# Physiological performance curves may shape environmental effects on social behaviour

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## ABSTRACT

As individual animals are exposed to varying environmental conditions, phenotypic plasticity will occur in a vast array of physiological traits. For example, shifts in factors such as temperature and oxygen availability can affect the energy demand, cardiovascular system, and neuromuscular function of animals that in turn impact individual behaviour. Here, we argue that non-linear changes in the physiological traits and performance of animals across environmental gradients - known as physiological performance curves - may have wide-ranging effects on the behaviour of individual social group members and the functioning of animal social groups as a whole. Previous work has demonstrated how variation between individuals can have profound implications for socially living animals, as well as how environmental conditions affect social behaviour. However, the importance of variation between individuals in how they respond to environmental conditions has so far been largely overlooked in the context of animal social behaviour. First, we consider the broad effects that individual variation in performance curves may have on the behaviour of socially living animals, including changes in the rank order of performance capacity among group mates across environments, environment-dependent changes in the amount of among- and within-individual variation, and differences among group members in terms of the environmental optima, the critical environmental limits, and the peak capacity and breath of performance. We then consider the ecological implications of these effects for a range of socially mediated phenomena, including social foraging, within-group conflict, collective movement, within- and among group assortment, disease and parasite transfer, and predator-prey interactions. We end by outlining the empirical work required to test the implications for physiological performance curves in social behaviour.

## INTRODUCTION

Within species there exists considerable among-individual variation in numerous physiological traits associated with energy demand (Burton et al., 2011; Metcalfe et al., 2016a), cardiorespiratory systems (Brijs et al., 2019; Walsberg et al., 1986), and neuromuscular function and movement (Marras et al., 2010; Wilson et al., 2004). A major aim in the field of ecophysiology is to understand how these traits are linked with organismal performance and behaviour in an ecological context, including the ability to escape predators and obtain resources (Jablonszky et al., 2017; Killen et al., 2017a; Mathot et al., 2017). More recently, there has been growing interest in how among-individual heterogeneity in physiological traits can modulate animal social behaviour, including social hierarchies (Kochhann, 2017), social networks (Moyers et al., 2018), and emergent collective behaviour (Jolles et al., 2017; Jolles et al., 2020).

Social grouping ranges from pairs of animals to large scale communities and enormous aggregations consisting of millions of individuals. Variation in this tendency to group, both at the individual and species level, can be explained by the balance between the benefits of reducing predation risk, improving foraging and saving energy during locomotion, versus the costs of competition within groups over food and the opportunity to breed, and a greater exposure to socially-transmitted diseases. These benefits and costs can be shifted, however, by individuals' behaviour within groups, with effects on social interactions and group functioning (del Mar Delgado et al., 2018; Jolles et al., 2017). However, increasing evidence suggests that social behaviour is also related to physiological traits associated with metabolic phenotype (Cooper et al., 2018; Killen et al., 2017b), stress responsiveness (Spencer, 2017), cognition (Wascher et al., 2018), locomotor performance and speed (Hansen et al., 2020; Jolles et al., 2017), and immune function (Raulo et al., 2018). Physiological traits associated with bioenergetics and locomotion may be especially important in this regard, because they are sensitive to environmental factors and can also influence performance in a social context, affecting both the capacity and motivation to express various behaviours. Metabolic rate, for example, has been linked with dominance and risk-prone behaviours (Mathot et al., 2019), which in turn have links with individual sociability (Jolles et al., 2017). There is also evidence of direct links between metabolic demand and sociability, with individuals with a higher metabolic rate being perhaps less social and therefore less likely to associate with conspecifics (Cooper et al., 2018; Killen et al., 2016b; but see Killen et al., 2021).

Social interactions can be influenced by environmental factors such as food abundance and potential predation risk (Beauchamp, 2004; Schaerf et al., 2017), but also by many aspects of the abiotic environment, including light levels (Ginnaw et al., 2020), temperature (Bartolini *et al.*, 2015), hypoxia (Domenici et al., 2017), turbidity (Chamberlain and Ioannou, 2019), and habitat structure (Takada and Minami, 2021), and by anthropogenic changes such as acoustic noise (Currie et al., 2020), and pollutants (Armstrong et al., 2011). While environmental factors can impact behaviour through the masking of cues and signals (McNett et al., 2010) and shifting attention to other tasks (Chan et al., 2010), environmental conditions can also affect behaviour via physiological changes. The effects of environmental variables on social behaviour via physiological changes can be indirect by inducing stress via stress hormones, or can directly affect the physiological traits associated with locomotor performance and movement speed, such as muscular function and aerobic and anaerobic capacity (Ord and Stamps, 2017). As movement speed plays a fundamental role in leadership, cohesion, and alignment (Pettit et al., 2015; Jolles et al., 2020b), these aspects of social behaviour may be sensitive to environmental perturbations. Hence, the ways in which physiological traits influence social behaviour, as well as the degree of among-individual trait variation and trait repeatability (Huang et al., 2020), may also vary with the environment (Killen et al., 2016a). These effects of environmental conditions on social behaviour are becoming increasingly important to understand due to human-induced rapid environmental change (Barrett et al., 2019; Fisher et al., 2021; Sih, 2013).

Breakthroughs in our understanding of the mechanistic underpinnings of sociality could be facilitated by studying the effects of individual performance curves on social dynamics. Performance curves depict shifts in physiological performance across the gradient of a continuous environmental variable. Such curves are generally determined for specific physiological traits or performance indices, such as maximum locomotor speed or aerobic capacity, with performance defined as the capacity to express a given trait across a range of environmental conditions. Performance curves are usually non-linear – though they may appear linear within narrow environmental ranges – with their exact shape depending on the trait and environmental variable being considered (Kingsolver et al., 2014) (Figure 1A). As an example, in ectotherms a typical performance curve for maximum locomotor speed would be a gradual increase with temperature, a peak level of performance at an optimal temperature, followed by a decline in performance capacity with further warming (yellow line in Figure 1A). It is important to note that performance curves are informationally richer and arguably more ecologically relevant than reaction norms, which are assumed to be linear in nature (Kingsolver et al., 2014). Performance curves often depict the change of a physiological trait in response to the environment and can therefore reflect environmental sensitivity (Jutfelt et al., 2018; Kingsolver and Gomulkiewicz, 2003; Lefevre, 2016). This sensitivity may, in turn, affect the capacity or motivation to perform specific behaviours, but these links are often uncertain and the focus of study to provide insight into intra- and intergenerational responses to environmental stressors (Metcalfe et al., 2016b; Norin and Metcalfe, 2019).

Here we argue that performance curves, and especially individual variation in performance curves within groups (Figure 1B), may be key in understanding how social behaviours are affected by shifting environmental conditions. In their natural environment, socially grouping animals can experience environmental changes at a scale of minutes, days, or months, but will also experience environmental changes over more protracted timeframes in response to broadscale phenomena such as climate change. For example, many animal species accommodate seasonal changes in temperature that are consistent across years, but due to human-induced climate change, such changes are becoming more extreme (IPCC, 2012). A more mechanistic, physiologically-based approach to the study of social behaviour will be key for understanding both how routine environmental shifts affect social behaviours as well as understand and predict how social behaviour may change or evolve in response to anthropogenic disturbances.

The study of animal social systems and particularly the study of collective behaviour has transitioned from a focus on uncovering universal mechanisms underpinning emergent behaviour and self-organisation (Couzin et al., 2002), to an increasing recognition that among-individual heterogeneity plays a critical role in these processes (del Mar Delgado et al., 2018; Jolles et al., 2020). We suggest that a promising next step in this line of research will be to examine how the degree of heterogeneity *itself* can change depending on the environment -- as is dictated by individual performance curves -- and how this will influence various dimensions of animal social behaviour. We first discuss the broad effects that individual variation in performance curves within social groups may have on the relative physiological capacity and behavioural motivation of individuals within social groups. Next, we discuss the specific consequences of these effects for an array of ecological phenomena related to social behaviour including within-group conflict, leader-follower dynamics, predator avoidance, and social foraging. Our aim is to highlight the enormous potential for performance curves to alter social behaviour at the individual, group, and community level and outline priority areas for future research.

