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Commentary

A primer on the relationship between group size and group performance

Mauricio Cantor [a, b, c, d, *], Lucy M. Aplin [c, e, f, 1], Damien R. Farine [b, c, g, **, 1]

[a] Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany
[b] Department of Biology, University of Konstanz, Konstanz, Germany
[c] Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany
[d] Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil
[e] Cognitive and Cultural Ecology, Max Planck Institute of Animal Behavior, Konstanz, Germany
[f] Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford, U.K.
[g] Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz, Germany

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Living in groups can benefit individuals in many ways, including in innovative problem solving. Several hypotheses have suggested mechanisms to explain why larger groups disproportionately outperform smaller groups, including the skill pool and pool of competence effects. However, disentangling these potential mechanisms from the effects of group size alone has been challenging. Here, we first outline key ways in which group size can shape performance in innovative problem solving. We then detail the nonlinear nature of the mathematical relationship between group size and various measures of group performance. Finally, we use simulations to confirm that measures of group performance in innovative problem solving scale nonlinearly with group size, even in the absence of any other effect. Our study provides guidance on how best to evaluate hypotheses about group composition on innovative problem solving, and clarity to help future studies make appropriate assumptions when developing null hypotheses against which to test their empirical data.

Many animals live in dynamic environments where they are constantly faced with new challenges. Behavioural innovations are key short-term responses to challenges, with novel or modified behavioural variants allowing individuals to fine-tune their behavioural repertoires to new local conditions and resource distributions (Griffin & Guez, 2014; Reader & Laland, 2003; Sol, Timmermans, & Lefebvre, 2002). For instance, a foraging innovation, whereby an individual adds novel food items to its diet or exploits a known item in a novel way, can facilitate invasion or persistence of innovators in novel environments (Ducatez, Sol, Sayol, & Lefebvre, 2020; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). Behavioural innovations can also be associated with social behaviour (see Reader & Laland, 2003). For one, by living in groups, individuals benefit from the well-known effects such as the dilution of risk, and the social transfer of information and knowledge (e.g. Caraco, 1981). As such, innovativeness may also be related to group size. Group living can reduce the ability to learn, or the benefit of learning, due to competition or scrounging (Hirsch, 2007). Conversely, group living can promote superior innovative problem solving, with individuals in larger groups solving novel problems and producing innovations disproportionately faster and/or more often than smaller groups (Berdahl, Torney, Ioannou, Faria, & Couzin, 2013; Couzin, Krause, Franks, & Levin, 2005; Pitcher, Magurran, & Winfield, 1982).

The relationship between group size and extraction of resources from the environment is well explored from an individual-centric approach, for example asking ‘how much energy does an individual in a group size of n accumulate over time?’ (Caraco, 1981; Clark & Mangel, 1986; Ranta, Rita, & Lindstrom, 1993). More recently, the interest has shifted to testing how foraging groups deal with new events: ‘has any individual innovated to access a new resource?’. Both field and experimental studies now suggest that larger groups

* Correspondence: M. Cantor, Max Planck Institute of Animal Behavior, Am Obstberg 1, Radolfzell, Baden-Württemberg, 78315, Germany
** Correspondence: D.R. Farine, Department of Biology, University of Konstanz, Konstanz, Germany
E-mail addresses: mcantor@ab.mpg.de (M. Cantor), dfarine@ab.mpg.de (D. R. Farine).
[1] These authors contributed equally.

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are more efficient at innovative problem solving when confronted with new food sources (Ashton, Thornton, & Ridley, 2019; Kerr & Tindale, 2004; Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011). For example, in Liker and Bókony (2009) groups of six captive house sparrows, *Passer domesticus*, were on average 11 times faster to solve a foraging task than groups of two, and all members of larger groups received food seven times faster. Similarly, Ashton et al. (2019) found a nonlinear correlation between the time to first innovation and group size in wild Australian magpies, *Cracticus tibicen*, with solutions emerging faster in larger groups (groups of 2–11). Note that being among many conspecifics can sometimes slow down or limit opportunities for individuals to engage in innovative behaviour (Overington et al., 2009; Griffin et al., 2013). Thus, counterexamples exist to highlight that the direction of the relationship between group size and performance is not always clear (e.g. Stöwe et al., 2006; Thornton & Samson, 2012; Thornton & Malapert, 2009).

