

REVIEW

Contemporary methods for studying animal sociality in the wild

Signalling in groups: New tools for the integration of animal communication and collective movement

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Alexander von Humboldt-Stiftung; Centre for the Advanced Study of Collective Behaviour, Grant/Award Number: EXC 2117 - 422037984; Human Frontier Science Program, Grant/Award Number: RGP0051/2019; Minerva Foundation; Gips-Schüle Foundation

Handling Editor: Erica van de Waal**Abstract**

1. Investigations of collective movement and animal communication have often followed distinct, though complementary, trajectories. Both subfields are deeply concerned with how information flows between individuals and shapes subsequent behaviour. Collective movement has largely focused on the dynamics of passive, cue-mediated group coordination, while animal communication has primarily examined the content and function of active dyadic signal exchanges in sender–receiver frameworks. However, in many social groups, network-wide signalling and collective movement decisions are tightly linked.
2. Here we discuss opportunities afforded by using multi-sensor tracking tags to simultaneously monitor the fine-scale movements and vocalisations of entire social groups. We highlight how such data can elucidate the role of vocal signals in individual and collective movement while illuminating the structures of entire vocal-interaction sequences at previously unexamined timescales and across entire communication networks.
3. We identify practical and analytical challenges associated with these new tools and datasets, and present avenues for addressing them. We specifically address issues associated with the deployment and synchronisation of multiple tags, the processing and interpretation of resulting multidimensional datasets, and the benefits of combining tag-based data collection with experimental approaches.
4. Finally, we argue that a comparative approach employing consistent methodologies across a range of environments, populations and systems is needed to shed light on the evolutionary ecology of communication and collective behaviour.

KEYWORDS

collective behaviour, communication, movement, social behaviour, vocalisations

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1 | INTRODUCTION

The study of collective behaviour seeks to understand the behavioural rules governing individual decisions, how information flows through groups and how these processes lead to emergent group-level outcomes. Perhaps due to their striking visual nature and ease of observation, 'canonical' examples of collective behaviour are coordinated movement patterns (e.g. flocks of birds, schools of fish and ungulate herds, Sumpter, 2010). The increasing ability to collect movement data on animal groups, both in the laboratory and in the wild, has advanced our understanding of how these behaviours function. However, while some collectively moving systems operate primarily based on visual cues, making relative position and movement (perhaps coupled with reconstructed visual sensory networks; Strandburg-Peshkin et al., 2013) good proxies for the flow of information, other systems rely on other mechanisms of information transfer. Many species communicate via active acoustic signalling that can mediate individual and collective movement decisions. Thus, to determine how social information shapes decision-making, one needs to consider the interplay of spatial configuration, movement, active production of signals and cue or signal-based sensory input.

Animal behaviour studies have highlighted the pervasive role of signalling in mediating most activities in the animal kingdom (e.g. mating, hunting, movement and competition) since the works of Darwin (1871). Darwin also hypothesised early on that passive