## INDIVIDUAL VARIATION IN PERFORMANCE CURVES

A key factor to consider when assessing the impact of performance curves on social behaviour is among-individual variation in how animals physiologically respond to changes in their environment (Bulté and Blouin-Demers, 2006). For example, different individuals can show different physiological sensitivities to factors such as temperature (Navas et al., 1999), or requirements in terms of oxygen (Killen et al., 2012b; Pang et al., 2015) or nutrition (Killen et al., 2011), with direct effects on among-individual variation in bioenergetics and capacity for locomotor performance. Such variation has traditionally been examined in the context of reaction norms whereby individuals are repeatedly measured for traits at around 2 or 3 environmental levels and modelled using mixed-models with random slopes (Dingemanse et al., 2010). However, assumptions of linearity may not be appropriate for all traits and particularly over broader environmental ranges. Therefore, to properly assess intra-individual variation in environmental sensitivity, the assessment of individual performance curves may be required (Gilbert and Miles, 2017). This work is still in its infancy, but investigations to date indicate that, similar to the case with linear reaction norms (Roche et al., 2016; van de Pol, 2012), individuals within species show variation in performance curves (Bartheld et al., 2017; Careau et al., 2014; Childress and Letcher, 2017; Nowakowski et al., 2020). There is also evidence that there may be within-individual variation in performance curves, in response to factors such as recent feeding history (Gilbert and Miles, 2016), which adds an extra layer of complexity.

If individual animals show variable degrees of behavioural and physiological plasticity in response to environmental variables, this has a wide range of potential consequences for social behaviour. To illustrate this, consider among-individual variability in performance curves for a physiological trait (e.g. aerobic capacity, movement speed) relevant to social behaviour, in relation to some environmental variable (e.g. temperature; Figure 1B; (van Berkum, 1988)). There are numerous effects that emerge from individual variation in environmental sensitivity that could have important consequences for how individuals interact with each other within social groups, which we discuss in detail below. Important to consider for any of these effects is the influence of acclimation to environmental conditions. During acute environmental changes, such as in temperature or oxygenation, individual animals tend to show much stronger changes in the expression of their physiology or behaviour (Guderley, 1990). These responses generally dampen with physiological acclimation to the new conditions, resulting in an overall “flattening” of the performance curve. Depending on the acclimation response of each individual groupmate and on the timescale of exposure to a given environment, the relative importance of each of the following considerations may change in prominence.

*Changes in the rank order of performance capacity*

Differences in sensitivity to the environmental variable in question may generate differences in the rank order of performance capacity among individuals within a social group, that directly depends on where along the environmental gradient performance is being measured (Figure 2). All else being equal, differences in this rank order could mean that, for example, the individual most likely to be dominant or a leader at one temperature may be subordinate or a follower at another temperature. Aside from having a direct effect on the social behaviour displayed by individuals, changes in trait rank order will also decrease trait repeatability and, potentially, the ability of that trait to be a target for selection in a social context. Another key consideration is that, if relative differences in energy demand (related to food-acquisition) or locomotor ability (related to predator avoidance) change among individuals, then the fundamental costs and benefits of sociality and group membership could change differently for individual group members depending on the current environmental conditions (Cooper et al., 2018). For example, if an individual has a relatively low energy demand (mediated via metabolic rate) or reduced escape performance at a low temperature, it may be more motivated to remain with its social group under these conditions. If the group moves to a warmer environment, however, that same individual may become less social and shift to a more independent foraging strategy, due to increased escape ability (via increased muscle contractile ability and nervous stimulation at warmer temperatures (Johnson and Bennett, 1995)) and decreased motivation to share or compete for discovered resources.

### *Change in among-individual variation*

As individual performance curves diverge or converge along the environmental gradient, the amount of phenotypic variation among individuals will correspondingly change. At a low temperature, for example, there may be a modest degree of among-individual variation in movement speed while at a higher temperature there may be wider variation (Killen et al., 2013) (Figure 3). This change in the degree of variation among-individual within a social group could have consequences for group coordination, cohesion, or intra-group conflict (Jolles et al., 2020). Changing environmental conditions and among-individual variation may therefore cause groups to split or merge, which in turn may increase the degree of phenotypic differences among groups. Importantly, changes in the amount of among-individual variation are fundamental in exposing traits to selective pressures in the social context (Farine et al., 2015).

### *Change in within-individual variation*

The effects of environmental conditions on variation among individuals may extend to physiological and behavioural flexibility within individuals. Depending on the environment, individuals may become more or less flexible in their behavioural expression. Physiological constraints at very low or high temperatures, for example, may limit the behavioural options available to individuals. At temperatures around their individual optimum, however, individuals should be less constrained and more able to express behaviour based on moment-to-moment changes in their motivation (Jolles et al., 2020) (Figure 4). Changes in within-individual variation along performance curves could also have consequences for the ability of natural selection to act on that trait, if there are changes in across- or within-context trait repeatability (Killen et al., 2016a).

*Among-individual differences in optimal environments*

Different individuals within a social group are likely to have different environmental conditions at which their individual performance is optimised (green and blue lines in Figure 5A). It is also possible that the environmental conditions selected by the individual (or the group as a whole) may have nothing to do with optimising their performance within a social group. For example, a group may choose to occupy a given location based solely on the availability of food or some other resource. In that case, the environmental conditions present at that point in space in time will determine how close each individual is operating to their individually optimal conditions and maximum capacity (Figure 5A and B). One possible consequence is that individuals may fit into vastly different social niches depending on the physiological constraints they end up facing within the group's chosen environment.

*Among-individual differences in peak performance regardless of optima*

Even if measured at their optimum environmental conditions, individual group members will show different absolute peak levels of performance (orange and purple lines in Figure 6). Individuals are likely to try and take advantage of an increased performance potential and consequently influence their behaviour and decision making within the context of the group. For example, an individual may choose to occupy a microhabitat within their group that brings that individual closer to its own peak performance capacity, or direct group movements to areas where that individual will derive an advantage due the local environmental conditions. For example, an individual that is relatively robust to variation in environmental oxygen availability (i.e. hypoxia; (Killen et al., 2012b)) could conceivably thrive socially in a moderately hypoxic environment if the competitive ability of its group-mates are reduced (although, the overall benefits of grouping for predator avoidance may decrease if overall group cohesion is impaired).

*Among-individual differences in performance breadth and critical limits*

Differences in performance curve shape may generate differences in the breadth over which individuals can function above particular thresholds of performance. For example, some individuals may be specialists (green individual in Figure 7A) and able to perform at a high level but only within a narrow environmental range, while others may be generalists (blue individual in Figure 7A) and able to perform over a wider range of environments but at a reduced absolute peak level of performance. The evidence for this trade-off between performance breadth and peak performance is however limited (Nati et al., 2016). There may also be among-individual differences in environmental tolerances of animals within a social group. Some individuals may simply be incapable of occupying the same environments as their conspecifics and even before this extreme point, have a sharper decline in performance (green and purple individual in Figure 7B). This variation in the breadth of environmental tolerance and critical thresholds for performance or survival should limit the habitats or environmental “options" available to groups with wide individual variation in such thresholds and may promote among-group assortment.

## EFFECT ON SOCIAL INTERACTIONS

### *Within-group competition and conflict*

Many social systems include dominance hierarchies, whereby individuals with greater resource holding potential have improved access to food, mates and/or other resources , and can often be found in locations within the group that reduce their risk of predation (Ward and Webster, 2016). Physiological traits are known to be important in the contests that establish dominance, as they correlate with competitive ability and also constrain the frequency, duration and intensity of contests, due to the build-up of lactic acid, for example, which limits anaerobic capacity (Briffa and Sneddon, 2007). A higher dominance status in contests has been shown to be associated with higher heart rate (Turbill et al., 2013), metabolic rate (Mccarthy, 2001), and aerobic scope (Killen et al., 2014). In turn, environmental variables can affect aggressive interactions via effects on physiology. For example, in cooler water, the cichlid fish *Cichlasoma paranaense* reduces aggressive interactions (Brandão et al., 2018), and the duration of fights between shore crabs (*Carcinus maenas)* is reduced in hypoxic conditions, associated with a greater accumulation of lactic acid during fights in hypoxia (Sneddon et al., 1998). Individuals experiencing cooler temperatures can compensate for reduced locomotor performance, however, through elevated aggression and be just as likely to win contests, as demonstrated in velvet geckos (*Oedura lesueurii*) (Kondo and Downes, 2007).

