Leadership in Animal Groups: The Interplay between Individual Traits and Coordination Mechanisms

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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.

Keywords: inter-individual variation[1]; collective behaviour[2]; followers[3]; leaders[4]; movement ecology[5]; sociality[6]

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). However, a critical aspect of collective coordination remains insufficiently understood — the variable level of influence that individuals have within groups (Delgado et al., 2018).

Social behaviour evolved independently in several different taxa (Krause and Ruxton, 2002; Ward and Webster, 2016). It offers various 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). Group living, however, presents challenges, with maintaining group cohesion being of prime importance. To maintain cohesion, animals combine environmental stimuli, monitor the movement of other group members, and adhere to behavioural rules facilitating within-group synchronisation (Couzin et al., 2002; Couzin and Krause, 2003; Sumpter et al., 2008; Kappeler, 2019; 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, repulsion, and/or behavioural amplification 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).

A dichotomous approach, that classifies individuals into leaders or followers provides important insights into coordination dynamics within a group. A fundamental question is whether leadership is an *intrinsic* trait that is selected for and hence 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 the same 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, it remains unclear whether leadership itself or associated traits, such as travelling speed and spatiotemporal position within the group, have any fitness benefits and are thus favoured by natural selection (Pettit et al., 2015; Strandburg-Peshkin et al., 2018). In this review, we aim to explore the literature on social evolution and leadership, highlighting knowledge gaps critical for understanding the *proximate* and *ultimate* properties of leadership in a social context.

The role of leadership for social information transmission

Social information, acquired by observing or communicating with knowledgeable conspecifics (Lesmerises et al., 2018), offers a faster alternative to personal information acquired through direct interactions with the environment (Sigaud et al., 2017; Vartparonian and Leu, 2024). This process is analogous to leadership, where a subset of group members, here the informed individuals, influence collective decision-making (Allen et al., 2020). In this context, observing the behaviour of knowledgeable individuals can influence the actions of naïve conspecifics, resembling a form of leader-follower dynamic. However, the reliability of socially transmitted information is paramount, as it may negatively impact the fitness of group members (Guttal and Couzin, 2010), particularly if the initial assessment of environmental quality is flawed (Sigaud et al., 2017). In situations where reliance on socially acquired information is exclusive and environmental cues are misinterpreted, there is a risk of sub-optimal behaviours and the selection of ecological traps (Giraldeau et al., 2002; Schlaepfer et al., 2002; Donaldson et al., 2012). This risk is further increased when individuals act as leaders but are misinformed, potentially leading to a group-wide loss of fitness if followers excessively rely on inaccurate information (Laland and Williams, 1998). For instance, the observed tendency of naïve bison (*Bison bison bison*) to follow informed individuals foraging on agricultural land despite the increased risk of mortality due to hunting illustrates the potential consequences of misinformed leadership (Sigaud et al., 2017). Similarly, bottlenose dolphin pods (*Tursiops aduncus*) led by misinformed individuals feeding on bycatch, experienced higher mortality rates due to collisions with boats (Donaldson et al., 2012). Thus, within the context of collective decision-making, the role of leaders on the use of social information and its outcomes is a critical aspect requiring further research.

The role of leadership in group synchronisation

Leadership's impact on group cohesion and behavioural synchronization can vary based on the interplay between individual characteristics and the underlying mechanisms influencing group dynamics. While simple interaction rules such as attraction, alignment, short-range repulsion, and behavioural amplification among neighbouring individuals play a fundamental role in facilitating synchronisation (Camazine et al., 2001; Couzin, 2009; Sumpter, 2010), the effectiveness of these rules can be further influenced by a subset of individuals that influence the behaviour of conspecifics. These leading individuals, if recognized by followers, ultimately promote greater synchrony among group members. For instance, in social systems where individuals discern between group members, conspecifics are likely to select specific interaction partners based on their shared history and identity (Gascuel et al., 2021).

However, the emergence of synchronization among group members can also be facilitated solely through the combination of these simple interaction rules and allelomimetic interactions (Camazine et al., 2001; Gautrais et al., 2007). In such cases, the leader-follower relationship may be case-specific, emerging as a consequence of localized interactions among conspecifics in proximity within "interaction neighbourhoods" (Rosenthal et al., 2015; Herbert-Read, 2016; Jiang et al., 2017). This dynamic suggests that the effectiveness of group cohesion relies on the spatiotemporal synchrony of activities among group members, rather than being exclusively dependent on a particular type of behaviour or the presence of identifiable leaders (Gautrais et al., 2007; King and Cowlishaw, 2009).

