

Re-wilding collective behaviour: an ecological perspective

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Summary

The earliest studies of collective animal behaviour were inspired by and conducted in the wild. Over the past decades much of the research in this field has shifted to the laboratory, combining high-resolution tracking of individuals with mathematical simulations or agent-based models. Today we are beginning to see a ‘re-wilding’ of collective behaviour thanks to technological advances, providing researchers with the opportunity to quantify and model the heterogeneity that exists within the social groupings they study, and within the environments in which these groups live. The perspective we present here aims to inspire and steer this research toward answering fundamental and outstanding behavioural and ecological questions, while also tackling pertinent conservation challenges.

Trends

The field of collective animal behaviour is transforming.
Continuous behavioural tracking in the wild affords an ecological perspective.
Collective behaviour can be studied in the environment in which it has evolved and is maintained.

Introduction to collective behaviour

How and why do animals form groups? The structure and functioning of animal aggregations have long intrigued scholars. Indeed, pivotal work by Nikolaas Tinbergen, Konrad Lorenz, and Karl von Frisch conducted during the last century won them a Nobel Prize (1973) for investigations of the “organization and elicitation of individual and social behaviour patterns” [1]. Their work, which included von Frisch’s discovery that bees use a type of “dance” to facilitate collective decisions [2], became the bedrock of studies of animal behaviour and ethology, and in particular, studies of differences in group structure and patterns of social relationships within and across species. Moving forward from these early descriptions, the past several decades have brought us a long way towards understanding the form and function of social interactions, resulting in the vibrant research field of collective animal behaviour (see glossary).

In this article we give a brief history of collective behaviour research and provide an overview of the state-of-the-art in this fast-developing field, highlighting some of the major gaps in our current understanding. We then introduce technological advances in bio-logging (see glossary) and new methods for remote environmental monitoring which enable us to gather high-resolution behavioural and ecological data in the wild, with a focus on vertebrates. We suggest that these new tools allow researchers to embrace and model the heterogeneity (see glossary) in their study systems [3] and to study collective behaviours in the social and ecological environments in which they have evolved and are maintained [4]. We thus expect to see a “re-wilding” of collective behaviour research. We end by proposing key behavioural and ecological questions and pertinent conservation challenges that we can address in the near future by combining wild and laboratory studies of collective animal behaviour.

A brief history of collective behaviour research

Research in collective animal behaviour tends to adopt a self-organisation (see glossary) perspective, with investigations of how global-level collective behaviours emerge from local interactions (see glossary) among individuals [5]. The majority of this work is informed by laboratory experiments which tend to combine high-resolution tracking of individuals [6], mathematical simulations or agent-based models of self-organising (see glossary) groups [7] (Figure 1). These works have provided a mechanistic and predictive understanding of the behaviour, structure, and performance of animal groups. For example, research on ant colonies has shown how simple rules (see glossary) of interaction among individuals can generate spatial structures in their societies which are critical to their organisation and decision-making [8-11]. Similarly, research with shoaling or schooling fish has uncovered the behavioural rules fish use to coordinate their motion [12-14] and make collective decisions about features of their environment [15-17].

Glossary Box

bio-logger: an electronic device attached on or in an animal providing data about that animal

collective behaviour: the coordination of individuals' behaviour in space and time

flexibility: capacity for an individual's behaviour or a collective's behaviour to be modified to respond to altered circumstance

global properties: group (or population) level dynamics that result from individual behaviours

heterogeneity: social units or the environment being composed of parts (individuals, habitats, etc.) of different kinds

keystone individuals: individuals that have a large effect on other group members' behaviours and/or the overall group dynamics

local interactions: interactions among individuals within a limited distance and/or range of each other

robustness: ability of an individual's or a collective's behaviour to remain stable following perturbations

self-organization: order at a global level arising from local interactions among individuals

