



Since January 2020 Elsevier has created a COVID-19 resource centre with free information in English and Mandarin on the novel coronavirus COVID-19. The COVID-19 resource centre is hosted on Elsevier Connect, the company's public news and information website.

Elsevier hereby grants permission to make all its COVID-19-related research that is available on the COVID-19 resource centre - including this research content - immediately available in PubMed Central and other publicly funded repositories, such as the WHO COVID database with rights for unrestricted research re-use and analyses in any form or by any means with acknowledgement of the original source. These permissions are granted for free by Elsevier for as long as the COVID-19 resource centre remains active.

Review

From Individuals to Groups and Back: The Evolutionary Implications of Group Phenotypic Composition

Damien R. Farine,^{1,2,3,5,*} Pierre-Olivier Montiglio,^{4,5,*} and Orr Spiegel^{4,5,*}

There is increasing interest in understanding the processes that maintain phenotypic variation in groups, populations, or communities. Recent studies have investigated how the phenotypic composition of groups or aggregations (e.g., its average phenotype or phenotypic variance) affects ecological and social processes, and how multi-level selection can drive phenotypic covariance among interacting individuals. However, we argue that these questions are rarely studied together. We present a unified framework to address this gap, and discuss how group phenotypic composition (GPC) can impact on processes ranging from individual fitness to population demography. By emphasising the breadth of topics affected, we hope to motivate more integrated empirical studies of the ecological and evolutionary implications of GPC.

Group Phenotypic Composition: An Emergent Topic

Many central questions in evolutionary biology rely on understanding how individual-level and group-level selective processes interact to shape phenotypic variation and specialisation. Individuals can aggregate into groups, and the composition of these groups, populations, or communities (herein **group phenotypic composition** or GPC, see [Glossary](#)) can affect group-level dynamics and self-organisation. For example, large groups of highly similar individuals can benefit from lower predation pressure by making it difficult for predators to track individuals (the confusion effect [1,2]). Eventually, this can drive selection operating on individual phenotypes [3,4], in this case by selecting against rare phenotypes because individuals who look different will be more likely to be taken by predators (the oddity effect [1]). Selection arising from GPC can lead to an evolutionary response of individual phenotypes. GPC can shape the evolution of behaviours that mediate individual movements between groups, phenotypic plasticity (individuals adjust their phenotype in response to particular GPCs), or **phenotypic traits** that allow individuals to manipulate the characteristics of their group. Selection from GPC can also directly modify the covariance between individual and group phenotypes through the removal of particular phenotypes within generations. All these evolutionary responses at the individual level are likely to modify GPC itself. Despite extensive theoretical considerations (see [5]), the role of GPC as an agent of selection shaping individual fitness and as an emergent property of the individual phenotypes have rarely been considered together in empirical studies.

Research across a range of disparate topics will benefit from simultaneously developing an understanding of how GPC affects individual fitness and exerts selection on individual

Trends

Members of animal groups often vary in their phenotypes (e.g., personality, morphology). Many recent studies have shown how different aspects (e.g., phenotypic average, variation, extreme) of GPC affect group-level outcomes (e.g., foraging success, mating system).

Group-level outcomes can shape selection when individual and group phenotypes co-vary. Selection arising from GPC can drive changes in traits that affect aspects of individual-to-group covariance, such as behaviours that determine group membership or by changing the expression of traits (via phenotypic plasticity or indirect genetic effects).

A framework based on interacting phenotype theory can quantify the selective consequences and evaluate the evolutionary implications of GPC. This framework is still largely unexplored empirically but it is applicable to many topics in evolutionary biology.

¹Department of Anthropology, University of California Davis, Davis, CA, USA

²Smithsonian Tropical Research Institute, Panamá, República de Panamá

³Edward Grey Institute of Field Ornithology, University of Oxford, Oxford, UK

⁴Department of Environmental Science and Policy, University of California Davis, Davis, CA, USA

phenotypes, and assessing how individual phenotypes respond to GPC, ultimately driving an evolutionary response to selection arising from GPC. For example, moving animal groups can contain both leaders and followers [6,7]. Much could be learnt about the evolution of leadership by simultaneously assessing how consistent behavioural differences affect **group-level outcomes** [8] and how group-level outcomes select for particular phenotypes or shape the distribution of phenotypes in the population. **Social selection** [4] and **social heterosis** [9] offer candidate frameworks to study selection arising from the social context, but these still need to be expanded to capture the complexities that can arise from the interactions between individuals (Figure 1). To study the consequences of group composition, we need to draw on evolutionary theory which integrates quantitative genetics and selection.

In this paper we propose that a framework based on the theory of interacting phenotypes [4,5,10] can integrate the key mechanisms determining how GPC affects selection acting on individual phenotypes and the subsequent **evolutionary implications of GPC**. We use this

⁵Authors have equal contribution, ordered alphabetically

*Correspondence:

damien.farine@zoo.ox.ac.uk

(Farine, D.R.), makitsimple@gmail.com

(Montiglio, P-O.),

orr.spiegel@mail.huji.ac.il (Spiegel, O.)