While empirical studies have yielded important insights into the individual benefits of living in a larger group, our understanding of these studies has been hampered by the lack of clarity on the underlying mechanisms driving the observed outcomes, and on the statistical patterns that different mechanisms are expected to produce. Our aim here is to provide clarification on the fundamentals of the relationship between group size and measures of group performance on innovative problem solving, whereby performance is measured by latency or propensity to innovate. First, we discuss the multiple hypotheses that have arisen to explain the relationship between group size and rates or propensity for innovations. Second, we highlight that the basic mathematical relationship between group size and group performance can sometimes be linear and sometimes nonlinear, depending on the type of actions that are being measured. Finally, we use a simple model to explore how the nonlinear relationships between group size and the time taken for innovations to emerge and to spread within social groups affects our ability to test some of the mechanisms hypothesized to underlie the effects of the group's size on the propensity to innovate. Our study highlights that nonlinear functions (1) are expected rather than surprising in studies of group performance and (2) make it difficult to quantify the role of alternative hypotheses. Variation in behavioural composition is likely to play a relatively minor role in the relationship between group size and innovation in all except the smallest groups. Rather, the mechanisms underlying the benefits of larger group sizes for innovation are largely simple and direct, with most circumstances not requiring the need to invoke complex hypotheses.

WHY DO LARGER GROUPS OUTPERFORM SMALLER GROUPS?

In theory, many drivers can lead to superior innovative problem-solving performance in large groups (Table 1). First, larger groups can solve a problem faster or more often because there is a clear effect of the additional effort of multiple individuals on the solving probability. This phenomenon is often referred to as 'swarm intelligence' or 'collective cognition' (e.g. Krause, Ruxton, & Krause, 2010). Second, individuals can directly cooperate to solve a problem, and being in larger numbers could facilitate the recruitment of good collaborators (see also Melis, Hare, & Tomasello, 2006). Third, there may be an indirect effect of the social context; for example, individuals in a larger group may have less aversion to novelty and be at lower risk of predation. Lower neophobia or reduced predator vigilance can then increase the expression of, or the time available to invest in, behaviours that lead to innovations (Coleman & Mellgren, 1994; Morand-Ferron & Quinn, 2011; Ryer & Olla, 1992; Stöwe, Bugnyar, Heinrich, & Kotrschal, 2006). Being surrounded by many conspecifics can increase cognitive performance (Thornton & Samson, 2012; Ashton, Ridley, Edwards, & Thornton, 2018; see also the 'social intelligence hypothesis' e.g. ; Reader & Laland, 2002), and it can also increase motivation to solve a problem (social facilitation) due to exposure to attempts and subsequent competition (Soma & Hasegawa, 2004).

One prominent hypothesis to explain increased performance in larger groups proposes that the probability of innovation is affected by emergent or pre-existing group heterogeneity, known as the 'skill pool' and 'pool of competence' effects, respectively. The skill pool effect implies that competition in larger groups will lead individuals to specialize on distinct foraging behaviours, representing a larger collective repertoire and translating into improved search efficiency and joint discoveries of food (Giraldeau, 1984). The pool of competence effect, instead, implies that larger groups are more likely to be composed of phenotypically diverse members (Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011) and, given that group diversity can leverage the chance of success (Hong & Page, 2004), larger groups should, by chance, be more likely to contain individuals with the skills to solve a given problem efficiently. In turn, members of larger groups will be more likely to benefit from the skill of these members of their group. Traits that are known to influence innovation include age, sex, dominance rank, motor tendencies, cognitive ability and personality (Amici, Widdig, Lehmann, & Majolo, 2019; Biondi, Bo, & Vassallo, 2010; Burns & Dyer, 2008; Gibelli, Aubin-Horth, & Dubois, 2019; Griffin & Guez, 2014; Keynan, Ridley, & Lotem, 2015; Morand-Ferron & Quinn, 2011; Smit & van Oers, 2019; Thornton & Samson, 2012).

THE SIMPLE MECHANISM OF GREATER PERFORMANCE BY LARGER GROUPS

The positive effect of group size and diversity on innovative problem solving has received support from both theoretical and experimental studies. Theoretical work suggests that individuals should vary in behavioural repertoires and competence (Bolnick et al., 2003; Sih, Sinn, & Patricelli, 2019), and that group diversity facilitates innovative problem solving that exceeds individual capacities (e.g. Hong & Page, 2004; Krause et al., 2010). A few empirical studies have also provided evidence for an effect of diversity by comparing groups of the same size but differing composition. For example, mixed-species passerine flocks, which have high phenotypic diversity, are more likely to approach and use a novel feeder than similar-sized flocks of single species (Freeberg, Eppert, Sieving, & Lucas, 2017). More directly, empirical comparison of bird flocks has consistently shown that larger flocks outperform smaller flocks in foraging tasks by solving them faster and more often (Ashton et al., 2019; Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011). As compelling as the evidence for greater innovative problem-solving performance in larger groups may be, however, an alternative mechanism is often overlooked.

The improved performance of larger groups can result from a simpler effect: that they contain more individuals that are available to attempt to solve a problem, and that this higher number of potential attempts per unit time can, in and of itself, result in greater group performance. In other words, larger groups should disproportionately outperform smaller groups without requiring any variation among group members. Indeed, a common misinterpretation of various hypotheses about the effects of group size on group performance has been that, all else being equal, there should be a linear relationship between group size and performance, for example that a group of 10 individuals should solve a problem, on average, twice as fast as a group of five individuals. This then implies that nonlinear relationships indicate the presence of some additional effect related to variation among group members or social facilitation (e.g. reduction in vigilance).

