

Review



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The importance of individual variation
in the dynamics of animal collective
movements

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Animal collective movements are a key example of a system that links two clearly defined levels of organization: the individual and the group. Most models investigating collective movements have generated coherent collective behaviours without the inclusion of individual variability. However, new individual-based models, together with emerging empirical information, emphasize that within-group heterogeneity may strongly influence collective movement behaviour. Here we (i) review the empirical evidence for individual variation in animal collective movements, (ii) explore how theoretical investigations have represented individual heterogeneity when modelling collective movements and (iii) present a model to show how within-group heterogeneity influences the collective properties of a group. Our review underscores the need to consider variability at the level of the individual to improve our understanding of how individual decision rules lead to emergent movement patterns, and also to yield better quantitative predictions of collective behaviour.

This article is part of the theme issue 'Collective movement ecology'.

1. Introduction

How does individual variability affect the properties and dynamics of biological populations? Individual variation in physiological, morphological and behavioural traits [1–3] constitutes the raw material for evolutionary change, and as such, has been a key focus of biological interest for decades [4]. Collective movements, a phenomenon emerging from local interactions between individual group members, provide a key example of a system in which two clearly defined levels of organization are linked: the individual and the group [5]. Initial Eulerian models investigating movements of schools, flocks and swarms assumed simple behavioural rules at the level of the individual (e.g. attraction, alignment and repulsion behaviours) and explored emerging patterns at the level of the group [6,7]. The general result of these studies is that, with an appropriate choice of parameters, simple local rules can produce a range of coherent collective behaviours. By design, these models assumed that all individuals were identical.

Under what situations are this simplification appropriate to capture the properties of collective behaviour observed in nature? In some cases, such as fish schools or bird flocks that rapidly change their shape in response to predation risks [8,9], heterogeneity among individuals may have no practical influence on group structure and collective movement dynamics. In such situations, group

dynamics provide the ecological and evolutionary context against which individuals make their behavioural decisions. Consequently, the social context may restrict individual differences to ensure increased conformity to the group [10]. In other cases, however, within-group heterogeneity may strongly influence collective movement behaviour [10,11]. Some studies have shown that individual variation in some attributes, such as sex and size [12,13], may influence group navigation and structure. Heterogeneity in social status, such as the presence of leaders and followers, may also be important for understanding the dynamics of some groups [14]. For example, group navigation in some species is guided primarily by a small number of individuals which contribute disproportionately to the relative success of other group members (e.g. [15,16]). Models that include different categories of informed individuals have shown that group composition can be critical to overall performance or even the persistence of populations [17,18].

Recent studies that explore how locally individuals lead to emergent group behaviours have revealed that differences among individuals can contribute to group functioning as well as drive the evolution, maintenance and behaviour of animal groups [10,19]. However, given the remarkable number of studies on collective movements, there is still relatively little research on the effect of heterogeneity within a group on aspects of collective motion [20]. Our goal in this paper is twofold. First, we review the current knowledge on sources of intragroup heterogeneity in collective movement across different taxa. Second, we review the current theoretical understanding of the importance of individual variation on a number of different metrics of collective motion. Specifically, we summarize how individual heterogeneity has been accounted for in existing models. We find a surprisingly narrow accounting, perhaps because, to date, such models have almost exclusively been developed to provide qualitative, theoretical predictions on the emergent properties of collective movements. The variables of interest for most collective movement studies are the suite of population-level phenomena (e.g. cohesion, group navigation) that emerge from lower-level features (e.g. individual-level properties, local factors). We thus sorted out the empirical and theoretical evidences based on how sources of intragroup heterogeneity at the lower-level features contribute to emergent phenomena. Further, we present results from a simulation model to illustrate whether adding heterogeneity among individuals has the potential to alter collective motion. We conclude by presenting testable predictions about the linkages between group heterogeneity and collective motion.

2. Empirical evidence for the importance of individual variation in animal collective movements

Empirical research indicates that within-group heterogeneity may strongly influence collective movement behaviour (electronic supplementary material, table 1). For example, as the relative position of individuals in the group, whether transient or persistent, is one of several key determinants of collective movement [21,22], sources of intragroup heterogeneity that establish and subsequently alter patterns of position may scale up to influence collective motion (electronic supplementary

material, table 1). Here we detail how heterogeneity among individuals in animal groups may derive from a variety of sources, none of which are mutually exclusive.

(a) Social, physiological and environmental factors

The behaviour of individuals is often influenced by the presence of neighbouring members via attraction, short-range repulsion and alignment between local neighbouring individuals. Interestingly, the sensitivity and reactivity of an individual to its social environment depends on the activity in which the individual is engaged [23], the specific differences between individuals (e.g. sex and size) in mixed groups [24], and the inter-individual differences in personality and established social affinities [25–28]. Further, social affiliations are a common source of internal structure in animal groups [29]. Because their innate structure is replicated across individuals, immediate family groups (e.g. mother–offspring units) and extended family units travelling together may impose hierarchical regularity on group structure.