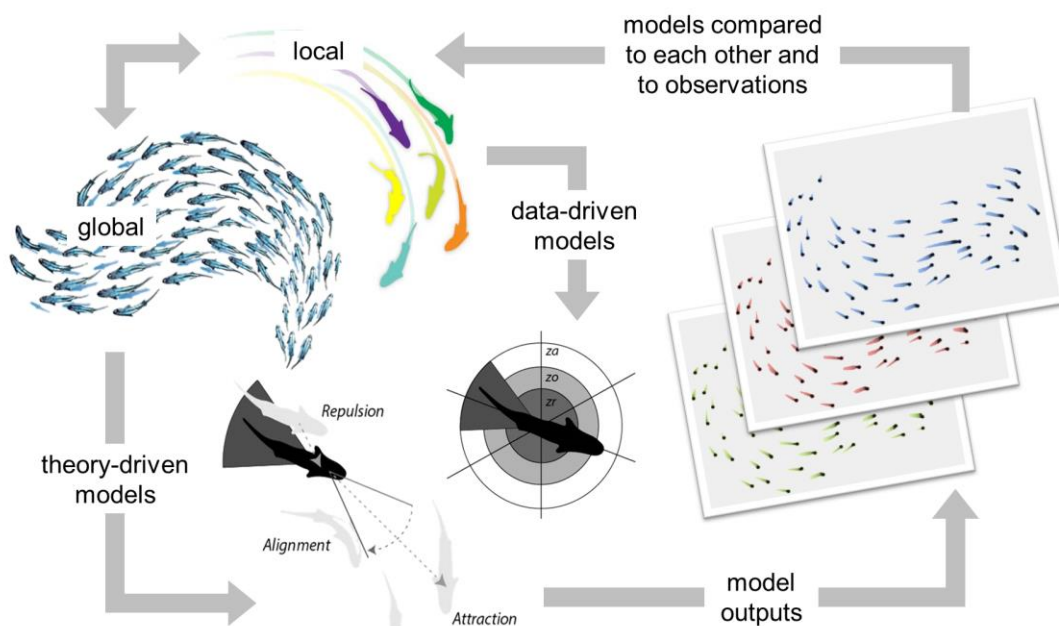


Figure 1. Collective animal behaviour research cycle. Almost all collective behaviour research is related directly or indirectly to mathematical models, and Sumpter et al. [18] explain how regular movement back and forth between mathematical models, experimental data and statistical fitting can provide a comprehensive understanding of how interactions between individuals produce group level patterns. Based on observations of global patterns, researchers use theory-driven approaches to try to replicate group-level dynamics. In contrast, individual-level observations can be used to produce data-driven models to quantify the response of individuals observed in experiments. Both approaches are complementary (and are also not distinct as portrayed here), tending to rely on simple local rules, such as the individual being submitted to a zone of attraction (zr), a zone of orientation (zo) and a zone of repulsion (za) ([19] as depicted) to produce model outputs. These model outputs can then be compared to each other, and the original or new observations, to quantify how closely each model approximates the real data [20].

Realism and heterogeneity

Early studies of the mechanisms of coordination in animal groups depicted individuals as essentially identical units: from Reynolds' "boids" [21] to Ballerini and colleagues' starlings [22], neither simulations nor analyses of real data accounted for potential individual heterogeneity (see glossary) among group members. This was due partly to the field showing (as yet) little interest in such heterogeneity, but also to the difficulties in quantifying individual variation in animal collectives that are often composed of thousands of individuals.

Constructing groups of (real or simulated) animals to study collective behaviours can ignore the very inter-individual differences – such as age, sex, reproductive or physiological state, social dominance, kin relations, personality, knowledge, or experience – which can result in differentiated social roles that can function to improve individual and group success [3]. For instance, inter-individual differences in flight speed, knowledge, personality and experience shape the collective dynamics of homing pigeons (*Columba livia*) (Box 1). Similarly, lab experiments with shoaling fish have shown personality differences can influence the structure of and movement dynamics within and between groups [23], but also that the influence of individual personality types can be context-specific [24]. Together, these empirical examples indicate how selection can drive behavioural differentiation between individuals within animal collectives [3].

Quantification and representation of heterogeneity in the environment (as opposed to within-groups as discussed above) has also been lacking. Research undertaken in the laboratory is typically optimised for the requirements of data collection (e.g. short periods of filming and subsequent tracking [6]) and wild studies tend to be restricted to short time periods or specific locations and/or contexts because of methodological constraints [22, 25, 26]. The challenge has therefore been for researchers to incorporate greater realism into their studies (Box 2). Where simple environmental heterogeneity has been introduced in laboratory experiments, their impact has been profound. For instance, studying fish under varying light conditions (dark and light patches varied in space and time) led to the discovery of emergent sensing in fish schools [27].