Table 1
Common hypotheses for the positive effect of group size on problem-solving performance and the emergence of innovative behaviour

Hypothesis	Effect
Swarm intelligence	Groups combine and process information independently collected by individuals, providing collective solutions to a problem that are unavailable to small groups or individuals alone
More collaboration opportunities	Problems may require collaboration to be solved and individuals in larger groups have access to a greater pool of potential collaborators
Reduced neophobia	Individuals in larger groups have less aversion to novelty and so can be more prone to exploration and to attempt to solve novel problems
Reduced predator vigilance	Individuals in larger groups experience lower predation risk and can reduce their predator vigilance, which facilitates investing in innovative problem solving
Increased cognitive performance	Living in groups either selects for cognition, or promotes cognitive development, which is useful for problem solving (akin to the 'social intelligence hypothesis')
Social facilitation	Individuals in larger groups are more motivated to solve a problem due to exposure to solving attempts, solutions and/or competition
Skill pool effect	Larger groups experience more competition, thus promote behavioural specialization, enlarging the collective repertoire and improving joint discoveries
Pool of competence	Larger groups are composed of diverse individuals with traits that increase problem-solving ability and are thus likely to contain skilful individuals

For references in support of or against these hypotheses, see the text.

The error in the assumption of linearity comes from confounding the additive and multiplicative nature of probabilities. In some cases, increasing group size will have additive effects on group performance. For example, when considering the amount of food items taken by a group of foragers, a group of n individuals will take ($n \times P_F$) food items, where P_F is the average number of food items that a single individual takes per unit time. Thus, the effect of increasing group size on the amount of food items taken is linear. By contrast, if we consider the probability of any one group member performing a specific action per unit time, then the relationship between group size and performance becomes nonlinear.

Take a simple case where all individuals have the same probability of innovating to solve a problem. The probability of individuals independently not solving such a problem in a given unit of time is

$$P(\text{not solve}|n) = (1 - P_I)^n$$

where n is the number of individuals in the group and P_I is the independent individual level probability of solving per unit time. This makes the probability that any given individual solves the same problem in the same unit time as

$$P(\text{solve}|n) = 1 - (1 - P_I)^n$$

in a single attempt, and

$$P(\text{solve}|n) = 1 - (1 - P_I)^{nt}$$

in t attempts (e.g. in t units of time). In other words, the probability that a group solves a problem is based on the innovation rate raised to the power of the effort (group size times the number of attempts), making the relationship between group size and the probability of solving the problem per unit(s) time multiplicative (i.e. nonlinear, Fig. 1). Should group members have opportunities to copy an innovator, then the probability of an individual solving the problem in a given time step becomes

$$1 - (1 - P_I) \times (1 - P_L)^n$$

where $P_L = 1 - (1 - P_S)^{n_s}$, which is the probability of socially learning per group member given n_s demonstrators at that time step. Thus, if individuals can then learn from one another, the time taken for all group members to solve the problem will decrease, but the basic shape of this relationship will not change.

Now, consider that individuals inherently differ in their past experiences, behavioural repertoires and/or motor abilities, a requisite for the pool of competence effect (Morand-Ferron & Quinn, 2011). When some individuals are more skilled in innovative problem solving than others, the probability of solving the same problem after multiple attempts becomes

$$P(\text{solving}|n) = 1 - (1 - P_I(\text{u}))^{n_u t} \times (1 - P_I(\text{s}))^{n_s t}$$

where n_u is the number of unskilled individuals, n_S is the number of skilled individuals, $P_I(\text{u})$ is the probability of an unskilled individual solving a problem per unit time and $P_I(\text{s})$ is the probability that a skilled individual solves per unit time. Note that adding skilled individuals would not change the basic nature (i.e. nonlinearity) of the group size and performance relationship.

The multiplicative nature of the group size and performance relationship means that while having skilled individuals in a group can lead to differences in performance among very small groups, as group size increases the contributions of skilled individuals become disproportionally smaller (groups with or without skilled individuals become indistinguishable, Fig. 1a). By contrast, adding more group members can greatly increase the probability of solving the problem, until this relationship levels off, at which point increasing group size no longer has a strong effect. The shape of this relationship for a given population and given a particular problem will be impacted by a range of factors, including boundary effects (the minimum time to solve a problem even if it is solved immediately) and social effects such as interference among individuals. We do not consider these further as they will not affect the overall nonlinear nature of the relationship.

The nonlinear relationship between group size and group performance at solving a problem means that the shape of the relationship is not prescriptive of the pool of competence effect (or other indirect effects). Thus, care is required to ensure that correct assumptions are made when developing the null hypothesis for group behaviours.