Individual position and movement behaviour within the group is also conditioned by the physiological state of individuals and the abiotic environment. For example, group migration of Australian locust (*Chortoicetes terminifera*) is influenced by cannibalism [30]. Deprived individuals move significantly faster within groups to avoid interactions with other group members. Body size and nutritional deprivation were also determinants of individual position in roach (*Rutilus rutilus*) shoals [31]. Further, movement patterns of individual olive baboons (*Papio anubis*) are highly affected by some habitat features such as roads and sleeping sites, resulting in changes in the group coordination and structure [32].

(b) Resource acquisition and risk aversion trade-offs

Resource acquisition and risk aversion is a classic trade-off in behavioural ecology, and the challenges of individually optimizing these two often-conflicting needs may influence animal groups [33]. Peripheral positions in a group are often associated with a higher predation risk as assumed by the selfish herd theory [34]. Thus, individuals tend to reduce their predation risk by occupying central positions while placing others in the moving group edges. For example, among vervet monkeys (*Chlorocebus pygerythrus*), dominant individuals traded off predation risk for food acquisition by consistently foraging on the front, outside edge of the group farther from conspecifics, where they obtained more resources [35]. Similarly, in Assamese macaques (*Macaca assamensis*), those individuals most vulnerable to predation (immatures and females with young infants) maintained positions closer to the group centre than adult males and females without infants [36].

(c) Aggression and dominance

Aggressive interactions, and dominance-based relationships more generally, may also provide structure to animal groups (electronic supplementary material, table 1). In many species, individuals seeking to avoid aggression often position themselves away from dominant individuals, including on the periphery of a group. For example, Aplin *et al.* [37] observed that in great tits (*Parus major*), the spatial position occupied by an individual in a moving group was related to individual differences, with more proactive individuals preferentially placing themselves at the periphery of flocks compared to

reactive ones which moved to high-density central flock areas. Among Assamese macaques, this positioning is translated into lower ranking individuals arriving later at feeding patches than higher ranking individuals, thereby reducing the negative impact of the highest aggression at the beginning of a patch feeding event [36]. Overall, the routine interaction between aggression-based factors and resource/risk factors in animal groups is a particularly clear example of how different organizing principles may jointly influence the spatial structure of animal groups.

(d) Opportunities for learning

Learning and information exchange among individuals are fundamental components of many social systems. The use of social information can lead to different behavioural actions, the decision rules behind which can be at least partly inferred from the realized individual movement patterns within the group [38]. Because proximity to experienced individuals may influence the success or rate of learning of naive or less-experienced individuals, the need to learn may influence how different individuals position themselves within a group. For example, in bearded capuchin monkeys (*Sapajus libidinosus*) that use rocks to break open nuts, young or inexperienced individuals position themselves within view of experienced monkeys that are proficient at nut cracking and maintain these positions when moving and foraging. Individual skill in route navigation is another trait typically heterogeneously distributed across group members, which can give rise to differences in within-group spatial positioning. Leading positions in a group are often occupied by individuals with greater navigational experience in a specific movement route or greater route confidence ([14]; but see [39]).

3. Theoretical representation of individual variation in collective movement models

While the empirical literature on behavioural variation of individuals within groups is rich, theoretical studies on collective movements that account for individual variation are much sparser. In this section, we review the questions asked and the approaches taken in theoretical models for collective motion that have accounted for individual variation (electronic supplementary material, table 2). In our view 'individual variation' refers to those differences among individuals that are either permanent or change slowly (e.g. body size, fat reserves) in relation to the dynamics of group movement. We distinguish these individual differences from other forms of 'noise' that represent individual variation that the model is not directly attempting to explain. For example, some studies have recognized that variability in individual movement alone is sometimes sufficient to produce collective patterns, like the circular structure generated by the ant *Messor barbarous* [40]. This variability, however, results from random fluctuations in the movement direction of individuals obeying identical behavioural rules.

(a) Individual movement characteristics

Many collective movement models that include individual variability commonly consider that the group consists of different types of individuals, each having the capacity to produce only a single type of behaviour. Early discrete-individual

(Lagrangian) models for animal aggregation were a variant of an n -body dynamics problem [41], where attraction or repulsion between individuals was often represented by a discontinuous function of the distance between them. Several such models assume the existence of leaders, or informed individuals, that have a greater effect on collective decision-making than other group members [26]. For example, Gueron *et al.* [40] investigated the dynamic behaviour of small herds using two-dimensional discrete stochastic models where individuals moved away from neighbours that were too close, and towards distant ones. Individual variation was accommodated by subdividing the group into two categories, namely speeders (i.e. dominants) and laggards (i.e. subordinates). They observed that in groups composed of identical individuals, cohesion and coordinated movements could be persistently maintained, whereas for heterogeneous groups, initial aggregations tended to fragment when the difference between the normal speeds of speeders and laggards exceeded a threshold. Because such sensitivity to group fragmentation is common in the natural world, this study illustrates the utility of individual-based models as vehicles for exploring group dynamics.

