Trends in Ecology & Evolution

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Review

The Role of Individual Heterogeneity in Collective Animal Behaviour

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Social grouping is omnipresent in the animal kingdom. Considerable research has focused on understanding how animal groups form and function, including how collective behaviour emerges via self-organising mechanisms and how phenotypic variation drives the behaviour and functioning of animal groups. However, we still lack a mechanistic understanding of the role of phenotypic variation in collective animal behaviour. Here we present a common framework to quantify individual heterogeneity and synthesise the literature to systematically explain and predict its role in collective behaviour across species, contexts, and traits. We show that individual heterogeneity provides a key intermediary mechanism with broad consequences for sociality (e.g., group structure, functioning), ecology (e.g., response to environmental change), and evolution. We also outline a roadmap for future research.

Highlights

Phenotypic variation is selectively maintained in populations and pervades animal social systems.

Considerable evidence shows that phenotypic differences among grouping animals drive the behaviour, structure, and functioning of animal groups.

This individual heterogeneity may thus be a key intermediary mechanism that regulates collective behaviour.

We lack a unified understanding to explain and predict the role of individual heterogeneity across different species, contexts, and traits.

An objective quantification of individual heterogeneity in physiological, cognitive, and behavioural components provides a common framework for understanding individual heterogeneity and its social, ecological, and evolutionary consequences.

The Effects of Phenotypic Variation in Collective Animal Behaviour: A Rising Topic

Social grouping (see Glossary) is ubiquitous across the animal kingdom, ranging from pairs of individuals to enormous **aggregations** and structured **communities**, and short-lived and unstable group membership to long-lasting and fixed group compositions. Animals time and coordinate their behaviour with others to gain potential benefits, including increased mating opportunities, improved foraging efficiency, lower predation risk, and reduced energetic costs [1,2]. These benefits are realised through individual-level behavioural processes that shape and are shaped by the social structure, leadership, movement dynamics, and collective performance of groups [2–4]. A key goal of **collective behaviour** research is therefore to understand and predict how collective patterns emerge from the behaviour and social interactions of individuals.

Scientists have long focused on identifying universal mechanisms underlying collective behaviour. Through a combination of theoretical and experimental work it has become clear that many complex collective behavioural patterns can emerge via **self-organising** processes from individuals using simple interaction rules [3–5]. However, individuals in groups are not all equal, and the **phenotypic variation** that is selectively maintained in populations results in **individual heterogeneity** within and among groups. Considerable theoretical (Box 1) and empirical evidence, from a broad range of taxa, suggests that such heterogeneity plays a fundamental role in collective animal behaviour. For example, the synchronised movements and social structure of fish schools and bird flocks [6,7], the leadership and collective decision-making of whale pods and primate troops [8,9], the colony performance of social spiders and honey bees [10,11], and the among-group **assortment** of ungulates [12] are all mediated by within-group individual heterogeneity.

While previous theoretical work discusses the important evolutionary implications of phenotypic variation among grouping animals [13], we still lack a unified mechanistic understanding of individual heterogeneity and its role in collective animal behaviour. This is in part because the study of self-organising patterns in collective behaviour and the ecological relevance of phenotypic variation in animal populations have remained largely separate endeavours. In this review we aim to bridge this gap. We present a common framework to objectively quantify individual heterogeneity, discuss the important modulating role of the social environment, and synthesise the broad literature to systematically explain and predict its consequences for collective behaviour across species, contexts, and traits. We show that individual heterogeneity provides a key intermediary mechanism that regulates collective behaviour with broad repercussions for ecology and evolution (Figure 1, Key Figure).

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Key Figure

Quantification of Individual Heterogeneity, Its Role in Collective Behaviour, and Its Ecological and Evolutionary Consequences