EXPLORING THE GROUP SIZE VERSUS GROUP PERFORMANCE RELATIONSHIP

We demonstrate the expected relationships between group size and two measures of group performance by building a simple model (see Supplementary Material). In our model, animal populations are composed of skilled and unskilled individuals, and individuals form groups of various sizes. We then simulate individuals attempting to solve a problem independently. Once the problem is solved, individuals can continue to solve independently but can also copy others. After all individuals have attempted to solve the problem, we record the group size, the time step and the

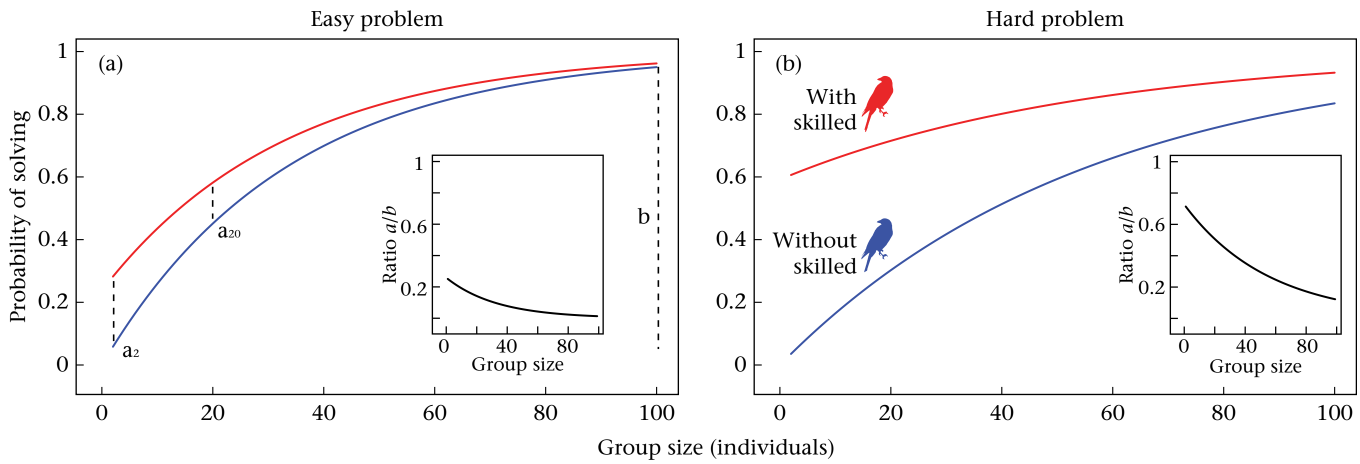

Figure 1. The mathematical relationship between group size and group performance. The relationship is shown for (a) an easy problem where a skilled individual is 10 times more likely to solve per unit effort than an unskilled individual and (b) a hard problem where skilled individuals are 50 times more likely than unskilled individuals to solve the problem. The probability of at least one individual solving the easy and the hard problems scales nonlinearly with number of individuals in the group both with and without a skilled individual. The influence of a skilled individual in the group performance in solving the problem will therefore be decreasingly important as group size increases and become insignificant in large groups. Inset plots indicate the relative effects of the presence of a skilled individual in the group versus the effects of increasing group size on the probability of solving a problem (ratio $\frac{a_n}{b}$), where a_n represents the difference in the probability of solving between groups with and without a skilled individual when group size is n, and b represent the increase in the probability of solving in small (here n=2) versus large (here n=100) groups without a skilled individual.

number of individuals that have solved the problem by that time step. We evaluate group performance in terms of both (1) the time taken to achieve the solution (solving or innovation efficiency) and (2) the proportion of the group that was successful over repeated time steps.

In our model, we vary four parameters: group size, presence of a skilled individual, individual probability of independently solving a problem per time unit and probability of socially learning from the innovator. We simulated 1000 replicated populations in which individuals formed groups varying in size, g, from 2 to 75 members (specifically: $g \in \{2, 3, 5, 7, 10, 13, 16, 20, 24, 28, 32, 38, 44, 50, 60, 75\}$) and gave groups a problem to solve until 100 000 time steps. Groups could or could not contain a skilled individual. Skilled individuals had a probability of independently solving $P_{\text{skilled}}(\text{solving}) = 0.01$, and so were expected to solve the problem relatively often. When the solution to the problem was relatively easy, $P_{\text{skilled}}(\text{solving})$ was 10-fold higher than the probability of independent solving by an unskilled individual, thus $P_{\text{unskilled}}(\text{solving}) = 0.001$; when the problem was hard, $P_{\text{skilled}}(\text{solving})$ was 50-fold higher, thus $P_{\text{unskilled}}(\text{solving}) = 0.0002$. The probability of any individual, skilled or not, of copying the solution from each other was set as $P(\text{learning}) = 0.1$. Our simulations produced three clear results: (1) both measures of group performance increase with group size; (2) the effect of individual variation in skill level was secondary to the effect of the group's size and contingent on group size; (3) the difficulty of the problem extended the time to reach a solution, but it did not change the fundamental relationship between group size and performance.