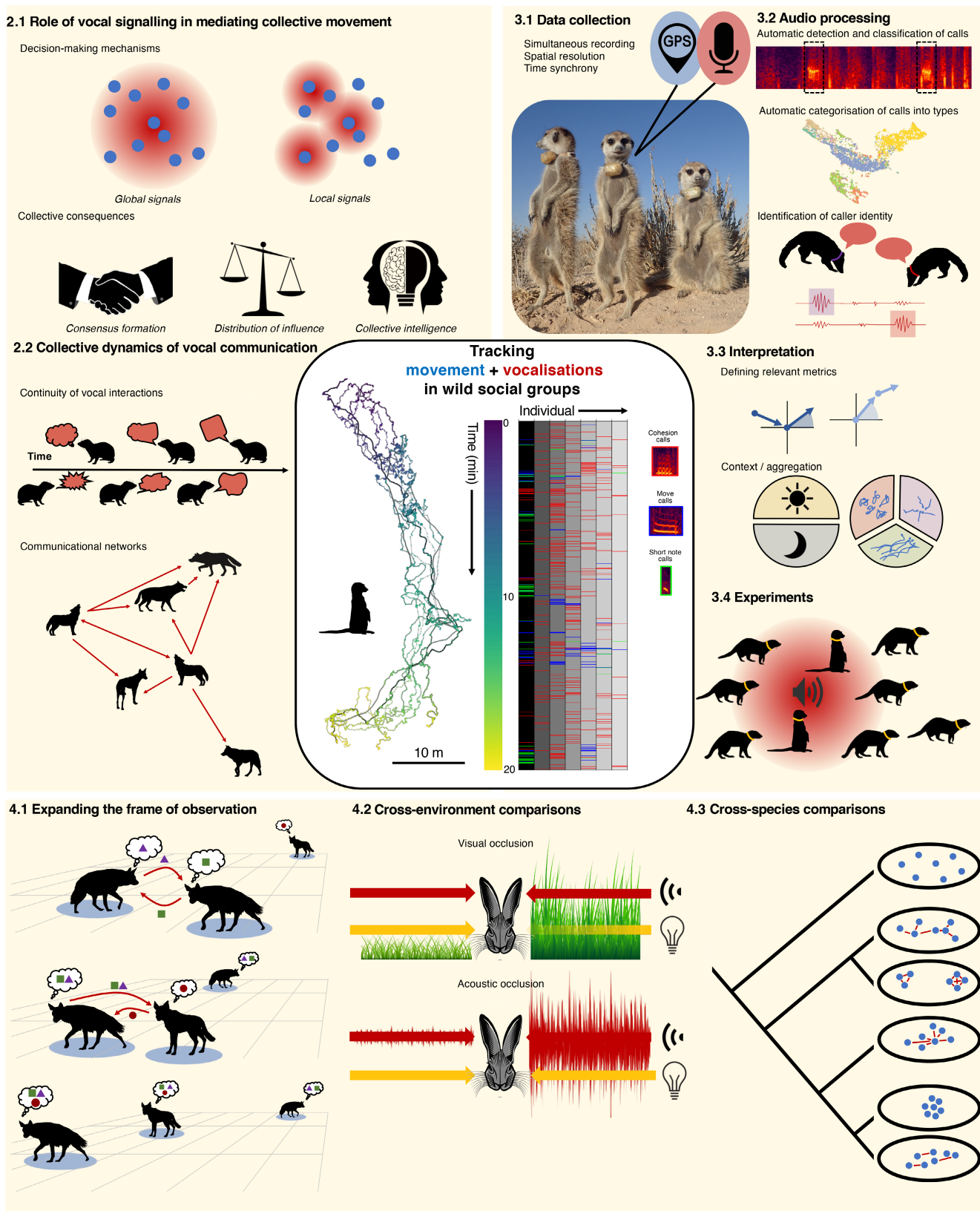
cues might evolve into active signals whenever more intentional communication enhanced the fitness of signallers or receivers. This clear theoretical relationship between signals and the fitness of communicating individuals may have influenced the animal communication literature's historical tendency to break communication events into discrete signal-response exchanges, and subdivide communicating groups into distinct roles of signallers, receivers and bystanders (Searcy & Nowicki, 2010). Signalling is frequently further discretised into informational units and into isolated communicational events. This is not to suggest that animal-communication theorists have overlooked the multi-agent nature of communication. Research on 'audience effects' in numerous taxa (Zuberbuhler, 2008) has highlighted the influence of neighbouring individuals, even those apparently uninvolved in a given interaction. Work on communication networks (McGregor, 2005) has provided a more formal framework to account for the effects of bystanders. Yet empirically investigating network-wide phenomena has remained challenging.

Direct human observation and recording have produced the data underlying a wealth of knowledge about the evolutionary drivers of communication systems, but capturing the dynamics of continuous, multi-participant behaviour presents unique obstacles to data collection in the field. Continuously tracking the simultaneous movements as well as recording high-fidelity audio of multiple individuals is often impossible for a human observer. New tag technologies now

FIGURE 1 Outline of the topics and methods discussed in the paper, from collection of combined acoustic and movement data to implications of expanding this methodological framework across multiple scales. Outer panels follow the section numbering of the text, with the central panel showing an empirical example. Central panel: Movement and signalling data from a single meerkat group over 20 min, collected during a study at the Kalahari Meerkat Project, South Africa. Lines show trajectories of each meerkat (individuals denoted by different shades of grey). Coloured points on lines indicate positions, with colour showing time elapsed. Inset shows the time series of vocalisations from all individuals (again denoted by different shades of grey) corresponding to the same 20 min. Horizontal coloured lines indicate call types, with examples shown as spectrograms in insets (red: cohesion call, blue: move call, green: short note call). 2.1: Role of vocal signals in mediating coordinated movement. Different group coordination mechanisms may be enabled by local vs global propagation of vocal signals, and collective properties are affected by the detailed mechanisms underlying decision-making. At top, blue dots indicate individuals and red circles indicate the source and spatial propagation of vocal signals. Below, examples of group-level properties that are likely to be affected by the decision-making dynamics at play. 2.2: Adopting a collective behaviour approach to communication research. Extended temporal frame for vocal interaction allows the detection of continuous informational constructs, conversation-like signal exchanges, signal convergence or entrainment. By accounting for contributions of multiple individuals to communicational events and long-term monitoring of communication networks, the role of communication in maintaining social relationships can be followed. Top subpanel illustrates multiple vocal exchanges between two individuals with the changing shape of the vocalisation bubbles illustrating signal convergence along the interaction. Bottom subpanel illustrates a network structure of a communicational event. 3.1: Main technical considerations for tag-based audio-GPS data collection in field conditions: position resolution, clock drift, multiple tag deployment. 3.2: Challenges in processing large volumes of audio data. Computational solutions for automated call detection and classification and a reliable separation of focal calls from calls of nearby conspecifics (See also Supplementary Text). 3.3: Interpretation of collected datasets by selecting or defining relevant metrics as well as segmentation of data into 'contexts' according to external variables or data emergent patterns. 3.4: Testing of observed patterns via playback experiments combined with tag-based data collection. Red circle denotes audio stimulus with colour intensity indicating distance-dependent signal degradation. Body posture of the animal silhouettes illustrate differential behavioural response to the playback. 4.1: Potential for expanding the frame of observation and detecting communicational events dispersed in space and time. Sub-panels illustrate temporally distant communicational events, the information shared in each and the informational state of the participating individuals. Vocalisation bubbles with geometrical figures represent different informational states, red arrows represent communicative exchanges in which individuals share information. 4.2: The effect of environmental constraints on the efficiency of communicational modalities. Cluttered environments (high and dense vegetation) may obstruct visual signals (yellow arrow) while having less effect on acoustic signals (red arrow), which could lead to their increased usage on short-term (behavioural) or long-term (genetic) levels. Conversely, in noisy environments (e.g. windy, rainy, urban), the visual modality can remain unaffected while the acoustic modality can be constrained. 3.3: Cross-species comparison for detecting similarities solving coordination tasks on different levels of social organisation.

