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Review

Bringing a Time–Depth Perspective to Collective Animal Behaviour

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The field of collective animal behaviour examines how relatively simple, local interactions between individuals in groups combine to produce global-level outcomes. Existing mathematical models and empirical work have identified candidate mechanisms for numerous collective phenomena but have typically focused on one-off or short-term performance. We argue that feedback between collective performance and learning – giving the former the capacity to become an adaptive, and potentially cumulative, process – is a currently poorly explored but crucial mechanism in understanding collective systems. We synthesise material ranging from swarm intelligence in social insects through collective movements in vertebrates to collective decision making in animal and human groups, to propose avenues for future research to identify the potential for changes in these systems to accumulate over time.

What Are Collective Behaviours and How Do They Arise?

Some of the most impressive biological phenomena emerge out of interactions among members of animal groups. Bird flocks, fish schools, and insect swarms perform highly coordinated collective movements that can encompass thousands of individuals, producing complex group-level patterns that are difficult to predict from the behaviour of isolated individuals only. Animal groups are also able to solve problems that are beyond the capacities of single individuals [1]; ant colonies, for example, tackle certain types of optimisation problems so effectively that they have inspired an entire field of computer science [2]. Despite the appearance of synchronised organisation, it is increasingly well understood that no central control acts on the collective as a whole; instead, the global patterns result from simple, local interactions among the group's neighbouring members – a form of biological **self-organisation** [3] (see Glossary). Recent years have seen a proliferation of both empirical and theoretical work on the mechanistic underpinnings of collective animal behaviour [4], with self-organisation emerging as a major principle in various contexts including collective motion [5], decision making [6] and construction [7], activity synchronisation [8], and the spontaneous emergence of leader–follower relations [9].

Nonetheless, a rigorous adaptive framework is yet to be applied to collective animal behaviour; little is known about the nature of the selective forces that act at the level of the individual behavioural rules to shape pattern formation at group level. Over shorter timescales, and crucially for this review, no major synthesis has yet examined **collective behaviour** from a **time–depth** perspective; we do not know: (i) what changes group-level organisation might undergo over the course of repeated executions of collective tasks; (ii) to what extent solutions arrived at collectively are retained (learned), either at the individual or at the collective level, with the potential to influence future interactions; or (iii) what effect changes in group composition, due to natural demographic processes, have on whether solutions are 'inherited' from previous generations.

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Collective animal behaviour arises when numerous, repeated behavioural interactions between individuals in groups produce intricate group-level phenomena. Studies of collective behaviour in animal groups typically focus on one-time or short-term performance, largely neglecting the potential of these systems to learn or to undergo changes over time.

Acting collectively with others exposes individuals to information that may be unavailable when learning through individual experience; repeated feedback from such information into subsequent collective action can, under some circumstances, progressively improve a group's performance. More empirical study of collective learning is needed to establish its contribution to the accumulation of knowledge in animal societies.

When animals have the capacity to evaluate some measurable quality of collective action (such as group decision speed and accuracy, group cohesion, or energetic efficiency), they may be able to adjust their contributions, or their interactions with others, to influence future collective outcomes. The process becomes adaptive, acting within individuals' lifetimes: changes in behaviour ('innovations') introduce variation on which selection via assessment of collective outcome can iteratively act.

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Why Time–Depth?