Although these previous studies have shown that environmental variables can affect average levels of antagonistic interactions, variation in performance curves suggests that differences between individuals in resource holding potential and other forms of competitive ability (e.g. the ability to detect food sooner than others) is plastic, being dependent on the prevailing environmental conditions. This may mean, for example, that under some environmental conditions, individuals are more closely matched in fighting ability, which tends to result in more frequent, longer, and more intense contests (Hack *et al.*, 1997; Schmitz & Baldassarre, 1992). Under other environmental conditions, differences in competitive ability between individuals may be magnified, resulting in clear winners, where contests are infrequent and easily won before they escalate. In cases where environmental changes over time are large enough to alter the rank order of physiological performance that determines dominance status, aggression may be more frequent and the dominance hierarchy less stable, which may explain changes in hierarchy stability with temperature (Kochhann *et al.*, 2015). Changes in dominance may also be delayed or may not occur at all if there are carryover effects whereby a dominant individual is more likely to stay dominant (Huber & Hock, 2009), even if the environmental conditions become less favourable for its own phenotype.

Also in groups without clear dominance hierarchies, more subtle forms of conflict can occur without obvious aggression. Groups often make decisions regarding when, where and how to move, which requires coordination to maintain cohesion of the group. Multiple sources of variation between individuals within groups, whether short-term and transient (Kerth et al., 2006) or long-term and consistent (Bevan et al., 2018), have the potential to result in conflict over these collective decisions that require consensus (Conradt, 2012). In contexts such as when behaviours should be performed, compromise can be reached; in others where behavioural decisions are mutually exclusive, such as where to travel to, compromise is not possible (Wade et al., 2020). In this latter case, the 'consensus costs' paid by individuals who do not get their preferred outcome should, on average, be higher than when compromise is possible (Conradt and Roper, 2009). If such consensus costs are too high relative to the benefit of remaining with the group, groups can split (Ioannou et al., 2015). As the extent of variation between individuals often determines the extent of conflicting preferences within groups, variation in physiological performance curves would mean that the degree of conflicting preferences will be sensitive to environmental conditions. When environmental conditions result in reduced variation between individuals in physiological performance, preferences should be similar and this reduced within-group conflict should result in fast decisions and more cohesive, coordinated groups. In contrast, if greater physiological differences result in conflicting preferences, decisions are predicted to be slower, and the group may change their decision more frequently or even split. For example, the speed of travel of a group can be determined by the physiological performance of the group members, and a consensus decision on that speed will be easier when preferred speeds, based on physiological performance capacities, are similar (Sankey et al., 2019). A potential, and somewhat paradoxical outcome, is that groups may be quicker to make consensus decisions in relatively harsh or extreme environments when performance capacity is limited or among-individual variation is constrained.

### *Social niches and social conformity*

While performance curves typically represent the maximum capacity that an individual has for a given physiological performance metric, individuals do not always opt to perform at their maximum capacity. This is partly because individuals within groups may need to coordinate behavior by either conforming to the group average or matching the behaviour of a particularly influential individual (Jolles et al., 2017; McCune et al., 2018). Alternatively, competition within groups can cause initial individual heterogeneity among group members to become amplified over time due to character displacement (the "social niche hypothesis"; Bergmüller and Taborsky, 2010; Montiglio et al., 2013, Jolles et al., 2020). Previous research has attempted to determine whether conformity or the social niche hypothesis is a larger driver of behavior within social groups (Munson et al., 2021), however, changes in the environmental context can either constrain or expose phenotypic variation such that behavioral conformity or differentiation within a group is more or less possible in different environments. For example, behaviors may appear to conform if interindividual variation in performance curves is low and there are limited differences in potential performance. Alternatively, social niche formation should be optimized in environments where the differences in performance curves are the highest because there are the greatest initial differences in individual capacity for behaviour.

If social dynamics influence behaviour to such an extent that individuals do not perform at their optimum across environmental contexts, then behavioral conformity and the formation of social niches could have important feedbacks that will affect responses to changing environments despite individual performance curves. If, even as the environment changes, individuals are constrained to behaving similarly (or dissimilarly) from other group members, the predicted changes in performance based on individual performance curves may not be evident. For example, if fish conform to slower individuals in a group that also do not change as rapidly in their swim speed in response to changes in the environment, then the whole group will be limited in how much they respond to changes in the environment. Similarly, behavioral conformity and social niche formation should limit acclimation to environmental change within an individual. Even if an individual's potential performance in one environmental context changes over time, they may not change their behavior if they are constrained to behaving similarly (or dissimilarly) from group members.

*Among and within-group assortment*

Animal groups are generally not randomly composed in nature, with individuals tending to assort according to various characteristics including body size, sex, age, or morphology (Jolles et al., 2020; Krause et al., 2000). Animals both assort at the among-group level, with different phenotypes occurring in different groups, and the within-group level, with individuals occupying different spatial locations according to their phenotype and/or non-randomly interacting with similar individuals within the group. Furthermore, animals assort both actively, with individuals selecting which individuals they associate with, or passively, with individuals exhibiting spatiotemporal overlap due to shared habitat selection or attraction to a resource (Killen et al., 2017b). The potential influence of individual metabolic traits and locomotor capacity on among- and within-group assortment have been discussed in depth elsewhere (Killen et al., 2017b), but there are a range of circumstances where performance curves could play a role in these processes.

As environmental conditions change, differences in individual performance curves could lead to an increase or decrease in within-group variation in performance capacity. For example, environmental conditions may increase group movement speed and thereby lead to more within-group spatial assortment, such as slower individuals occupying posterior positions within the group. This has been observed in fish schools, in which the flow of water increasingly leads to individuals with lower aerobic scope to occupy positions in the back of the group (Killen et al., 2012a). Such effects could be further amplified or reduced depending on interactions among multiple environmental factors, such as faster flowing water may carry more oxygen, which may thereby partly reduce assortment effects caused by the higher water flow. In contrast, an increase in water temperature may generate increased variation in locomotor capacity among group members and thereby enhance such assortment effects. In environments that produce greater amounts of variation among individuals within groups, groups may even split according to performance capacity, essentially leading to among-group assortment based on individual sensitivities to a particular environmental variable.

Among individual differences in environmental optima, tolerance breadths, or habitat preferences may also cause among-group assortment. For example, individual sensitivity to hypoxia stemming from performance curves may dictate which individuals occupy specific habitats or depths in aquatic environments (Joyce et al., 2016), and thus which conspecifics are available for them to interact with socially. Differences in energy requirements due to performance curves may also cause individuals to select different habitats and therefore spatially segregate (Michelangeli et al., 2018). Among-individual variation in changes in maintenance or active metabolism at different temperatures could cause individuals with a lower energy demand to select safer habitats, even if it means less access to food. Individuals with steeper increase in energy demand in response to temperature, however, may choose riskier habitats if it grants them increased access to food, and thereby group with individuals with a similar physiological and behavioural phenotype.

### *Leader/follower dynamics*

Choices in social group behaviour (e.g. movement or a feeding event) can be reached by egalitarianism where all individuals reach consensus, or can be initiated by one or few individuals (i.e. leaders) (Conradt and Roper, 2009). Leaders are only successful if followed by other group members, instigated voluntarily or as a result of hierarchical influence or dominance. Leaders in these groups often have better access to resources and make decisions for the group which may be at cost to others (King et al., 2008; although see

McComb et al., 2001). In self-organised moving groups, leadership has been shown to propagate from the front of the group (Bumann and Krause, 1993; Nagy et al., 2010). Front positions are thought to be occupied by individuals who have more information about the surrounding environment, a greater need for resources and motivation to locate preferable environments (Ioannou et al., 2015). The group members that successfully lead others and achieve their preferred outcome may be those with the highest physiological performance, for example those with the greatest aerobic capacity (Killen et al., 2012a) who can sustain more energetically-demanding positions or be better able to escape from attacks by predators, both costs of leadership associated with being at the front of moving groups (Ioannou et al., 2019). The ability to lead through spatial position or behavioural signalling could thus be constrained by physiological capacity, governed by an individual's performance curve.

What is particularly interesting when considering group movement and physiological performance curves is that group movement may result in substantial changes to the environment that individuals experience. Those with greater influence on group movement may lead the group to locations with environmental conditions that improves (either absolutely or relatively to others in the group) their physiological performance, which may reinforce their position as leader. On the other hand, leaders' preferred locations may be driven by factors other than their physiological performance, and due to inter-individual variation in physiological performance curves, a changed environment may shift which individual is most physiologically capable to lead subsequent group decisions. If groups are moving between locations which vary considerably in environmental parameters, individuals with narrower environmental tolerances may have the greatest motivation to lead, as they are likely to experience greater consensus costs if collective decisions take the group into locations of unpreferred environmental conditions. Additionally, other group members with wider tolerances may be less affected by environmental conditions, and may have less motivation to lead the group, despite potentially having a higher peak performance in changing environments. As the group encounters a less optimal environmental gradient then a leader's capacity to lead may decrease due to variation in environmental tolerance. Moreover, if individual capacity to lead changes with performance curves, individuals may be more influential in different environments and could cause a switch in leadership from one individual to another.