Nonetheless, the costs associated with maintaining cohesion may outweigh the benefits, leading to a decrease in behavioural synchrony among group members. In stable social systems, this process helps regulate optimal group size (Markham et al., 2015). In fission-fusion systems, characterized by frequent changes in group size and composition, 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). The leader-follower relationship may play an important role in this process by facilitating effective responses to behavioural asynchrony. Notably, in situations where behavioural asynchrony arises, a subset of individuals responsive to such cues may choose to depart or join others, thereby contributing to intragroup interactions through fission-fusion events.

Leadership dynamics in heterogenous groups

Within-group heterogeneity may arise due to variation in access to information, for example, due to its spatiotemporal occurrence or individuals' varying internal states (King and Cowlishaw, 2007). Such variation can alter group decision-making and lead to the evolution of conflict resolution mechanisms, such as quorum responses (Conradt and List, 2009; Papageorgiou and Farine, 2020) or voting (Ramos et al., 2015). For instance, once a critical number of group members exhibit a certain behaviour, for example, leaving a foraging patch, the entire group may follow (Sumpter and Pratt, 2009; Ward et al., 2012; Marshall et al., 2019).

Nonetheless, group members often exhibit consistent differences in movement patterns, driven by factors such as foraging strategies, habitat preferences, and social interactions, leading to assortative mixing among conspecifics (Toscano et al., 2016). This intraspecific trait variation affects foraging, influencing resource acquisition and energetic expenditures among group members (Milles et al., 2020). Moreover, individuals appear to modulate their movement across a foraging resource gradient, adjusting their behaviour to optimize access to foraging resources as resource distribution shifts from uniform to clumped (Webber et al., 2020). While some individuals exhibit adaptive phenotypes, showing plasticity in adjusting their space use across the resource gradient, there is high interindividual variation in the direction and magnitude of this plasticity, with some individuals showing no plasticity at all (Webber et al., 2020). Importantly, a recent meta-analysis further supports the widespread nature of intraspecific variation in movement behaviour across animal taxa (Stuber et al., 2022).

The leader-follower relationship is intricately connected with the within-group heterogeneity, if individuals vary in the propensity and plasticity to lead or follow conspecifics (Harcourt et al., 2009). In social systems where certain individuals consistently exhibit marked differences in their influence on the group, leaders emerge (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), offering benefits, such as reducing free-riding and coordination errors (Frank, 2003; Hooper et al., 2010). Followers, on the other hand, are often less likely to co-opt leadership roles, indicating a degree of specialization in decision-making roles within the group (Nakayama et al., 2013).

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. For instance, subordinate guineafowl individuals (*Acryllium*

vulturinum) exhibit behavioural flexibility in response to dominant individuals monopolising resources, choosing to move away and triggering the group to abandon a food patch once a critical threshold of departed subordinates is reached (Papageorgiou and Farine, 2020).

Contrasts between leaders and followers

The contrasts between leaders and followers might stem from variations in social attraction and responsiveness to 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). Followers are often socially responsive and prioritise social interactions and proximity to other conspecifics. Whereas leaders are less socially responsive, favouring environmental cues and preferences over group cohesion (Lamprecht, 1996; Wolf et al., 2008; Johnstone and Manica, 2011; Pettit et al., 2015).

The coexistence of followers and leaders in a population is hypothesised to be maintained through negative frequency-dependent selection because the benefits of social responsiveness vary among leaders and followers (Wolf et al., 2008; Wolf and McNamara, 2013). When group size and/or population density increase, individuals with lower sociability, such as leaders, are increasingly negatively affected, thereby selecting against them. Instead selection favours followers. In contrast, when group size and/or population density decrease, selection favours leaders. Theoretical models indicate that even in large groups, only a small proportion of leaders is sufficient for high coordination accuracy (Couzin et al., 2005). Hence, the frequency-dependent coexistence of leader-follower strategies remains evolutionarily stable even in large groups (Guttal and Couzin, 2010). A socially responsive cohort, receptive to socially transmitted cues, can act as a social adhesive, maintaining group cohesion. Conversely, a socially unresponsive cohort determines group movement and decision-making (Harcourt et al., 2009; Pettit et al., 2015).