The first outcome of our simulations demonstrates that solving efficiency decreases nonlinearly with group size, and that the shape of these curves fits an exponential decay model (Fig. 2a,d). When comparing the fit of models to the latency to solve by groups of different sizes, a likelihood ratio test reveals that models with nonlinear terms fit significantly better than models without them (Table 2). For groups without skilled individuals, the most important contributor to the fit is the nonlinear term ($\frac{x}{g}$, where x is a constant fitted by a nonlinear least-squares estimate and g is group size); all models that have this term fit equally well (models 1–3, Table 2) and better than all linear models without it (models 4–6, Table 2). By contrast, when groups contain skilled individuals, the linear term ($z \times g$, where z is a constant) becomes a significant contributor to the fit (model 7 versus models 8–12, Table 2), along with the nonlinear term. Thus, in neither case do linear models better explain the relationship between group size and solving efficiency. Further, it is only situations where groups perform the task efficiently (with low latency), such as when they contain skilled individuals, that the relationship appears more linear (see red line in Fig. 2d which has a significant linear component).

The second outcome of the simulations demonstrates that the time difference in solving between groups with skilled and unskilled individuals is similar across all group sizes, except for very small groups (Fig. 2). Further, the number of individuals that have not solved a problem over a given time also decreases with group size, but while this proportion is distinct between small groups with and without a skilled individual, it becomes indistinguishable when groups are large (Fig. 2b, c, e, f). The third outcome demonstrates that while the members of larger groups solve the problem sooner than those in smaller groups, the presence of skilled individuals in a group only makes a difference when the problem to solve is considerably harder, and so skilled individuals have a much higher probability of solving it than the unskilled individuals (Fig. 2). However, a difference in latency to solve the problem may not be a statistically robust test, as in our simulations the 95% range in the difference in latencies for small group sizes, even for the hard problems, overlaps zero (insets of Fig. 2a,d).

Our simulation supports empirical findings that larger groups should exhibit overall greater innovative problem-solving performance than smaller groups (Ashton et al., 2019; Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011), but it demonstrates that comparing the performance of differently sized groups is generally a poor test of the pool of competence effect. Even if larger groups are more likely to contain skilled individuals, the sheer number of individuals in a group, and thus their multiplicative probabilities of solving a problem, can produce the same net positive and nonlinear relationship, between group size and different measures of group performance. Our simulations further show that irrespective of how difficult the problem is, the effect of having a skilled individual in the group is likely to be important only in small groups. Across problems with increasingly difficult solutions, there is a consistent

