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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.

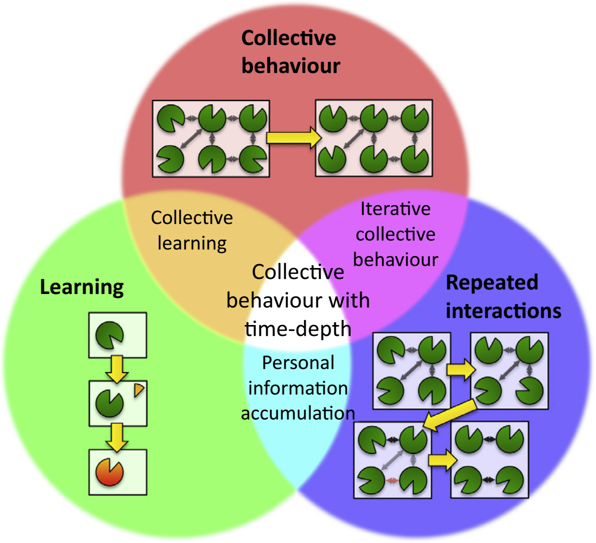

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Figure 1. Schematic Representation Showing How Different Processes Combine to Produce Time–Depth in Collective Behaviour. Coloured circles represent individuals and thin arrows between them represent their interactions. Collective behaviour (the appearance of patterns at group level based on interactions between individuals) combines with individual learning capacities to allow individuals to acquire novel information through their interactions with others ('collective learning'). Through repeated executions of a collective task, collective behaviour becomes iterative and personal information regarding the quality of the collective outcome continues to accumulate from each round of feedback, with the potential to inform subsequent collective action. Adjustments based on repeated performance of collective tasks and through learning via such experiences give collective behaviour time–depth: groups can adapt their problem-solving based on feedback detected at the individual level from the group's performance. Procedural (how to solve tasks) as well as content-based (what information to use to solve tasks) knowledge can effect these changes.

Time–depth: the interpretation of a trait in question (e.g., language, behaviour, technology, process, species) as the product of a series of changes in state that it has undergone over time. Changes can be due to selective forces acting on evolutionary timescales or to learning in the lifetimes of individuals or groups.

beyond what individuals are capable of inventing in a single lifetime. Such 'ratcheting' [19] is argued to have been key to the scope that culture has attained in humans but not in other species [20]. From religion to the Mars rover, much of present-day human behaviour and technology is the product of information accumulation over thousands of generations.

Models that attempt to explain what factors might have driven CCE in hominins frequently incorporate demography, focussing on population size or density [21,22]. These parameters (representing the pool of social learners) determine how likely novel behaviours – generated with a given probability – are to be retained. In a recent review, Fogarty *et al.* [23] briefly suggest that these models fall short on taking into account interactions between individuals as potential factors influencing innovation rates. We strongly agree with this suggestion and propose it deserves much more detailed consideration. What previous approaches lack is a role for groups as generators rather than simply repositories of information on which culture is built and can accumulate. In other words, not only is the final product (knowledge accumulation) dependent on group size, but so is the mechanism; larger groups might: (i) generate more innovations because they have a higher probability of including an innovator; and/or (ii) generate more innovations because **collective intelligence** operates more strongly the more individuals contribute to problem solving.

As an example, laboratory studies of CCE in humans, pioneered by Caldwell and Millen [24,25], have shown progressive improvements in solving tasks (such as building increasingly tall towers of spaghetti and Plasticine) when these are given to successions of 'microsocieties' comprising a mixture of previous solvers and novices. These transmission chain designs are notable for their use of groups of participants at each stage and are highly informative in terms of outcome (the accumulation of improvements) as well as mechanisms (emphasising features such as prosociality, teaching, and collaboration [20,26]). However, they are not explicit about the potential role that solving the task as a group might itself have had on the generation of innovations, particularly if each link in the chain had comprised more than the study's maximum of three individuals [25].

The issues explored above raise many interesting questions about what is necessary for collective tasks to benefit from pooling the contributions of multiple individuals (‘collective intelligence’). What are the necessary social, ecological, and cognitive prerequisites for animal groups to generate and retain solutions to problems in ways that allow the accumulation of these over time? In what measurable aspect can collective solutions improve? In the next section, we examine how we can evaluate behavioural solutions before returning to address these questions.