The value of leadership 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). In this context, the distinction between net fitness gains for leaders and followers blurs. Both leaders and followers may benefit from their individual behaviour, for instance, in a scenario where leaders lead naïve individuals to known resources, they gain an advantage by accessing it first (Merkle et al., 2015), while simultaneously benefiting from the dilution effect as others join them (Hamilton, 1971). Conversely, following is advantageous for naïve individuals, as they discover food patches faster than if they had to forage independently. For example, Rands and colleagues (2003) introduced a state-dependent game-theoretical model that demonstrates the emergence of leaders in foraging dyads when individuals have different

158 energetic requirements, enabling them to synchronise their foraging activities (Rands et al., 2003; Rands et al., 2006;
159 Rands et al., 2008). Empirically, this effect has been observed in food-deprived fish occupying front positions in shoals
160 more frequently and influencing the movement preferences of others (Krause, 1993; Hansen et al., 2015b). Likewise,
161 lactating zebras, driven by their elevated nutritional needs, initiate group movement more frequently, highlighting the
162 dynamic interplay between individual needs and the emergence of leadership within the group (Fischhoff et al., 2007).

163 Analogously, gregarious species often engage in a producer-scrounger game, where some individuals forage
164 independently (producers) and others rely on the discoveries of others (scavengers). This tendency is supported by
165 studies showing that the scrounging tactic tends to spread within populations (Dumke et al., 2016). Drawing parallels
166 to leader-follower dynamics, we suggest that leaders can be likened to producers, while followers can be considered
167 scroungers. The decision to lead or follow is influenced by the perceived payoffs of each strategy, and individuals rely
168 on social cues to make these decisions. Individuals that forage effectively alone (producers/leaders) likely benefit
169 conspecifics by providing information about the availability of resources (Morand-Ferron and Giraldeau, 2010). While
170 theoretical models provide insights into these dynamics, the lack of empirical data limits the generalizability of these
171 findings.

172 Nonetheless, despite potential costs like increased predation risk from occupying peripheral positions as a leader
173 (Gillet et al., 2011), theoretical models suggest that voluntary followership can maintain this relationship if leadership
174 enhances group productivity (Hooper et al., 2010; Powers and Lehmann, 2014). However, a comprehensive
175 understanding of this phenomenon requires consideration of both within-group and between-group effects. Within-
176 group analysis suggests that followers receive greater benefits compared to leaders, but leader-follower dynamics may
177 not emerge in homogeneous populations unless both leaders and followers benefit (Koykka and Wild, 2015).
178 Conversely, incorporating between-group effects reveals a more nuanced perspective. While leaders may face
179 challenges, such as increased predation risk, they benefit from the presence of followers during inter-group conflicts
180 and competitions with leaders from other groups (Gavrilets and Fortunato, 2014). Empirical evidence from a range of
181 species supports the notion of unequal energetic expenditures of high-ranking individuals during intergroup conflicts.
182 Studies on chimpanzees (*Pan troglodytes*) (Amsler, 2010) and blue monkeys (*Cercopithecus mitis*) (Cords, 2007)
183 show that territorial border patrols and defending the communal feeding territory are undertaken more frequently by
184 dominant individuals. These findings highlight the role of individuals likely occupying leadership roles in resource

defence. In grey wolf packs, older and more aggressive males assess opponents from rival groups and adjust their behaviour based on relative pack size. Packs with a numerical advantage are more likely to engage in aggressive intergroup interaction (Cassidy et al., 2017). Consequently, the net benefit of leader-follower relationships may extend beyond immediate group dynamics, encompassing a broader context of group competition and individual self-interest. Thus we argue, that a complete understanding of leader-follower dynamics requires examination of both within-group and between-group interactions, considering the implications for group productivity and the potential costs and benefits for leaders and followers.