By bringing greater realism to the social and physical environments of animal collectives, researchers can better understand both the mechanism and function of the behavioural rules and emergent patterns identified. Clever experiments with an evolvable simulation of small prey that were 'preyed upon' by a bluegill sunfish [28] show how this can be achieved. Researchers were able to observe how group formation and specific individual interaction rules can provide collectives with anti-predatory benefits. Embedding animals in such reactive, virtual reality environments provides a fascinating new line of investigation that will afford an "evo-mecho" approach to collective animal behaviour. In the sunfish experiments the researchers were able to observe how group formation and specific individual interaction rules can provide collectives with anti-predatory benefits. In essence, this can reveal which rules "work best". Future VR environments [29] and/or robots [30-32] can help us achieve "closed loop" experiments in which freely moving animals can be precisely perturbed or stimulated, improving our ability to probe the social patterns we observe, as well as their underlying processes. However, we maintain that it will be difficult to test if and how the rules and mechanisms uncovered are adaptive without studying real-life, wild systems over sufficient time and context [33].

BOX 1. A birds-eye view



Images: Z. Ákos

Individual tagging of free-flying birds, and, in particular, the use of study systems in which individual variation can be not only quantified but also manipulated, has provided significant insights into the role of within-group heterogeneity in shaping collective dynamics. Homing pigeons (pictured) provide an experimental model especially amenable to both quantification and manipulation. These birds' long history in studies of individual spatial cognition and navigation [34] allows models to incorporate numerous known sources of individual variation, and, crucially, to do so in collective decision-making scenarios on ecologically valid scales. For example, we know that different birds prefer to fly substantially different routes when navigating home over familiar landscapes [35] and that these differences can give rise to conflict that needs to be resolved when birds with different preferred routes are made to travel together [36]. Rather than choosing the best available route, how "stubbornly" a given bird tries to keep to its own route, even whilst flying with a partner, seems to predict leadership in pairs [37]. In larger flocks transitive leadership hierarchies emerge [38], whose temporal stability and robustness to manipulations of individual navigational knowledge [39] suggest structuring by inherent individual differences among flock members. Perhaps unexpectedly, neither social dominance [40] nor individual navigational competence [41] seem to be significant predictors of leadership. However, solo flight speed [41] and a tendency for greater exploratory behaviour [42] do: faster and "bolder" birds are significantly more likely to assume higher leadership ranks. In combination, variation in these traits provides a simple and elegant link between individual heterogeneity and the organisation of collective movement. Similar mechanisms have now also been identified in fish [23], and confirmed to explain multiple aspects of collective functioning. Interestingly, the observation that there can exist feedback between leadership and the individual traits that structure it (such as knowledge gained through the experience of leading reinforcing leadership [41]) opens up many new and fascinating questions about changes that collective behaviour can undergo over time. Future work will need to further explore such feedback for a longer-term perspective on collective behaviour [4], incorporating the role of learning during collective action as an additional source of individual heterogeneity.

BOX 2. A Fish-Eye Lens



Image: A. Ward.

The challenge for researchers interested in the collective behaviour of shoals and schools is to incorporate greater realism to their laboratory studies and, where possible, to conduct studies in the wild. Wild studies of fish aggregations have a surprisingly long history. Sund applied echo-sounding to the study of cod shoals over 80 years ago [43], while in the 60s, Radakov filmed wild fish schools from aircraft [44]. Recent technological developments offer the tantalising prospect of building on these early advances. Improvements in camera technology now facilitate filming of fish in their natural habitat. One interesting outcome of a recent study of the collective behaviour of wild stickleback shoals [45] was the remarkable concordance between the behaviour of free-swimming shoals and shoals of the same species under the oft-criticised environs of the laboratory. Nonetheless, studies in the wild represent our best opportunity of developing a deep understanding of collective behaviour in its proper ecological context. Until recently, one obstacle has been the difficulty in tracking fish in the wild, due to problems with variable light and contrast, among other issues. The application of artificial intelligence to this problem offers a way forward, for example, the use of trainable algorithms to assist in the detection of target animals. Another challenge for studying fish in the wild is that visibility is often restricted in aquatic systems. Active acoustic techniques provide an alternative to cameras in these cases. Collective manoeuvres and information transfer within pelagic shoals and the interactions of predators and prey have been quantified using sonar and the development of techniques to effectively resolve collective responses in space and time [46-49]. As yet, acoustic techniques lack the resolution to be able to identify individuals consistently over time; however in cases where this is of particular importance, telemetry can offer an alternative solution. Reductions in the size, mass and price of tags now allows for the possibility of tracking individual fish over extended periods of time [50].