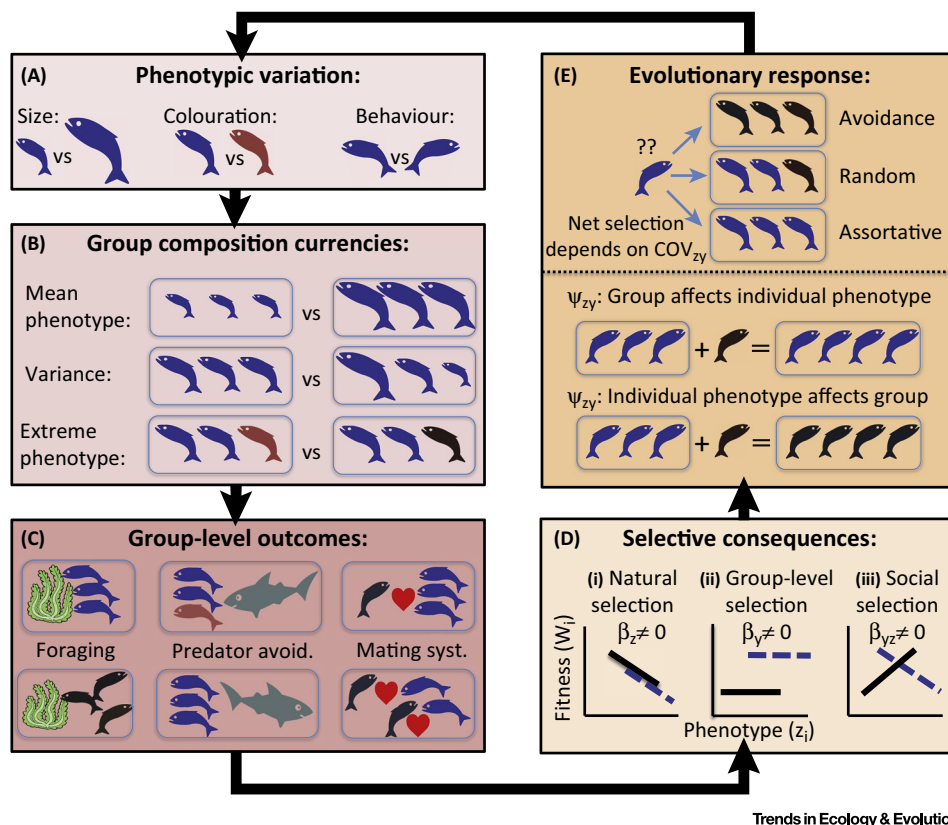


Figure 1. The Evolutionary Implications of Group Phenotypic Composition (GPC) in a Nutshell. (A) Individuals show remarkable phenotypic variation in their morphology, behaviour, and life history. (B) Hence, groups (or populations/communities) can vary in their GPC (e.g., their mean phenotype or within group variation). (C) GPC affects group-level outcomes (e.g., the total amount of food a group acquires), thus (D) impacting on individual fitness (Box 1). Beyond the consequences of individual phenotypes on fitness (natural selection), GPC can favour all members (**group-level selection**) or favour particular phenotypes over others (social selection). Blue (dashed) and black (solid) lines represent two groups with different GPCs. (E) GPC can drive different evolutionary responses. These include traits affecting covariation between individual phenotypes and their GPC (e.g., decisions to join or leave particular groups), the evolution of individual phenotypic plasticity in response to GPC (e.g., individuals change their phenotypes to match the group), or the evolution of individual contributions to GPC (e.g., individuals change the behaviour of group members). These evolutionary responses can then affect the distribution of phenotypes in subsequent generations.

framework to draw general predictions about how GPC affects the evolution of individual phenotypes and ecological processes, and how the feedback between the evolution of individual phenotypes and group-level outcomes alters GPC. We then show how this framework can be applied to an array of fields by detailing empirical studies that have investigated the role of GPC in either shaping individual fitness or generating emergent properties of animal groups. We hope that outlining the similarities among topics will help to create an integrated research agenda to begin addressing the effects of GPC on individual fitness (selective consequences) and the response of individuals to the **selective consequences of GPC** (evolutionary implications) in unison.

When Should GPC Matter: A Framework

Understanding the evolutionary implications of GPC requires quantifying its effect on individual fitness, its net selective force on individual phenotypes, and its evolutionary implications across generations (Box 1). These three components are usually studied in isolation, but here we outline how they can be integrated.

Variation in Individual Fitness Resulting from GPC

Many studies have investigated how phenotypic variation among individuals is associated with variation in individual fitness, and how GPC affects the relationship between the phenotype of an individual and their fitness. GPC can be a function of the phenotypes of its members (such as the frequency of fast-exploring individuals, or the phenotype of the least-exploratory individual) [11] or an emergent property that is not attributable to any single individual, such as the mating system (see section 2.2 in [12]). GPC can affect individual fitness by influencing the overall performance of the group on collective tasks, affecting all the members of any given group equally, or by affecting the relative performance of different phenotypes within groups. For instance, a group with more aggressive individuals can be more successful at foraging, but aggressive individuals can have a higher fitness than non-aggressive individuals because they can monopolise a larger share of the total resources. It is interesting to note that the selection acting on individual phenotypes within groups can conflict with the selection acting on the individual phenotypes among groups [13]. Studying fitness in the context of phenotypes and how GPC modulates fitness, both within and across species, provides good insights on the overall potential selective consequences of GPC for the individuals within them.

Net Selection Arising from GPC

In addition to requiring phenotypic variation in fitness, net selection strongly depends on the covariance between the phenotype of an individual and the phenotypes of those it associates with [4,14]. For example, if individual phenotypes experience all possible types of GPCs (i.e., GPC is effectively random) then no net selection will arise from GPC (although other mechanisms, such as genetic drift, may still shape GPC). A key insight is that a range of behavioural traits and ecological processes can determine the covariance pattern in GPC, and hence drive net selection. For example, limited dispersal can result in individuals with similar phenotypes forming groups more often than random. Thus, behaviours can therefore modulate the strength of selection arising from GPC on other traits [4]. For instance, aggressive male water striders (*Aquarius remigis*) respond to negative fitness effects of aggressiveness within their group by moving between groups [15]. Similarly, many species respond to competition under different ecological conditions by switching between single-species groups and mixed-species groups [16].

Evolutionary Response to GPC

Extensive work on the mechanisms of inheritance, phenotypic plasticity, and indirect genetic effects have detailed the evolutionary response of phenotypes to selection forces (i.e., via

Glossary

Baldwin effect: evolution in changing environments facilitated by increased plasticity across generations. For example, individuals that can adapt by learning new behaviours have more offspring, resulting in a higher average learning capacity in subsequent generations.

Evolutionary implications of GPC: the effect of GPC on the changes in the distribution of phenotypes. Such a change can arise through changes in the genotypes present or through indirect effects.

Group-level outcome: any aspect of a group of individuals that affects the fitness of individual members. For example, the mean amount of food that individuals in a group consume, the group's mating system, or the group's migration route.

Group-level selection: selection arising from differences in the mean fitness among groups of individuals.

Group phenotypic composition (GPC): any descriptor of the types of phenotypes found within a group. Examples include the average body size of individuals, the variation in male colour, or the aggressiveness level of the most aggressive individual in the group. In this framework, 'groups' can represent many aspects of the social environments of individuals, including breeding units, social networks, neighbourhoods, populations, and communities.

Indirect effects: the effect of an individual or a group of individuals on the expression of the phenotype of a given organism. For example, small individuals can grow faster if they are in a group containing larger individuals.

Net selection force: the net difference between the average phenotypic value in the population before selection and the average phenotypic value in the population after selection.

Niche construction: the ability for an organism to modify its environment to favour its own phenotype. For example particular individuals can adaptively control group membership or alter the phenotype of other group members.

Parameter COV_{zy} : covariance between GPC and individual phenotypes, or the extent that particular phenotypes are consistently found either together or apart. For example, high covariance in body

'indirect effects' [5,14] or the **Baldwin effect** [17]). These theoretical tools are applicable to studying the evolutionary implications of GPC (Box 1). Individuals can respond to the effect of GPC by altering the phenotypic composition of the group (for example by controlling access to the group) and/or by changing their own phenotype (phenotypic plasticity in response to the

Box 1. A Framework to Study GPC

Understanding the selective consequences and evolutionary implications of GPC requires considering in concert (i) the fitness consequences of individual and group phenotypes, (ii) how selection affects individual and group phenotypic variation within a generation, and (iii) how phenotypes are transmitted across generations. First, it is important to consider how group composition can affect the relationship between the phenotype of an individual and their fitness. This can be done by partitioning the effects of individual traits, group composition and their interaction on fitness through a regression (i.e., a social selection approach) or a contextual analysis approach [3,14] using:

$$w_i \approx z_i * \beta_z + y_j * \beta_y + z_i * y_j * \beta_{yz} \quad (\text{Equation I})$$

where w_i is the fitness of the individual (relative to the population), z_i the phenotype of the individual i , β_z the selection gradient associated with this phenotype (i.e., how an increase in one phenotypic unit translates to a fitness change), and y_j is the phenotypic composition of group j (for example its average z value or any other GPC characteristic). β_y is the social or group selection gradient (*sensu* [4]), describing how changes in group composition affect the fitness of its members. Note that social selection gradients are usually estimated using the GPC excluding the focal individual, whereas group selection gradients are estimated using the overall GPC of the group [3,4]. β_{yz} describes the extent to which the selection gradient associated with the phenotype of an individual changes with GPC.