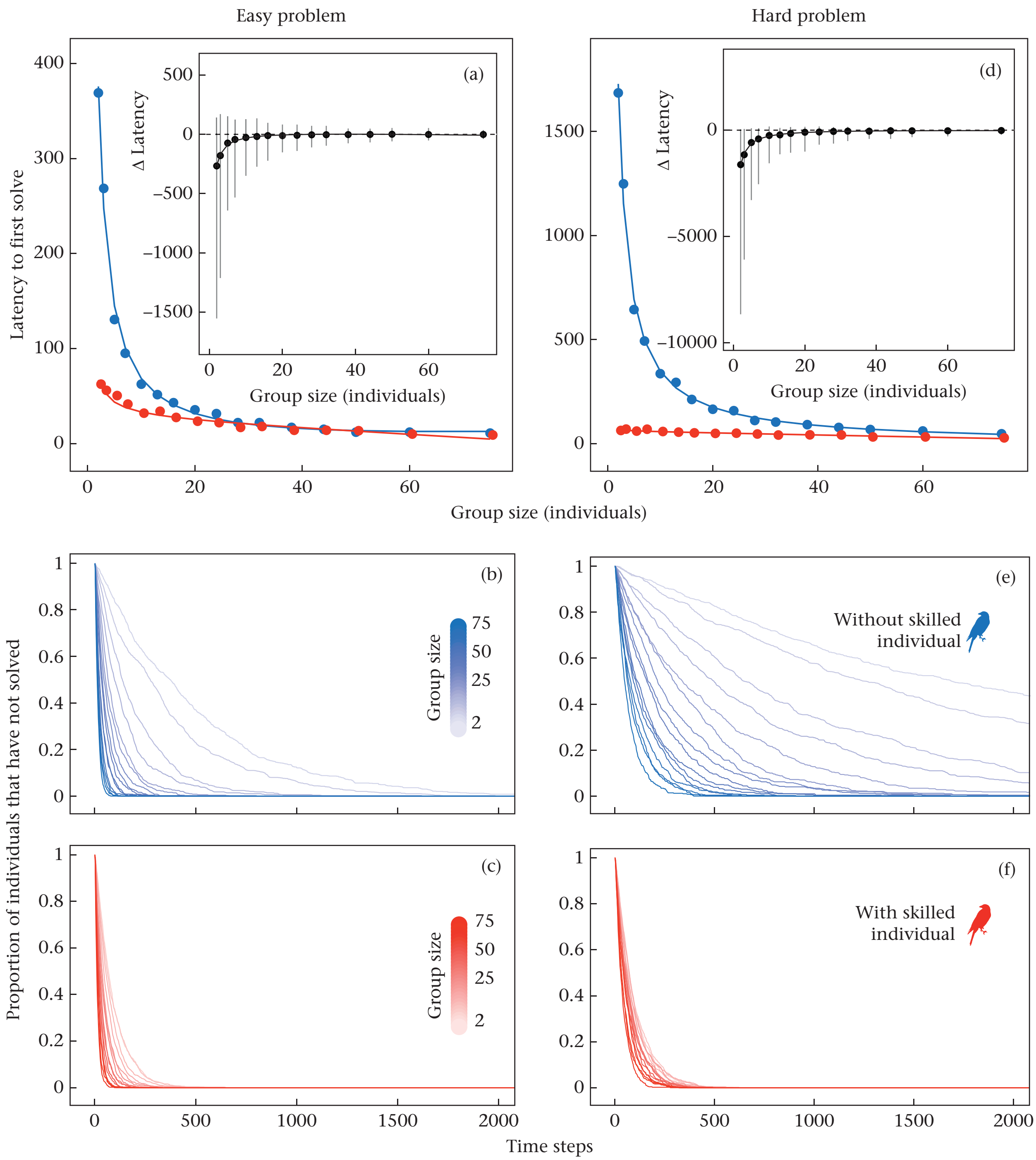

Figure 2. Larger groups perform inherently better, regardless of the members' skill level. Groups containing skilled individuals do not always perform better when solving a given problem than those that do not contain a skilled individual, with the average performance becoming indistinguishable when groups are large. (a) The time until one individual in a group solves a relatively easy problem decreases nonlinearly with group size for groups both without (blue points and line) and with (red points and line) skilled individuals. For the easy problem, the solving probability of a skilled individual was 10-fold that of an unskilled individual. Points show the means of 1000 simulated populations with group sizes of 2–75 individuals; lines show the fit of an exponential decay model (models 1 and 7 from Table 1 for unskilled and skilled groups, respectively). Inset plot shows that the difference in performance (Δ latency) by groups without and with skilled individuals is statistically indistinguishable, especially for larger groups, as the confidence intervals (whiskers) always overlap with the horizontal dashed line indicating no time difference ($y = 0$). (b, c) The proportion of individuals in the groups that have not solved the problem decreases with time, and it decreases faster in larger groups, for groups both (b) without and (c) with skilled individuals. Colour shade indicates group size. Simulations were run for 100 000 time steps but are truncated at 2000 for better visualization. (d, e, f) These patterns are consistent when the problem is hard (skilled individual's solving probability was 50-fold that of an unskilled individual) only that (d) it takes longer for any individual to reach a solution and (e) members of small groups without skilled individuals take particularly longer than those of (f) groups with skilled individuals (however, this distinction disappears when groups are very large).

Table 2
Likelihood ratio test of alternative models describing the relationship between group size and the latency to solve a problem

Fitted model		Easy problem				Hard problem			
		df	Log likelihood	χ^2	*P*	*df*	Log likelihood	χ^2	*P*
Without skilled individuals									
1	$L \sim \frac{x}{g} + (z \times g) + c$	4	-54.366			4	-77.270		
2	$L \sim \frac{x}{g} + c$	3	-55.456	2.179	0.140	3	-77.277	0.015	0.902
3	$L \sim \frac{x}{g}$	2	-56.639	2.368	0.124	2	-77.278	0.002	0.967
4	$L \sim (z \times g) + c$	3	-92.277	71.275	<0.001	3	-116.241	77.925	<0.001
5	$L \sim (z \times g)$	2	-99.637	14.720	<0.001	2	-124.292	16.102	<0.001
6	$L \sim c$	2	-96.242	6.789	<0.001	2	-120.606	7.371	<0.001
With skilled individuals									
7	$L \sim \frac{x}{g} + (z \times g) + c$	4	-40.98			4	-43.038		
8	$L \sim \frac{x}{g} + c$	3	-50.599	19.238	<0.001	3	-56.644	27.212	<0.001
9	$L \sim \frac{x}{g}$	2	-62.867	24.537	<0.001	2	-78.21	43.133	<0.001
10	$L \sim (z \times g) + c$	3	-57.131	11.472	<0.001	3	-44.623	67.175	<0.001
11	$L \sim (z \times g)$	2	-76.756	39.251	<0.001	2	-81.59	73.934	<0.001
12	$L \sim c$	2	-67.414	18.685	<0.001	2	-63.049	37.083	<0.001

The time until one individual in a group solves a problem (latency, L) as a function of group size (g) was fitted to six models containing a nonlinear (x), a linear (z) and/or a constant (c) term. The probability of a skilled individual solving an easy problem was 10-fold that of an unskilled individual and that of solving a hard problem was 50-fold. Statistical significance ($P < 0.05$) indicates rejection of the null hypothesis that a submodel (2–6 and 8–12) provides a better fit than the full models (1 and 7, respectively). Data are from simulations shown in Fig. 2a,d.

inflection point (around 10 individuals) in the relationship between group size and the benefits of having a skilled individual on group performance (Fig. 3).