Re-wilding collective behaviour

Whilst there is a long tradition of wild studies in collective behaviour research – von Frisch’s work on the collective decisions of honey bees was undertaken in the wild [2] – we have not yet been able to collect the same sorts of data that have become the norm in the lab (Figure 2). For instance, we know from direct observations of primate groups that a type of “embedded leadership” can emerge from simple and local interactions [51] whereby socially connected or dominant individuals steer group activities [52, 53]. We assume that this process might result in faster collective decisions because transmission of information via central individuals will be quicker than via peripheral individuals (and possibly more accurate too, since it will pass through fewer individuals) [53]. Similarly, decision accuracy might also be enhanced since highly connected individuals tend to be dominant and/or elders which can have superior knowledge of features in their environment [54]. However, whilst correlational data from elephants (*Loxodonta africana*) [55], and orcas (*Orcinus orca*) [56] offer some support for these ideas – because individuals in elephant herds and orca pods gain significant benefits from following older, socially important leaders – we do not yet fully understand why certain rules evolve. To achieve this, we need more and better data, adopting similar approaches to those used in the laboratory (Figure 1), but over longer time periods and in more depth [4]. Only then will researchers be afforded a fully integrated study of collective behaviour.



Figure 2. Collective animal behaviour research: traditional observation techniques. (a) Observation of chacma baboon troops on foot to study collective movement and decision-making [52, 57] (image: A. King); (b) Observations of orcas by boat to study leadership and collective behaviour of pods [56] (image: The Center for Whale Research). (c) Observations of wild dogs in Botswana to study the collective movement decisions of packs [58] (image: N. Jordan).

Tools for re-wilding

Field researchers tend to gather data on one or a few individuals at a time, or else conduct repeated scans of all individuals’ behaviour at some interval. Where animals cannot be followed, observations tend to be restricted to certain resources (e.g. water or food sources, or at sleeping locations). These are noisy and patchy data. New developments in bio-logging [59] – which use animal-attached devices to provide data on the individual’s movement, behaviour, or physiology, without the need to directly observe the animal – can enable researchers to generate wild data comparable to the “whole-system” information afforded by laboratory experiments [60] (Figure 3). Three-dimensional accelerometers and magnetometers, for instance, allow us to reconstruct not only animal movement but also behavioural states [61, 62], and global positioning systems can provide animal location with high accuracy [63, 64]. With devices and batteries getting smaller, cheaper, and more powerful, there is now a real possibility of attaching loggers to the majority or all individuals in a social group as has recently been done with baboon troops [65-68]. Similarly, high-resolution sonar imaging can be used to track the motion and interactions among aquatic

organisms under water [47], and drones used to track them at the surface [69]. Imaging techniques can be used to reconstruct the 3D position and velocity of individual birds within large mobile flocks, too [70]. Note that with all the excitement of new data from these technologies, researchers must also carefully consider the ethical questions such technologies raise, related to animal capture and tagging, and disturbance to animals and habitats via drone use [71].

New tools are also available for remotely gathering environmental information. For example, with easy-to-deploy mapping drones we can capture accurate aerial imagery and generate 2D maps and 3D models of research sites on demand [72]. At larger scales, remote sensing data can not only classify objects and landscapes at high resolution, but also provide estimates of environmental heterogeneity (and its 'productivity') [73]. In aquatic landscapes high-resolution mapping data can be generated by Autonomous Underwater Vehicles (AUVs: [74]), while in aerial landscapes, fine-scale data on variability and predictability in airflows can be mapped using an Ornithodolite (binoculars with an inbuilt laser-rangefinder, compass and inclinometer) which can provide a series of coordinates of a target to estimate groundspeed [75].

Combining bio-logging and remotely sensed data creates "individual-environment" data streams that can enable researchers not only to model interactions between individuals according to their relative positions and movements, but to also explicitly measure and explore the influence exerted by local and global heterogeneity (i.e. how individual traits, relationships between individuals, and environmental features interact to modify movement and interaction rules). For example, a recent study of wild baboons in Kenya combine bio-logging data collected for a majority of individuals in a troop over a number of days together with environmental mapping [66], providing a benchmark for future wild studies of collective behaviour.

A new era?