Leadership in socially stratified systems

In gregarious species, social stratification often leads to the development of hierarchies, which can reduce instances of free-riding and aggression within the group (Issa and Edwards, 2006). Dominant individuals tend to monopolise resources and occupy advantageous positions within the group (Ward and Webster, 2016). While 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), disentangling the effect of social hierarchy is challenging due to its interplay with other factors. These factors include 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). Additionally, in some species, the most dominant individual is not the sole leader; instead, leadership is distributed among several high-ranking group members (Peterson et al., 2002; King et al., 2008).

What is more, most animal social interaction patterns are non-random, with individuals connected to different numbers of conspecifics or having ties of varying strength. This variation suggests that individuals differ in their importance within the social interaction network (Wey et al., 2008). Specifically, focusing on social network metrics can shed light on keystone individuals within a group, potentially underlying leadership dynamics (Makagon et al., 2012; Sumpter et al., 2018). For instance, individuals with a high degree or high centrality are likely candidates for holding key social positions (Krause et al., 2009; Sih et al., 2009). Furthermore, indirect connections may play a crucial role in determining leadership, with leaders potentially exhibiting a high reach (Sih et al., 2009). Measures such as eigenvector centrality have also been identified as a strong predictor of successful recruitment (Sueur et al., 2018).

While some progress has been made in this area, with theoretical research highlighting 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), further empirical studies are needed to improve our limited understanding of the role of leaders in the network (Briard et al., 2015; Lerch et al., 2021).

Notably, dominance plays an important role in within- and between-group interactions and conflict mediation (Smith et al., 2016). Dominant individuals, often leaders, may induce followership by acting independently and being less socially responsive (King et al., 2009), which could also mean that they are less connected in their social network. Alternatively, strongly connected individuals who occupy key social positions may disproportionately influence their group (King, 2010; Briard et al., 2015; Tokuyama and Furuichi, 2017; Strandburg-Peshkin et al., 2018). The contrasting dynamics between dominance- and social network position-mediated leadership underscores its nuanced nature. While dominance-driven leaders may shape group dynamics through coercion, socially central individuals may leverage their network positions to wield influence. The key distinction is how leadership emerges and is maintained within these systems.

Future directions of leadership research

Researchers are successively broadening the list of individual characteristics associated with leadership, encompassing factors like movement characteristics (Gueron et al., 1996; Couzin et al., 2005; Conradt and List, 2009; Sasaki et al., 2018), 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.

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, is it linked with certain individual characteristics, such as size, sex, personality, or social status, which may remain constant or semi-persistent over time? Or does leadership emerge as a consequence of group coordination, driven by spatiotemporal variation in traveling velocity and positioning among group members? These two scenarios are not mutually exclusive, necessitating rigorous experiments to disentangle

the interaction between individual-driven leader characteristics (Ramseyer et al., 2009), and group-driven allelomimetic processes (Taylor et al., 2011).

Moreover, understanding the consistency of leadership is crucial. Does the same individual or a subset of individuals repeatedly assume leadership roles, or does leadership change between movement events? Examining the repeatability and context-dependence of leadership can reveal patterns of stability and variability of leader-follower dynamics. The consistency of leadership may also depend on socio-ecological factors and potentially have a heritable component. Exploration of the impacts of these factors on leadership can provide insights into its adaptive value and contribute to our understanding of the evolutionary processes shaping social systems. If leaders are consistently more successful in acquiring resources or mating partners, then this could lead to the selection of traits that make individuals more likely to become leaders. This feedback loop could potentially drive the evolution of specialized leadership roles within a population.

A noteworthy challenge in studying leader-follower relationships is the need to monitor multiple potential decision-makers in a group simultaneously, 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). This necessitates the ability to track the movements and behaviours of multiple group members all at the same time, particularly at the movement initiation stage, across the entire group (Ramseyer et al., 2009; Nagy et al., 2010; Herbert-Read, 2016).

Furthermore, the investigation of how leadership differs between species, populations, and different social groups within the context of social responsiveness across the sociability spectrum can provide valuable insights. One approach to address this issue is to establish an artificial selection experiment, where lines of animals are selected based on their sociability score, ranging from low to high sociable type. By establishing homogenous and mixed groups of animals across the sociability spectrum, researchers can investigate if social responsiveness affects the formation of leader-follower dynamics, movement coordination, decision-making, and social organization.