Couzin *et al.* [42] presented a self-organizing model of group formation in three-dimensional space to show how individual decisions may influence group behaviour and structure. Individual-level heterogeneity was introduced by drawing speed and turning rate values independently for each individual. These values (drawn from Gaussian distributions) remained fixed for each individual for the duration of the simulations. The authors assumed that all individuals attempted to maintain a given minimum distance between themselves and others. If individuals were not repulsed, they were attracted towards and aligned themselves with other individuals. As a result of individuals modifying their interactions with one another, this model successfully replicated transitions commonly observed in natural animal groups [42]. These behavioural rules depended on individual local perception, which was assumed to be the same across all individuals. Individual variation in local perception, however, as well as the specific mix of individual perceptual ranges within a group, may also affect group properties such as group size, polarization, group shape, density and segregation [43,44].

(b) Individual local perception and cognitive traits

Recent studies of the evolution of collective motion have treated individual behavioural characteristics as continuous traits [9,45–47], emphasizing the need for detailed observations of individual-level characteristics for understanding, for example, cooperation in animal social groups [48] and the use of social information of individuals within groups [49]. By using stochastic asynchronous updating of fish positions and orientations, Bode *et al.* [50] observed that higher updating frequency led to more synchronized group movement, with speed and nearest-neighbour distributions becoming more uniform. Hein *et al.* [51] developed an evolutionary model of collective responses to the environment to study how individual behavioural rules produce collective behaviours, and conversely how collective behaviours provide the ecological and evolutionary context against which individuals make their decisions. The authors assumed individual heterogeneity by allowing each individual to achieve its fitness as a function of the resource level each animal experiences over its lifetime. They observed spontaneous changes in the collective state of

groups as a consequence of individual responses to local conditions [51].

As stated above, individual differences may lead to the emergence of leadership. Couzin *et al.* [22] built a model to look at the mechanisms of leadership and decision-making in animal aggregations. First, they asked how a small number of individuals with information on the location of resources could influence the rest of the group. Second, they asked how groups can overcome conflicts in individual preferences to achieve consensus. In this study, individuals were identical except that some were given a directional preference representing, for example, the direction towards a known resource, whereas others had no preferred direction of travel. The model predicted that a small proportion of informed individuals could successfully guide an uninformed group, and that for any given group size, the accuracy of group motion increased as the proportion of informed individuals increased. By extending this model, Couzin *et al.* [52] further showed that the presence of uninformed individuals is essential in achieving consensus.

While some studies have assumed equal navigation abilities for all individuals in a group (e.g. [44,45]), others [46,47] have explored the evolution of group behaviour by incorporating the costs and benefits of obtaining directional cues from the environment and evolvable social interactions among individuals. These studies have shown that, even though collective migration appears to be a shared navigational process, populations typically have only a small fraction of individuals actively acquiring directional information, whereas the majority of individuals use socially facilitated movement behaviour. To test whether an individual's preferences for an optimal target may result in within-group conflicts of interests, Conradt *et al.* [53] simulated a scenario where each individual preferred to move to either of two mutually exclusive target destinations. In their model, individuals were assigned speeds independently and then decided where to move based on a trade-off between the desire to maintain group cohesion and the desire to move towards its preferred target destination. They found that the decisions of individual members could influence the direction of group movement by increasing alignment or by reducing both speed and the radius of attraction to neighbours.

(c) Individual personality and internal state traits

Other theoretical models have explored how individual differences in biophysical traits can modulate collective decision-making. For example, Sueur *et al.* [54] built a state dynamic simulation model where they assumed that an individual's probability to lead the group increased when its energy reserve decreased. Because movement velocity was constant and equal for all individuals, only the position of the individual was affected by its energy reserve. As a further example, Kunz *et al.* [55] studied how body size and body form of artificial fish affected school formation. By assuming that the perceptual field of fishes (i.e. their lateral line) follows the body form, the repulsion and alignment regions were assumed elliptical rather than circular. As a consequence of these assumptions, individual biophysical constraints controlled group behaviour and stability.

On related topics, the concepts of personality, temperament and coping style have all received increasing attention from modellers [56]. Michelen *et al.* [26] combined experimental data with a theoretical approach to investigate the links

between animal personality and collective decision-making processes in groups of large vertebrates foraging across patchy resources. By using an individual-based model where crowding and conspecific attraction affected the probability of entering or leaving patches, they proposed a simple mechanism whereby interaction rules depended on personality type (i.e. bold and shy individuals). This model predicted that collective choices emerge through the nonlinear dynamics of interactions between individuals.