Second, one needs to assess whether the selection gradients associated with group composition (β_y and β_{yz}) truly translate to fitness differences in the population. This is achieved by quantifying the covariance between the individual phenotype and GPC:

$$S_z = \text{VAR}_z * \beta_z + \text{COV}_{zy} * \beta_y \quad (\text{Equation II})$$

where S_z is the net selection differential acting on individual phenotypes z , VAR_z is the phenotypic variation in z values in the population, and COV_{zy} is the covariance observed between the phenotype of individuals and the composition of their group [4].

Third, to predict the response to selection, one needs to take into account that the group can simultaneously affect, and contribute to, the expression of the phenotypes of its members (i.e., indirect genetic effects, [5,18]). The phenotype of an individual, z_i , is the sum of its breeding value (the additive effects of its genes), a_i , and the effects of the environment the individual experiences, e_i [70,71]. However, z_i is also determined by the group composition. The parameter Ψ_{zy} determines the strength and direction of the effect of y_j on the phenotype of the individual z_i (see [5]). Similarly, group composition y_j , can also have a breeding value, and is affected by the phenotype of its members (through Ψ_{yz}). Note that the breeding value of the group (a_j) is a function of the breeding values of its members.

$$z_i = a_i + e_i + \Psi_{zy} * y_j \quad (\text{Equation IIIA})$$

$$y_j = a_j + \Psi_{yz} * (a_i + e_i + \Psi_{zy} * y_j) \quad (\text{Equation IIIB})$$

If the group phenotype is a function of all members of the group, rather than just one, then a_j will be the sum, average of variance or individuals' breeding values. Note also the potential feedback between GPC and individual phenotypes via phenotypic plasticity (Ψ_{zy}). Thus, the response to selection would be:

$$\Delta z_i = (G_z + \Psi_{zy} * G_{zy}) * \beta_z + (G_{zy} + \Psi_{zy} * G_z) * \beta_y \quad (\text{Equation IVA})$$

$$\Delta Y_j = (G_y + \Psi_{yz} * G_{zy}) * \beta_y + (G_{zy} + \Psi_{yz} * G_z) * \beta_z \quad (\text{Equation IVB})$$

where G_z is the additive genetic variance (the variance in breeding values, a) associated with group members' phenotype z , G_y , the genetic variance in GPC, and G_{zy} is the genetic covariance between individuals' phenotypes z and group composition Y . If feedback is allowed, the evolutionary response of z_i and Y_j will include an additional term $\{1/(1 - \Psi_{zy} * \Psi_{yz})\}^2$ (see [5] for derivation and also [10]).

Integrating these three approaches into a single set of equations is not developed here (see [10]), but these enable us to describe the change in individual phenotypes, Δz_i , and changes in group composition, ΔY_j , following selection from one generation to the next. The complexity of this equation arises from the multiple contributions of indirect effects (Ψ_{yz} , Ψ_{zy}) to the response to selection (i.e., through their effect on the variance in individual phenotype, their contribution to individual breeding values, and their impact on the covariance between the phenotype of an individual and the composition of their group [10]). This integrated approach also outlines that group composition has selective consequence through a limited number of interacting key parameters (G_z , G_{zy} , G_y , Ψ_{zy} , Ψ_{yz} , β_z , β_y , and β_{yz}).

size implies that groups are composed of either all large or all small individuals.

Parameter β_y : the relationship between the fitness of an individual and GPC.

Parameter β_{yz} : the interaction between the effect of GPC and the phenotype of an individual on their fitness. This is the extent to which the selection gradient associated with the phenotype of an individual changes with GPC.

Parameter β_z : the relationship between the phenotype of an individual and their fitness.

Parameter Ψ_{yz} : the effect of an individual with a particular phenotype on GPC. For instance, an aggressive individual can increase the overall number of aggressive interactions in a group.

Parameter Ψ_{zy} : the indirect effect of GPC on the expression of the phenotype of an individual. For example, a group can constrain the maximum movement speed of its members.

Phenotypic trait: any aspect of an individual organism that can be measured. Examples of traits include behaviours such as aggressiveness, exploration or patterns of space use, and morphology (e.g., body size and colouration).

Selection gradient: the relationship between the fitness of an individual and their phenotype, or the relationship between their fitness and the GPC they experience.

Selective consequences of GPC: the extent to which GPC changes the distribution of individual phenotypes within groups owing to differences in fitness within a given generation. This can happen through direct removal of particular phenotypes or their failure to reproduce.

Social heterosis: an increase in fitness of a phenotype (or genotype) arising from its interaction with different phenotypes (or genotypes). Individuals with a particular allele or trait value have higher fitness in the presence of individuals carrying a different allele or expressing a different trait value.

Social selection: differences in fitness among individuals arising from differences in their social environment. Social selection differs from natural selection, which arises from differences in phenotype among individuals. Note that social selection arising from GPC is usually estimated

phenotypic composition of their group). The strength and shape of such individual responses will largely determine whether selection can drive an evolutionary response to GPC [5, 18]. Interestingly, phenotypes can differ in how much they can or do contribute to the group's outcome (e.g., by manipulating the GPC) or in how much they can or do adjust their phenotype to their GPC. For example, a larger body size or higher aggressiveness could enable an individual to alter its social environment to a greater extent. Such individuals might also exhibit a lower plasticity level than smaller or less aggressive individuals.

by excluding the contribution of the focal individual to GPC.

Applying an Integrated Framework to Study the Evolution of GPC

Combining the effect of GPC on individual fitness with an analysis of its selective consequences and evolutionary implications allows us to identify five main ways in which group composition can matter for the evolution of individual phenotypes or for the maintenance of phenotypic variation (Box 1). First, GPC can simply alter the fitness consequences associated with individual phenotypes (i.e., via direct selection, β_y , or by selection mediated by the properties of their group, β_{yz} , Box 1). Second, individual phenotypes can co-vary with group composition (high COV_{zy}) and thus modulate the **net selection force** exerted on individual phenotypes. Third, GPC can affect the expression, and therefore the heritability, of individual phenotypes. Hence, GPC can amplify or weaken the ability of the population to respond to selective pressures (high or low Ψ_{zy}). Fourth, if GPC modulates selection, and individual phenotypes can respond to selective pressures, this can drive a feedback between them. A synergy between the effect of the group on individual phenotypes (Ψ_{zy}) and the contribution of individual phenotypes to the group composition (Ψ_{yz}) can substantially increase or decrease the pace of evolutionary change in response to selection arising from GPC. Fifth, GPC is also an emergent property of genotypes and their patterns of expression. Hence, GPC or group-level outcomes could also be associated with genetic variation, respond to selection, and be an adaptation. The exact function linking genetic variation (or variation in breeding values) at the individual level to GPC at the group level, $f(G_z, G_y)$, will determine how much genetic variation in group composition is available for selection to shape group-level processes. Further, interacting phenotype theory typically considers only the group mean, although indirect genetic effects can make the group mean phenotype very different than a simple mean of the mean of the breeding values. In cases where group variance or extremes are important, linking GPC to individual breeding values remains unclear. Determining the amount of genetic variation in group mean phenotype, in the phenotypic variation, or in the phenotypic range still requires proper mathematical formalisation and is a major gap in this area.