Measureable Outcomes

How can we measure the quality of collective performance? This question is relevant both to researchers seeking to identify changes in said quality and to the individuals involved in collective action (i.e., how does an individual within a group assess success and effectiveness in a group task?). The former speaks to our ability to study changes in collective outcomes longitudinally and the latter to the mechanisms that would allow such outcomes to promote learning by individual agents within the collective. As broad categories, the speed, accuracy, cohesion, and **energetic** efficiency of collective performance are all credible candidates – theoretically detectable by individuals in collectives and subject to adjustment as a function of individual behaviour. We illustrate each briefly below.

The capacity of groups to make accurate consensus decisions due to information pooling has entered popular science lore (as the ‘wisdom of crowds’ [27]) and the relationship between group size and decision accuracy has extensive theoretical and empirical support. Shoals of fish become capable of finer-scale discriminations [28] and of better predator avoidance [29], flocks of birds select routes closer to the beeline path to their nests [30,31], and human crowds move more accurately towards a target destination [32] as the number of individuals in these groups increases. Condorcet's jury theorem, the ‘many wrongs’ principle, and increased information processing power are typically relied on to explain the mechanism [6,33,34]. With the assumption that there is no population-level bias in opinions and that group members contribute information independently and equally, individual errors are averaged out to approach the optimum and/or the population majority tends towards the correct decision.

Often just as vital as decision accuracy, decision speed provides another measure of collective performance. This is particularly evident when under threat through predation or other forms of ecological pressure, where a group's capacity to respond rapidly is of fundamental importance. Here, too, increases in performance quality have been documented with increases in group size. For example, how quickly shoals of fish choose a path that avoids a predator [35] or how quickly honeybee colonies acquire and evaluate information about suitable nest sites [36] is improved by larger numbers of individuals contributing to the processing of available information.

Quorums often contribute to these effects, allowing groups to switch from information gathering to rapid convergence on a decision. Cross-inhibition, one mechanism through which such convergence operates, shows interesting parallels between social insect and neuronal decision-making [37]. Although quorums link decision speed and accuracy, the two can also be involved in a trade-off. For example, much like in individual decision making [38], decision accuracy can be traded off against decision speed; theoretically, the speed of a collective decision can be increased by decreasing the steepness of the quorum function, but this will also cause a decrease in the accuracy of the decision [33]. Ants in harsh environments where decisions have to be made rapidly, potentially sacrificing accuracy, respond just so [39] (see also Box 2).

Since many of the benefits of social living depend on group cohesion [33,40], group fragmentation might be viewed as a suboptimal outcome during collective action. Antipredatory effects such as predator confusion and dilution will be compromised [41] while information-processing advantages will be correspondingly scaled back [6,36]. However, differing interests or preferences over the best course of action can generate conflicts where individuals will typically pay a 'consensus cost' for remaining with the group [42]. Under such circumstances groups can fragment: differing preferences in the direction of travel have been shown to break up homing pigeons [43] and king penguins [44] (although, perhaps due to different balancing of long- vs short-term costs, not meerkats [45] or baboons [46]). Cohesion can also be involved in trade-offs with speed and accuracy [47]. Analyses of baboon group movements suggest that decisions are delayed when opinions within the group diverge widely [46], probably because forces maintaining cohesion compete with individual preferences, reducing decision speed.

Lastly, collective action can generate energetic savings that might be detectable to individuals. These savings can be accrued through, for example, positive aero- or hydrodynamic interactions: crustaceans [48], fish [49], adult [50] and juvenile [51] marine mammals, and birds during both flight [52] and surface swimming [53] have been shown to benefit energetically from moving together with conspecifics. Box 3 details a case study for flying birds.

How Can Measureable Outcomes Feed Back into Collective Behaviour?

It seems reasonable to assume that individuals in groups are sensitive to some combination of the measurable outcomes of collective action outlined above. Although absolute evaluation might not be possible in many circumstances (a bird in a flock might not know whether the flock is flying an efficient route to a destination or an ant with limited knowledge of the environment might not be able to judge whether the colony was delayed in choosing a new nest site), relative judgements based on comparisons with previous group performance could be available to guide evaluation. Based on such comparisons, individuals might, for example: (i) choose to adjust their own contribution on subsequent occasions; (ii) redistribute the relative weighting they assign their personal versus social information; or (iii) change the way they interact with specific group mates. Similarly, increases in an individual's experience or competence as a result of previous collective action might affect what information it contributes and how it interacts with others in future. We now explore examples of both these processes – adjustments based on judgement of previous performance quality and on learning as a result of previous collective action – with reference to theoretical and empirical examples.

