordan, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour* 75**,** 333-344. doi: https://doi.org/10.1016/j.anbehav.2007.06.020.

Wolf, M., and McNamara, J.M. (2013). Adaptive between-individual differences in social competence. *Trends in Ecology & Evolution* 28(5)**,** 253-254. doi: https://doi.org/10.1016/j.tree.2013.01.006.

Wolf, M., van Doorn, G.S., and Weissing, F.J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences of the United States of America* 105(41)**,** 15825-15830. doi: https://doi.org/10.1073/pnas.0805473105.