Alternatively, multiple individuals with similar performance curves could have the capacity to lead when experiencing a change in environment, causing a disruption to hierarchy and may lead to group splitting if the cost to staying with a group is too large (Ioannou et al., 2015). Considering these factors, we predict there may be complex feedbacks between environmental conditions, physiological performance and leadership in collective decision making due to inter-individual variation in physiological performance curves within groups.

### *Collective dynamics*

Collective patterns, including the speed, alignment, synchronization, and movement tendency of animal groups, emerge via self-organizing mechanisms from the behaviour and interactions of the individual group members (Couzin et al., 2002; Couzin and Krause, 2003). Hence, the phenotypic composition of groups, including the average behaviour of and heterogeneity among group members, and its change over time, may strongly impact on collective dynamics (del Mar Delgado et al., 2018; Jolles et al., 2020). Furthermore, changes in individual behaviour and the interactions among grouping individuals in response to their environment coincides with changes in group-level patterns (Schaerf et al., 2017). Both the movement speed and social responsiveness of individuals are strongly linked to a range of physiological characteristics that may change depending on the environment, and thereby impact collective dynamics. For example, at higher temperatures, ectothermic animals may have less aerobic scope available, reducing their optimal and preferred movement speed and in turn result in slower, but potentially more cohesive groups. Alternatively, temperatures colder than optimal may also increase cohesion if overall activity is reduced via effects on individual performance curves (Bartolini et al., 2015). Similarly, changes in oxygen availability may differently impact the muscular functioning of individuals and, by changes in movement speed, impact collective dynamics.

Importantly, if individuals are far from their performance optimum, this could negatively impact their social responsiveness as they may be less able to and/or motivated to cognitively focus on their group mates. If environmental conditions push groups further from their physiological optima, this could then result in less synchronised groups and potentially cause groups to break apart. In a similar way, differences in metabolic requirements may, across changing resource availability in the environment, cause relative changes in individuals' focus on goal-oriented versus socially-oriented movements (i.e. motivation to stay together) and thereby impact the cohesion, speed, and alignment of groups. In many cases, social responsiveness is affected by sensory input, such as the extent to which individuals can see each other, and conditions such as increased water turbidity or habitat complexity will require individuals to slow down and be more socially responsive to not break social contact. This in turn may actually provide more scope for individuals with different physiological optima or different breadths of performance curves to stay together. Finally, the limits of group members' physiological performance curves (or environmental tolerances) will determine how well they will be able to stay together and move across increasingly extreme conditions, as individuals may simply differ in the upper limits they can survive, such as in refuge pools of streams during extreme droughts.

### *Social learning and the spread of information*

Many animals rely on social learning as a shortcut for behaviours linked to predation avoidance, migration, foraging, and reproduction (Brown and Laland, 2003; Mueller et al., 2013). The efficiency and benefits of social learning may change across an environmental gradient because of changes in the transmission of information from demonstrators, and perception and processing of information from learners. Information is mainly transmitted via sensory signals (cues), perceived, and transduced via sensory organs and processed via neurological pathways. Variation in the transmission, perception and processing of information may arise from alteration of the sensory signals themselves, which may be disrupted directly by changes in the environment, such as acoustic cues masked by human noise pollution (Radford et al., 2014), or visual cues reduced by increased water turbidity (Nieman and Gray, 2019). Physiological changes across environments can also impact the perception and processing of cues, as well as indirectly by changes in group cohesion and coordination, which will influence how well information will spread within groups (MacGregor et al., 2020).

Although in extreme environments sensory organs may even be directly damaged, less dramatic changes may occur in response to environmental changes that lead to physiological effects and impact individual signaling and perception. An example is hormonal disruptions such as modification of melatonin rhythms in birds with variation in night lighting (Dominoni et al., 2020). Neural transmission, brain functioning, and cognition may also vary across an environmental gradient with impacts on social learning capacities. A well-known example is honey bees exposed to pesticides, which have reduced brain functioning (Klein et al., 2017) that may translate into a weaker ability to learn how to localize food from waggle dances (von Frisch, 2013). As with the development of social niches and leader and follower behaviours, greater within-group variation in individuals' physiological performance should favour more distinct demonstrator and learner roles, which can result in conflict over preferred group dynamics (MacGregor et al., 2020). Furthermore, variation in rank order across environments, such as a change in rank order of performance capacity at higher temperature (Figure 2), may result in a change in which individuals are demonstrators and which are learners. If relative changes in physiological performance and preferences promote a less stable group composition, reduced familiarity with the demonstrator and other individuals belonging to the group may affect the social transmission of information (Barrett et al., 2019; Hasenjager and Dugatkin, 2017).

Group-level behaviours and dynamics are likely to vary across environments (e.g. increased water temperature and hypoxia may decrease group cohesion in aquatic ectotherms), which can strongly affect how social information is transmitted (e.g. visual information, MacGregor et al., 2020). Any changes in group cohesion could in turn alter the potential for information transfer among groupmates due to changes in spatial distances among individuals and their ability to give and receive social cues (Pineda et al., 2020). In addition, the extent that individuals use social learning can be dependent on group behavioural composition. For example, using network-based diffusion analysis it has been found that, in guppies, social learning rate is higher in both bold and risk averse individuals when they are part of groups dominated by risk-averse individuals or mixed groups and there is a bold demonstrator (Hasenjager et al., 2020). Across gradients of environmental variation, among- and within-individual differences in behavioural expression in relation to performance curves may therefore lead to variation in social learning. If, across such gradients, the risks and benefits associated with social learning change (e.g. different reliability and efficiency of the transmission and perception of information within groups), non-optimal environments may lead to changes in social learning (e.g. I'Anson Price et al., 2019).

## EFFECTS ON THE COSTS AND BENEFITS OF GROUPING

### *Social foraging*

Individuals in groups can benefit by increased access to food sources and the potential to exploit food resources discovered by others, but grouping can also result in competition (Ranta et al., 1993). As discussed earlier when considering within-group conflict, differences in physiological performance can allow some individuals to have disproportionately greater access to food. When physiological performance curves differ between individuals, the variability in how food is distributed between individuals should be driven by variation in physiological performance under the current environmental conditions. This could favour less competitively able individuals to actively leave groups, and the reduction in group size to potentially impact foraging efficiency and anti-predator benefits experienced by those group members that remain (Krause & Ruxton, 2002).

Predicting the role of physiological performance curves on social foraging may be dependent on the feedback between individuals' physiological performance and changes in physiological state that occur during foraging. If the intake of food and time to satiation differs between individuals (Gifford et al., 2014; MacGregor et al., 2021), which could be determined by differences in physiological performance in the current environment, there may be conflict in the optimal time to stop foraging at that patch. If those with higher physiological performance have both faster food intake and greater influence over group decisions, then other individuals in the group will be less likely to forage for an adequate duration. This may act as a positive feedback which magnifies differences in physiological performance between individuals over the longer term. Because of variation in physiological performance curves, such a feedback would however be suppressed if foraging occurs under variable environmental conditions, favouring food intake of different individuals at different times.

Due to the metabolic cost of digestion (Norin and Clark, 2017), which can impact physiological traits such as locomotion (Dupont-Prinet et al., 2009), negative feedbacks are likely to influence the role of physiology during social foraging. In common minnows (*Phoxinus phoxinus*), individuals show consistent inter-individual differences in being at the front of a shoal and that this results in greater consumption of food (McLean et al., 2018). After feeding, however, individuals at the front would move toward the back of the shoal, explained by the reduction in aerobic metabolic scope from digestion (McLean et al., 2018). Satiated individuals may also reduce foraging and increase anti-predator vigilance to the benefit of others in the group (Arbon et al., 2020), dampening differences between individuals in food intake. Thus, both changing environmental conditions and inter-individual variation in physiological performance curves have potential to disrupt positive and negative feedback and thereby result in either a reduction or strengthening of inter-individual variation in food intake.

Feedbacks among physiological performance, environmental conditions and social behaviour can be informed by recent research exploring how individual differences based on state can drive behaviour, and how behaviour can in turn drive differences in state (i.e. state-behaviour feedbacks; Sih et al., 2015). Experimental tests with sticklebacks (*Gasterosteus aculeatus*) support the existence of feedbacks between risk-taking behaviour and satiation, but even in this relatively simple case, these studies show that these feedbacks are unpredictable, without strong evidence in favour of negative or positive feedbacks (MacGregor et al., 2021). This suggests that integrating feedbacks into the interaction between physiological performance curves and social foraging will be challenging. Simulation modelling based on assumptions and parameters that are empirically determined may thus be an essential tool in this endeavour.