4. The effect of individual heterogeneity in collective motion: a simulated example

In the above section, we learned how theory can be enriched by considering greater detail about individual heterogeneity. Together with emerging empirical information, individual-explicit models can yield quantitative predictions and improve our understanding on how individual decision rules lead to emergent collective movement patterns. While several of the models included some individual behavioural variability, this variability has—in many cases—been limited to having a small countable number (usually, two) of individual 'types'. What has been less often investigated is the effect of total individual heterogeneity, e.g. increasing variability throughout the individuals in a population, on group dynamics (but see e.g. [41,57]). To round out this review, we explicitly introduce increasing heterogeneity in a simulation model and explore the effects on collective movement dynamics.

Our model is a somewhat modified version of the Couzin *et al.* [42] agent-based model, which combines simple behavioural rules of repulsion, long-range attraction and intermediate-range alignment. We considered that individuals were heterogeneous in three behavioural parameters—speed, radius of interaction and degree of sociability. Following Gueron *et al.* [40] we analysed the movements of individuals and explored how the cohesion of groups changed over time. In particular, we studied whether groups became unstable or changed their characteristic shapes in relation to the degree of individual heterogeneity assumed in behavioural rules.

(a) Behavioural rules

We simulated N individuals moving on a two-dimensional space with wrapped boundaries in Netlogo 5.2.1 [58]. Each individual is characterized at each discrete time t by a movement direction $d_i(t)$, speed $s_i(t)$ and degree of sociability $\alpha_i(t)$. An individual i was surrounded by a circular perception field defined by a radius r_a with a blind angle β behind the animal. Within the perception field, a zone of repulsion was defined around an individual i at radius r_r . A zone of alignment was delimited by the radii r_r and r_l , with $r_r < r_l < r_a$. A zone of attraction was defined as the area between r_l and r_a . At each time step, each individual assessed the presence of other individuals or neighbours within its perception field and adjusted its direction and speed for the next time step accordingly. If an individual i detected any neighbours n_r within the zone of repulsion, it would move away from n_r , so that the expected direction in the next time step would be given by

$$d_i(t+1) = - \sum_{i \neq j}^{n_r} \frac{r_{ij}(t)}{|r_{ij}(t)|},$$

where the summand is the unit vector in the direction from

target j to subject i . The speed at the next time step would stay unaltered, so that $s_i(t+1) = s_i(t)$. Response to n_r neighbours was prioritized over responses to neighbours in other zones of the perception field.

In the absence of neighbours within the repulsion zone ($n_r = 0$) and the presence of neighbours only within the zone of alignment ($n_l > 0$), an individual would attempt to align to n_l depending on its degree of sociability α_i according to the following formulas:

$$d_i(t+1) = d_l(t+1) = \alpha_i \sum_{i \neq j}^{n_l} \frac{d_j(t)}{|d_j(t)|} + (1 - \alpha_i)d_i(t)$$

and

$$s_i(t+1) = s_l(t+1) = \alpha_i \left(\frac{1}{n_l} \sum_{i \neq j}^{n_l} s_j(t) \right) + (1 - \alpha_i)s_i(t),$$

that is, an α weighted combination of movement towards all other individuals within the radius and previous movement. A value $\alpha = 1$ means movement is entirely dictated by neighbours; $\alpha = 0$ is independence of movement.

If all neighbours were outside r_l (i.e. $n_l = 0$ and $n_a > 0$), then the expected direction and speed of individual i at the next time step would also depend on the degree of sociability α_i and would be, respectively, estimated as

$$d_i(t+1) = d_a(t+1) = \alpha_i \sum_{i \neq j}^{n_a} \frac{r_{ij}(t)}{|r_{ij}(t)|} + (1 - \alpha_i)r_i(t)$$

and

$$s_i(t+1) = s_l(t+1) = \alpha_i \left(\frac{1}{n_l} \sum_{i \neq j}^{n_l} s_j(t) \right) + (1 - \alpha_i)s_i(t).$$

If $n_l > 0$ and $n_a > 0$, the expected direction would be $1/2(d_l + n_a)$. In those cases where no other individuals were present within the perceptual field, individual i followed a correlated random walk. We also assumed a maximum turning speed of γ every time step (i.e. at every time step an individual could only turn up to γ towards the expected direction).

(b) Parameterization and simulations of individual heterogeneity

We used two different combinations of r_l and r_a values that produce either parallel directed movement or swarming as group behaviours in the absence of individual heterogeneity (electronic supplementary material, table 3). Parallel directed movement consists of collective movement with a high level of alignment and cohesion (proximity). By contrast, swarming behaviour is characterized by poor alignment but cohesion among individuals ([42]; figure 1). To explore individual heterogeneity in behavioural rules, we allowed three of the parameters to vary across individuals: the radius of orientation r_l , the speed s and the degree of sociability α (electronic supplementary material, table 3). These parameters represent, broadly, three distinct aspects of movement and individual interaction, namely: s —movement, r_l —detection range and α —influence of neighbours. To add individual heterogeneity, we allowed each of these to vary among individuals as truncated normal distributions with increasing coefficients of variation (c.v. = s.d./mean) from 0 (no heterogeneity) to 1 (maximum heterogeneity). We ran 20 simulations at each

combination of parameter values and heterogeneity levels for over 6000 time units to let the system attain stationarity. After that we recorded the position and direction of all individuals at 10 time steps separated by 60 time units.