allow us to overcome many of these hurdles and record the movements and vocalisations of all or most members of social groups simultaneously using combined Global Positioning System (GPS)/acoustic tags (Figure 1; see also O'Bryan et al., 2019).

In this paper, we explore the opportunities offered by these new methods to answer questions at the interface of vocal communication and collective movement. In Section 2, we detail the potential applications of simultaneous sound-and-movement trackers and discuss how



the two fields can benefit from integrating data, tools and concepts. In Section 3, we describe the methodological challenges of whole-group tagging field studies and provide suggestions for tackling them. In Section 4, we discuss the wider implications of research that links communication and collective movement across different contexts and species, and how future comparative work could address broader questions in behaviour, ecology and evolution.

2 | THE MECHANISMS OF COLLECTIVE BEHAVIOUR

2.1 | Role of vocal signalling in mediating collective movement

Theoretical models of collective behaviour demonstrate that co-ordinated movement (Couzin et al., 2002; Reynolds, 1987; Vicsek et al., 1995), effective leadership (Couzin et al., 2005) and even democratic decision-making (Couzin et al., 2011) can emerge without the need for explicit signals to be exchanged. Nevertheless, across a wide range of species, signals are intricately linked with the coordination of group movement. In the vocal realm, many species emit contact calls, which are thought to play a role in group cohesion while moving (Boinski, 1993; Gall & Manser, 2017; O'Bryan et al., 2019) or to aid individuals in finding one another and initiating a meet up (Teixeira da Cunha & Byrne, 2009). Vocal signals are also commonly used to initiate changes in group state, such as collective departures (Bousquet et al., 2011; Walker et al., 2017), and are frequently associated with the coordination of cooperative behaviours, such as mobbing of predators (Naguib et al., 1999; Rubow et al., 2017) or collective action against competing groups (Gersick et al., 2015; Seyfarth & Cheney, 2018). Monitoring the locations and signals of all group members simultaneously unlocks the potential for a more complete understanding of the social mechanisms underlying these behaviours.

Vocal signals could be used as an alternative to self-organisation for achieving group-wide coordination: if the range of signal propagation spans the entire spatial extent of a group (global communication, Conradt & Roper, 2005), a signaller might be able to directly influence all others and exert centralised control. However, even under global communication, group decisions could still emerge in a decentralised fashion, for instance if vocalisations from multiple individuals are required to initiate a collective action. Furthermore, many signals propagate only to nearby group members (local communication; Conradt & Roper, 2005), mediating local interactions that ultimately give rise to group-wide coordination. Thus, signalling and self-organisation often work in concert with vocal signals, both global and local, mediating collective dynamics (Figure 1, panel 2.1).

2.1.1 | Global signals

A simple example of coordination mediated by global communication is the use of vocal quorums, where a group travels only after

multiple group members produce a particular vocalisation (Bousquet et al., 2011; Walker et al., 2017). While common, the dynamics of such vocal quorums remain poorly understood, and the ability to monitor the timing of each individual's vocalisations as well as the spatial organisation of the group would allow us to distinguish between different possible mechanisms for their formation. One possibility is that vocalisations are triggered independently by an individual's motivation to move, with collective movement initiated once a certain threshold of calling group members is crossed. Alternatively, the call of one individual might elicit calls or movement from others in response, resulting in a positive feedback mechanism. Furthermore, calls given to initiate movement might have a different effect depending on the relative position of the caller; for example, calls given from specific locations in the group (edge vs centre) might be more or less likely to result in collective movement. When combined with an individual's position or movement, calls might also convey information about the proposed movement direction and not just the intention to leave (Boinski, 1993).