Changing one's relative contribution to collective decisions might depend on a judgement of the quality of one's own information. That such adjustments – a function of individual certainty – are possible has been demonstrated in various species. How well informed human participants in a collective decision-making task judge themselves to be influences how readily and quickly they contribute information to the group [54]. Male bottlenose dolphins perform specific behavioural signals that initiate group travel more frequently the greater their knowledge about the optimal timing of such activity shifts [55].

Changes in the organisation of decision making represent perhaps more subtle adjustments. Modelling work examining changes in information flow within groups over repeated iterations of task solving found that links between individuals were reinforced when they judged each other to have contributed high-quality information on previous occasions [17]. In a sense, individuals chose to rely on group mates that had proved themselves competent. Similar mechanisms might be at work in several of the systems we discuss in previous sections and in Boxes 1–4, although cases could be limited to species that have stable and small enough groups and the

Box 1. Navigational Problem Solving in Homing Pigeon Flocks: Leadership Hierarchies, Collective Learning, and Competence

Homing pigeons (*Columba livia*) have long served as model animals in the study of large-scale spatial cognition [65]. One of the most consistent findings emerging in recent research is that, with experience, pigeons establish idiosyncratic routes home (based on memorised chains of landmarks) that they recapitulate faithfully whenever flying solo [66]. When flying as a flock, the collective route emerges as a compromise between individuals' preferred paths via a self-organised process, often, but not always, leading to 'better' (closer to the beeline) routes overall [14,30,43] (Figure I). Furthermore, pair-wise leader–follower relations are spontaneously generated within the group and condense into robust, fully transitive leadership hierarchies [67] that reflect the flow of information within the flock. Consequently, how these leadership hierarchies are structured will have important implications for the quality of the group's navigational performance [68,69] and changes in rank allocations have the capacity to dynamically modulate group performance.

Interestingly, since leaders are by definition responsible for more of the flock's navigational decisions than followers, recent work has shown that they are also the ones that learn most through the experience of moving collectively [31]. This raises the possibility – as yet unexplored – that there exists a feedback loop between leadership, learning, and competence with the potential to effect improvements in collective performance over time. In other words, although leaders might not necessarily be the most competent navigators at the outset, they improve in their roles through the experience of leading, which can in turn improve the flock's performance and reinforce their leadership role in future.

Pettit *et al.* [14] have shown that while individual birds eventually reach a plateau in the efficiency of their routes, adding a locally naïve individual as a flight partner allows the pair to improve beyond this individual constraint. This tantalisingly suggests that collective intelligence and social (collective) learning can interact to produce increasingly efficient group solutions over successive 'generations'. Input from new individuals, combined with what experienced individuals had previously learnt, effectively acts as the 'innovation' on which novel, better solutions are built. Such improvements – that go beyond the capacities of single individuals – are hallmarks of cumulative culture [18], a process so far argued to be unique to humans [20].

Key questions for future work will be to determine how flocks' organisational structure changes as a function of individuals' prior experiences (do leadership hierarchies become progressively more stable, more stratified, or more or less heavily weighted in favour of input by birds at the top?) and whether improvements (reflected in increasingly more efficient homing routes) can accumulate over time through iterative rounds of navigational innovation followed by collective learning.

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Figure I. Homing Pigeons Solving a Navigational Task Collectively. Photograph by Zsuzsa Ákos.

requisite cognitive capacities for individual recognition. Through such recognition and selective targeting of attention, the contributions not only of competent group mates but, conversely, also of 'persistent offenders' might change over time.

In systems that use quorums in reaching consensus decisions, quorum size can be adjusted to tune decision speed and thus to modulate how decision speed is traded off against decision accuracy (Box 2). Honeybee colonies vary in how they trade off speed for accuracy according to their size [36]: larger colonies invest larger numbers of scouts in discovering nest sites but make decisions at the same speed as smaller swarms, allowing higher accuracy. Combined with the

Box 2. Nest Emigrations in Social Insects: Do Ant Colonies Get Better at House Hunting?