IMPLICATIONS FOR THE STUDY OF GROUP SIZE AND OVERALL PERFORMANCE

We have shown analytically and using simulations that larger groups are expected to have a disproportionate increase in measures of group performance. Even without any differences between individuals, or any interactions among group members, we expect

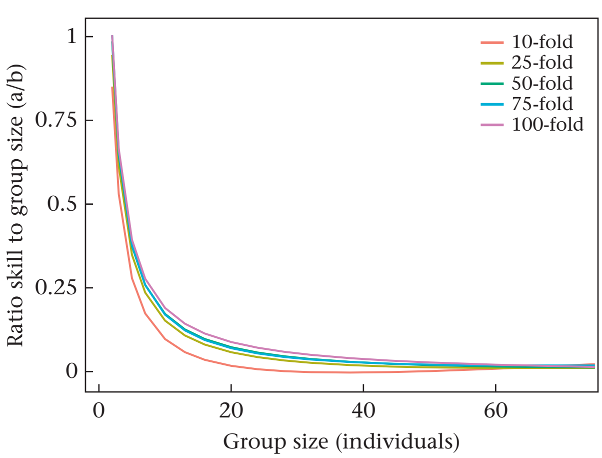

Figure 3. Larger groups perform inherently better, regardless of the difficulty of the problem to solve. The relative effects of group size versus the presence of a skilled individual in the group on the probability of solving a problem is given by the relative increase in the effect of having a skilled individual with increasing group size, given by $\frac{a_n}{b}$, where a_n represents the increase in the probability of solving between groups of the same size with and without a skilled individual and b represents the increase in the probability of solving in small versus large groups without a skilled individual (see Fig. 1). Colour-coded lines indicate increasingly harder problems to solve. For instance, for an easy problem a skilled individual is 10 times more likely to solve the problem per unit effort than an unskilled individual (10-fold higher probability), whereas for a very hard problem, this probability is 100-fold.

nonlinear relationships between group size and metrics of group performance, such as the time to first solve a problem and the rate at which group members subsequently learn. Further, our simulations suggest that it is likely to be impossible to distinguish a pool of competence effect from the relationship between group size and measures of group performance alone. So, if there are indeed individual differences in skills, experience and motor abilities affecting innovation (e.g. Ashton et al., 2019; Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011) but the nonlinear relationship between group size and innovative problem solving is mathematically expected, how can one can detect the contributions of skilled individuals to group performance?

Our simulations suggest that the best, and perhaps only, way to study the relationship between group composition and group performance is by comparing groups of exact same size with differing compositions of skills. If specific traits can be associated with the propensity to innovate, or if the solver status of individuals can be tracked (e.g. Morand-Ferron & Quinn, 2011), then studies can also explore how group composition covaries with group size and/or group performance. However, four considerations should be borne in mind when designing such studies. First, when studying group composition, it must be considered that larger groups may be more likely to contain skilled individuals because these groups have, independently, been more likely to have had a group member previously innovate. Thus, while larger groups could be more likely to contain a greater pool of competence, care should be given to understanding the precise mechanisms generating such a pattern. Second, the effect of group composition is best studied in small groups, at sizes where the contributions of skilled individuals would be more prominent. The group size and performance relationship between groups with and without skilled individuals is more similar and thus much harder to distinguish in larger than in smaller groups. Third, the differences in performance between skilled and unskilled groups is clearer when measuring solving efficiency rather than propensity to solve (i.e. whether a group has solved in a given time). Thus, we recommend that all groups should be given as much time as required for individuals to solve a task before examining performance as a function of group composition. Fourth, the nonlinear nature of the group size to group performance relationship suggests that it may not be appropriate to control for group size statistically (e.g. by fitting group size as a fixed effect), unless the relationship can be modelled accurately and explicitly.