2.1.2 | Local signals

In many cases, vocal signals may not be broadcast to the entire group, but only propagate to a local neighbourhood of receivers. Such signals often play a role in governing the types of local interactions that give rise to emergent coordination as classically studied in collective behaviour. For example, many species produce short-range contact calls thought to be involved in the maintenance of group cohesion (Chaverri et al., 2013; Gall & Manser, 2017). Such signals are particularly important in visually occluded environments, or when individual foraging strategies impede visual monitoring of group mates (Caine & Stevens, 1990; Reber et al., 2013). However, these signals are not always limited to simply broadcasting individuals' locations to their neighbours (i.e. as a replacement for visual observation). For example, in meerkats *Suricata suricatta*, contact calls have different acoustic properties when given after an individual was vigilant, and these 'guarding' contact calls reduce vigilance in other group members (Townsend et al., 2011). Meerkats also change the structure of their close calls after a successful foraging attempt (Reber et al., 2013; Townsend et al., 2011). These findings suggest that contact calls can transmit the caller's behavioural state and influence the behaviour of receivers, potentially facilitating the coordination of vigilance within the group, or enabling collective sensing of the resource distribution (Berdahl et al., 2013).

2.1.3 | Mechanistic details affect collective outcomes

It is important to understand the detailed decision-making mechanisms underlying group coordination because even seemingly subtle differences can have important consequences for collective outcomes and ultimately group functioning. For instance, if calls given as

part of quorums reflect only individuals' internal motivation to move, the integration of such independent estimates of the environment could lead to increased collective intelligence (Surowiecki, 2004). In contrast, if calls are given in response to other calls they no longer represent independent estimates, thus potentially disrupting collective intelligence (Lorenz et al., 2011) but perhaps facilitating more rapid consensus formation (Sumpter, 2006).

Vocal signalling is also likely to affect the balance between shared and unshared decision-making in collective decisions. Individuals might regard individually distinctive (Knornschild et al., 2012; Mathevon et al., 2010; Pollard, 2011) calls from certain members of their groups as more important or reliable; thus, vocal distinctiveness could cement relationships of influence within groups. On the other hand, individuals may also include variable components to their signals, encoded in aspects such as signalling rate, frequency shifts or other modulations. Such vocal modulations can then affect how strongly conspecifics respond to their calls, for example if certain characteristics are perceived as higher urgency (Gall et al., 2017). Revealing these detailed mechanisms is made more challenging by the fact that responses to many frequently emitted calls can be subtle, and individuals may not show a clear and immediate response to a specific signal but rather their behaviour likely depends on a complex social, spatial and acoustic landscape. Tracking the movements and vocalisations of entire groups allows this landscape to be revealed.

Question summary box 1:

Role of vocal signalling in mediating collective movement	To what extent are group coordination processes driven by local vs. global communication, and how does communication range affect coordination dynamics?
	How does vocal feedback (individuals responding to received signals by producing signals) affect the dynamics and outcomes of collective decision-making, for example, in vocal quorums?
	How does vocal signalling affect the balance between shared and unshared decision-making in social groups?

2.2 | Collective dynamics of vocal communication

Understanding the contribution of multiple agents to both individual and group actions is the basic task of the field of collective behaviour, and this approach has generated substantial insights into the mechanisms governing coordinated movement (Couzin et al., 2002; Vicsek et al., 1995). Taking a similar approach in the signalling domain, that is, measuring the collective dynamics of vocal exchanges and how these are driven by individual-level rules, will allow us to address questions regarding social regulation and coordination of signalling in unprecedented detail.

Each signalling event generates a multi-participant communicational space, including non-signalling bystanders who both affect

and are affected by the signalling behaviour (Zuberbuhler, 2008). The ability to continuously monitor the vocalisations and positions of multiple individuals allows us to move beyond a discrete designation of signallers, receivers and bystanders and instead focus on spatial fields of effect, which can change dynamically according to an individual's presence and actions. As we extend the boundaries of our analyses beyond the 'signalling dyad', and perhaps also strive to account for multi-modal informational streams, we are also bound to revise the temporal boundaries of observed interactions (Figure 1, panel 2.2).

2.2.1 | Continuity of vocal interactions

While some signalling is momentary and does not progress beyond the short-term transmission of a single informational packet, most natural interactions consist of a continuous chain of events with no well-defined 'start' and 'end' point. Addressing communication as a stream of events can highlight information constructs that may only be meaningful in the context of previously exchanged signals. Over the long term, prior knowledge about interaction partners has been shown to affect the decision to engage in signalling (Goll et al., 2017), the type of response (Reber et al., 2013), and decisions regarding mating and competition (Mowles & Ord, 2012). It is therefore likely that over shorter time-scales, such as in the course of multiple rounds of sequential signal exchange, responses to later rounds may be conditioned on earlier signals. The informational state of the participants, their arousal and their motivational levels can vary with additional information received over the course of the interaction and according to each individual's previous experience in similar behavioural contexts. Collecting continuous data on multiple individuals simultaneously allows us to flexibly expand the interaction time window, allowing it to span over several rounds of signal exchange and potentially enabling us to determine whether the information transmitted at different time points along the interaction is a simple repetition or whether more complex information exchange is at play.