The integrated framework (Box 1) provides insights into the evolutionary impact of GPC by predicting when it will matter and its consequences for individual phenotypes. GPC can only matter when it introduces differences, or equalises existing differences, in fitness across different phenotypes (β_y and β_{yz} differ from zero). Assuming this is the case, GPC will have stronger selective consequences when the phenotypes of the members of a group or community are non-random (the covariance COV_{zy} is high). An important prediction here is that net selection has the potential to be stronger in smaller groups (because, by definition, COV_{zy} decreases with group size). Similarly, relatedness among group members leads to a higher covariance (COV_{zy}), and therefore groups with high relatedness should experience stronger selection arising from GPC. Higher covariance can also arise from habitat preferences, segregation, or local adaptation coupled with limited dispersal. Hence we expect GPC to be associated with stronger selection in these situations. Note that some aspects of GPC (e.g., the average phenotype of a group) can co-vary with the phenotype of its members to a greater extent than other aspects (e.g., the variance, or the highest phenotypic value).

In addition to predicting when GPC should have important selective consequences, this framework allows us to predict the particular evolutionary implications of selection arising from

GPC (Figure 1). When individual phenotype is fixed (non-labile), selection resulting from GPC should result in the evolution of behaviours that will affect the covariance between the phenotypes of members of the group or community (COV_{zy}), such as decision rules for joining or leaving, habitat selection, or manipulation of group composition by individuals (e.g., evicting particular members from the groups). On the other hand, when traits are labile and can be modulated in response to the environment (e.g., individuals can express varying levels of aggressiveness in different contexts), then we expect that selection associated with GPC will affect the evolution of individual phenotypic plasticity in response to their social environment (Ψ_{zy}) and/or the evolution of the effect that individuals have on the characteristics of their group (Ψ_{yz} , which can eventually lead to **niche construction** [19,20]). These traits (Ψ_{zy} and Ψ_{yz}) could evolve [21] to differ among individuals [22] and co-vary according to other aspects of individual phenotypes [23].

Empirical Evidence for the Selective Consequences of GPC

In the following section we show how outstanding questions in ecology and evolution from apparently disconnected topics all rely on understanding the selective consequences of GPC. This framework applies across topics relevant to the ecology of individuals in groups (i–iii), emergent properties of groups (iv–vi), and community or population dynamics (vii). We argue that these empirical examples can be studied by quantifying the key parameters outlined above (see also Box 1).

(i) Foraging

Animals can vary in how they search for and/or handle food. Variations in foraging skills within groups can create variation in fitness among groups (β_y) by simply introducing differences in the amount of food different types of groups acquire: for example, shoals of fish with bolder or more-exploratory individuals found and approached novel food faster [24,25]. Similarly, colonies of social spiders with more-aggressive individuals have a higher foraging success because aggressive individuals approach prey faster [26]. Individuals can also vary in the ability or propensity to innovate [27] and socially learn [28], hence GPC might affect the ability for groups to acquire and exploit novel foraging opportunities (β_y). GPC can also affect the relative fitness of members within groups (β_{yz}): for example, food is shared more equally in mixed-personality shoals of guppies compared to shoals with only shy or bold individuals [24].

(ii) Niche partitioning

GPC can also modulate the benefits of group-living by varying competition (Ψ_{zy} or Ψ_{yz}) [29]. Many species participate in mixed-species foraging groups, in which one proposed benefit is that resource competition is reduced via niche partitioning. Reduced competition can facilitate larger flocks, resulting in secondary benefits such as rapid information transfer (β_y or COV_{zy}) [30–33] and better problem solving [34]. Within species, different individuals might also specialise on specific resources or vary in the range of food items they eat [35], which affects competition for food resources [36]. When competition within groups introduces differential access to resources, (i.e., strong social selection component through β_{yz} and COV_{zy}), we expect groups to contain individuals with of a greater range of food preferences or specialisations than would be expected by chance [29,37].

(iii) Predator–prey (or host–parasite) interactions

GPC can affect phenotype-dependent predation risk via confusion and oddity effects [1]. Thus, GPC can affect the fitness of all group members equally by collectively reducing their predation risk (confusion effect, β_y) or favour particular phenotypes (oddity effect, β_{yz}). For example, predation risk for prey of particular body sizes varies depending on the ratio of small to large individuals [2], and odd fish are disproportionately likely to leave their shoal (thus affecting COV_{zy})

[38]. The defensive ability of a given group also varies with group composition: in honey bee *Apis mellifera* colonies, the proportion of defensive individuals affects the recruitment of workers against intruders, the defensive response of the colony, and the fitness of all the colony members [39]. Disease dynamics and parasite prevalence can also depend on the presence of a few highly social or promiscuous individuals in groups acting as super-spreaders [40–42]. For example, ‘Typhoid Mary’, or the flight attendant spreading the severe acute respiratory syndrome (SARS) virus between Asia and America, disproportionately contributed to major disease outbreaks. The consequences of group composition for disease dynamics is usually thought to decrease the fitness of all the group members in a similar way (β_y). However, GPC could also affect disease dynamics that differentially impact on particular phenotypes (β_{yz}). High levels of kinship could favour disease transmission if kinship promotes physical contact among kin members [43], and net selection force can be stronger due to higher phenotypic covariance among group members (high COV_{zy}). By contrast, groups with higher genetic variation (G_z) can have lower disease prevalence if this reduces contact or transmission rates.

(iv) Altruism and Eusociality

GPC is a central mechanism in the evolution of cooperation, altruism, and eusociality [44]. Cooperation among colony members is more common in colonies with high relatedness, either because it is beneficial for individuals to cooperate with kin (increase their Ψ_{zy}) or because related groups with cooperative individuals outcompete other groups (β_y and COV_{zy}) [45]. Beyond these well-established effects, overall colony fitness can depend on the personality composition of its members. In North American ants *Temnothorax longiniosus*, colonies with greater variance in worker aggressiveness and exploration have increased *per capita* productivity via greater specialisation (β_y) [46,47]. In the fire ant (*Solenopsis invicta*), a threshold frequency of ‘tolerant workers’ determines the acceptance of multiple queens into the colony [48]. This could potentially impact on the reproductive output of the colony. Similarly, in honey bees, workers vary in their responsiveness to queen pheromone (i.e., Ψ_{zy}), and less-responsive workers are more likely to activate their ovaries and compete with the queen over reproduction [49]. Hence, worker responsiveness can affect the extent of competition over reproduction within the colony (β_{yz}). GPC can evolve in response to different environments: in social spiders, where all individuals reproduce and have no caste specialisation, colonies with more-docile individuals fair better in communities with less competitors [50] (Box 2). GPC can also become adapted to specific ecological conditions: when perturbed, colonies of social spiders recreate the specific optimal composition of their native environment [51].