(c) Emergent properties

We calculated several response metrics from the simulations—each of which corresponds to a measure of the cohesion of the group—and plotted them against individual heterogeneity in the three parameters (s , r_l , and α). The metrics include: (i) mean and s.d. of nearest neighbour distance; (ii) number of isolates, defined as the number of individuals and any given time-point whose nearest neighbour is at a distance greater than the interaction radius r_l ; (iii) the mean and s.d. of speed; (iv) a coefficient of alignment, estimated as the mean cosine of the difference in orientation of each individual compared to an overall average orientation (thus, values of 1 correspond to perfect alignment, values of 0 correspond to totally random alignments); and (v) group size mean and standard deviation (electronic supplementary material, table 4). Groups were identified using a medoid partitioning of clusters, using optimum average silhouette width to determine the number of groups [59] estimated with the pamk package in R [60]. We explored variation in these response metrics against increasing individual heterogeneity in the three parameters. Broadly, we expected that the emergent collective properties would break down with greater individual heterogeneity, but the robustness of those properties was difficult to predict *a priori*. All analyses and visualizations were performed in R.

(d) Results and discussion

In our simulation study, we added a continuous form of individual heterogeneity to one of the foundational models of collective movement. We interpreted the results of the simulations qualitatively, based on visual assessments of figure 2 and electronic supplementary material, figure 1. Including individual heterogeneity into simulation models led to looser aggregations, smaller groups and a shift from aligned to swarming behaviour (see examples in figure 1). The three parameters had different effects on collective movement. In particular, heterogeneity in alignment radius and speed had less impact on collective behaviours (electronic supplementary material, figure 1) than individual heterogeneity in sociability. This may be partly explained by the fact that we only considered heterogeneity in speed and in alignment radius in their initial values, thus its effects washed away completely. Therefore, we focus our discussion here on the heterogeneity in sociability (figure 2).

As shown in many empirical systems (including several discussed earlier), we found that heterogeneous individuals manage to behave collectively with one another. The very presence of social interactions tempers the effects of non-conformity (consistent with some empirical/theory results above, e.g. [39,61]). However, when heterogeneous groups contained individuals whose behaviours were too extreme (i.e. after a heterogeneity coefficient (c.v.(α)) of 0.4 in our specific case), we observed that groups become looser and more isolates are found (figure 2*a–c*). Interestingly, the mean number of isolates was near zero for the larger populations at total homogeneity, but—in particular in the swarming scenario—overtook the number of isolates for the