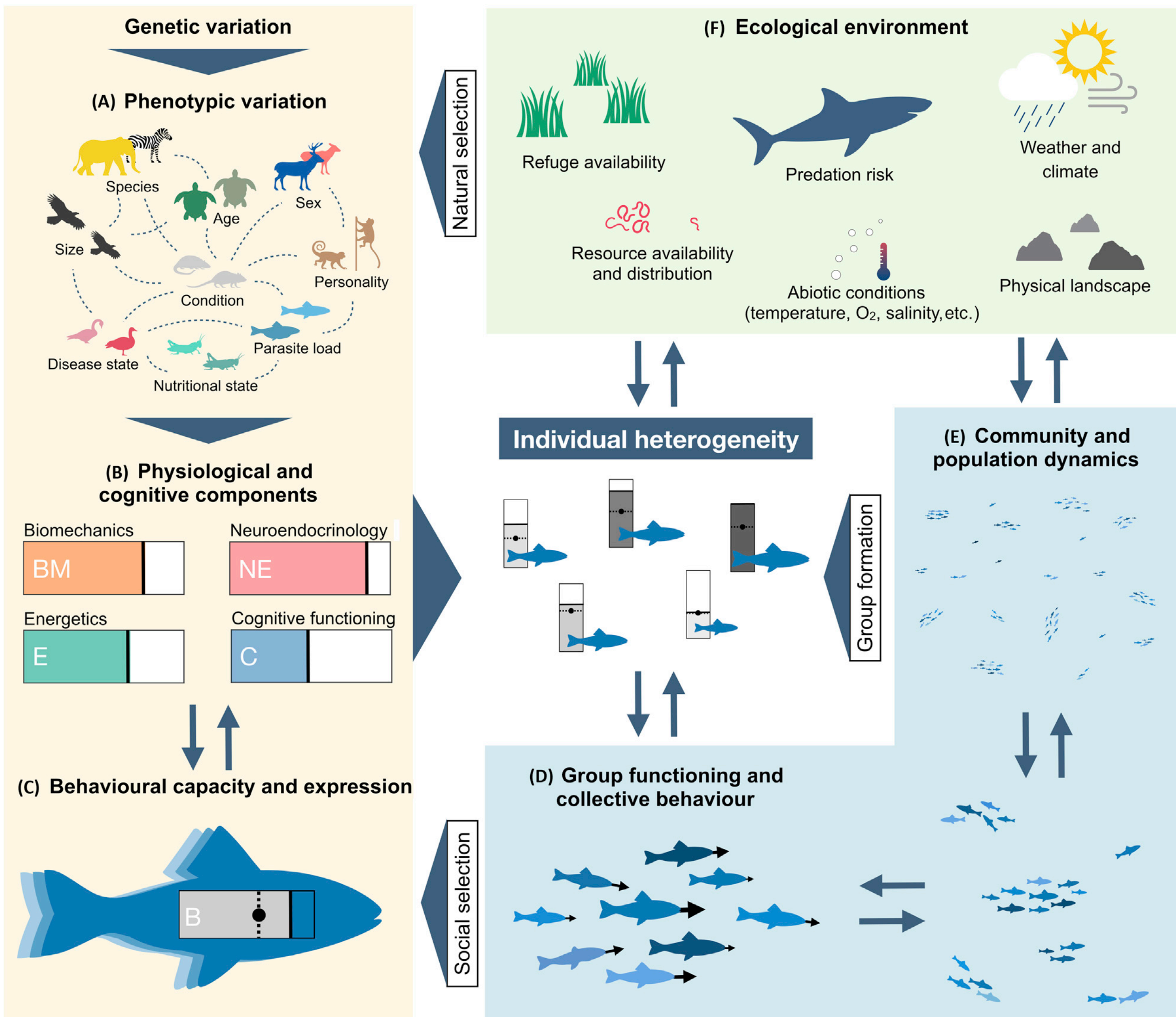

Figure 1. Our premise is that (A) phenotypic variation among grouping animals can be reduced to (B) fundamental physiological (i.e., biomechanics, energetics, and neuroendocrinology) and cognitive components that determine (C) behavioural capacity and expression. Overall, such individual heterogeneity drives (D) collective behaviours and group-level pattern and assortment, which in turn affect (E) the structure and dynamics of animal communities and populations. In turn, the social environment modulates individual heterogeneity and drives the formation of animal groups. (F) The ecological environment and conditions that animals encounter may directly affect individual heterogeneity and thereby reduce or enhance its role in collective behaviour but may also itself be a result of the effects of individual heterogeneity. Ultimately, the fit of individual and collective behaviours with the social and ecological environments (that may change) will influence individual fitness and result in natural and social selection, which selectively shapes phenotypic variation in populations (and species).

Box 1. Theoretical Work on Individual Heterogeneity in Self-Organised Groups

Theoretical modelling is a central component of collective behaviour research. In particular, agent-based model simulations of self-organised groups have been fundamental in revealing how global patterns can emerge from simple interaction rules [3,4,95,96]. In contrast to the large empirical literature on phenotypic variation and collective behaviour, relatively few theoretical studies explicitly account for individual heterogeneity (Figure I). However, those studies that do demonstrate that even small differences among individuals can have large consequences for the collective behaviour, structure, and functioning of groups. Specifically, via self-organising processes, individuals with faster speeds, slower turning behaviour, and weaker social attraction/repulsion functions tend to end up at positions towards the front and edge of groups [7,74,97,98]. The greater the number of such individuals, the higher the groups' velocity and alignment and the lower its cohesion [7,58,97–100]. When heterogeneity among agents is large, groups are predicted to fragment over time, leading to phenotypically assorted subgroups [97,99] and the most extreme behavioural types to be isolated [69]. Models that have considered variation in individuals' preferred movement direction, such as towards a known resource, show that goal-oriented individuals tend to end up in the front of groups and thereby obtain a larger share of potential resources [7,61,98]. Such individuals can thereby play a large role in determining the direction and speed of the group as a whole [31,61], and even lead large numbers of uninformed individuals to novel resources [71,101]. However, the right balance of goal- and socially oriented behaviour is required for such leading individuals to not risk splitting from their group [31,61,71]. Importantly, as individual heterogeneity within and among groups increases, its effect on collective behaviours becomes greater [102], and these effects persist even after perturbations [61,97]. Other theoretical models have explored the role of individual differences in biophysical traits and shown that individuals with higher energetic needs can spontaneously emerge as leaders during foraging bouts [38] and that small heterogeneity in needs can result in large, nonlinear differences in leadership [36]. Despite this knowledge however, there are major gaps in our understanding of the fundamental sources of heterogeneity and how these bridge phenomena from the individual to the group and community level.

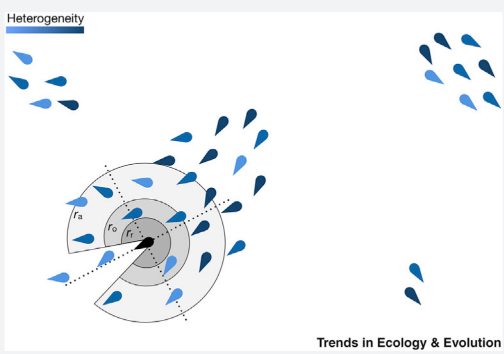

Figure I. Individual-Based Model of Self-Organised Heterogeneous Agents.
Schematic representation of heterogeneous agents, depicted by the degree of blue, following interaction rules based on a zonal model of self-organised behaviour with the repulsion (r_r), alignment (r_o), and attraction (r_a) zones shown for a single individual.