Another promising opportunity afforded by continuous monitoring of communication is identifying and characterising acoustic convergence/vocal accommodation (Babel, 2010; Gallois et al., 2005). It has been shown, for example, that closely affiliated female Campbell's monkeys share similar vocal variants (Lemasson et al., 2011) and Diana monkeys match the frequency contour of immediately preceding calls (Candiotti et al., 2012). An intriguing possibility would be to trace selective, continuous convergence within a group of communicating individuals. Vocal accommodation across vocal exchange rounds could function as a communicational link with a specific individual, independent from physical proximity. This direction has the potential to shed light on animals' ability for targeted signalling and their capacity to perpetuate a signalling interaction, with potential implications for communicational and informational intentionality (Pougnault et al., 2020).

2.2.2 | The social role of communication networks

The immense complexity of animal communication systems frequently forces us to focus on edge cases with relatively clear cut 'cause and effect' relationships. Conditions such as alarm (Fichtel & Hammerschmidt, 2002), distress (Lingle & Riede, 2014), mating (Simmons et al., 2013) and competition (Reby et al., 2005) often make it easier to formulate clear hypotheses as well as to define the participants of a communication event. However, while such events are crucial for survival and fitness, they are nevertheless usually rare. For most animals, the bulk of their time budget is dedicated to an apparently unremarkable routine (Ilany et al., 2013) of sleeping, resting, eating and moving around. Those 'unremarkable' behaviours are frequently accompanied by signals which are often hard to define and analyse due to their subtle effects, interwoven sender–receiver roles and complex causation relationships. But these types of calls often have a crucial function in the formation and maintenance of social bonds and relationships in a group.

It is not uncommon for the first encounter between individuals to be by exposure to vocal signals, and for repeated exposures and signalling exchanges to facilitate familiarisation and establishment of 'relationships'. The role of vocalisations in social relationships continues to be valuable even for individuals who have opportunities to interact physically. For example, vocal interactions have been suggested to function as 'remote grooming' behaviour contributing to the strength of social ties (Dunbar, 1993; Kulahci et al., 2015).

Long-term monitoring of the behaviours and vocalisations of entire social groups opens the possibility of determining the stability of communication networks and their link to networks based on physical behaviours. Whether communication drives physical association or vice versa is likely context dependent. For natal members of a social group, physical associations often precede fully developed communication repertoires. In contrast, immigrating individuals can establish a communication link with residing group members before reaching physical proximity (Wiley, 2013). While the role of inheritance and nurture in determining social association has been addressed in several animal systems (Cantor & Farine, 2018; Ilany et al., 2021), the role of signalling in priming or improving social association is rarely described (Kulahci et al., 2015). To what extent are communication-based bonds different from inherited or kin-based ones, and can an individual's social niche be stably divided into signalling-based and physical interaction-based domains? For instance, signal-mediated bonds could be used either to reinforce physical interaction-based bonds, leading to a positive relationship between the two domains (Kulahci et al., 2015), or could be used as a replacement for them as originally proposed by Dunbar (1998), leading to a negative relationship (Chereskin et al., 2022). It is likely that both processes have the capacity to support equally strong bonds, however exploring social systems and ecological contexts in the latter case would increase our understanding of the coevolution between social living and communication.

Question summary box 2:

Collective dynamics of vocal communication

To what extent are vocal interactions affected by memory of previous exchanges, and how does information accumulate over a sequence of communication interactions?

When and how does vocal convergence occur in social groups?

How are vocalisations used to establish and maintain social bonds, and how do communication-based bonds interact with other forms of bonding based on physical interactions?

3 | CHALLENGES AND CONSIDERATIONS FOR GROUP-WIDE TRACKING EFFORTS

While the potential of whole-group tagging for animal behaviour research is immense, effectively using these new tools poses a number of technical and analytical challenges. Here we highlight some challenges encountered when employing these techniques and discuss promising avenues towards tackling them.

3.1 | Data collection

3.1.1 | Logistics of tracking groups

Tracking entire social groups (Figure 1, panel 3.1) requires not only that many individuals be tagged, but also that tags record simultaneously. Programmed 'delayed start' capabilities are often crucial because they allow tag deployment over multiple days and synchronous activation. Delayed activation also enables retrieval or redeployment of malfunctioning units (when a tag's proper functioning can be verified by observers), and allows animals a period of accommodation to tags before data collection. In habituated groups, it may also be feasible for observers to continuously follow individuals that could not be tagged with a microphone and GPS unit, to minimise gaps in the data (Gall et al., 2017).

To justify the effort and disruption to animals associated with tagging, it is often beneficial to include additional sensors on the same deployed unit. While not addressed here, accelerometer and magnetometer sensors can increase the value of collected data by providing information on the heading, posture and behavioural state of the animal (Chakravarty et al., 2019; Sankey et al., 2021) and contribute to drawing biologically relevant conclusions. These sensors typically have low battery consumption relative to high-resolution GPS, and thus impose only small increases in tag weight.