What will all these complex individual-level data paired with environmental information do to advance the field of collective behaviour? Will it be worth all the effort? We think so. This new era will provide opportunity to integrate knowledge of the rich, complex, and changing environments in which social groups live with the behavioural data which are collected. The approaches we have discussed will allow for a synergy between laboratory and field experiments, providing insight into why specific rules of interaction evolved and how they are maintained, enabling better integration of function and mechanism, and therefore a platform for a more explicit comparative perspective. However, to achieve this requires a degree of restraint from researchers because it will become all too easy to gather vast datasets on the movement, behaviour, and environment of wild animal collectives. We therefore urge researchers to carefully consider (1) what the data are for, and (2) how they will be analysed. Data should be collected to allow systematic testing of hypotheses and predictions generated by researchers with good knowledge of the systems being investigated. A discussion of analytical tools requires a methodological review that is beyond the scope of this article, but we would point researchers towards new open-access analytical tools and software for storing, visualising, processing, analysing, and integrating data streams that will be crucial [e.g. 76, 77]. Below, we provide three inter-linked research themes that represent the sort of advances that will be possible (see the questions box some for more).

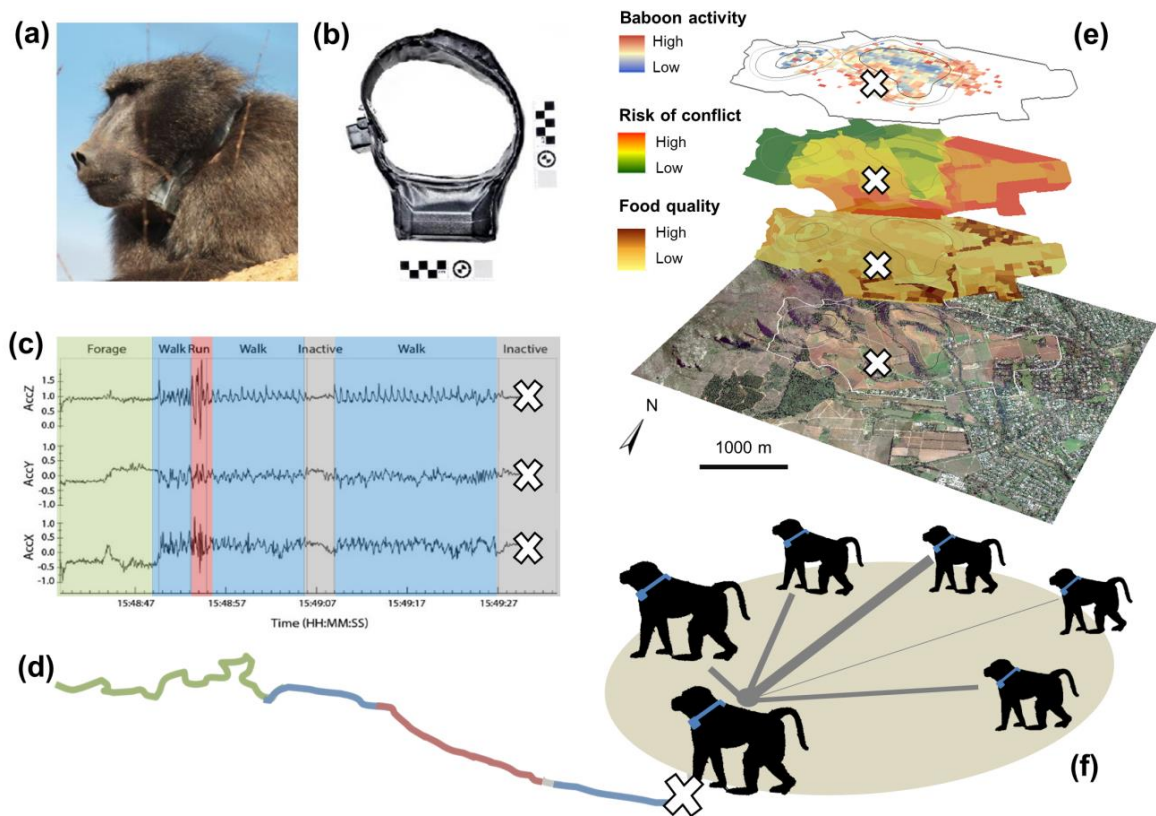


Figure 3. “Whole-system” information in the wild. (a) chacma baboon (*Papio ursinus*) wearing a F2HK.v2 baboon tracking collar pictured in (b) which can be used to create an acceleration ethogram (a catalogue of different acceleration footprints produced by different behaviour of an animal) as pictured in (c). For full details on how to build, deploy, and interpret data from the F2HK.v2 collar see [62]. (d) Represents a schematic of a baboon GPS track coloured by behaviours depicted in the acceleration ethogram and at the end of the GPS point “X” marks a location in time and space (Cape Town suburbs) for which information has been gathered on habitat types, food quality, risk of conflict with humans [78] and which has been combined with information on the average activity type performed by baboons from past data to produce a series of landscape layers in (e). The schematic in (f) shows that if multiple individuals are collared this allows for individual behaviour and positions can be recorded at each time point. In this image, the frequencies of recent interactions (e.g. spatial proximity based on GPS data or behavioural interactions based on acceleration data) are represented by line thickness. Combining these data one can investigate spatial or temporal synchrony in activities and explore variation within these as a function of the physical and/or social environment. Supplemental animation 1 provides a visualisation of how these data can be combined.

Simple rules: fixed or flexible?

Over the past decade, one of the major goals for collective behaviour research has been to uncover the “rules of interaction” (normally with reference to motion) used by individuals in animal groups, but even with sophisticated model selection processes, these are difficult to infer [79]. One reason for this could be that the rules might change (i.e. a fixed rule set that varies with context or a rule set that changes over time). A ‘flexible phenotype’ [80-82] is hypothesised to be a primary causal factor determining individuals’ success when dealing with uncertainty in their environment [83]. However, an infinitely flexible phenotype is not possible due to the genetic and developmental basis of species-specific traits [84] which limit