Characterising Individual Heterogeneity: A Framework

Considerable phenotypic variation exists among grouping animals, ranging from relatively fixed and stable phenotypes such as species and sex to those that may change over longer to shorter timescales, such as size, **personality**, parasitic infection, and energy reserves. Generally, empirical work studying the effects of phenotypic variation in animal groups carefully characterises the traits of interest but tends to lack detailed quantification of the potential underlying mechanisms. We advocate that for a proper understanding of the role of phenotypic variation in collective animal behaviour, we need to go beyond coarse categorisation of phenotypic traits and focus on the universal components that underpin this variation.

Glossary

Aerobic scope: the capacity to perform oxygen-consuming physiological processes above those required for basic maintenance, including physical activity, growth, and digestion; functionally defined as the absolute difference or ratio between maximum and minimum metabolic rates.
Aggregation: any form of gathering of individuals; typically used to refer to loosely structured social groupings.
Animal personality: interindividual differences in behaviour that are consistent over time and/or across different contexts.
Assortment: the social sorting of animals, which may arise actively through attraction or repulsion of certain (types of) individuals or passively from individual differences as a result of mechanical processes, habitat preferences, nutritional requirements, or environmental tolerances.
Behavioural capacity: the range of behaviours an animal is capable of performing; determined by animals' physiological and cognitive capacity.
Behavioural expression: an animals' behavioural action within the limits of its behavioural capacity, driven by its biomechanical, energetic, neuroendocrine, and cognitive functioning.
Cognitive functioning: how an individual acquires, processes, retains, and acts on information.
Collective behaviour: the higher-order behavioural patterns and social structure of animal groups and communities; largely emerges from self-organising processes but may also require sequential behavioural processes.
Communities: the set of structured social relationships among individuals within which breeding typically occurs.
Conformity: an individual's tendency to change its behaviour to match that of others it interacts with.
Individual heterogeneity: the measure of phenotypic variation among grouping animals, at the group, community, or population level; can be categorised in terms of physiological, cognitive, and behavioural components.

Fundamental Components of Individual Heterogeneity

First, we need a comprehensive way to quantify individual heterogeneity across species and traits. Key is that the spectrum of phenotypic traits seen among grouping animals is strongly hierarchical, with broader sources of phenotypic variation, such as sex and size, comprising more fundamental phenotypic components (Figure 1A). Additionally, previous work has highlighted the role of individual differences in physiological and motivational processes as a key driving force underlying collective processes [14–16]. We build on this knowledge and propose that phenotypic variation can be fundamentally attributed to variation in three **physiological components** – (i) biomechanics (e.g., muscular ability, mobility), (ii) bioenergetics (e.g., **minimum** and maximum **metabolic rates**, **aerobic scope**), and (iii) neuroendocrinology (e.g., hormone expression and the regulation and activity of certain brain regions; fundamental to emotions) – and (iv) **cognitive functioning**, which includes sensory acquisition, information processing, knowledge, and learning ability. Interindividual variation in physiological and cognitive processes determines the **behavioural capacity** of individuals and, in combination with environmental conditions such as predator risk and temperature, determines an animal's **motivation** to particular behaviours and thereby their behavioural expression. It is important to consider the feedback between behavioural, physiological, and cognitive capacities (Figure 1), such as the short-term effects of foraging and subsequent digestion on available aerobic scope [17], and long-term effects of sustained activity on cardiovascular performance [16]. Characterising individual heterogeneity in terms of these behavioural, physiological, and cognitive components provides a lens to quantify and understand the fundamental, intermediary mechanisms that regulate collective behaviour (see Box 2 for a case study).

Quantifying Individual Heterogeneity

How do you characterise individual heterogeneity and quantify relevant physiological, cognitive, and behavioural components that underlie the trait of interest? Let us look at some examples. To study the role of body size in leadership, detailed measures of size should be accompanied by a quantification of fundamental phenotypic components to shed light on how body size may affect leadership, such as muscular performance, metabolism, and behavioural capacity in terms of mobility and movement speed – all measures that may be impacted by body size (Box 2). This also enables the objective characterisation of differently sized individuals in specific physiological and behavioural components that are comparable with those of other traits. In a similar way, a study interested in the effects of group sex composition on group cohesion could quantify males' and females' movement speeds and **social responsiveness**. Researchers studying the effects of behavioural traits, such as boldness and sociability, on collective behaviour should conduct comprehensive tests to assure validity [18] and to determine the potential underlying physiological (e.g., hormonal profile), cognitive (e.g., learning style), and behavioural (e.g., optimal movement speed) components. To conceptualize individual heterogeneity, capacities can be visualised as bars and expression as sliders on the bars (Figure 1 and Box 2). Ultimately, a more objective quantification of individual heterogeneity in empirical work will help to improve individual-based models that can be used to further test underlying mechanisms (Box 3).