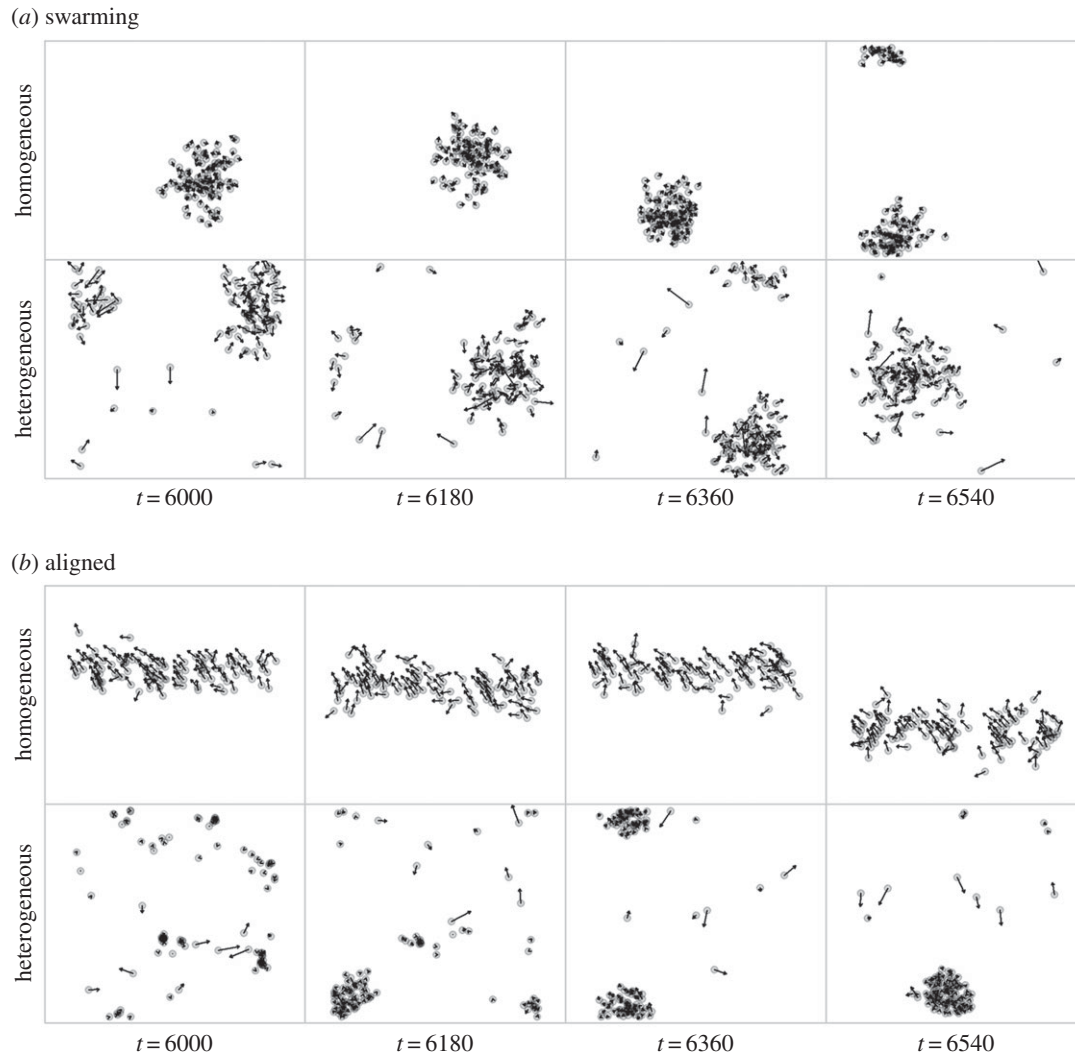


Figure 1. Example snapshots of simulations. Locations (grey dots) and velocity vectors (dark arrows) for each individual are presented across four time points (left to right). In the upper panels (*a*), the parameterization corresponds to a swarming scenario, where the individuals are spatially coherent but oriented in random directions (note, due to toroidal boundary conditions, what appears to be two groups in the top-rightmost panel is actually one group). The top row of panels shows the homogeneous case, while the second row shows what happens when heterogeneity in all parameters is introduced: looser aggregations and more isolated individuals. The lower panels (*b*) show the aligned parameterization, where (in the homogeneous case, third row) there is not only spatial coherence but also similar alignment across individuals, and in the heterogeneous case (bottom row) the grouping is much more diffuse and no longer aligned.

smaller populations at higher values of heterogeneity ($0.4 < \text{c.v.}(\alpha)$). The consistent resilience of the collective movement structure up to a coefficient of variation of between 0.3 and 0.4 was striking in our specific simulation study. The probability of fragmentation we found depends on parameter values, and thus there is no guarantee that this will happen under all conditions. Yet, as some other theoretical studies have reported similar kind of thresholds [40,51,62], we believe that further investigation is necessary to see how generally that principle holds and whether it is predictive of anything that might be observed in nature.

Increasing heterogeneity had no strong effect on the mean speeds of motion but a very marked effect on the standard deviation of the speed (figure 2*d,e*), which was near zero at low values, then shot up after 0.4 rapidly and identically in all scenarios. Also of interest is the eventual transition we observed from aligned behaviours to swarming behaviours. The alignment coefficient was low (under 0.3) in the swarming scenario, and higher (over 0.6) in the aligned scenario as expected. However, that alignment decreased steadily under heterogeneity, becoming indistinguishable from the swarming scenario at heterogeneity levels over 0.8

(figures 1*b* and 2*f*). That transition in group shape caused when adding heterogeneity is different from the one making the groups become ‘unstructured’, as in that case we would have expected to observe an even, rapid increase in the mean nearest neighbour distance (figure 2*a,b*). Group fragmentation is a common natural phenomenon that may happen under different conditions where groups are composed by different individuals [40,42].

In terms of mean group size, the effect of individual heterogeneity differed between swarming and directed scenarios. In swarms, the mean group size remained fairly stable as heterogeneity increased. For directed scenarios, mean group size decreased with increasing individual variation in sociability, reaching minimum values at $0.4 < \text{c.v.}(\alpha) < 0.6$ and slightly increasing after $\text{c.v.}(\alpha) > 0.6$ (figure 2*g*). More dramatic and consistent was the increasing variation in group size for both swarming and directed movement behaviours with increasing heterogeneity.