the range of possible physiological and/or behavioural responses individuals might exhibit [80]. Ecological constraints too (e.g. predation risk) can limit the types of social interaction that are possible [84]. As an alternative to flexibility, species can evolve sub-optimal, but resilient or robust phenotypes that operate well across a broad range of environments [80]. Studying social animals in the wild and collecting “whole-system” information (Figure 3), we can start to test whether these rules are flexible and/or robust (see glossary). Such characterisation will be especially important with respect to novel environmental changes and challenges caused by humans. In doing so, we can also investigate if and how interaction rules change with greater heterogeneity in systems and the environment (Figure 4a).

Networks and resilience

All manner of collective behaviours can be represented and analysed using a network approach [85, 86], and one of the most exciting avenues for network research and collective behaviour is to link the rules of interactions (see above) to global network structure and function. If rules turn out to be flexible, then individuals in animal collectives should adaptively change their behaviour and/or restructure their social networks to maintain performance under change. If rules are robust, then individual behaviour or the resulting social networks should not drastically alter when experiencing change, but instead show temporary “dips” in performance (Figure 4b). Work on ants in the laboratory has begun to tackle such questions [87], but, as yet, we have very little idea of how wild animal networks respond when their physical or social environment is perturbed [88] (Figure 4b). However, work investigating the effect of short- and long-term differences in predation risk upon fish collective behaviours offers a useful platform from which to build [89, 90].

Keystone roles

Similarly, if specific ‘keystone’ individuals are particularly important for collective animal behaviour [91, 92] and these same individuals are preferentially hunted, exploited, or exposed to risks via their own behaviour or via human activity, then this can impact on the structure and functioning of social units [93] (Figure 4c). Investigations of keystone roles and complementarity in roles within social units will offer insight for decision-makers tasked with managing the consequences of harvesting or human-wildlife conflicts. For instance, in the case of human-wildlife conflicts, if certain individuals play “keystone” roles and steer group activities, it could be more efficient to attempt to manage these individuals [78]. In the case of harvesting, research into keystone roles and collective behaviour can be employed to understand – and crucially, predict – if the removal of specific individuals will result in temporary or more permanent changes to social dynamics (Figure 4b). In extreme cases, these data and/or predictions might even help prevent catastrophic change to group stability and viability [94].

Concluding remarks

The frontier of collective behaviour research is riding on a wave of technological developments, but for the field to progress and answer fundamental behavioural and ecological questions and solve challenges concerning the consequences of environmental change (Figure 4) requires technology-enhanced learning and research within a broad multi-disciplinary research environment. That mouthful of a sentence requires students and researchers capable of this. Karl Popper, the famous Austrian-British philosopher said in 1963: “We are not students of some subject matter, but students of problems. And problems may cut right across the borders of any subject matter or discipline.” [95]. We urge Universities and funding agencies to enable such scientific endeavour [96].