3.1.2 | Movement data resolution

Modern GPS technology can provide relatively precise location data, with error typically on the scale of a few meters. While this spatial resolution is often sufficient, it is important to note that movement and social interactions below the device resolution will be unresolvable. Additionally, positioning accuracy can be reduced in terrain with steep height changes or under dense canopy. A field comparison of tag models might help to decide whether collection conditions will produce usable output, and which devices perform best for a given location. Beyond GPS, for animal groups that remain within a reasonably small home range local tracking systems may also be an option (Beardsworth et al., 2022). If available, information from inertial sensors can also be integrated with intermittent position data to obtain a finer-scale reconstruction of the animal trajectory ('dead reckoning', Wensveen et al., 2015). Higher precision (cm-level accuracy) is in principle also possible via differential GPS technology, using stationary GPS loggers to correct errors, however to our knowledge there are currently no commercially available tracking systems using this technology.

3.1.3 | Time synchrony

Reconstructing the temporal structure of vocal interactions relies on all deployed audio recorders being accurately time synchronised. All recording units exhibit gradual clock drift, leading to the misalignment of internal clocks. The magnitude of drift depends both on properties of the recorder's clock and on external factors such as temperature. While this misalignment can be ignored when addressing questions about repertoire structures and communication budgets, any analysis relying on the correct timeline for recorded calls across tags must come up with a solution for re-alignment of recordings. The level of synchrony required will vary by study system and planned subsequent analyses. For example, some call-response exchanges occur at time-scales on the order of 200 ms (Stivers et al., 2009), requiring sub-second accuracy.

An ideal approach is to provide a direct time feed from the GPS that can be used for correcting the timestamp of the audio files. However, this solution requires tags specifically engineered for this purpose. A relatively simple alternative is to produce an external audio ping that is recorded by neighbouring units. Playing pings at regular intervals throughout data collection allows alignment of audio streams in post-processing. Naturally, this approach requires regular acoustic contact with study animals, and that the sound not interfere with their behaviour. When regular access is not possible, a speaker could potentially be integrated into the tags, with tones played at specific times and recorded by neighbouring devices, allowing synchronisation across tags (Goll Y & Geffen E., pers. commun., 2018), though the relationship to absolute time may then drift.

3.2 | Audio data processing

Extracting vocal signals from raw audio traditionally requires time-consuming manual annotation by trained labellers, which may also suffer from subjective and inconsistent assignment of call types. While some manual labelling will likely always be necessary, processing the vast quantities of audio recorded across multiple tags requires a more scalable approach, that is, automated detection and recognition of calls (Figure 1, panel 3.2). While an in-depth discussion is beyond the scope of this paper, in Supplemental Text A we provide a general introduction to automated approaches for the processing of acoustic data, emphasising how they can be used to detect and classify calls based on human-labelled data (supervised approach), as well as to characterise vocal repertoires without human-specified categories (unsupervised approach). We also discuss challenges and potential solutions associated with disentangling collar-wearing individuals' calls from the calls of neighbours. See also Stowell (2022) for a review of deep learning approaches applied to bioacoustics.

3.3 | Interpretation

The methods described here produce multidimensional datasets that are inherently open-ended and complex. Interpreting these datasets requires first extracting relevant features from them, which can then be modelled (Figure 1, panel 3.3). For example, a common question might be which individuals in a group influence collective movement decisions. To address this question, one needs an operational definition of 'influence' that is extractable from the data. However, different approaches (see Strandburg-Peshkin et al., 2018 for a review) might lead to different conclusions. There is no simple solution to this conundrum; however, prior knowledge of the study system, or similar systems, can help in developing meaningful measures. For example, for continuously moving groups such as bird flocks, heading correlations might give insight into influence (Nagy et al., 2010), however for animals whose movement is more 'stop-and-go' with less well-defined headings, approaches based on spatial displacements may be more appropriate (e.g. Strandburg-Peshkin et al., 2015). Similarly, prior knowledge about vocal repertoires can help guide analyses. For example, calls that are known to be associated with movement initiations might be interpreted as initiation attempts, with subsequent movement of the group being interpreted as following. Because all approaches make assumptions, using multiple approaches to address the same question can be important to the critical evaluation of the robustness of results.

Another challenge arises in determining which periods of tracking data to use for a given analysis. Continuously recorded behavioural data typically consist of multiple contexts (e.g. resting, foraging), and considering these contexts separately can facilitate analysis and interpretation. 'Lumping together' data from multiple contexts can obscure patterns or lead to the detection of spurious relationships, whereas 'over-splitting' data reduces sample size and may introduce biases as well. Often, behavioural contexts are clear, such as when

they are determined by external factors that are measured in the dataset (e.g. time of day). However, sometimes context may be unobserved, hard to measure, or hard to define, leading to questions of how to segment the dataset. Behavioural observations and environmental data can help with the establishment of context, and hence with the problem of how to aggregate data for behavioural analyses. It may also be possible to determine context from the tracking data itself, for example by identifying group-level behavioural states and transitions among them (Tunstrom et al., 2013). However, group states that seem 'distinct' in the field (e.g. 'slow-moving' vs 'rapid travel') often form a continuum when viewed through the lens of tracking data. In these cases, assessing how behavioural rules change as a function of continuous metrics (e.g. speed, group spread) may be more appropriate. Oftentimes, it may still be practical to break data into contexts based on some criteria (e.g. considering group speeds faster than a threshold as 'travel'), but here sensitivity analyses should be conducted where decision criteria are varied and the results checked for robustness. A benefit of tracking data is the ability to vary contextual and behavioural definitions post hoc to perform such robustness checks, which is often not possible when using conventional approaches to field data collection.