While there is strong evidence that group living improves rates of finding and exploiting food sources (Cvikel et al., 2015; Ioannou, 2017), if individuals' performance during collective foraging is related to their performance in physiological traits, then physiological performance curves are likely to impact group-level performance in foraging. If groups are reliant on a small proportion of individuals to lead, for example those with information regarding the presence and location of food (Ioannou *et al.*, 2015), and the ability of these individuals to lead is positively associated with their physiological (e.g. locomotory) performance, group foraging success will be greatest when environmental conditions are optimal for leading individuals. In contrast, if foraging is dependent on pooling information from many individuals in the group, such as in many eusocial insect colonies (Detrain & Deneubourg, 2009), then environmental conditions which favour the greatest average physiological performance may maximise foraging success. The environmental conditions that optimise group performance in foraging may thus be dependent on whether influence on foraging performance is distributed between many individuals or a few.

### *Predator Avoidance*

Reduced predation risk has been proposed as one of the main drivers for why most animals live in social groups (Krause & Ruxton, 2002). Importantly, the environmental context may alter predation risk for grouping animals, both by affecting predator behaviour (Grigaltchik et al., 2012) as well as effects on group behaviour. For example, if in a particular environment, phenotypic variance is high due to among-individual variation in performance curves, this may result in less cohesive groups, potentially reducing the anti-predator benefits for those individuals (Sogard and Olla, 1997). Groups that are more cohesive with less phenotypic variance benefit from the confusion effect whereby visual predators have reduced targeting accuracy when prey are phenotypically homogenous (Jeschke and Tollrian, 2007). Because of this, phenotypically different individuals can experience increased risk of predation relative to their group mates (the oddity effect; Theodorakis, 1989). As individual behavior and group behavioral composition are important aspects of predator avoidance (Blake et al., 2018; Farine et al., 2015), this suggests that not only should groups differ in their anti-predator success across environments as performance curves converge and diverge, but that individuals may prefer different groups as environments change. Different individuals are affected by the oddity effect to different extents (Rodgers et al., 2015). For example, an individual with particularly high-performance capacity in a given environment may be less susceptible to predation than an individual who has a low performance capacity relative to its groupmates, especially if these differences in physiological capacity manifest in behavioural differences (e.g. activity level) that make them more of less obvious to predators. Thus, as environments change, there may be differences in group membership, as individuals opt to forego or receive the full anti-predator benefits of being in a group. Additionally, there may be important ramifications on group level success if group predator avoidance is influenced by a leader, and if the identity or influence of a leader changes across an environmental gradient due to variation in performance curves.

*Disease and parasite transfer*

Disease transfer and parasite load can both be affected by the environmental context (Aeby and Santavy, 2006) and by the social behavior of animals (Hawley et al., 2011). Social behavior can increase risk of disease and parasite transfer between individuals (Ezenwa, 2004), especially when groups are more cohesive because of the closer proximity between individuals. As group cohesion changes as a result of changes in phenotypic variance in performance curves, rates of disease and parasite transfer could also change. Furthermore, if changing environmental conditions affect optimal group membership due to changes in physiological performances and individuals then change groups, this can increase disease transfer between groups. Previous work suggests that increased space use relates to parasite load (Boyer et al., 2010) and that this can be influenced by the environmental context (Spiegel et al., 2015). If environmental conditions change more rapidly this could also result in decreased group stability and more rapid transfer of individuals (and their diseases) between groups as individuals spread out.

### *Migrations and range expansions*

Group movement occurs at different spatial and temporal scales. At small scales, within a population's distribution, group movement is generally driven by organisms' motivation and necessity to find resources or shelter. Such movements, from one resource patch to another or from one tree to the other for shelter, often relies on social interactions where the presence of more experienced individuals or with knowledge for specific information such as the location of food resources can guide naïve individuals or transmit the information to the other group members (Berdahl et al., 2018; Mueller et al., 2013). At a larger scale, movements are associated with migration or range expansion (Cote et al., 2017) and social interactions still have a central role. Indeed social interactions can improve the accuracy of group navigation (Berdahl et al., 2018; Simons, 2004) and reduces energy expenditures (Herskin and Steffensen, 1998; Marras et al., 2015). However, despite numerous advantages there are also potential costs to individuals associated with group movement, including coordination (Nagy et al., 2018) and consensus costs (Conradt and Roper, 2009) such as adjustment of individual performance to match the group performance and individual differences in lower or upper limits of physiological performance across environmental gradients (Figure 1, 7). Therefore, as groups move across various spatial scales and environments, environmental effects on performance curves will continuously modulate group functioning and performance of individuals within the group.

One response of organisms to unsuitable environmental conditions is to relocate into more favorable habitats. However, relocation is strictly linked to movement behaviour including group movement and to the ability to settle. If individual variation in performance curves affects group movement then reduced relocation opportunities may be expected under certain environments. For example, during drought, especially in mediterranean climates, parts of rivers dry up completely, requiring individuals within fish populations that live in the river to move to deeper safe refuges that do not dry up. In those conditions individual physiological and behavioural traits may be essential for group movement - see Box 1 for more details. However, not all individuals perform equally well in new environments and even if large scale movements occur, they may come at the cost of group re-arrangement.

## EXPERIMENTAL APPROACHES

While gaining a better understanding of the relationships between performance curves and social behavior is critically important in a changing world, these are not easy relationships to decipher. Ideally, we need performance data for individuals tested repeatedly across an environmental gradient and then in groups across the same range. Acquiring detailed data to be able to construct individual performance curves requires many repeated measures of the same individuals across a range of conditions of the same environmental variable. Accurate and precise estimates of individual variation in a reaction norm require relatively large sample sizes and each individual tested multiple times (Allegue et al., 2017; Martin et al., 2011; van de Pol, 2012). Estimating performance curves can be even more sample intensive, particularly because the important variation is typically greater in estimating higher order parameters associated with curve shape than for those associated with offset or slope (Murren et al., 2014). To then consider the social axis as we discuss here, the number of individuals required for a study will be even larger.

Still, these studies are possible, particularly with the advent of automated techniques and low cost open source electronics (Jolles, 2021). The general approach begins with measuring the same individuals repeatedly for a physiological trait and their behavior (e.g. locomotor capacity, temperature preference, spatial position) across a range of conditions (e.g. temperature, oxygen availability, turbidity) to construct individual performance curves. It is important to consider that, due to the large number of measurements required, not all traits can be easily investigated, especially those that are relatively invasive such as those relating to tissues or organ level physiological performance. Notedly, because lab studies often test animals when they are otherwise at relatively benign conditions, there have been recent calls to improve ecological relevance by confirming laboratory studies of performance curves with field data (Childress and Letcher, 2017). This may be particularly important when seeking to understand group behavior—the patterns of which are often the result of tradeoffs between individual foraging needs and the benefits of groups for predator protection—but it adds further methodological challenges.

After repeatedly measuring individual performance curves in isolation, animals should be assigned to groups. The method for group assignment should be considered carefully depending on the exact question being asked. For example, if researchers are interested in how performance in a given environmental context affects group assortment, animals should be allowed to assort themselves. However, if the question relates more to how groups manage performance of different individuals as conditions change, group assignment can be done by the experimenter. This also requires careful consideration such as whether to optimize the performance of all individuals, the performance of the group as a whole or the differences between individuals.

Additionally, experimenters will need to decide whether they are going to measure the performance of a few focal individuals or all individuals in the social groupings. Due to the time and work involved in collecting performance curves on each additional animal, this is a serious consideration. While measuring every individual in a group provides more information, it can functionally limit the number of groups that can reasonably be measured. Whether fewer individuals per group can be measured depends on the exact question being asked. Importantly, even if the ultimate question relates to individual performance, it may be important to construct performance curves for all individuals in a group if the question focuses on how the individual relates to group performance and whether the important metric is average group performance or individual rank. While this type of experiment can be time intensive, without a better understanding of how individual performance curves influence social behavior traits and group performance, we will be unable to adequately predict how animal groups respond to changing environmental conditions.