Social Modulating Effects on Individual Heterogeneity

To understand the effects of individual heterogeneity on collective behaviour, it is important to consider the modulating effects of the social environment. Individuals must time and coordinate their behaviour if they are to maintain group coherence and consensus [1,2] and therefore modulate their behaviour based on the behaviour and phenotype of others [19–23]. This is reflected in animals showing generally low behavioural variance within [21,24,25] and high behavioural plasticity between [26] social contexts. The behavioural differences arising from phenotypic variation among grouping individuals may thereby be partly or even completely overridden by individuals' tendency to conform [20]. A clear example of social **conformity** is the convergence of the spontaneous speeds of groups of moving animals, such as bird flocks and fish schools [7,21,27]. Such effects that decrease the variability within groups may drive increased differentiation between groups [25,28]. The extent that individuals adjust their behaviour and/or conform can also be linked to their phenotype [20,29]. For example, individuals may be constrained, such as by their physiological, cognitive, or behavioural capacities, or differ in their level of social responsiveness, such as by differences in speed, nutritional state, or

Minimum metabolic rate: the minimum energy required by physical and chemical processes to sustain life, termed basal or standard metabolic rate in endotherms and ectotherms, respectively; measured in inactive animals in a post-food-processing state.
Motivation: an animal's disposition to perform a specific behaviour, mainly influenced by (evolutionary) cost:benefit trade-offs; is inherently goal-directed and can be influenced by an animal's behavioural capacity.
Phenotypic variation: interindividual differences in phenotype, ranging from fixed phenotypes (e.g., species, sex) to those labile to change (e.g., nutritional state).
Physiological components: the range of an animal's biomechanical, energetic, and neuroendocrine functioning; determines an animal's behavioural capacity but can also but altered by an animal's environment and behaviour over time.
Self-organisation: the process by which dynamic and structural patterns arise in nature due to local interactions between individuals; underlies collective behaviour and decision-making.
Social grouping: the process and outcome of individuals maintaining proximity with one another in space and time through social attraction.
Social responsiveness: the extent that individuals respond to the position or behaviour of others; can be driven by both the motivation and the capacity to respond.
Social scales: the hierarchical levels of sociality, from the individual, dyads, and groups to communities and populations.

Box 2. A Worked Example: Individual Heterogeneity in Size

Variation in body size is one of the most salient sources of individual heterogeneity among grouping animals. Body size is linked to many other phenotypic traits in a hierarchical way and can be decomposed into more fundamental physiological characteristics, especially the biomechanics that drive individual and thereby collective behaviour (Figure I). For example, larger individuals tend to have higher muscular capacity for forward locomotion [103] but also tend to be less manoeuvrable and as a result have larger repulsion areas [100], two characteristics that drive them to positions towards the edges and front of their group [97,100]. These effects on spatial positioning may be further enhanced by passive effects arising from small individuals having higher social attraction due to being more vulnerable to predation [102], and small individuals being more motivated to occupy positions in the centre and back of the group to gain energetic advantages [88] due to their higher relative cost of transport. As a result, groups may show within-group assortment, with individuals interacting more with similar-sized individuals [91], driving social network characteristics [104]. Because larger individuals predominantly occupy leading positions, they have a greater influence on group movements and decisions, potentially amplified by their higher competitive ability. Interestingly, smaller individuals also have higher vigilance [105], and group heterogeneity in size may therefore be expected to affect the acquisition and transfer of information among grouping animals. Smaller individuals tend to have higher mass-specific metabolic rates and, depending on the prevailing environmental conditions, may be more motivated than large individuals to occupy frontal positions while foraging [106]. As long as differently sized individuals are able and willing to conform in their speed, they may be able to group and move together, explaining why individuals in schools of fish may differ up to 30% in size [107]. However, under circumstances that require individuals to move very fast, over longer periods of time, or over larger areas, groups will segregate by size through passive sorting of size-related differences, such as in movement speed [91]. Animals may also actively assort by size to optimise the energetic costs of movement [16], to minimise foraging competition [16], or to reduce phenotypic oddity, which could increase predation risk [108]. Large among-group-level differences may arise between such homogeneous groups, with groups comprising larger individuals, for example, being faster and more aligned as a result of higher individual speeds [100].

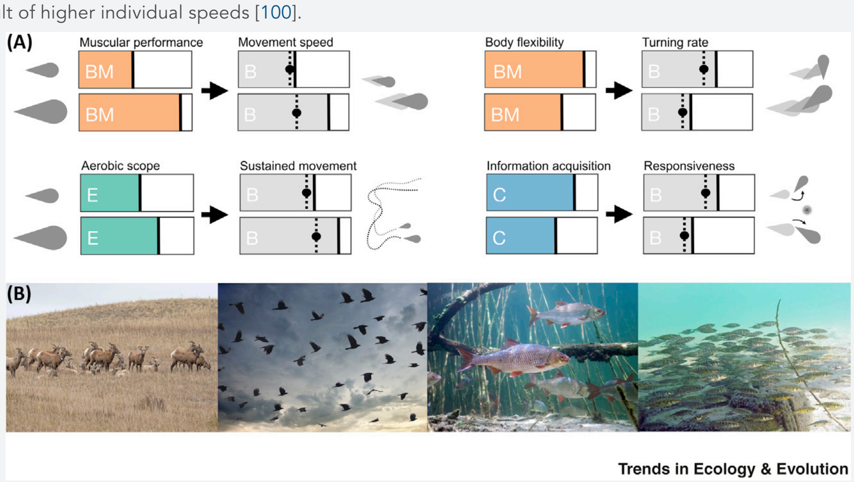

Figure I. Effects of Body Size on Individual and Social Behaviour.