When their nest becomes uninhabitable, ants of the genus *Temnothorax* (Figure I) make collective house-hunting decisions that emerge from differential recruitment efforts for different potential new nest sites by scouts [70]. These decisions can be superior to those made by individuals, as colonies are less susceptible to error when the discrimination task is difficult [71] or involves a larger number of choices [6] or in cases where a 'decoy' leads to irrational decisions in single ants [72].

How the organisation and quality of house-hunting collective decisions change over repeated emigrations by the same colony has received surprisingly little attention, despite the fact that such successive events have powerful ecological relevance. Not only are colonies likely to face similar emigration problems repeatedly over their lifespan, but the process might be undertaken after at least partial turnover in colony membership due to normal demographic processes.

Langridge *et al.* [62] were the first to examine the effect that repeated emigrations have on a colony's collective problem solving. They demonstrated that emigration time decreased with repeated task solving, with the improvement apparently due to learning by individuals. All components of the total emigration time (discovery, assessment, and transport of colony mates) were reduced on repetition; however, interestingly, there was no change in division of labour (scouts vs non-scouts, transporters vs non-transporters) across the colony. Instead, further work by the same authors identified changes in the behaviour of ants actively involved in previous emigrations: they switched to carrying colony contents (other individuals or brood items) sooner than ants that had not previously acted as transporters [73]. Thus, decision speed was accelerated. However, whether colonies could also improve in other ways – for example, in the resolution of their discriminative capacity or in their resistance to decoys – as a result of repeated task solving remained to be established. Interestingly, Sasaki and Pratt [74] showed that colonies are indeed capable of more subtle improvements: they can adapt the weighting they place on different attributes used to distinguish between potential nest sites as a function of which of these attributes had proved the more informative during previous emigrations. Again, learning by ants (specifically, how scouts change their individual weightings for different nest attributes) is implicated in the observed improvements.

As results in both sets of studies rely on individual rather than collective learning (in other words, ants learn through their own independent actions rather than through collective action), it seems likely that demographic turnover would limit the extent to which any improvement is able to accumulate over time in these systems. This is in contrast with cases where naïve individuals introduce novel innovations that can build on previously reached solutions and where learning is influenced not just by an individual's own actions but by what it experiences as a consequence of group action (e.g., Box 1). Nonetheless, much remains to be explored with respect to *Temnothorax* collective decision making, and if individual ants also change their interactions with others as a function of previous experience (suggested but not confirmed in [62]) and if these interactions in turn shape learning in new recruits, longer-term effects indeed become possible.

Figure I. Ants of the Species *Temnothorax rugatulus* Inside their Nest in the Laboratory. Photograph by Takao Sasaki.

Box 3. Energetics of Group Movement in Bald Ibis: Practise Makes Perfect?

Aerodynamic theory predicts that when birds fly in V formations, energy savings can be achieved by capturing the upwash produced by the preceding bird – positive aerodynamic interactions occur between members of the V formation [75,76]. As impressively coordinated as such flocks appear, developmental studies reveal that they do not spontaneously assemble but result from learning by individuals in a collective setting.

The critically endangered northern bald ibis (*Geronticus eremita*) is currently being reintroduced back into its Central European range, a process involving imprinted birds following a microlight paraplane containing a human foster parent [60]. Such migratory flights would traditionally be undertaken in groups comprising juveniles and adults in small family groups, implicating kin selection [77]. Training flights pre-migration are critical, particularly for juveniles, since, as in many other species, the first migration is the greatest cause of mortality in the lifespan of an individual [78].

The onset of V formation in juvenile birds post-fledging had previously been investigated in the American white ibis (*Eudocimus albus*) and was assumed to develop through repeated interactions and flights with adult birds [79]. During the course of the observations, the tendency of juveniles to fly in formation increased from 17.8% of all juveniles immediately post-fledging in late June to 88.0% of juveniles by late August (Figure IA). Among 64 000 observations, only once was a juvenile seen flying out of a mixed-age flock, suggesting that the presence of adult birds plays a role in the development of formation flight in young birds.