### Box 1. Methodological Case Study: Using performance curves and social dynamics to understand how fish deal with droughts

Many freshwater ecosystems are characterised by natural seasonal fluctuations of their water cycle, including droughts and floods (Lennox et al., 2019). Despite being an integral part of the ecosystem, droughts have strong impacts on fish and other aquatic biota by increases in water temperature, deoxygenation, and reducing habitat availability and connectivity by reductions in water flow (Magoulick and Kobza, 2003; Mas-Martí et al., 2010). In fluvial systems in particular, severe droughts can result in complete sections of rivers to dry up, confining fish to few refugia with very extreme abiotic conditions, intense competition, and high predation risk (Magoulick & Kobza, 2003). Physiological performance curves are likely to directly affect how individual fish cope with these strong environmental changes, but also indirectly through various social effects, whereby the responses and capabilities of individual animals to drought may be compromised or enhanced, influenced by the phenotypic composition of groups (see main text; Killen et al. 2017; Jolles et al., 2020). For example, fish more sensitive to temperature increases may be the first to leave areas that may dry up later and thereby could act as leaders that "rescue" individuals with broader performance curves and correspondingly wider thermal tolerances. It is also possible that, in pools with low oxygen availability and warm water, competitive interactions change considerably relative to non-drought conditions, putting individuals with narrower performance curves (e.g., in terms of aerobic scope) at risk.

To better understand the above types of scenarios in terms of how fish may deal with the severe effects of droughts, we first need to understand how individual fish cope with changes in their environment related to drought at both the behavioural and physiologic levels. To start, one could decide to focus on hypoxia linked to drought and determine the physiological performance curves in terms of metabolic capacity and activity change across decreasing oxygen levels. To do this, a replicated setup of 16 respirometry chambers could be used to measure the standard metabolic rate and aerobic scope of fish during acute exposure to various levels of oxygen availability observed in the wild, e.g., 100%, 75%, 50%, and 25% air saturation. Fish would be tested in a random order in terms of oxygen treatment to avoid temporal effects, and fish could be tested on alternative days to test two batches on following days. In that way it would be possible to test 32 fish on all four treatment levels in 8 days' time.

Physiological experiments could be complemented with automated behavioural experiments to determine how fish behaviourally respond to different levels of oxygenation, particularly spontaneous activity, air-breathing, and potential escape (longer directed movement) behaviour. For this, fish could be tested individually in medium-sized arenas, filled with water at a specific oxygen level and containing rocks and partitions to provide structure. A system of replicated setups could be used with automated recording (e.g. pirecorder) and tracking of the fishes' movements, such that all 32 fish could be tested on one treatment level per day (randomized).

After acquiring the individual measures, fish could be tested for social behaviour in larger arenas in small groups of different compositions in terms of their physiological performance. A range of different questions could be investigated, each requiring a different type of homo- and heterogenization. To start, one could focus on understanding the effects of individuals' breadth of performance curve in terms of metabolic phenotype on competitiveness in a social foraging scenario. Thereby groups, such as with a group size of 6 fish, could be composed of individuals with small and large performance breadths and exposed to an open arena with hidden foraging patches and repeatedly tested across the four oxygen treatment levels. Manual video observations will help determine the cumulative food intake of the individual fish with automated tracking linking this to changes in the individual movement and social interaction rules (see e.g. Jolles et al., 2017; McGregor et al., 2020). Additional experiments could be performed in which social trials are run at differing levels of hypoxia such that among-individual variation in performance capacity and behaviour could be manipulated according to each individual's performance curves, and the resulting effects on social behaviour observed.

With careful planning of the physiological and behavioural measurements, while properly accounting for acclimatisation and randomizing for order and treatment effects, it should be feasible, following the above, to get a sample size of 96 fish tested within 6-8 weeks. In the foraging experiment described above, the dataset would have 384 unique individual scores in terms of SMR, AS, individual activity, and social activity to determine individual physiological performance curves and heterogeneity therein as well as the effects of this heterogeneity on group functioning in terms of social foraging (at the baseline foraging condition, presumably at normoxia). Note that this experimental design only considered acute exposures to the various levels of oxygen availability. A study could also start with fish acclimated (for at least two weeks) to the various hypoxia treatments, but this would obviously increase the amount of time needed for the project if individual performance curves are to be constructed after acclimation and subsequent testing at each condition.

## CONCLUDING REMARKS

It is becoming increasingly clear that: 1) animal social behaviour is linked with the physiological performance capacity of individuals; and 2) physiological performance is strongly influenced by environmental factors. Accordingly, it is apparent that a research approach that involves estimation of performance curves is required to fully understand how environmental factors influence social behaviour. Conversely, the measurement of performance curves has been a central feature of the study of comparative physiology and ecophysiology during the last several decades, but in virtually all cases has only been applied to individual animals and devoid of any social context. As individual heterogeneity within groups is a known driver of leadership, conflict, cohesion and coordination, environmental effects on phenotypic variation should ultimately influence behaviours at the group level. As wild animals are being exposed to increasing environmental changes, an integration of physiological performance curves with the measurement of social behaviour will be key for understanding how such changes affect group living and associated ecological phenomena. We therefore encourage increased collaboration among ecophysiologists and researchers that investigate animal social behaviour to achieve a more complete understanding of how species will respond to environmental change.

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## AUTHOR CONTRIBUTIONS

SSK and CCI contributed to conception and design of the manuscript. DC, LC, JJ, and AM contributed to further idea development and refinement. SSK coordinated manuscript writing and compiled manuscript drafts; all authors drafted specific sections of the manuscript. SSK, DC, JJ, and CCI designed and produced figures with additional input from LC and AM. All authors contributed to manuscript revision, read, and approved the submitted version.

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## FIGURES

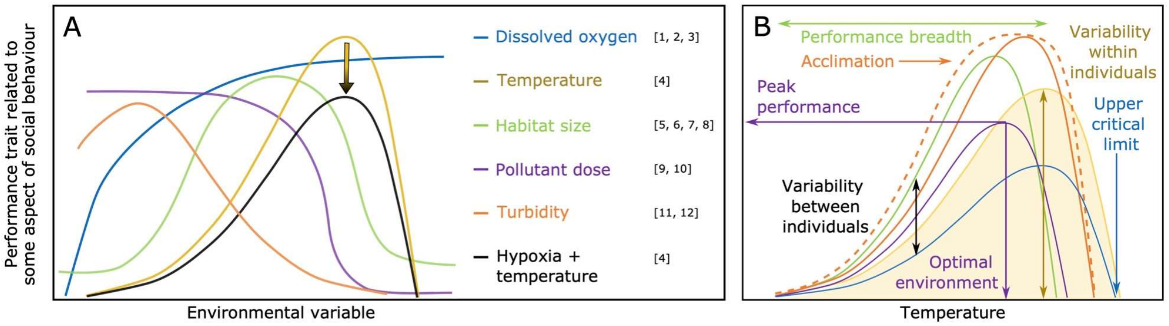

**Figure 1.** (A) Performance curve shape is heavily dependent on the environmental factor being examined. In this panel, different types of environmental factors are represented by different colours. The arrow represents an overall depression of trait expression when potential effects of hypoxia are combined with the effects of temperature. Note, when habitat size increases, greater protection/space to hide from predators and/or increase food availability may enhance performance, thus reducing endocrine stress level [6, 7]. However, when territory is very large the performance traits may be reduced again in territorial animals (e.g. anemonefish [8]) due to increased stress and/or energy investment to protect a larger area from competitors or predators. (B) Potential effects of among-individual variation in performance curves for a trait related to the expression of social behaviour (e.g. aerobic capacity, cognitive ability, locomotor capacity, muscular function) in response to temperature (environmental variable). In this panel, the performance curve of different individuals within a social group are represented in different colours. The dashed orange line shows variation in the performance curve (solid orange line) caused by acclimation to the environmental variable (temperature in this example). Acclimation generally results in an overall “flattening” of the performance curve, but may also cause an increase in the peak performance. Arrows illustrate the different points of individual variation in performance curve that have implications for animal social behaviour, especially in ectotherms. Each point and its consequence on social behaviour is highlighted in Figures 2, 3, 4, 5, 6 and 7. References: [1] Barrionuevo and Burggren, 1999; [2] Fry, 1971; [3] Pörtner 2010; [4] Pörtner and Farrell 2008; [5] Maierdiyali et al. 2020; [6] Bauer et al., 2013; [7] Breves and Specker 2005; [8] Ross, 1978; [9] Gomez Isaza et al., 2020; [10] McKenzie et al. 2010; [11] Meager et al. 2006; [12] Chamberlain and Ioannou,2019.