(A) Schematic overview of heterogeneity in physiological and cognitive capacity and in turn its effects on behavioural capacity and expression, with capacity represented by coloured bars and unbroken lines and behavioural expression by points with broken lines on the horizontal sliders. BM, biomechanics; E, energetics; C, cognitive functioning; B, behavioural capacity. (B) Body size drives vigilance in bighorn sheep [105], spatial positioning in mixed-species corvid flocks [65], leadership in roach shoals [59], and among-group assortment among stickleback schools [108]. Photographs by Philip Schwarz, Alexander Novikov ©123RF.com, Krzysztof Odziomek ©123RF.com, and Jolle Jolles.

knowledge [7,30,31]. If individuals cannot or will not adjust their behaviours, not only may groups become phenotypically assorted by plasticity, but less-plastic individuals are expected to have a disproportionate effect on collective patterns [16,32,33].

Individual heterogeneity within groups can also increase or decrease independent of conformity effects. On the one hand, increased heterogeneity may occur where individuals become more proficient over time through training, such as improved movement efficiency [16] and social learning [34], and canalize interindividual differences in behaviour and underlying physiology. Similarly, prolonged differences in food intake can lead to differentiation in metabolic rates among group members [35]. On the other hand, individual heterogeneity may diminish or disappear due to social feedback. For instance, intrinsic differences in physiology and foraging motivation are reduced when individuals become satiated due to efficient and coordinated group foraging [36]. Also, animals that persistently move at high speeds or above their optimal speed to stay with others could gain increased muscular and aerobic performance that results in reduced heterogeneity in associated traits [16]. The restriction or enhancement of heterogeneity via social feedback can therefore act to increase the consistency of social roles ('social niche construction' [37]). For example, small differences in the tendency to lead, which can arise from differences in movement speed or resource needs, may be enhanced by social feedbacks and result in stronger leader and follower roles [38–40].

Individual heterogeneity in capacity for movement, aerobic scope, or metabolism will also result in asymmetry in competitive abilities (e.g., aggression over resources) that can generate and maintain social dominance hierarchies and structure animal groups [41]. This may further lead to social stress and result in both dominants and subordinates experiencing altered metabolic rates and lasting physiological costs [42]. An intriguing avenue that requires additional research is the possibility that the effects of social dynamics on individual trait expression may act over very different timescales

Box 3. A Roadmap for Studying Individual Heterogeneity in Collective Behaviour

For a more complete understanding of collective behaviour, we advocate the need to focus on individual heterogeneity as an intermediate mechanism that regulates collective behaviour. We suggest that, to yield the greatest insights (Table 1 and see Outstanding Questions), an integrated, collaborative research approach is needed (Figure I) that incorporates the following elements.

- Much research has examined links between specific traits and collective outcomes, with little consideration of the physiological and behavioural attributes underlying trait expression. We encourage researchers to first collect accurate behavioural, physiological, and cognitive data at the individual level to obtain common fundamental measures of individual heterogeneity. Researchers should thereby use mechanistic descriptions to provide proper functional insights about the effects of individual heterogeneity on collective outcomes. Recent advances in tracking technology enable the refined and automatic quantification of individual behaviour, such as exploration, movement ability, and sociability [109], and the use of social interaction rules, which should be combined with relevant physiological and cognitive metrics, such as biomechanics, metabolic rates, digestive efficiency, neuroendocrine status, and sensory processing. Without such information, we risk overlooking the mechanistic processes that link local and global patterns and erroneous conclusions via inaccurate characterisation of individual heterogeneity.
- There is a need for further improvement of theoretical models by the proper integration of realistic and empirically quantified sources of individual heterogeneity. Furthermore, agent-based and state-dependent models [96] have so far primarily focused on behavioural interaction rules, and physiological information should be further incorporated to match empirical data. An iterative approach may help to refine models and make them applicable across different contexts, including group compositions, group sizes, and environmental conditions. Empirical and theoretical studies should be carefully designed to be compatible and modular such that smaller studies can address specific workflow components.
- Data from free-ranging and wild animals with detailed knowledge of individual phenotypic variation is critical to improve our understanding of how group-level phenomena scale to the population and ecosystem level [110]. Predictions stemming from laboratory studies and modelling should ultimately be tested in the field by observing wild animals experiencing broad spatiotemporal environmental variation. Deviations from expected collective behaviours in the field can in turn be examined with further controlled experiments to determine underlying mechanisms. Although the precise measurement of individual behaviour and physiology has been a major challenge for field studies, technological advances now enable researchers to automatically record continuous behaviour, movement, physiology, and environmental factors with increasing detail in the wild [110,111].

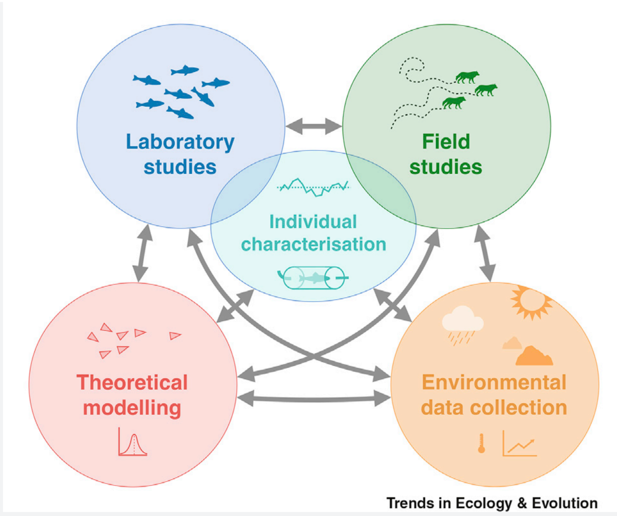

Figure I. Studying Individual Heterogeneity in Collective Animal Behaviour.