The imprinted northern bald ibis, however, presents a different scenario. Unlike in a wild-type setting, the imprinted ibis did not have knowledgeable leaders to follow or learn from: there were no adult birds to demonstrate V-formation flight and no experienced individuals to impart knowledge via social interactions. Using biologging technology [60], it was possible to document the onset of V-formation flight in the young birds (Figure IB–D). Successive training flights, followed by actual migratory flight, show a clear and gradual move from apparently uncoordinated flight akin to that of cluster flight in pigeons [80] to the distinctive V formation. While it is possible that the delayed onset of formation flight is linked to flight capabilities and younger birds do not have the requisite skills to fly in such a controlled manner, the results do suggest that a group of naïve birds is able to self-sort over a period of time and learn the optimal positions to maximise upwash capture. It is likely that positive feedback fine-tunes positioning within the flock while the motivation to fly in a V is genetically determined [64]. The group was able to work as a collective to progressively find not only the most energetically profitable flock shape but also where within that flock each bird should be optimally positioned.

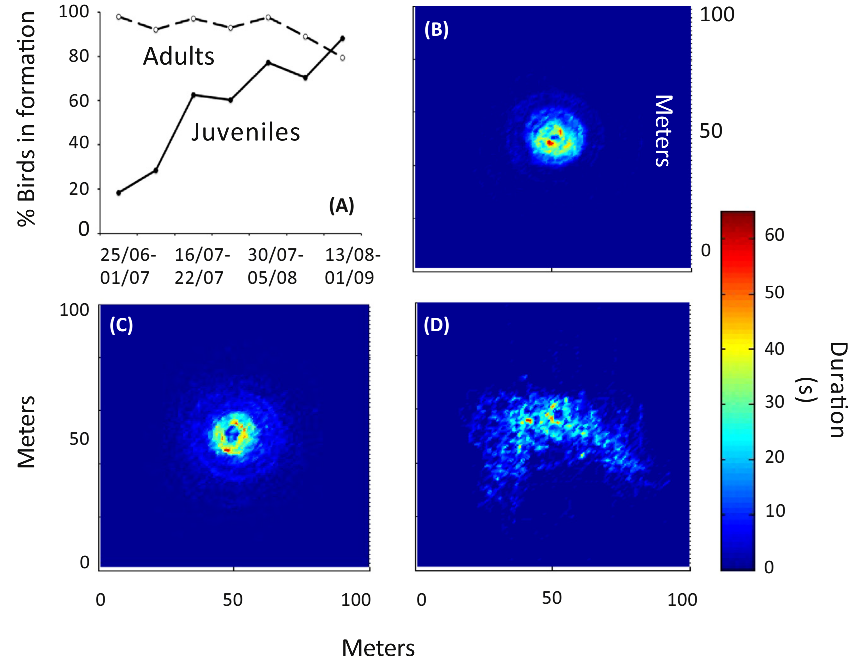

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Figure I. Development of V-formation Flight in Juvenile White Ibis. (A) Percentage of adults and juveniles flying in V formation over the course of a single summer. Redrawn from Figure 1 in [79]. (B–D) 3D location histogram showing the position of individual juvenile ibises ($n = 14$) flying as a flock, with respect to the flock centroid, measured by a 5-Hz GPS data logger. The colour scale refers to the duration (in seconds) that a bird was present in each 0.25 m × 0.25 m grid. The sequence of histograms shows the development of organised V-formation flight over time, with the birds flying in training flights in (B) late July and (C) early August before (D) embarking on the first migratory flight in late August (2012). Data adapted from [60] and from online supplementary data in [61].

Box 4. Candidates for Time–Depth?

Animal groups come in many shapes and sizes and the degree of usefulness of a time–depth component to collective behaviour is likely to vary along with certain key parameters. We suggest that the usefulness and likelihood of time–depth will primarily be related to three important factors: (i) levels of interindividual conflict within the collective (itself linked to the relatedness of individuals comprising the group); (ii) stability of group membership; and (iii) the regularity of the collective task undertaken (Figure IA). A group is unlikely to benefit from a capacity for time–depth if group members: (i) are unrelated; (ii) are fluid in composition; and (iii) perform a given collective task only sporadically. For example, collectively migrating passerines that travel in large clusters of unrelated individuals are unlikely to accumulate significant improvements over time: the task is so rarely undertaken and the fission–fusion nature of groups means that time invested in developing individual roles or expertise would not be recouped in the absence of recurring interactions with the same individuals or with individuals with closely aligned interests. Similarly, large group sizes can negate the advantages that time–depth can bring, if sheer numbers mean that repeated interactions between individuals will be limited and feedback between individual and group performance will not be transparent. By contrast, a group is likely to benefit greatly from time–depth if members: (i) are related; (ii) are static; and (iii) regularly perform tasks as a collective.