(v) Collective Decision-Making and Collective Movement

Phenotypic composition can modulate the emergent properties of animal groups, potentially leading to persistent group-level differences in fitness. Complex collective behaviours often arise from simple interaction rules, such as groups pooling information to make accurate decisions [52,53]. Having a mix of informed and uninformed individuals can promote better decision-making because the latter support consensus via a majority [54]. Informed individuals can also lead groups to resources [55]. In homing pigeons, experienced individuals contribute more to the route of the group back to the coop [56], while old female matriarch killer whales (*Orcinus orca*) lead the group to resources when food abundance is low [57]. In great tits (*Parus major*), phenotypic variance in groups is important because slow-exploring individuals maintain group cohesion, while fast-exploring individuals sample new patches, thus ‘leading’ the group [8]. Thus, who is in moving groups can affect how well the group makes decisions (through Ψ_{yz} or β_y), and potentially the fitness of group members (z_i). Group composition can even have carry-over effects on behaviour if new individuals acquire the behaviours of group members via conformist or cultural transmission (Ψ_{zy}) [58]. For example,

Box 2. Empirical Example I: GPC in Social Spiders

To demonstrate how our framework can be applied to an empirical study system, consider the case of social spiders. These have been studied extensively in the context of the selective importance of group composition. Initial studies in three species showed how colonies are made up of docile and aggressive individuals (*Anelosimus studiosus* [26,72,73]; *Stegodyphus sarasinorum* [74]; *Stegodyphus dumicola* [75]). Studies repeatedly quantified individual behaviour and tracked the overall performance of group composition using observational and experimental approaches. These studies have tackled the classical question of how individual specialisation and consistent behavioural variation can evolve through multi-level selection and social interactions. Docile and aggressive individuals specialise on different tasks, such as colony maintenance, defence, or foraging [72,76,77].

Many aspects of the phenotypic composition of a colony (y) affect its dynamics. The frequency of aggressive or docile individuals determines the foraging success or defensive abilities of the colony (i.e., β_y [26]). In addition, the phenotype of individuals at the extreme of the phenotypic distribution of the colony [74], and the personality of founder individuals [78], have important effects on the overall colony behaviour, performance, and the fitness of individuals (i.e., β_y). These effects of colony composition on performance are especially likely to lead to selection pressures when the contribution of an individual to colony-level performance depends on their phenotype (e.g., a higher value of z is associated with a greater absolute value of Ψ_{yz}). For example, bold individuals disproportionately affect the prey capture rate of a colony [79]. Moreover, colony composition can have an impact on the interactions between the colony and its community [50].

Overall, through these different mechanisms group composition affects the fitness of all colony members in two ways. First, mixed group composition increases the fitness of all colony members equally, with both docile and aggressive individuals benefiting from having a diverse group (β_y is strong [72]). Second, particular group compositions will interact with the surrounding community to favour greater mass gain in either docile or aggressive individuals (β_{yz} is strong [80]). Eventually, the selective consequences of group composition could lead to the evolution of adaptations enabling colonies to express particular group compositions, and to regulate it once perturbed [51]. However, how colony performance selects for particular phenotypes (S_z) and how individuals respond to selective pressure (i.e., by modifying traits affecting COV_{zy} , Ψ_{yz} , Ψ_{zy}) largely remain to be investigated.

juvenile whooping cranes (*Grus americana*) learn the migration routes from older individuals [59], which could lead to consistent and maintained differences in migration costs between groups.

(vi) Mating System

Classical work on the evolution of alternative mating tactics via negative frequency-dependent selection has extensively considered the selective consequences of the frequencies of different phenotypes in a population or a group (β_{yz}) (e.g., evolutionary stable strategies [60]). However, other aspects of GPC, such as the presence or absence of particular phenotypes, can affect mating systems. For example, the presence of aggressive individuals in groups of water striders has a well-known effect on the operational sex ratio and mating activity within mating pools (e.g., [61]). The presence of aggressive individuals drives other individuals out of the local area and decreases the intensity of scramble competition for females (aggressive individuals exhibit a strong Ψ_{yz}). This reduces the overall mating rates of the group (β_y), but under these new social conditions more-aggressive males can get a bigger share of the mating (β_{yz}) (when measured at the individual level [13]). Similarly, GPC is likely to have strong impact on group reproductive success in family groups, cooperatively breeders, and monogamous species with bi-parental care [62,63].

(vii) Population and Community Dynamics

The link between GPC and population level outcomes is at the heart of classical hypotheses on population regulation, where population composition in aggressiveness or territoriality can both drive and be driven by population density (through β_{yz} and potentially an interaction between Ψ_{zy} and Ψ_{yz}) [64]. We are not aware of any study empirically linking population or community composition in behavioural traits to their dynamics, and these dynamics to fluctuations in selection acting on behavioural traits. Nevertheless, the distribution of particular morphological [65], life-history [66], or behavioural traits [67] can affect the overall population growth of all members (β_y) or favour particular phenotypes relative to others

Box 3. Empirical Example II: GPC in Mixed-Species Flocking

The presence or absence of particular phenotypes in the community can impact on the dynamics of social interactions, group formation, and subsequent group-level behaviours. A useful model for studying the impacts of community-level [81] and group-level [82] phenotypic composition on individual fitness is mixed-species flocking in birds. Individuals can often choose between joining mixed-species flocks or forming single-species flocks (thus affecting COV_{zy}): mixed-species flocking is generally hypothesised to reduce predation risk (increasing the fitness of all individuals) by combining individuals with different predator-detection skills and through forming larger groups (which is thought to reduce the overall COV_{zy} , and act via β_y , β_{yz} , and Ψ_{zy}).

Individuals can also modulate selection pressure by influencing the behaviour of heterospecifics. Several studies document the importance of key species in the formation and maintenance of interspecific groups. For example, mixed-species flocking in the Brazilian Atlantic forest depends on the presence of red-crowned ant-tanagers (*Habia rubica*) [83]. Similarly, birds on New Guinean islands only flock in the presence of particular species [84]. In both these cases, the same species flocked in patches with these key species, and did not flock when in their absence (thus the presence or absence of species affects z_i through Ψ_{zy}). These dynamics have been verified experimentally: removing nuclear species (tufted titmice, *Baeolophus bicolor*; Carolina chickadees, *Poecile carolinensis*; and black-capped chickadees, *P. atricapillus*) from some, but not other (control), isolated patches of woodland affected flocking dynamics in a range of attendant species (including white-breasted nuthatches, *Sitta carolinensis*; and downy woodpeckers, *Picoides pubescens*) [85]. At experimental sites, individuals were less likely to forage at exposed food sources, potentially because the flocking reduces perceived predation risk [86], and individuals had lower body condition [87] than in control sites. Similar patterns were observed in guilds of carrion eaters where particular species facilitate resource discovery and others resource utilisation (through β_y [32,88]).

By forming mixed-species flocks (changing Y_i), individuals can benefit from reduced competition or from forming larger groups, and change the benefit they gain relative to others (through β_y and β_{yz}). More importantly, mixed-species flocking provides an opportunity to quantify the effects of community composition on individual phenotypes (through Ψ_{zy}) and the contribution of particular phenotypes to community composition (Ψ_{yz}).

(β_{yz}). Group diet or niche composition can also alter the interactions between a population and its community [36]. Eventually, the characteristics of interspecific interactions or other higher levels processes can co-vary with particular individual phenotypes, and act as agents of selection on the phenotype of the individual (β_y or β_{yz} , and COV_{zy}) [68,69]. Note that changes in GPC can occur either because individuals join or leave a group or community, or because individuals plastically modulate their phenotype in response to their group (Ψ_{zy} , Box 3).