The ability of unskilled individuals to also solve tasks makes the analysis of group composition effects challenging to analyse. One reason is that easy tasks make the performance of groups much more similar across a range of group sizes. Thus, an additional suggestion is that the effect of group composition will be clearer in studies where the solution to the problem is not trivial, so that individual variations in skills is more easily detectable because the average latency for groups to solve is longer. One design could be to study situations where only some individuals either naturally have information about the problem or have been trained in advance. For instance, groups of tits (Paridae) known to contain an individual that had previously solved a task were faster at solving the same task in a subsequent attempt (Morand-Ferron & Quinn, 2011). Other fields, such as collective animal behaviour, have also created situations in which some individuals have information ('informed') and others do not ('uninformed individuals') to demonstrate that few knowledgeable individuals are needed to lead groups to resources (e.g. Couzin et al., 2005; Kao & Couzin, 2014). Yet if all individuals in such a test are naïve, then identifying whether some individuals have traits that enable them to be faster than others at solving problems is less likely to succeed.

While our simulation focuses on the pool of competence hypothesis, we would suggest that the general conclusions may also apply to other proposed effects, such as social facilitation, including positive correlations between group size and reduced neophobia or predator vigilance (Table 1). That is, such additional effects will be unlikely to change the fundamental shape of the relationship of group size and group performance, but rather mainly act to decrease the latencies to solve, both of the first innovator and of the subsequent social learners. Again, this effect is most likely to be observed at small group sizes. Similarly, while we did not consider the potential negative effects of increasing group size, including competition, scrounging and aggression, these will generally not alter the fundamental relationship. For example, monopolization of the new problem by a few individuals would potentially lead to a reduction in innovation rate (see also Ashton et al., 2019) or the rate at which solving the problem can be attempted, but this change would be unlikely to affect the latency to first solving it. Moreover, the increased risk of scrounging could reduce the benefit of innovation, but while this might increase the latencies for individuals to learn, it will simply stretch the relationship, which could potentially make it appear more linear but, at least in our simulations, does not remove the nonlinear component. However, it would be an interesting question for future studies to identify cases where within-group effects, such as social obstruction, might alter the predicted expectation of the group size to group performance relationship in ways that increase the effects of having skilled individuals in the group.

Finally, we turn to another common assumption of empirical studies on group performance: that larger groups are not only more likely to innovate, but also to promote a rapid transmission of the innovation among members, thereby increasing the performance of the average group member (Ashton et al., 2019; Morand-Ferron & Quinn, 2011). The fact that innovations spread faster and with fewer errors via social learning among socially cohesive groups has received strong support of theoretical (Cantor & Whitehead, 2013; Voelkl & Noe, 2008) and experimental field work (Aplin et al., 2015; Whiten, Caldwell, & Mesoudi, 2016). Further, collective learning has also been proposed to convert individual experiences into superior group decisions and performance (Kao, Miller, Torney, Hartnett, & Couzin, 2014). However, simply observing larger groups more quickly reaching a collective solution could stem from multiple processes. While it could be the result of one or a few innovation events being copied and transmitted quickly within the group, it could also stem from indirect effects (e.g. larger groups having information sooner; see also Clark & Mangel, 1986) translating to a positive relationship between group size and individual learning rates. Studies should consider the contribution of different effects when evaluating hypotheses (e.g. removing the effect of larger groups having information sooner by recording latencies since the initial innovation event). In line with our general warning that the nonlinear relationship between group size and group performance is not diagnostic of the pool of competence effect, the pattern of innovation spread is also not diagnostic of the type of learning (Hoppitt, Kandler, Kendal, & Laland, 2010). Thus, it remains important to test for social learning of the studied innovation using two-action and control experimental paradigms, where social learning can be clearly distinguished from individual learning (Aplin et al., 2015; Ashton et al., 2019; Whiten et al., 2016).

FINAL REMARKS

Larger groups of animals innovate disproportionally more often, and faster, than small groups. Empirical studies have been influential in advancing explanations for the relationship between group size and group performance. However, we emphasize the need to further consider a fundamental mechanistic explanation for why larger groups so convincingly outperform smaller groups. Our model highlights two important points. First, it shows that the nonlinear relationship between probability of solving a problem and group size is expected to arise from mathematical properties alone, i.e. from the strength in numbers, without needing to invoke any further explanatory factors. Second, it is not possible to draw conclusions for or against any hypothesis by solely looking at the shape of the curve representing the relationship between group size and performance. A positive nonlinear relationship should not be mistaken as evidence for any effect of group size on group performance beyond group size alone.

In clarifying the fundamentals of the group size and performance relationship, we do not intend to criticize existing research, but inspire more mechanistic investigations into the benefits that can arise from living in a larger group and, most importantly, the development of more robust null hypotheses against which to evaluate empirical data. Studies interested in inferring group composition in terms of skill levels should control for group size in their data collection by comparing the performance of groups of identical sizes, rather than in their statistical tests. Doing so will help us better tease apart the roles of individual variation and learning in the innovative problem-solving skills of animal collectives as they cope with an increasingly changing world.

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Supplementary Material

Supplementary material associated with this article can be found online at https://doi.org/10.1016/j.anbehav.2020.06.017.

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