Despite the ongoing effort to unravel the mechanisms underpinning leadership in gregarious animals, little is known about the effect of leaders on group decision-making in economically valuable species (Briard et al., 2015). Beyond the academic inquiry, understanding the impact of leadership in these species could have significant practical implications. Leveraging leader-follower relationships for practical applications, such as improving agricultural

practices, informing conservation strategies, and enhancing animal welfare, holds promise. For example, by optimizing group composition and strategically utilizing individuals with leadership predispositions, we may be able to enhance productivity, welfare, and overall management of animal populations.

Concluding Remarks

In conclusion, we argue that leadership plays a crucial role in the functioning of animal social systems of different complexity. However, it is important to acknowledge that the nature of leadership can vary significantly depending on the context in which it occurs across species, populations, and even within different social groups of the same species. While this manuscript primarily offers a vertebrate-centric explanation of leader-follower relationships, we recognize the richness of sociality among invertebrates. Their intricate collective behaviours present an equally promising avenue for deeper insights, urging inventive studies to unravel the dynamics of leadership across taxa.

Over the past two decades, methodological advances in animal tracking technologies and statistical methods have offered valuable insights into animal spatial behaviours (Kays et al., 2015; Hughey et al., 2018; Tuia et al., 2022). While traditional GPS collars offer simultaneous and continuous georeferenced data from group members, they lack the capability to discern specific types of social interactions and can pose logistical challenges to be deployed on all individuals concurrently. An emerging and promising approach involving the combination of Unmanned Aerial Vehicles (UAVs) and deep learning techniques presents an exciting opportunity to overcome the limitations of traditional tracking methods (Kellenberger et al., 2018; Tuia et al., 2022; Koger et al., 2023). By collecting aerial imagery and employing machine-learning video analysis methods, we can simultaneously track the movement of multiple individuals, and identify the type of social interactions, individual characteristics, and behaviours (Corcoran et al., 2021). This multi-faceted information provides the opportunity for in-depth investigations of leader-follower dynamics within natural context, all while minimizing disturbances to the subjects under study (Corcoran et al., 2021). While only a nascent effort (Rathore et al., 2023) has delved into incorporating drones and deep learning to study leader-follower relationships, it underscores a transformative potential for future research. The application of these methodological innovations is set to significantly advance our understanding of leader-follower dynamics, integrating behavioural ecology into the broader domains of population ecology and conservation.

This manuscript aims to provide an overview of recent advancements in the field of leadership within animal social systems. While acknowledging the unresolved debate surrounding the nature of leadership as either *inherent* or

emergent, our review underscores the importance of considering contextual factors and individual variability. As we move forward, we hope to inspire future research to embrace this nuanced perspective and stimulate the study of leadership across taxa, ultimately advancing our understanding of collective behaviours in the natural world.

Table 1 The table below outlines key questions in the study of leader-follower dynamics, along with suggested study systems and methodological approaches for each.

Questions	**Study Systems**	**Suggested Approaches**
Leader-follower relationship and its adaptive value	Socially stratified species (e.g. primates, canids)	Long-term field observations, and genetic analyses to explore the links between leadership, individual traits, and fitness.
Consistency of leadership within and between species	Long-lived animal groups with clear leadership roles (wolf packs, primate troops, ungulates)	Longitudinal studies spanning the lifetime of focal individuals, behavioural observations, kinship estimations and trait inheritance analyses to explore the repeatability and context-dependence of leadership.
Factors contributing to the emergence and maintenance of leadership	Species with different social structures (fission-fusion societies, swarming invertebrates) exposed to varying environmental and social contexts	Comparative analyses across species, considering social structure, group size, and ecological factors (e.g., predation pressure, habitat heterogeneity). Experimental manipulations to identify causal factors.
Traits associated with leadership roles	Managed species exhibiting leadership dynamics (schools of fish, domesticated ungulates)	High-resolution tracking devices (e.g., biologging, drones) combined with behavioural experiments to examine the behavioural correlations between individual traits and leadership.
Practical applications of leader-follower dynamics	Domesticated animals, managed wildlife populations	Integration of leader-follower dynamics into practical strategies (e.g. trained individuals, virtual fences, sentinel animals), considering the implications for agriculture, conservation practices, and animal welfare.

Author Contributions

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

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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.

Data availability

Data sharing does not apply to this article as no datasets were generated or analysed during the current study.

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