Overall, our simulation study illustrates whether adding heterogeneity among individuals has the potential to alter collective motion: greater individual variability frays collective behaviours, but social interactions (to a point) effectively

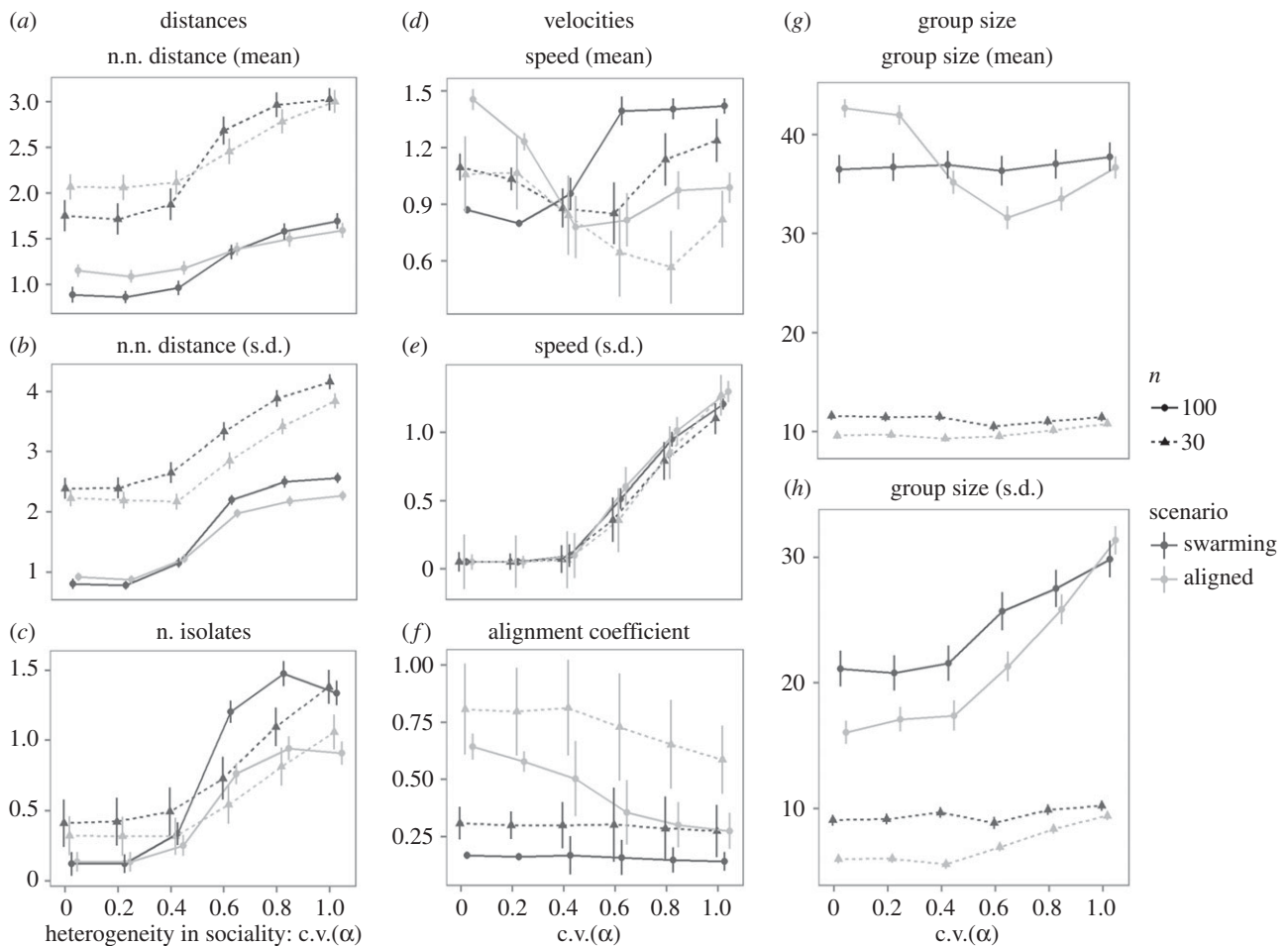


Figure 2. Collective movement statistics presented against increasing heterogeneity in sociability (coefficient of variation in parameter α , ranging from 0 to 1). Each point represents an average across 10 snapshots in 20 scenarios against 36 values of parameters r_1 and s (7200 simulations per summary point). Darker and lighter lines show result from the swarming and aligned scenarios, respectively. Circles and solid lines represent simulations with 100 individuals, triangles and dashed lines represent simulations with 30 individuals. Vertical bars are the standard errors around the means. The collective movement metrics are related to distance (left panels): nearest neighbour distance (a) mean and (b) standard deviation, (c) number of isolates (i.e. total number of individuals at a distance greater than r_1); related to velocities (middle panels), with (d) mean and (e) standard deviation of speed, and (f) the alignment coefficient which ranges from 0 (total randomness) to 1 (perfect alignment of all individuals); and group size (g) mean and (h) standard deviation.

dampen the impacts of variability. Both are, however, important for maintaining fitness and for survival. The improved ability of social groups to navigate, forage and protect themselves is well documented (including here). But when a few outlying individuals behave independently of the majority by dispersing or straying, they may eventually part and form a separate group. There may be fundamental trade-offs, linked to the behaviours and resources that individual organisms pursue and risks they are exposed to, that might explain the relative success and adaptability of different taxa in different environments.