3.4 | Hypothesis generation and experimental tests

Multimodal tracking data allow us not only to address existing questions, but also to detect new behavioural patterns via exploratory data analyses, leading to the formulation of novel questions and hypotheses. For instance, tracking datasets can be mined for naturally occurring instances of a specific signal, and the subsequent behaviour of individuals and groups can be examined to investigate the function of that signal. While such data mining approaches can be highly informative, with such large and complex datasets spurious patterns are also bound to emerge, highlighting the need for experimental tests to help resolve causal relationships (Figure 1, panel 3.4).

Tag technology offers great potential when used in combination with experiments. For example, playback experiments (a common method for testing the function of animal calls where recorded calls are broadcast

from a speaker) can be conducted on groups of tagged individuals. Such an approach effectively increases sample size, since multiple individuals are observed simultaneously, and intrinsically includes balance and variation in factors that would otherwise have to be controlled or limited by experimental design (e.g. distance from stimulus, receiver traits). It is important to note that responses of multiple individuals to the same playback cannot be considered true biological replicates of a given stimulus type, and furthermore animals are likely to influence one another's responses, thus pseudo-replication and non-independence must be taken into account in the experimental design and subsequent analyses (Kroodsma, 1989). However, this challenge is also an opportunity: exposing a fully tracked group to a playback stimulus allows us to observe in detail the interactions among group members after a stimulus is heard. For example, it could enable investigation of how receiver responses propagate through the group, amplifying or diminishing the initial informational input, and to what extent collective outcomes are driven by the cascading social facilitation rather than by the primary stimulus. Tracking entire groups before and after an experimental manipulation also allows pre- and post-experimental behaviours to be incorporated into analyses, effectively expanding the time window of observation. For instance, territorial species that hear calls associated with territorial incursions might be more likely to engage in 'border patrols' later in the day, or groups might change their behaviour in particular locations in response to earlier simulated predation threats in that area.

3.5 | Combining approaches

While the methods describe here open many opportunities, it is important to note that not all of the experiences, information and abstract social structures that influence individual and group decision-making are best observed via remote sensing. For this reason, we believe the most promising approaches will be collaborative efforts that deploy the methods described here in concert with longitudinal field studies. Long-term studies possess the data on relatedness, relationships, past interactions and life histories that can put our models of collective behaviour in context. Moreover, in our experience both successful data collection and meaningful interpretation of tracking data rely on prior biological knowledge of, and experiences with, a given study system.

Question summary box 3:

Challenges and considerations for group-wide tracking efforts	<p>Can sufficient portions of the animal group be tagged in a practically reasonable time period, and what measures for tag time synchronisation can be used?</p> <p>How will the audio data be processed and prepared for analysis?</p> <p>Which complimentary data collection and experimental procedures could be done in parallel to improve the interpretability of the tag-based data?</p>
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4 | THE ECOLOGY AND EVOLUTION OF COMMUNICATION AND COLLECTIVE BEHAVIOUR

As technologies continuously improve, the range of species and environments wherein comparable data can be collected is constantly expanding. Comparing coordination across spatiotemporal scales, environmental contexts, populations, and species, will allow researchers to investigate both the unique behavioural features and the common building blocks of communication and coordination systems. Ultimately, this will allow connecting our understanding of

these systems to long-standing questions about how and why they evolve. In this section, we outline questions that could be addressed in the future and argue that collaborations across study systems and disciplines are required to tackle these broader questions.

4.1 | Expanding the frame of observation

Continuous, coordinated movements by cohesive groups are just a fraction of the coordination feats that group-living species accomplish. Many forms of collective action, such as extended migrations (Flack et al., 2018; Foss-Grant et al., 2018), threat-mobbing by dispersed groups (Gersick et al., 2015; Lehmann et al., 2017) and fission–fusion cycles (Aureli et al., 2008), must be coordinated across large spatial gaps between individuals, and long temporal gaps between interactions (Figure 1, panel 4.1). Coordinating across these gaps can demand specialised cognition and behaviour to support information sharing and facilitate consensus. Dispersed groups lose access to passively transferred informational ‘cues’ about the actions of groupmates, increasing the need for active, explicit communication (‘signalling’). Spatial dispersion also reduces shared access to contextual information such as resource availability, forcing individuals to rely on second-hand information from signalling group mates. To evaluate the weight and reliability of these signals, receivers must use data stored in memory about signallers’ identities, relationships and past actions, introducing new dimensions of potential variation into the flow of information through group networks. The techniques described in this paper offer a way to observe these complex, large-scale processes as they unfold, and to investigate spatiotemporally dispersed behaviours using data that matches the breadth and detail of datasets on short-term, cohesive collective action.