A good example of the latter scenario is provided by cooperative hunting (Figure IB). Cooperative hunting has been reported in several mammal species [81] and one bird [82]. It is particularly prevalent in the delphinids (e.g., [83,84]), with a variety of hunting approaches utilised depending on prey type, habitat, and group size and some dolphin species even hunting cooperatively with humans [85]. Many of the cooperative hunting strategies (e.g., intentional beach stranding [86,87], pack-ice breaking [88,89]) used by dolphins appear region or pod specific [87,88], suggesting an element of culture in cetacean society [90,91]. Furthermore, delphinids exhibit role specialisation, where specific group members repeatedly take the same role over many years in each cooperative hunt. Such division of labour within a stable social group potentially allows an individual to perfect its role. It remains unclear why a division of labour with role specialisation is so rare in species that hunt cooperatively. One theory proposes that practice might not improve performance sufficiently to warrant such role specialisation [83]. Why it should prevail in marine mammals is likely to be linked to prey diversity, prey biomass, mobility, and, crucially, practice rewards [92]. In cooperative group hunters, some highly skilled individuals can exert more influence during hunts. The full effect that these 'keystone individuals' [93] have, and, most importantly, how long their influence lingers after their departure, is a topic of current research effort. What remains unknown is how such cooperative hunting techniques improve over time, both within the lifespan of an individual and over successive generations. Thus, cooperative collective hunting in cetaceans can potentially offer an intriguing future case study for examining time–depth in collective action.

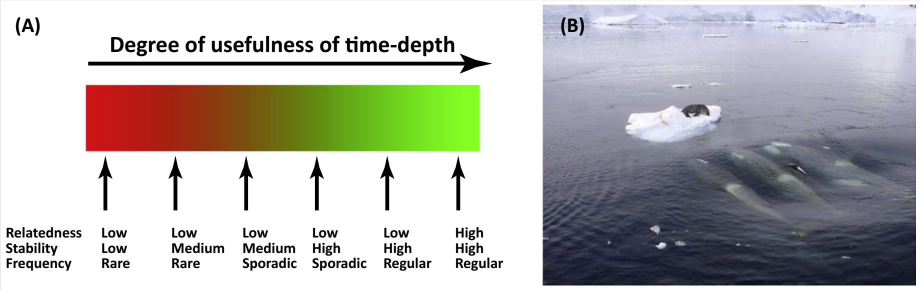

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Figure I. Searching for Candidates for Time-Depth. (A) Hypothesised likelihood and/or degree of usefulness of a time–depth element in collective behaviour as a function of various parameters relating to group composition and the task undertaken. We suggest that a capacity for time–depth will be least relevant in cases where groups comprise individuals of low relatedness and are transient or unstable in composition and where tasks are repeated only rarely within individual lifetimes. At the other end of the scale, time–depth is envisaged as most relevant where groups are small and stable, members have high relatedness, and the task frequently recurs. (B) Killer whales (Antarctic type B) coordinate to 'wave wash' a Weddell seal off an ice floe in Antarctica [88]. Such cooperative hunting falls at the 'high relatedness, high group stability, high task frequency' end of the spectrum in (A) and hence might be a potential candidate for time–depth. Photograph by John Durban, NOAA Southwest Fisheries Science Center.

observation that prior knowledge contributes to collective decisions in social insects [56], flexibility in lowering quorum size when individuals are well informed could lead to progressive improvements in colony performance in terms of speed without sacrificing accuracy.

While many of the examples above deal with collective decisions, improvements in collective performance are also attainable in cases where there is no explicit 'decision'. Groups of prey, for example, might streamline their escape responses following successful interactions with predators (much like certain types of collective motion rules are suggested to reduce group fragmentation following predator attacks [43]). Similarly, increases in energy savings derived from moving in formation can be obtained by individuals learning, during group movements, where best to position themselves for more efficient exploitation of the aero- or hydrodynamic benefits offered by group travel (Box 3). On the other side of predator–prey interactions, cooperative hunting presents an interesting case study in which we suggest there is potential for collective learning and time–depth (Box 4). Where there is division of labour – not only in group hunting but also in more discretised roles within society such as in social insect temporal and physical castes – flexibility in the roles assumed by individuals, coupled with feedback on how well they fulfil their roles [57], can tune collective performance over time.