To summarise, GPC (i.e., the average phenotype, presence of keystone individuals, or variability in phenotypes) affects individual fitness in a variety of contexts (e.g., mating, foraging, decision making) over a wide range of temporal and spatial scales. In some cases, GPC impacts upon individual fitness long after the initial group members are gone (e.g., if behaviours are culturally transmitted), but GPC can also exert selection in populations consisting of highly ephemeral group membership [30]. Considering such group-level dynamics in the context of GPC opens up a range of questions, such as ‘do species with fission-fusion exhibit more or less phenotypic variation in groups than socially-stable species?’ Further issues are listed in the Outstanding Questions. Notably, the evolutionary implications of GPC are still rarely studied, as is the potential for GPC to shape the patterns of social organisation we observe in animal groups across multiple levels of selection (Box 4 gives a description of the types of data needed to study this). Individual behaviour and ecology not only determine the effects of GPC on individual fitness but also influence to what extent individual phenotypes co-vary with their group composition, and how groups and individuals determine each other’s behaviours. Moreover, group-to-individual covariance, the constraints placed on individual phenotypes by the group, and individual contributions to group-level outcomes are thought to have the ability to evolve in response to selection [4,5] generated by GPC. Nevertheless, no theory or empirical work has investigated the implications of such a claim for the evolution of individual and group phenotypes.

Box 4. What Types of Data are Necessary to Study GPC?

Understanding the evolutionary implications of GPC requires data at both the individual and group levels. Estimating selection gradients (β_z , β_y , and β_{yz}) requires a dataset containing measurements of fitness (or relevant proxies) for individuals of known phenotypes, observed in groups of known composition [89]. A linear model can be used to assess how much fitness (as a dependent variable) varies as a function of individual phenotype, GPC, and their interaction [89,90]. Whereas in nature particular phenotypes might only be found in particular GPCs, an experimental approach can be used to generate all possible combinations, representing the full spectrum of all individual phenotypes in all possible GPCs.

Estimating the variance in individual phenotypes (VAR_z), and its covariance with GPC (COV_{zy}) in natural populations, requires data on the natural range of individual phenotypes and their GPCs when individuals are free to choose which groups to join or leave. The behavioural mechanisms generating the covariance between individual phenotypes and group compositions can vary from one system or community to the next (e.g., non-random interaction patterns, habitat preferences [4]). Hence, it is essential to take the biology of the system into account when designing studies, for example to avoid constraining individual decisions to join or leave groups. Mixed models facilitate analysing such datasets [91] because they can estimate individual phenotypic variation and its co-variation with group composition while accounting for temporal or spatial changes in these aspects and correcting for covariates [92,93]. Such a dataset could eventually be extended to include repeated measurements of individual phenotypes as they sequentially join multiple groups, or to monitor changes in group structure as individuals join and leave them. Such a dataset can be used to quantify how much the GPC affects the expression of individual phenotypes (Ψ_{zy}) and how much individuals contribute to group-level outcomes (Ψ_{yz} , [5,94]). Finally, when coupled with some knowledge of the pedigree of individuals and of the environmental conditions, such datasets can also be used to quantify how much of the variation in individual phenotypes and group structures is associated with additive genetic variation (G_z , G_y), as opposed to how much phenotypic variation arises from environmental factors, to estimate indirect genetic effects, and to compute individual breeding values (a , a , [71,95,96]).

Concluding Remarks

The group, community, or population phenotypic composition has both pervasive consequences for individual fitness and fascinating evolutionary implications. GPC has the potential to shape many attributes of individual phenotypes and/or the distribution of phenotypes in populations. Importantly, understanding what drives the evolutionary implications of GPC requires not only quantifying how GPC affects individual performance (i.e., estimating **selection gradients**) but also considering the patterns of phenotypic covariance within groups (or aggregations at other levels). Another key aspect to studying the impact of phenotypic variation is to quantify the extent to which individuals and those they interact with modulate each other's behaviours. How this underpins phenotypic covariance is rarely studied. A fascinating area for further theoretical and empirical research is the idea that these parameters can evolve (or co-evolve), and this could potentially have profound effects on the dynamics of phenotypic adaptation. We emphasise the urgent need for theory to be expanded to support empirical research, and the need for future research that is tightly focused on the mechanisms determining the formation of groups in terms of individual phenotypes and group composition (for example, do groups reflect the underlying distribution of individuals in the wider population, or do individuals actively choose groups according to phenotypic composition?). We further emphasise the need for theoretical advances in understanding the co-evolution or co-dependence of group composition with the expression or value of individual phenotypes (through indirect effects). The study of the selective consequences and evolutionary outcomes of GPC is an area of increasing interest across a breadth of research areas. It will continue to be an exciting area of research, with potential to contribute to many classical questions in ecology and evolution.

Outstanding Questions – The Evolutionary Implications of GPC

A key challenge in answering key questions in many disciplines is to analyse both the effects of group composition on group outcomes and the effect of group outcomes for group composition [(i) and (ii), respectively].

Foraging

- (i) How do interference competition, foraging tactics, and facilitation determine the relative foraging success of different phenotypes in the group?
- (ii) How do different phenotypes resolve conflicts of interest in forming or maintaining GPC?

Niche Partitioning

- (i) Do particular individuals control GPC, or does GPC emerge from a shared process determined by existing niche preferences? What ecological conditions favour phenotypic segregation (or mixing) via niche preferences versus niche construction?
- (ii) Can selection emerging from GPC lead to phenotypic segregation and ultimately the divergence of new species? Or maintain phenotypic variation in the species?

Predator–Prey (or Host–Parasite) Interactions

- (i) How does GPC in prey and predators affect synchronisation between predator–prey dynamics?
- (ii) How do predator–prey dynamics impact on GPC within species?

Altruism and Eusociality

- (i) How does the mix of cooperators and defectors affect group dynamics? How does colony caste composition affect its performance?
- (ii) How do group dynamics favour the evolution of cooperation? Do particular caste compositions favour further division of labour among colony members?

Collective Decision-Making and Collective Movement

- (i) Do groups with particular GPCs make better decisions, and under what conditions?
- (ii) How does GPC affect the evolution of leaders and followers?

Mating Systems

- (i) Does GPC determine the mating systems?
- (ii) How do mating systems maintain variation in sexually selected traits (e.g., lek paradox)?

Population and Community Dynamics

- (i) Does the GPC of a population determine its ability to respond to environmental change?
- (ii) When does GPC lead to spatial segregation of similar phenotypes or favour overdispersed phenotypic distributions?

Acknowledgments

The authors thank Lucy Aplin, Meg Crofoot, Grace Davis, Simon Garnier, Charles Goodnight, Allison Jones, Allen Moore, Jonathan Pruitt, Raphael Royauté, Ben Sheldon, Andrew Sih, Paul Smaldino, Ariana Strandburg-Peshkin, Kelly Weiner-smith, Tina Wey, Jason Wolf, and the Human Behavioral Ecology Group at UC Davis for insightful discussions or comments on the manuscript. We also thank three anonymous reviewers for constructive comments on the manuscript. D.R.F. was supported by grants from the National Science Foundation (NSF-IOS 1250895) awarded to Margaret C. Crofoot and the Biotechnology and Biological Sciences Research Council (BBSRC: BB/L006081/1) awarded to Ben C. Sheldon. P.O.M. was funded by a Fonds Québécois Recherche Nature et Technologie fellowship. O.S. was supported by a grant from the NSF awarded to Andrew Sih (NSF-DEB 1456730).