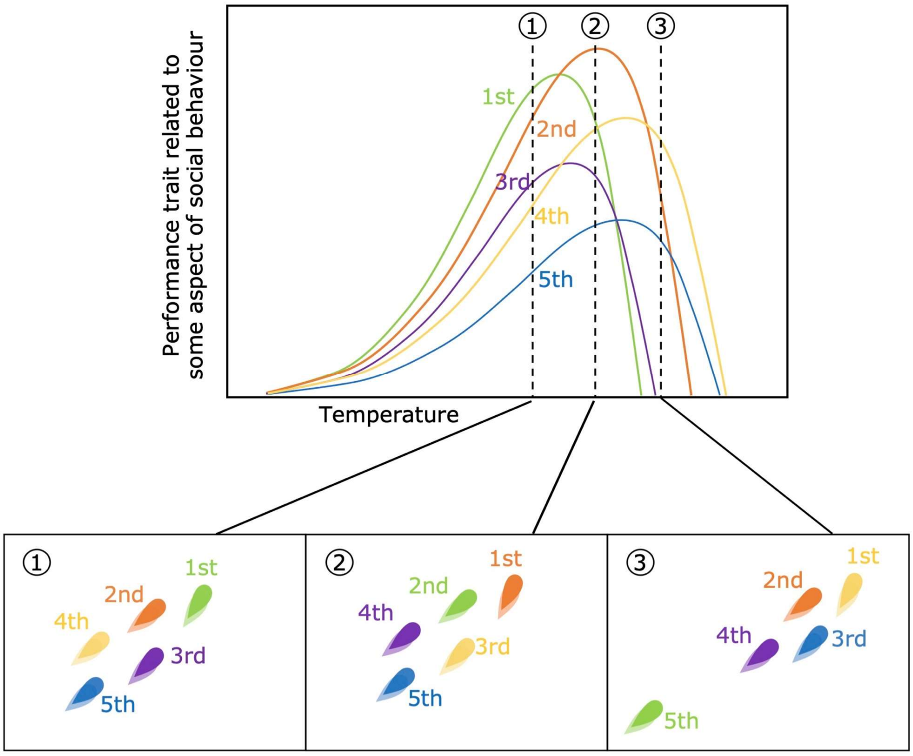

**Figure 2.** Changes in the rank order of performance capacity across three different temperatures (top panel). Each colour refers to an individual within the same social group. In the bottom panels the rank-assortment within the group is shown for each temperature (1, 2 and 3), assuming that higher-ranked individuals are positioned on the front of the group. For example, the green individual is the highest rank-individual (leader) at temperature 1, but a follower with 2nd rank position at temperature 2, and is no longer part of the group at temperature 3, given that the individual's performance capacity decreases to 0 before temperature 3, while the rest of the groups has not.

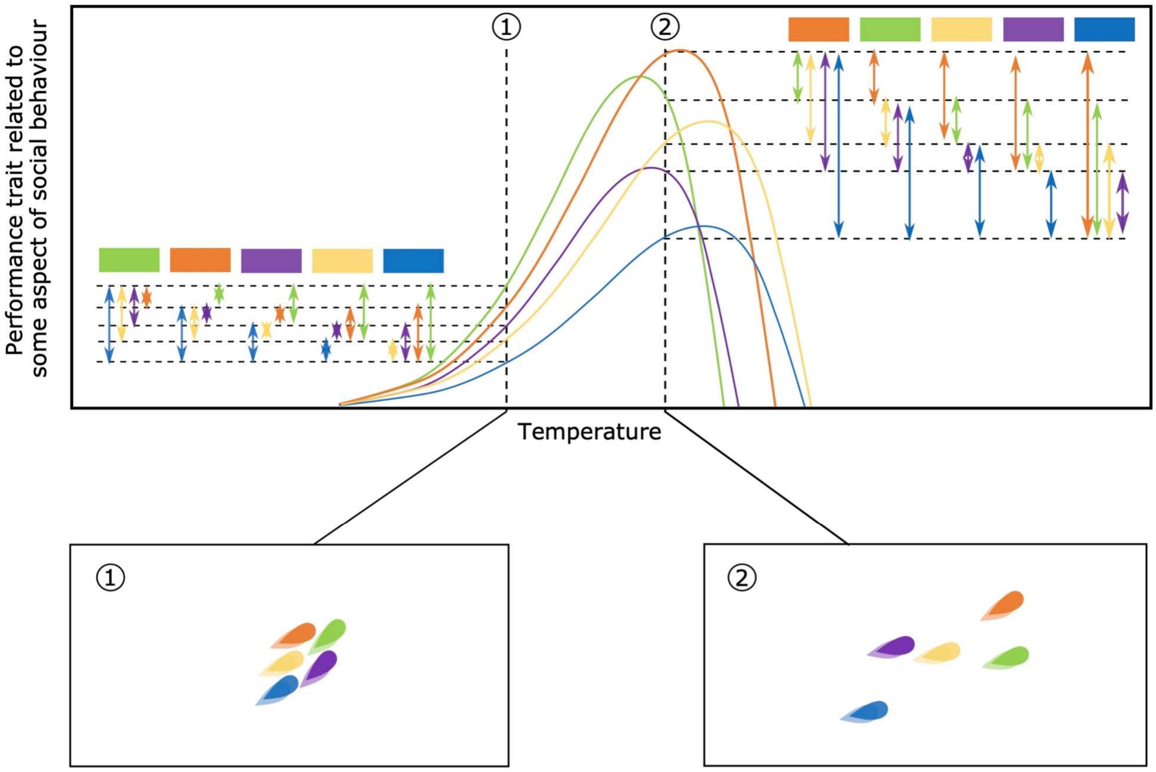

**Figure 3.** Change in among-individual variation along the environmental gradient. On the top panel the among-individual variation is highlighted at 2 different temperatures, when individual performance curves converge (temperature 1) or diverge (temperature 2). Each colour refers to an individual within the same social group. Square boxes represent individuals used as a reference to show the amount of variation. Arrows show the amount of variation between individuals. In the bottom panels is shown an example of the consequences of among-individual variation in performance curves on social groups. Wider variation could lead to less cohesion, i.e. higher distances among individuals within the same group, here shown at temperature 2 compared to temperature 1.

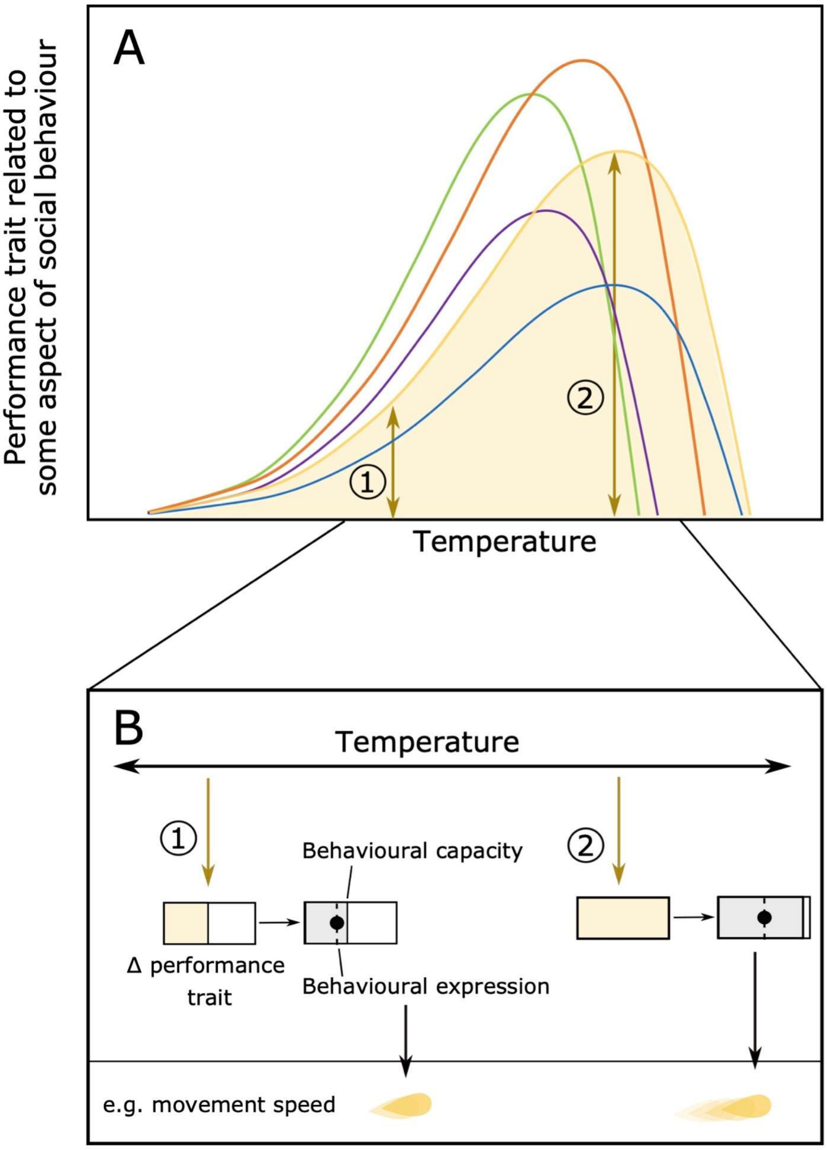

**Figure 4.** Change in within-individual variation across an environmental gradient (e.g. temperature). The area below the performance curve indicates the variation in individual performance (A, individual in yellow used as an example). Differences in individual variation in performance trait at two different temperatures (1 and 2, B) can result in different behavioural capacity and expression. For example, at temperature 1 the yellow individual has only little variation in performance and its behaviour is only expressed as low movement speed, while at temperature 2 (close to its optimum) the same individual has a higher variation of movement and can move up to very high speeds. Panel (B) reproduced from Jolle et al. 2020.