The precise characterisation of individual heterogeneity in individual behavioural, physiological, and cognitive components is central in our approach to understanding its role in collective behaviour. Such data can be combined with the observation of animal groups under laboratory conditions and in the wild and funnelled into theoretical models. Integration of dynamically recorded environmental data will allow the further objective assessment of individual heterogeneity across changing environments. Strong interdisciplinarity will be needed to facilitate such an integrated approach and help to generate a more unified and fundamental understanding of individual heterogeneity across social and ecological scales.

depending on whether the focal trait is behavioural or physiological. Acute behavioural shifts during conformity, for instance, may occur rapidly and so trait expression may shift on a moment-to-moment basis. In contrast, training effects or other socially induced plastic responses that alter physiological trait expression are more likely to occur over more prolonged timescales [43,44].

Ultimately, when grouping with others, the different forms of social conformity and feedback described above mean that animals' performance and ultimately fitness are determined not only by their own phenotype but also by the phenotypes of the individuals they interact with [13]. This may have positive effects, such as when grouping leads to higher foraging gains [7,45,46], and negative effects, such as when grouping induces higher costs in terms of energetic requirements for locomotion or stress and injury due to dominance interactions [47]. Individuals may contribute equally to the functioning and performance of their entire group or this may be disproportionately influenced by a few keystone individuals [48]. Similarly, the phenotypic composition of the group as a whole could affect all group members equally or affect the relative performance of different phenotypes in the group [13]. Such effects may have various important ecological and evolutionary consequences (Table 1) and may mask or expose traits as targets for selection, such as behavioural conformity reducing individual heterogeneity in activity and risk-taking behaviour.

Collective Consequences of Individual Heterogeneity

In the following section we describe how individual heterogeneity results in a series of hierarchical effects that influence collective behaviour, from within-group positioning, group coherence, leadership, and collective decision-making to group functioning, fission–fusion dynamics, and among-group assortment. We thereby synthesise the broad literature using our framework and focus on key patterns across species and traits. For the specific role of eusociality in collective behaviour, see [49] for a recent review.

Table 1. Ecoevolutionary Consequences of Individual Heterogeneity in a Nutshell

	Implications
Environmental change	Traits related to leadership and spatial positioning may affect individuals' sensitivity to environmental stressors (e.g., thermal sensitivity, hypoxia) and thereby disproportionately affect the behaviour of groups under conditions of environmental change
	Changes in the environment could substantially alter the expression of phenotypic variation within populations and expose or mask traits from selection, thereby reducing the ability of populations to respond to ongoing change
	More extreme environmental conditions may increase the energetic costs and required physiological capacity of individuals and push individuals to the maximum of their behavioural capacity, resulting in more behavioural disparity between phenotypes and in turn more dispersed animal communities
	Altered thermal conditions may select for individuals with different locomotor capacity and aerobic scope and thereby affect collective behaviour and performance
Dispersal and invasion	Individuals with higher locomotor and metabolic capacities and those with less social- and more goal-oriented behaviour may disperse and forage further and potentially act as leaders that encourage group movements during range expansion
	Social feedbacks that affect the locomotor capacity of individuals within groups may directly determine the dispersal potential of entire groups
	Phenotypic traits linked to greater competitive ability and foraging efficiency may enable invasive species to outcompete native species during social foraging
	Greater connectedness of individual phenotypes may increase the spread of environmental information and drive invasion success
Disease and parasite transmission	Disease and parasite infection may alter trait expression and thereby the potential for selection to act on specific traits
	Individual heterogeneity may drive the spread of infections at the community and population level by differential effects of phenotypes on the number and strength of their interactions and the likelihood of individuals to move between groups
	Phenotypic variability at the population level may play a role in parasite transmission via group-size effects as group size may be influenced by phenotypic composition and affects the prevalence of contagious parasites
Spread of social information	Differences in biomechanical, energetic, and neuroendocrine functioning may lead some individuals to be more informed about their environment and, because of differences in interconnectedness, play a key role in the information's spread and maintenance across generations
	Linked to physiological differences, highly social, less goal-oriented individuals may drive the spread of social information by greater numbers and strength of social interactions
	The spread of information may be compromised in animal communities because of the clustering of individuals with low motivation and capacity due to the passive assortment of phenotypes within and among groups

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Table 1. *Continued*

	Implications
Habitat selection	Individuals differ in their physiological requirements and optima, which may lead to segregation of physiological phenotypes by habitat and influence the associated biotic and abiotic conditions they will experience
	Individuals with a phenotype that makes them more likely to lead may result in disproportionate effects on the habitat experienced by other group members and potentially result in suboptimal physiological functioning of those individuals
Reproduction	Individuals within groups may have differential reproductive success related to their locomotor potential, their aerobic or anaerobic capacity, and their expression of aggressive behaviour
	Passive assortment within and among groups could lead to assortative mating, affecting the gene flow within populations, and ultimately result in genetic divergence of populations
	Individuals may select group members based on the potential for mating opportunities, thereby affecting within- and among-group assortment and the potential for gene flow