References

1. Landeau, L. and Terborgh, J. (1986) Oddity and the confusion effect in predation. *Anim. Behav.* 34, 1372–1380
2. Rodgers, G.M. *et al.* (2015) Prey body size mediates the predation risk associated with being 'odd'. *Behav. Ecol.* 26, 242–246
3. Goodnight, C.J. *et al.* (1992) Contextual analysis of models of group selection, soft selection, hard selection, and the evolution of altruism. *Am. Nat.* 140, 743–761
4. Wolf, J.B. *et al.* (1999) Interacting phenotypes and the evolutionary process. II. Selection resulting from social interactions. *Am. Nat.* 153, 254–266
5. Moore, A.J. *et al.* (1997) Interacting phenotypes and the evolutionary process. 1. Direct and indirect genetic effects of social interactions. *Evolution* 51, 1352–1362
6. Hodgkin, L.K. *et al.* (2014) Leaders benefit followers in the collective movement of a social sawfly. *Proc. Biol. Sci.* 281, 20141700

7. Nagy, M. *et al.* (2010) Hierarchical group dynamics in pigeon flocks. *Nature* 464, 890–U899
8. Aplin, L.M. *et al.* (2014) Individual-level personality influences social foraging and collective behaviour in wild birds. *Proc. Biol. Sci.* 281, 20141016
9. Nonacs, P. and Kapheim, K.M. (2007) Social heterosis and the maintenance of genetic diversity. *J. Evol. Biol.* 20, 2253–2265
10. McGlothlin, J.W. *et al.* (2010) Interacting phenotypes and the evolutionary process. III. Social Evolution. *Evolution* 64, 2558–2574
11. Brown, C. and Irving, E. (2014) Individual personality traits influence group exploration in a feral guppy population. *Behav. Ecol.* 25, 95–101
12. Smaldino, P.E. (2014) The cultural evolution of emergent group-level traits. *Behav. Brain Sci.* 37, 243–254
13. Eldakar, O.T. *et al.* (2009) Aggressive mating as a tragedy of the commons in the water strider *Aquarius remigis*. *Behav. Ecol. Sociobiol.* 64, 25–33
14. Frank, S.A. (1997) The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis. *Evolution* 51, 1712–1729
15. Eldakar, O.T. and Gallup, A.C. (2011) The group-level consequences of sexual conflict in multigroup populations. *PLoS ONE* 6, e26451
16. Grubb, T.C. (1987) Changes in the flocking behavior of wintering English titmice with time, weather and supplementary food. *Anim. Behav.* 35, 794–806
17. Simpson, G.G. (1953) The Baldwin effect. *Evolution* 7, 110–117
18. Wilson, A.J. *et al.* (2011) Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, *Cervus elaphus*. *J. Evol. Biol.* 24, 772–783
19. Odling-Smee, F.J. *et al.* (2003) *Niche Construction: The Neglected Process in Evolution*, Princeton University Press
20. Saltz, J.B. and Nuzhdin, S.V. (2014) Genetic variation in niche construction: implications for development and evolutionary genetics. *Trends Ecol. Evol.* 29, 8–14
21. Chenoweth, S.F. *et al.* (2010) Experimental evidence for the evolution of indirect genetic effects: changes in the interaction effect coefficient, ψ , due to sexual selection. *Evolution* 64, 1849–1856
22. Wolf, M. *et al.* (2011) On the coevolution of social responsiveness and behavioural consistency. *Proc. Biol. Sci.* 278, 440–448
23. Kazancioglu, E. *et al.* (2012) The evolution of social interactions changes predictions about interacting phenotypes. *Evolution* 66, 2056–2064
24. Dyer, J.R.G. *et al.* (2009) Shoal composition determines foraging success in the guppy. *Behav. Ecol.* 20, 165–171
25. Laskowski, K.L. and Bell, A.M. (2014) Strong personalities, not social niches, drive individual differences in social behaviours in sticklebacks. *Anim. Behav.* 90, 287–295
26. Pruitt, J.N. and Riechert, S.E. (2011) How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proc. Biol. Sci.* 278, 1209–1215
27. Cole, E.F. *et al.* (2011) Individual variation in spontaneous problem-solving performance among wild great tits. *Anim. Behav.* 81, 491–498
28. Aplin, L.M. *et al.* (2013) Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Anim. Behav.* 85, 1225–1232
29. Araújo, M.S. *et al.* (2011) The ecological causes of individual specialisation. *Ecol. Lett.* 14, 948–958
30. Farine, D.R. *et al.* (2015) The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds. *R. Soc. Open Sci.* 2, 150057
31. Magrath, R.D. and Bennett, T.H. (2012) A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring hetero-specifics. *Proc. Biol. Sci.* 279, 902–909
32. Spiegel, O. *et al.* (2013) Factors influencing foraging search efficiency: why do scarce lappet-faced vultures outperform ubiquitous white-backed vultures? *Am. Nat.* 181, E102–E115
33. Farine, D.R. *et al.* (2015) Interspecific social networks promote information transmission in wild songbirds. *Proc. Biol. Sci.* 282, 20142804
34. Morand-Ferron, J. and Quinn, J.L. (2011) Larger groups of passerines are more efficient problem solvers in the wild. *Proc. Natl. Acad. Sci. U.S.A.* 108, 15898–15903
35. McMahon, K. *et al.* (2014) Dietary wariness influences the response of foraging birds to competitors. *Anim. Behav.* 89, 63–69
36. Bolnick, D.I. *et al.* (2011) Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26, 183–192
37. Kobler, A. *et al.* (2009) Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia* 161, 837–847
38. Wolf, N.G. (1985) Odd fish abandon mixed-species groups when threatened. *Behav. Ecol. Sociobiol.* 17, 47–52
39. Paleolog, J. (2009) Behavioural characteristics of honey bee (*Apis mellifera*) colonies containing mix of workers of divergent behavioural traits. *Anim. Sci. Pap. Rep.* 27, 237–248
40. Anderson, R.M. and May, R.M. (1992) *Infectious Diseases of Humans; Dynamics and Control*, Oxford University Press
41. Lloyd-Smith, J.O. *et al.* (2005) Superspreading and the effect of individual variation on disease emergence. *Nature* 438, 355–359
42. Paull, S.H. *et al.* (2012) From superspreaders to disease hotspots: linking transmission across hosts and space. *Front. Ecol. Environ.* 10, 75–82
43. Shykoff, J.A. and Schmidhempel, P. (1991) Parasites and the advantage of genetic-variability within social insect colonies. *Proc. Biol. Sci.* 243, 55–58
44. Hamilton, W.D. (1964) Genetical evolution of social behaviour I. *J. Theor. Biol.* 7, 1–16
45. LeBoeuf, A.C. and Grozinger, C.M. (2014) Me and we: the interplay between individual and group behavioral variation in social collectives. *Curr. Opin. Insect Sci.* 5, 16–24
46. Modlmeier, A.P. and Foitzik, S. (2011) Productivity increases with variation in aggression among group members in *Ternothorax* ants. *Behav. Ecol.* 22, 1026–1032
47. Scharf, I. *et al.* (2012) Characterizing the collective personality of ant societies: aggressive colonies do not abandon their home. *PLoS ONE* 7, e33314
48. Ross, K.G. and Keller, L. (2002) Experimental conversion of colony social organization by manipulation of worker genotype composition in fire ants (*Solenopsis invicta*). *Behav. Ecol. Sociobiol.* 51, 287–295
49. Hoover, S.E.R. *et al.* (2005) Retinue attraction and ovary activation: responses of wild type and anarchistic honey bees (*Apis mellifera*) to queen and brood pheromones. *Behav. Ecol. Sociobiol.* 59, 278–284
50. Pruitt, J.N. and Ferrari, M.C.O. (2011) Intraspecific trait variants determine the nature of interspecific interactions in a habitat-forming species. *Ecology* 92, 1902–1908
51. Pruitt, J.N. and Goodnight, C.J. (2014) Site-specific group selection drives locally adapted group compositions. *Nature* 514, 359–362
52. Couzin, I.D. and Krause, J. (2003) Self-organization and collective behavior in vertebrates. *Adv. Study Behav.* 32, 1–75
53. Simons, A.M. (2004) Many wrongs: the advantage of group navigation. *Trends Ecol. Evol.* 19, 453–455
54. Couzin, I.D. *et al.* (2011) Uninformed individuals promote democratic consensus in animal groups. *Science* 334, 1578–1580
55. Couzin, I.D. *et al.* (2005) Effective leadership and decision-making in animal groups on the move. *Nature* 433, 513–516
56. Flack, A. *et al.* (2012) What are leaders made of? The role of individual experience in determining leader-follower relations in homing pigeons. *Anim. Behav.* 83, 703–709
57. Brent, L.J.N. *et al.* (2015) Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Curr. Biol.* 25, 746–750
58. Aplin, L.M. *et al.* (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* 518, 538–541