Finally, it is worth noting that the idea that iterative collective performance in animal groups might be influenced by the group's previous states has been suggested to present intriguing parallels with neuronal processes (e.g., [58]). In both cases interactions among populations of units, as well as the properties of the units themselves, can be tuneable as a function of prior history; the succession of collective states thus assumed can be regarded as reflecting ‘collective memory’ [59]. Future work linking processes such as memory formation in organismal and neural collectives is likely to provide cross-disciplinary insights on both sides of this analogy [58].

When Might Capacity for Time–Depth Be Most Useful?

Although in our descriptions above we deal with examples where time–depth is both feasible and potentially operates, we acknowledge that there are situations in which it will be either impossible to implement or of limited use. First, in cases where collective outcomes are not necessarily or directly linked to mechanisms at the individual level but are instead ‘emergent’ properties, by definition behaviours that improve group performance cannot be learnt. Second, it might be that adjusting the collective outcome has utility only in certain situations where, for example, there is need, room, or capacity for improvement (Box 4). In this second case, changes might be generated and implemented flexibly, thus increasing the mechanism's functionality and fine-tuning its effectiveness to the given scenario. The role, or best use, of time–depth is, therefore, situation dependent.

In a task or event, a time–depth element might be utilised to either be: (i) in progress – to learn, innovate, and problem solve as a collective, for future use; or (ii) static – to benefit from previous innovation and iterative interactions as a collective, to maximise potential gains to be made through working cooperatively. The propensity of a group to work collectively will require alternative functions, in progress or static, of a time–depth element depending on the task in hand. During collective tasks where solutions are open ended or shifting, groups comprising knowledgeable and naïve individuals might facilitate finding the best solutions. During such tasks, innovations (or, more simply, ‘noise’) from naïve individuals added to the knowledge of those more experienced can work together to bring about improvements in the measurable outcome. In this instance a stable, static society would perform worse than one with immigration or demographic turnover, with the time–depth element needing to be considered in progress. If, however, solution quality can or has reached a plateau where no further innovation will better any measurable outcome, a static state would be more effective, reducing the element of risk. For example, if a group has found a continually productive foraging site, once the best route (e.g., straightest and/or safest) has been located between the foraging site and home, the best solution would be to continue benefiting from route innovations before that point but to then remain static. The decision, or feedback, to remain static and cease innovation can be spontaneous or a consequence of a lack of demographic turnover at a given time point.

It is likely, therefore, that there will be times and events where the potential noise from innovation could have deleterious effects. Such events might be at specific times in the annual cycle where resources are limited or due to an energetic bottleneck whereby deleterious noise could have a significant impact on survival rates and/or energy expenditure. For example, where collective action results in energetic savings through cooperative group locomotion, the situation could be considered quite different. To maximise energy savings during a long migratory flight in a V formation, an important component of success is learning the correct positioning ([60]; Box 3) and the requisite social rules for positional swapping within the V [61]. In this scenario a stable group of 'experts' would be best – a static use of time–depth. During critical events such as migration, innovations might be too risky.

Concluding Remarks

We have highlighted a hitherto largely overlooked aspect of collective animal behaviour: that many collective outcomes we observe and study at a given time might be contingent on the collective's previous history and memory. There is evidence that collective performance – measured in terms of the speed and accuracy of group decisions, group cohesion, and/or energetic efficiency – can change over time, both in groups where the same members solve the same task repeatedly and in those that experience at least partial turnovers in group membership over the course of such repetition (e.g., [15,31,62–64]; Boxes 1–4).

Key to our argument is that if collective learning not only influences individual knowledge but also has the potential to affect how future collective decisions are made, we must acknowledge collective behaviour as a flexible process and explore its capacity to adapt using feedback from the group's prior performance. We suggest that, in future research on biological self-organisation and collective animal behaviour, crucial insights will be achieved by focusing explicitly on four issues (see Outstanding Questions). Through the synthesis of these questions with mechanistic and functional studies of collective behaviour, it will be possible to illuminate in hitherto unprecedented detail how animal groups acquire, process, store, and build upon information.

Outstanding Questions

To what extent are solutions arrived at collectively retained by individuals and to what extent do they influence future contributions to and interactions during subsequent task solving?

What changes does group-level organisation undergo over repeated executions of collective tasks, and over what timescales?

What effect do changes in group composition due to natural demographic processes have on solutions 'inherited' from previous generations and on producing innovations that modify these solutions further?

What role does energetic optimisation play in the streamlining of collective actions?

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