4.2 | Variation across environments and populations

Communication requires transmitting information through the environment, and environmental features can facilitate or impede propagation (Figure 1, panel 4.2). Thick vegetation can neutralise visual communication, while having a smaller effect on acoustic signals (Schamberg et al., 2017; Uy & Safran, 2013). Conversely, environmental noise may disrupt acoustic communication but leave visual channels unaffected (Drijvers et al., 2018; Grafe & Tony, 2017). Environmental features often vary across landscapes, change temporally (e.g. due to seasonality, weather or climate change) or are modified by human activities (logging, road building, marine development). Which environmental circumstances might evoke plasticity of coordination systems and which might cause their collapse? What components of coupled communication–coordination systems (e.g. signal structure or modality, group spacing) create bottlenecks or facilitate adjustment? And how do human-driven modifications to the landscape affect groups’ abilities to coordinate?

The traits, behaviours and mechanisms that compose coordinated action may flex under varying ecological conditions, or new

mechanisms may emerge to cope with new situations. Alternatively, species’ ranges may be limited to areas where ecological conditions facilitate existing coordination mechanisms, and rapid environmental changes may cause fitness-critical collective behaviours to break down. Tracking how the communication-and-coordination dynamics of social groups respond to varying environmental conditions will enable a new perspective on these topics.

4.3 | Variation across species

The tracking methods discussed here also have the potential to generate relatively comparable data across multiple systems, enabling cross-species comparisons. While collective behaviour research has focused primarily on the mechanisms underlying coordination, socioecologists have largely examined coordination-and-cooperation systems to understand the evolution of traits that help individuals overcome complex ecological or social challenges (Ashton et al., 2018; Byrne & Whiten, 1994). This focus treats group dynamics as sources of external pressure, while collective-behaviour scientists have viewed group dynamics as akin to behavioural traits in their own right, albeit with mechanisms dispersed across individuals pursuing their own individual fitness. By facilitating cross-species comparisons, the methods described here could help to bridge the perspectives that collective-behaviour scientists and evolutionary socioecologists have taken on common questions about the evolution of social traits and behaviours (Figure 1, panel 4.3). Species that rely on coordination to occupy their niches will face common challenges. Ecological and social variation, meanwhile, will influence the behavioural phenotypes of species’ adaptations to those challenges over evolutionary time. Comparing the coordination systems of species facing similar challenges in different physical or competitive environments can illuminate both the fundamental elements of complex coordination and the areas of adaptation or flexibility that fuel or restrict adaptation and speciation. Such comparative work also has the potential to reveal to what extent there has been co-evolution between species’ communication systems, the ways they solve coordination challenges, and what factors drive diversification of coordination systems across species.

Question summary box 4:

Ecology and evolution of communication and collective behaviour

- How do social groups coordinate across large temporal gaps and vast spatial scales?
- How do environmental factors influence communication and coordination systems? When and how can these systems adjust to changing environmental conditions, including human-driven modifications to the environment?
- How have communication and coordination systems evolved? To what extent has there been co-evolution between communication systems and the ways animals solve coordination challenges, and what factors drive diversification of coordination systems across species?

5 | OUTLOOK

This paper has described the purpose and potential of new methods for collecting and analysing data on animals' communication and collective behaviour in the field. When used in concert with long-standing methods of direct field observation and experiments, we argue that these tools will open up exciting new avenues of research at the interface of communication and collective behaviour and ultimately comparisons across species. Such comparative research on animal coordination requires identifying comparable elements across different systems (i.e. call types or coordination contexts) to draw meaningful parallels, which can only be achieved by deep knowledge of each biological system. Thus, collaboration among researchers working within multiple study systems to coordinate data collection and analytical approaches will be key. Ultimately, such a collaborative approach has the potential to facilitate broad-scale insights into the evolution and ecology of coupled communication-coordination systems.

AUTHORS' CONTRIBUTIONS

A.S.-P. and V.D. conceived the idea for the manuscript and led the writing. M.R., M.T., F.J., and A.G. contributed to writing the manuscript. M.M. and A.S.-P. collected the example data shown in Figure 1. All authors contributed to development of the ideas contained in the manuscript, and all authors approved the final version of the manuscript.

ACKNOWLEDGEMENTS

We are grateful to the members of the 'Communication and Coordination Across Scales' project team for helpful discussions inspiring many of the ideas in this manuscript. Dr. Gabriella Gall contributed to the collection of meerkat data shown in Figure 1. We acknowledge funding from the Human Frontier Science Program (RGPO051/2019 to A.S.-P., M.R., and M.M.), the Gips-Schüle Foundation (to A.S.-P.), the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy—EXC 2117—422037984 (to A.S.-P.), the Alexander von Humboldt Stiftung (to V.D.), and the University of Zurich (to M.M.). Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13939>.

DATA AVAILABILITY STATEMENT

This manuscript does not include data.

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SUPPORTING INFORMATION

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How to cite this article: Demartsev, V., Gersick, A. S., Jensen, F. H., Thomas, M., Roch, M. A., & Strandburg-Peshkin, A. (2022). Signalling in groups: New tools for the integration of animal communication and collective movement. *Methods in Ecology and Evolution*, *00*, 1–12. <https://doi.org/10.1111/2041-210X.13939>