Within-Group Positioning

Positions near the front and edge of moving groups tend to have better access to resources but come with a higher risk of predation [1,2]. Studies in various taxa have, for example, shown that hungrier individuals are more likely to be in the front of moving groups [50,51]. Because larger individuals require more food, they are often found to lead collective movements, such as in migrating schools of cod (*Gadus morhua*) [52]. Similarly, in ungulate herds, pregnant and lactating females that have higher resource requirements often assume leading positions to gain a finder's advantage [53]. Positions near the front of moving groups also generally come with higher biomechanical and energetic costs of locomotion [54]. As a result, faster individuals tend to emerge as leaders, as observed in pigeon flocks (*Columba livia domestica*) [55] and shoals of roach (*Rutilus rutilus*) [56]. By contrast, individuals with a lower aerobic or locomotor capacity tend to occupy positions in the back of the group [33], especially in demanding environments [57], and parasitized individuals with impaired movement capacity similarly move towards the rear of groups [58]. Importantly, these patterns are not fixed: lead individuals fall back in the group [59,60] because they become satiated and/or experience reduced aerobic and locomotor capacity due to food-processing costs [16]. Also, variation in social responsiveness can cause less-social individuals to arrive at more peripheral and leadership positions [61]. This may arise from physiological and behavioural differences linked to social attraction [62] and the number of neighbours an individual responds to [63], as well as from differences in body shape or manoeuvrability (especially for groups moving in water or air). Furthermore, individuals with stronger social affiliations tend to cluster within groups and occupy more posterior positions, such as jackdaws (*Corvus monedula*) flying in pair formation in mixed-species flocks [64,65]. Also, individual heterogeneity in sensory performance may affect spatial positioning, such as the cataract formation induced by certain parasites [66]. In general, while individuals sort themselves by similarities or differences in morphology and behaviour [67], these traits can be correlated with physiological traits, including metabolism, growth rate, immune function, and endocrine status [16]. Via these different mechanisms, phenotypic variability is expected to have a large influence on how individuals use social interaction rules (i.e., social responsiveness in terms of repulsion, attraction, and alignment), something which has so far received little attention [5].

Group Coherence

The effects of individual heterogeneity on spatial positioning within groups have a direct impact on group coherence and performance. Social cohesion and coordination both require individuals to possess similar movement capacities and, over time, can result in individuals acquiring similar energetic (metabolic) costs of locomotion [16]. Therefore, groups with too great a mix of physiological capacities [15], extreme variation in motivation [25,68], or low social responsiveness are expected to have low cohesion, alignment, and coordination [69], which may compromise the transfer of information. By contrast, groups of individuals with high social motivation will improve group cohesion [7,45,70], and because such individuals are generally less assertive [31], they may furthermore help to reduce conflict and improve decision-making [71] but lack directedness [7]. Groups of larger individuals may also show stronger alignment as a result of the physical space they occupy while staying cohesive, as has been shown for tadpoles (*Xenopus laevis*) [72]. External factors that differentially compromise individual heterogeneity (e.g., locomotor capacity) will also affect group cohesion by increasing within-group heterogeneity. For example, fish infected with endoparasites have impaired mobility, which makes them less able to respond to the position and movements of others and so disrupts overall group coordination and alignment [58,73].

Leadership and Collective Decision-Making

Phenotypes that end up in the front of groups generally tend to have a larger influence over group movements and decision-making simply by the natural flow of information [7,55]. Furthermore, the trade-offs (conflicts of interest [74]) associated with individuals moving towards their own desired target and maintaining group cohesion can result in the group becoming fragmented [31,61] (Box 1). As a result, those individuals that have pertinent information or experience are more likely to elicit followers [19,31,71]. For example, in groups of elephants (*Loxodonta africana*) and killer whales (*Orcinus orca*), knowledgeable and older individuals lead foraging decisions, especially during uncertainty created by environmental change, bringing significant fitness benefits for followers [9,75]. Individual heterogeneity in knowledge or experience (i.e., cognitive performance) can also enhance collective decision-making and problem-solving in fish [76,77], illustrating the hierarchical nature of individual heterogeneity (Figure 1). Such leaders do not enforce followership. Instead, leaders show more directed movement paths [19,31,71] or greater likelihood of initiating motion [37], which elicits following from naïve conspecifics. In social systems with a stable social structure, group movements are commonly led by the more dominant individuals, such as in mountain gorillas (*Gorilla beringei*) [78], and may result in despotic group decision-making even when such individuals do not occupy leading positions [79]. Social networks can also mediate leader–follower dynamics, with highly socially embedded individuals, which also tend to be older and to have more experience, more likely to act as leaders because group mates are more strongly motivated to associate and follow them [8,80]. Although successful leadership may require the right combination of goal- and socially oriented behaviour [31], being followed can benefit leaders by lowering their risk of predation [81].

Group Functioning

Individual heterogeneity also affects the ability of groups to derive shared benefits associated with factors such as foraging and predator avoidance. In social spiders (*Anelosimus studiosus*) for example, collective foraging success is increased by the proportion of aggressive individuals in a group because of their higher tendency to approach prey [82], and in fish (*Gasterosteus aculeatus*), a composition of bolder, less sociable phenotypes enhances group foraging but with the cost of compromised cohesion [7]. In social arthropods, greater variance in behaviour and physiology can affect the division of labour and thereby drive colony performance [49], and, in lions (*Panthera leo*), phenotypes with different morphologies have different roles during group hunts [83]. In some cases group-level behaviour is determined by keystone individuals, such as in social spiders, where one bold individual can shape the behaviour and foraging success of the whole colony [84]. The phenotypic composition of groups is also expected to affect predator avoidance. For example, predators attacking groups are predicted to be less successful when their composition is linked with increased group cohesion and alignment, such as has been shown for predatory fish attacking virtual prey [85], or increased defensive responses, such as shown in honey bee (*Apis mellifera*) colonies [10]. Still large gaps remain in our understanding of the effects of individual heterogeneity on group functioning and individual survival in the context of predator–prey interactions.