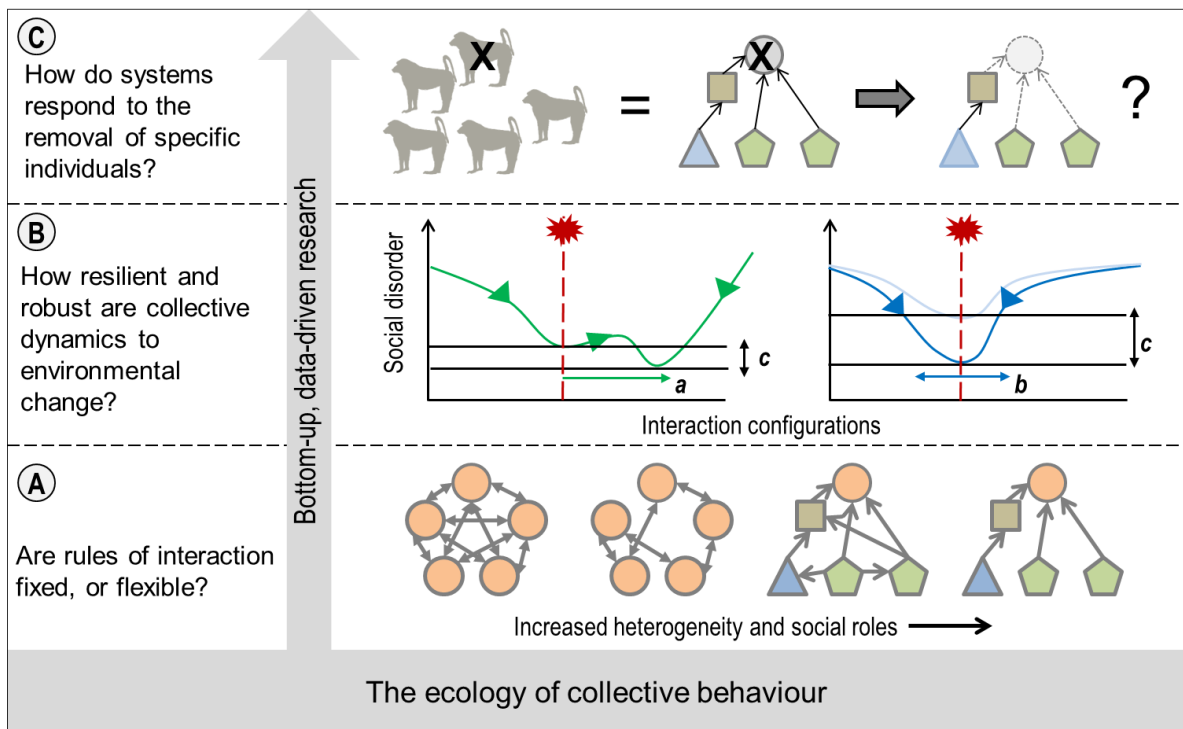


Figure 4. Environmental change and adjusted phenotypes/networks. (A) Detailed individual level data paired with environmental information will enable researchers to track individual interaction rules and resulting collective dynamics, and quantify the level of heterogeneity and social roles within their study system. We can then investigate if and how interaction rules change with greater heterogeneity in systems and the environment. (B) Schematic of social disorder (e.g. a breakdown of social hierarchy or cooperation) as a function of possible interaction (network) configurations: Stable states are indicated by the horizontal black lines, and a rapid environmental change indicated by the red comic-book style crash icon and red dashed vertical lines. Possible routes to maintaining stability: ‘a’ represents flexibility where interaction configurations adaptively change and social networks restructure. ‘b’ represents robustness where there is no significant change to interaction configurations and individuals/networks accommodate the change without any impact on social order. c represents resilience in the system. (C) Represents a case where individuals with specific behaviour (e.g. risk-takers) or morphology (e.g. big horns) die or are removed because of human impacts. For example, these individuals can be preferentially hunted or a particular exposed phenotype. If these individuals have a disproportionate influence on collective behaviours, this can alter the functioning and efficiency of social units. If such individuals play keystone roles, then the network might reconfigure (B).

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