5. General conclusion

Our review of the empirical and modelling literature allows us to make some testable predictions about the linkages between individual heterogeneity and collective motion. Given that the relative spatial position of individuals is so central to collective motion [21,22], the impact of individual variation within a group should be observable on a variety of different metrics of collective motion, such as group cohesion, movement speed and directedness of motion. These metrics, in turn, scale up to affect other measurable quantities of group performance such as the efficiency of group travel or navigation.

A variety of biological systems exemplify the kinds of effects of group heterogeneity on collective motion that we might expect. For example, across a variety of systems where heterogeneity among individuals includes hierarchical social structure, several studies have linked experience or dominance to group movement efficiency [14,32,61,63–65]. As noted above, animal groups in which kinship strongly determines relative spatial positioning can feature a kind of spatial regularity that emerges from the existence of repeating subunits (e.g. mother–offspring pairs) in which two or more heterogeneous individuals remain close to each other, both while resting and while moving. We expect that learning-based mechanisms of group spatial structure should perform like those based on kinship in that individuals of one particular subtype (learners) will seek locations preferentially close to one or more individuals of a different subtype (experienced individuals). Whether originating from kinship or differences in experience, these repeated structures within animal groups ensure a degree of group cohesion, but also establish clear fault-lines along which group fissioning can occur when elemental units split from the larger group.

While recent modelling studies on collective motion have greatly helped to understand how individual decision rules lead to emergent movement patterns, relevant empirical

long-term data in wild conditions continue to lag behind. One important problem here is the need for simultaneous data on a large number of individuals—ideally the entire set of potentially interacting individuals. However, recent advances in tracking technology [66] make high-resolution movement data on a significant proportion of individuals in some populations increasingly feasible and available [13]. The availability of accurate information at the individual level could facilitate the development of more realistic frameworks that reflect ecological realism [19]. The analyses of movement trajectories from individuals within a group would allow us to capture the essential dynamics of the group by assessing how individuals respond to different types of biological influences, and to identify what details at fine scales are necessary and sufficient for understanding patterns at larger scales [38,67]. The statistical toolbox for the analysis of trajectory data is currently quite developed [68,69] and researchers are starting to apply many of these tools to the study of group movement [70–72]. We believe that these tools will allow researchers to extend the domain of previous mechanistic models to explore plastic responses of individuals within a group. These responses will derive from stimuli in individuals' immediate social environments, biophysical constraints and internal states, driving the group reaction to and success in coping with its experiences. For example, many collective movement models exploring the effects of individual variability consider a heterogeneous group of individuals moving with constant parameters over time. However, adaptive individuals can modify their behaviour substantially according to environmental cues, and they can learn from past experience or from other individuals. By individually scaling and statistically exploring the variables of interest, animal movement models may represent an ideal framework in which to use bottom-up modelling to explore how individual-level mechanisms give rise to group dynamics. Furthermore, continued efforts to merge collective motion modelling and animal movement analyses will provide the foundations for improved, quantitative understanding of animal movement.

Compared to the vast literature on the general topic of collective motion, only a few studies have examined how individual variation in behavioural rules lead to different emergent properties. Most animal collective movement studies have generally been interested in emergent population-level properties, and thus have traditionally neglected variation among individuals, the uniqueness of individuals, and the fact that individuals change in these characteristics during their lifetime. Yet, recent theoretical models regarding collective motion based on individual movement decision rules are becoming increasingly sophisticated, and are challenging the

established approach by relying on more mechanistic, individual-based models [20]. These models represent an important step towards increasing biological realism when modelling collective motion.

Starting from our model as a very illustrative example, we observed that when assuming groups composed of identical individuals, cohesion and shape remain mainly unchanged. However, when adding individual heterogeneity, we were able to capture a more realistic dynamic, where group size and shape depend on the specific composition of the group. As this sensitivity to group fragmentation, commonly observed in nature, may influence how the group respond to predation risks and environmentally changing conditions, the composition of a group may have fitness consequences at the population level [73]. Conversely, collective behavioural dynamics may act as the selection pressures to maintain inter-individual variation, such that the presence of particular individual phenotypes may depend on the ensemble of phenotypes in a particular group [74]. Understanding the interplay between these two processes is central not only for basic collective motion research, but has implications for applications, including how animal groups respond to changing environmental conditions.

In this paper, we have highlighted empirical cases showing the importance of considering how animals make decisions regarding movements, and the need to theoretically start from a bottom-up approach based on our existing knowledge and data to ensure that we will not sacrifice key explicit processes of interacting individuals by otherwise focusing on specific subsets of average properties only when modelling animal collective movements.

Data accessibility. This article has no additional data.

Authors' contributions. M.M.D conceived the idea and wrote the article. S.A. and E.G. performed the simulated model and interpreted the results. M.M., V.P. and W.F.F. reviewed the empirical literature, while M.M.D., A.V. and J.M.M. compiled the theoretical studies. All authors made substantial contributions to (i) drafting the initial manuscript, (ii) providing useful comments on intermediate drafts; and (iii) getting the final approval of the version to be published.

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