Fission–Fusion Dynamics and Among-Group Assortment

Where conflicts between individual physiological behavioural capacities and the collective common ground of the group are too great [74], fission–fusion dynamics occur, with profound ecological and evolutionary consequences (Table 1). For example, groups themselves may split and reform over time [11,25,86], with certain phenotypes (e.g., high foraging motivation, high movement capacity, low sociability) being more likely to move between groups, as observed in wild populations of guppies (*Poecilia reticulata*) and great tits (*Parus major*) [6,87]. Phenotypes may also opt to remain solitary, such as those with high resource requirements to avoid competition with groupmates. As grouping with others can be more energetically efficient than staying alone [64,88], animals with low energy reserves or low aerobic scope may be more compelled to (stay in their) group to reduce energetic costs of movement. Importantly, the overall size of the group shifts the costs and benefits and thereby the relative trade-offs that motivate individual phenotypes to join the group. As a result of this effect, the size of groups may be predicted to depend on the group phenotypic composition. Fission processes may also be directly linked to individual physiology. For example, individuals with low muscular and cardiovascular capacity may simply not be able to keep up with others, or individuals with similar environmental tolerances or habitat preferences may end up occupying the same space [89]. Physiological differences may also lead to differences in activity budgets that lead to the (temporary) fission of groups. These fission–fusion processes provide a parsimonious and mechanistic explanation for the observation that groups are often assorted by size, species, sex, and parasite status [90,91]. For example, the sexual segregation that is common in social ungulates arises from males needing more time to forage and fill their rumen [12]. Importantly, among-group assortment may also arise through active processes [91], such as individuals grouping with similarly efficient or competitive individuals to optimise their food intake, with similar-sized individuals to reduce the energetic costs of grouping [15,16], or with individuals with similar appearance or movement capacities to lower predation risk [2]

Individual Heterogeneity and the Ecological Environment

Ecology plays a fundamental role in the behaviour of animal groups and shapes how individual heterogeneity drives collective behaviour and its broader consequences (Table 1). First, sources of individual heterogeneity may not be relevant under certain ecological conditions, such as phenotypic variation linked to foraging motivation playing no role in environments devoid of resources [7]. Context-dependent effects may, however, emerge over time, such as food deprivation resulting in increased behavioural heterogeneity when linked to differences in metabolic rates [92]. Environmental conditions may also temporarily reduce heterogeneity in behavioural expression, such as when motivation to forage is altered by changes in food availability or predation risk [1]. More generally, ecological pressures and environmental stressors tend to increase the potential effects that arise from individual heterogeneity in capacity [93]. For example, heterogeneity in movement ability and aerobic scope may be relevant only in demanding environments, such as in the acute context of a predator–prey interaction or where groups move over steep terrain. Similarly, individual heterogeneity in thermal tolerance will affect the ability of individuals to stay together under exceedingly hot or cold conditions and could cause phenotypic assortment along temperature gradients and associated habitats [15,89]. The ecological environment can also strongly modulate the effects of individual heterogeneity by shaping the trade-offs of grouping. For example, animals generally decrease their distance to group mates when threatened and increase it when foraging or hungry [7,68], but individuals aim to occupy optimal positions relative to others based on their physiological and behavioural capacity in relation to their environment and thereby influence such outcomes. The spatial variability of the environment itself, such as in terms of resources, may also affect the scope for conflict between group members and differently affect the costs and benefits of grouping for different phenotypes [32], mediated by social and reproductive factors [94]. Hence, the environment and changes therein strongly influence the role of different phenotypes within groups and the overall measure of behavioural heterogeneity and shape collective patterns with large potential ecological consequences (Table 1).

Concluding Remarks

Research on social grouping to date can be generally divided into strong quantitative studies focussed on the self-organising patterns of collective behaviour and those with a more ecological

Outstanding Questions

To what extent are social responsiveness and the use of interaction rules driven by social motivation versus effects of physiology (biomechanics, energetics, and neuro-endocrinology)?

How does individual heterogeneity in cognitive functioning affect social interactions and influence collective decision-making?

In what way do the effects of individual heterogeneity depend on the phenotypic distribution (normal, bimodal; range; keystone individuals) and group size?

How does individual heterogeneity in behavioural expression (constrained/enhanced by behavioural, physiological, cognitive capacities) change according to short-term socio-environmental changes and what are its implications for collective behaviour?

In what ways can social grouping over time lead to an increase in similarity in behavioural capacity among group members?

To what extent are phenotypic effects on collective behaviour a result of variability in social plasticity in terms of behavioural capacity or responsiveness?

What phenotypic mechanisms determine the switch point at which individuals will join/stay with a group and does this lead to phenotypically assorted groups that differ in size and stability?

To what extent does social network structure across different **social scales** result from self-organising effects linked to individual heterogeneity in behavioural capacity?

How are predator–prey interactions impacted by group phenotypic composition, in terms of both predator performance and prey avoidance of predators?

What are the ecological and evolutionary consequences of the effects of individual heterogeneity in the context of human-induced environmental change?

focus and attention to individual variability. The time is right to bridge these approaches and acquire a proper mechanistic understanding of individual heterogeneity in collective behaviour across species, contexts, and traits. Using our common framework to objectively quantify individual heterogeneity in fundamental physiological, cognitive, and behavioural components, we synthesised the broad literature and provide key mechanistic and predictive insights into how and when individual heterogeneity matters for collective behaviour and its broad eco-evolutionary consequences (Table 1). Strong interdisciplinary research that integrates experimental, observational, and theoretical approaches (Box 3) will be crucial to properly understand the causes and consequences of individual heterogeneity in the collective behaviour of animal groups (see Outstanding Questions).

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