We use the term 'time–depth' as applied primarily in linguistics and archaeology, where it is used to refer to the length of time a trait in question (e.g., language, behaviour, technology) has been undergoing change (e.g., [10]). Thus, implicit in the term is an appreciation that any current observations of a phenomenon are only snapshots that represent the outcome of a potentially long history of previous states. Correspondingly, we argue that, in the case of collective behaviour, the collective performance we observe at any given time has a history on which its current state is contingent. Such contingencies can be rooted both phylogenetically and ontogenetically. First, natural selection can fine-tune individual interaction rules in ways that modulate global-level phenomena [3,11], even in systems with very low levels of relatedness [12]. Second, individuals can adjust their contributions as a function of, for example, the quality of a previous collective action as they perceive it. In this review we focus on the latter scenario and examine the changes that collective phenomena can undergo over repeated performances of a collective task. Crucial to our perspective is the idea that individuals can learn from their experiences of acting collectively with others, making collective behaviour a plastic process that can allow groups to adapt their collective problem solving dynamically. In that sense, time–depth is what distinguishes collective behaviour in biological systems from that in the physical or chemical domain: the component units possess memory and are capable of learning. By considering changes to collective outcomes that are the products of learning as a result of collective experience rather than merely that of the individual, we can pursue a novel perspective on collective animal behaviour.

The Case for Collective Learning

Although pedagogical research and developmental psychology have long acknowledged that humans interacting in a group context influence each other's learning, this has typically been framed in terms of sophisticated cognitive mechanisms such as joint attention and mental-state attribution [13]. However, the same premise – that knowledge can be constructed from the interactions of multiple individuals – applies equally to collective behaviour. For example, previous research has shown that during collective navigation by homing pigeon flocks, birds less well informed about the terrain nonetheless contribute to the route-finding process and can thus improve the performance of both naïve and knowledgeable flight partners [14] (see Box 1 for more detail). We refer to this phenomenon as **collective learning** [15]. A theoretical treatment of this topic by Kao *et al.* [16] modelled collective learning to demonstrate that individual experience gained during collective action results in superior group decisions under a range of hypothesised environmental conditions. Empirical data on how such predictions relate to the performance of real animal groups is, however, largely lacking.

We suggest that collective learning not only influences knowledge held by individuals (and hence these individuals' subsequent behaviour whether alone or in a group setting) but also has the potential to affect how collective decisions are made on future occasions. For example, following a successful collective action, links between specific individuals might be reinforced as they recognise the usefulness of the information received or, conversely, a failed collective decision might weaken bonds between individuals and promote social reorganisation. Agent-based models suggest many interesting potential outcomes of such reorganisation, including social stratification and elite formation [17], but the empirical relevance of such models to real biological systems is unclear. Figure 1 summarises the interrelationships among the different conceptual elements we have so far highlighted.

Groups as Generators Rather than Only Repositories of Information

The progressive increase in the breadth, complexity, and efficiency of cultural phenomena in hominins is commonly described as **cumulative cultural** evolution (CCE) [18]. With behavioural **innovations** continually building on previous innovations, CCE gives rise to behaviours that go

Glossary

Collective behaviour: behaviour observed at one level of a biological, physical, or chemical system that emerges from interactions between lower-level units of the system. When these units comprise whole organisms (animals), collective patterns are those that are observed at the level of the social group.

Collective intelligence: shared or group intelligence that emerges from pooling information from many individuals.

Collective learning: the process of acquiring knowledge through interactive mechanisms where individual knowledge is shared. The content of what is learnt is generated through co-action or interactions between individuals and is thus unavailable to the same individuals when learning alone.

Cumulative culture: the accumulation of sequential modifications over time, and typically over generations, in culturally transmitted traits (i.e., those passed on through social learning) in a population. Cumulative cultural evolution is often likened to a ratchet-like effect where successful iterations are maintained until they are improved on, reflected in incremental increases in the efficiency and/or complexity of the behaviour.

Energetics: the study or exploitation of energy contained in chemical bonds. In respiration some fraction of this energy is converted into biologically useful forms for biosynthesis, membrane transport, muscle contraction, nerve conduction, movement, etc.

Innovation: a process resulting in new or modified behaviour that can be learnt by the innovator, by observers, by others the innovator acts collectively with, or by none of these.

Quorum: the minimum number of individuals that need to agree on a course of action for others in the group to copy them. Quorums accelerate decisions by effectively ending deliberations when the group is in the process of deciding between multiple options.

Self-organisation: the emergence of group-level patterns from local interactions between the group's neighbouring component units, resulting in organised behaviour without global or centralised control.