59. Mueller, T. *et al.* (2013) Social learning of migratory performance. *Science* 341, 999–1002
60. Maynard-Smith, J. (1982) *Evolution and the Theory of Games*, Cambridge University Press
61. Sih, A. and Watters, J.V. (2005) The mix matters: behavioural types and group dynamics in water striders. *Behaviour* 142, 1417–1431
62. Both, C. *et al.* (2005) Pairs of extreme avian personalities have highest reproductive success. *J. Anim. Ecol.* 74, 667–674
63. Schurch, R. *et al.* (2010) The building-up of social relationships: behavioural types, social networks and cooperative breeding in a cichlid. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 365, 4089–4098
64. Chitty, D. (1967) The natural selection of self-regulatory behaviour in animal populations. *Proc. Ecol. Soc. Aust.* 2, 51–78
65. Pelletier, F. *et al.* (2007) The evolutionary demography of ecological change: linking trait variation and population growth. *Science* 315, 1571–1574
66. Ezard, T.H.G. *et al.* (2009) Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 364, 1491–1498
67. Pelletier, F. and Garant, D. (2012) The population consequences of individual variation in behaviour. In *Behavioural Responses to a Changing World: Mechanisms and Consequences* (Candolin, U. and Wong, B.M., eds), pp. 159–174, Oxford University Press
68. Fussmann, G.F. *et al.* (2007) Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.* 21, 465–477
69. Pruitt, J.N. *et al.* (2012) Iterative evolution of increased behavioral variation characterizes the transition to sociality in spiders and proves advantageous. *Am. Nat.* 180, 496–510
70. Falconer, D.S. and Mackay, T.F.C. (1995) *Introduction to Quantitative Genetics*, Longman
71. Lynch, M. and Walsh, B. (1998) *Genetics and Analysis of Quantitative Traits*, Sinauer Associates
72. Pruitt, J.N. and Riechert, S.E. (2011) Within-group behavioral variation promotes biased task performance and the emergence of a defensive caste in a social spider. *Behav. Ecol. Sociobiol.* 65, 1055–1060
73. Pruitt, J.N. *et al.* (2010) Population differences in behaviour are explained by shared within-population trait correlations. *J. Evol. Biol.* 23, 748–756
74. Pruitt, J.N. *et al.* (2013) Linking levels of personality: personalities of the 'average' and 'most extreme' group members predict colony-level personality. *Anim. Behav.* 86, 391–399
75. Keiser, C.N. *et al.* (2014) Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. *Behav. Ecol. Sociobiol.* 68, 839–850
76. Grinsted, L. *et al.* (2013) Individual personalities shape task differentiation in a social spider. *Proc. Biol. Sci.* 280, 20131407
77. Keiser, C.N. and Pruitt, J.N. (2014) Personality composition is more important than group size in determining collective foraging behaviour in the wild. *Proc. Biol. Sci.* 281, 2014281
78. Pruitt, J.N. (2012) Behavioural traits of colony founders affect the life history of their colonies. *Ecol. Lett.* 15, 1026–1032
79. Pruitt, J.N. and Keiser, C.N. (2014) The personality types of key catalytic individuals shape colonies' collective behaviour and success. *Anim. Behav.* 93, 87–95
80. Keiser, C.N. and Pruitt, J.N. (2014) Spider aggressiveness determines the bidirectional consequences of host–inquinine interactions. *Behav. Ecol.* 25, 142–151
81. Daily, G.C. *et al.* (1993) Double keystone bird in a keystone species complex. *Proc. Natl. Acad. Sci. U.S.A.* 90, 592–594
82. Farine, D.R. *et al.* (2012) Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Anim. Behav.* 84, 1271–1277
83. Maldonado-Coelho, M. and Marini, M.A. (2004) Mixed-species bird flocks from Brazilian Atlantic forest: the effects of forest fragmentation and seasonality on their size, richness and stability. *Biol. Conserv.* 116, 19–26
84. Diamond, J.M. (1975) Assembly of species communities. In *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 342–444, Harvard University Press
85. Dolby, A.S. and Grubb, T.C. (1999) Functional roles in mixed-species foraging flocks: a field manipulation. *Auk* 116, 557–559
86. Dolby, A.S. and Grubb, T.C. (2000) Social context affects risk taking by a satellite species in a mixed-species foraging group. *Behav. Ecol.* 11, 110–114
87. Dolby, A.S. and Grubb, T.C. (1998) Benefits to satellite members in mixed-species foraging groups: an experimental analysis. *Anim. Behav.* 56, 501–509
88. Buckley, N.J. (1996) Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. *Auk* 113, 473–488
89. Lande, R. and Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution* 37, 1210–1226
90. Arnold, S.J. and Wade, M.J. (1984) On the measurement of natural and sexual selection – theory. *Evolution* 38, 709–719
91. Bolker, B.M. *et al.* (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135
92. Dingemanse, N.J. and Dochtermann, N.A. (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.* 82, 39–54
93. Dingemanse, N.J. *et al.* (2010) Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* 25, 81–89
94. McGlothlin, J.W. and Brodie, E.D. (2009) How to measure indirect genetic effects: the congruence of trait-based and variance-partitioning approaches. *Evolution* 63, 1785–1795
95. Kruuk, L.E.B. (2004) Estimating genetic parameters in natural populations using the 'animal model'. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 359, 873–890
96. Wilson, A.J. *et al.* (2010) An ecologist's guide to the animal model. *J. Anim. Ecol.* 79, 13–26