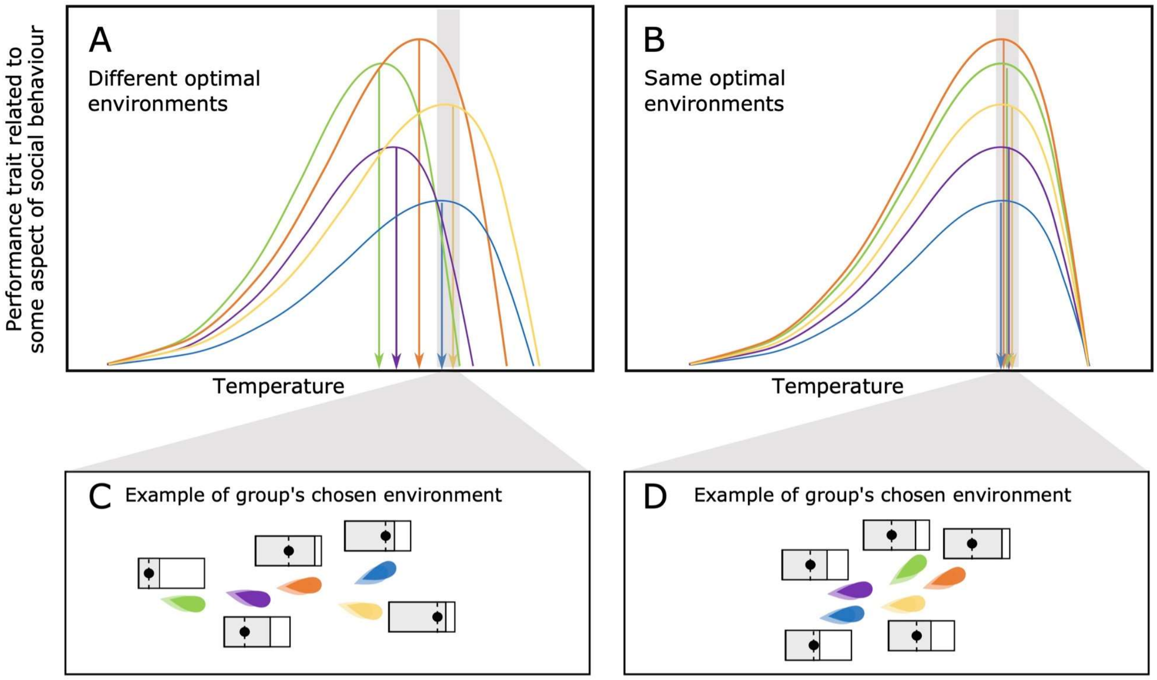

**Figure 5.** (A) Among-individual differences in optimal environments *vs.* (B) equal optimal environment among individuals belonging to the same social group. One of the consequences of among-individual differences in optimal environments is that individuals may fit into different social “niches”, each with a different behavioural capacity and expression, depending on the physiological constraints they end up facing within the group’s chosen environment (C). On the other hand, an similar optimal environments may lead to behavioural conformity among individuals (D).

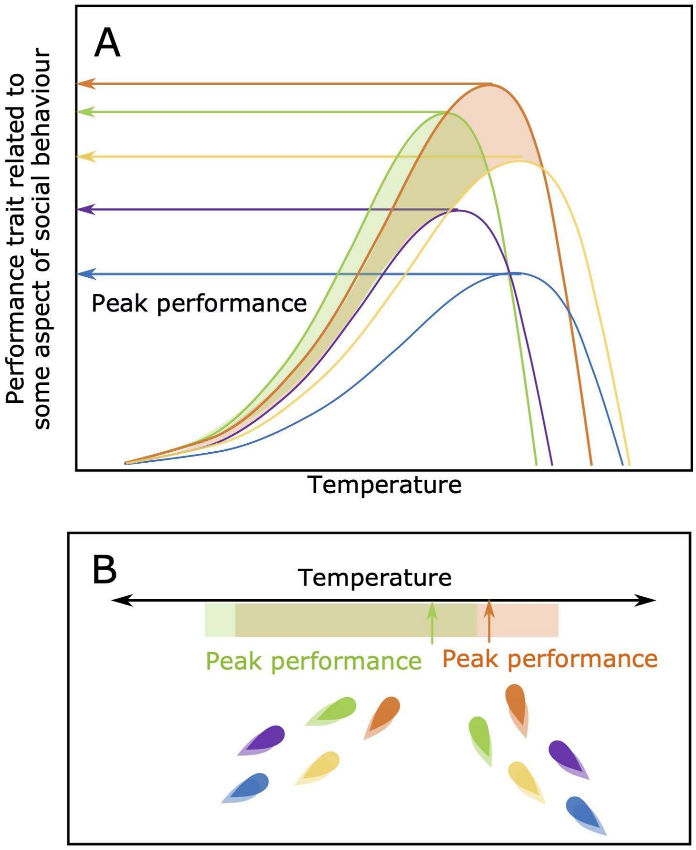

**Figure 6.** Among-individual differences in peak performance regardless of optima. In panel (A) across a large range of temperatures, individuals green and orange have a higher peak in their performance compared to the other individuals within the group and regardless of optima.

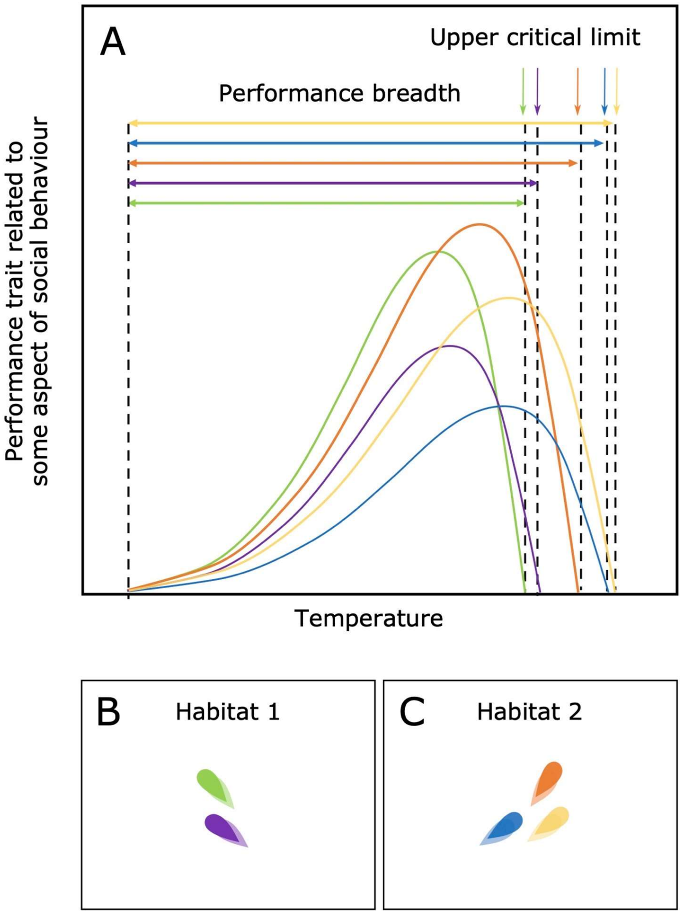

**Figure 7.** Among-individual differences in performance breadth and critical limits (A) and its consequences (B and C). Variation in the breadth and critical thresholds limit the options of habitats available for each individual and promote among-group assortment (e.g. B and C).