An efficient method for sorting and selecting for social behaviour

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\textit{Abstract:} Social and collective behaviour cannot be understood by studying only isolated individuals. Yet, it is often the social traits of individuals that researchers are interested in identifying. Many social traits must instead be studied in terms of behavioural differences at the group level. However, a simple randomised approach to forming groups makes these differences negligible. This paper presents and analyses a novel method for arranging a population into groups so that the between-group variation of social behaviour is maximised. The method works by subjecting groups to several rounds of evaluating, sorting and permuting, without the need for any individual labelling. The process is simulated using various models of group performance, indicating that efficient directional, stabilising or diversifying artificial selection can be achieved based on this method. In addition, we demonstrate that the data produced during this procedure can be used to test multiple relevant models of group performance.
1 Introduction

Using a ruler and measuring scales, it is straightforward to assess the size and weight of an individual. And by observing or testing an individual’s behaviour in isolation, we can measure its behavioural traits. However, social behaviour, by definition, only occurs when more than one individual interact. Collective behaviour emerges from these interactions, and so cannot generally be attributed to individual traits. The extent to which individual traits are measurable depends critically on the structure of the groups they live in [1]. And while we may be able to identify differences between group-level behaviour, linking this to differences in individual traits is a more significant challenge [2].

There are situations where the social behaviour of individuals in well-structured groups can be effectively analysed. When social behaviours arise as a division of labour, individuals can be assessed on their contributions, such as the level of maternal care [3]. Similarly, stable social networks based on dyadic interactions can be analysed to find the most gregarious or influential individuals [1, 4]. In larger aggregations, individuals can be assessed according to some related trait. For instance, group sheltering dynamics can be compared to the individual sheltering behaviour of cockroaches [5]. More generally, group behaviour can be related to personality composition [6], as is also done in studies of human teamwork [7]. In all of these cases, there is a requirement of using natural or artificial markings or tags in order to identify the roles adopted by individuals.

A challenge in identifying differences in social behaviour thus arises when it is difficult to identify individual roles. Social behaviour often emerges from local interactions, with group members changing positions and contributing in a variety of ways to the overall collective structure [5, 6, 10]. To assess the different individual contributions to group performance requires both precise observations and exact knowledge of how the members behave and respond to each other. Precise observations are increasingly available [11, 12], but detailed knowledge of how individuals respond to each other is more difficult to infer from this data [13]. While it has been possible to identify, for example, which birds are leading and following in groups of pigeons [14, 15] other behaviours are much more difficult to quantify. Identifying which individuals are most influential in aggregation [5, 16], group alignment [17], determining speed and direction of collective motion [18] and in collective decision-making [19, 20, 21] is far from straightforward. These difficulties present a fundamental challenge to accurate identification and quantification of social behaviour at the individual level.

Here, as an alternative to individual assessment, we propose a method of sorting populations into groups that maximise the between-group variation in social behaviour. Individuals are sorted, not according to behavioural roles or interactions, but on the basis of the collective properties of the group they currently belong to. This method bears many similarities to a standard team selection method used in rowing squadrons. In rowing, the execution of roles within a team is not as important as the team’s overall synchronisation which, like in a bird flock, cannot generally be predicted in advance [22]. The ultimate goal is to compose a team with maximum performance, and this is usually done using “seat racing”, a heuristic method of exchanging players between two teams until the difference in performance (i.e. racing time) between the teams is maximised [23].

The method we propose can be used to investigate a wide range of questions in behavioural ecology and sociobiology. For example, we may be interested in whether individuals in a population have very different tendencies to aggregate. This is a common question when studying animal personality, where we are interested in the existence and extent of repeatable differences [2, 10, 24, 25]. If we randomly sample groups from a natural population and test their aggregation levels, for example, then a very large number of trials will be required to find personality differences [10, 24, 25]. If we systematically change the membership of the groups in order to sort them into high and low levels of aggregation, then this can be used as evidence that repeatable differences in social traits exist between the groups.

Increasing the behavioural variation between groups also enables the study of interactions between
dissimilar groups. Such experiments can be used to investigate whether, for example, co-operative behaviours increase the chance of success in intergroup conflict [26]. In all such experiments, the inter-group variation — and hence the statistical power — is far from optimal if groups are randomly selected from the same population. The larger the groups that are sampled, the lower this variation, and hence the more improvement offered by sorting them.

Our method can also be used to understand the roles of individual personalities within groups [6]. For example, a group’s speed might be driven by one individual, or alternatively by some average of the constituent members’ preferred speeds. For each of these cases, exchanging random members between groups would, on average, have a different effect on the group-level behaviours. The outcome of a sorting process could therefore allow us to distinguish between these two hypotheses.

Sorting according to social traits can be used to investigate correlations between these and other phenotypic traits such as brain size or other aspects of brain anatomy [27] [28] within a population, rather than across species and environments. A powerful way of establishing such correlations is through artificial selection [29] [30], where individuals with the most (or least) prominent implementation of a trait of interest are paired to produce offspring whose average trait value will be above (or below) that of the previous generation. While one can measure and select for behavioural traits [31], this selection is made more difficult for social behaviour that cannot be directly attributed to individuals. In this case, it is clearly sub-optimal to randomly sample groups from a population and selectively breed members of the most prominent groups. This is because the more members per group, the lower the genetic variation between random samples, and thus the more generations of breeding required for the desired phenotypic effect. Partitioning groups efficiently, so that social traits are highly homogeneous within groups, is therefore key to rapid success of selection regimes on social behaviour.

The aim of this paper is to provide a method for sorting and selecting individuals for social behaviour. We first propose a simple, highly efficient method for sorting groups to increase between-group variation. The technique is illustrated by simulating simple limiting cases where the group performance depends on the mean, maximum, minimum or standard deviation of the underlying individual traits. We conclude by discussing how the method can give insight into questions in behavioural ecology.

2 Methods

2.1 Sorting algorithm

The sorting begins by randomly dividing the population of $N$ individuals into $m$ physically separated groups, each with $n$ individuals. Without loss of generality, we assume that $m$ and $n$ are both even numbers and the population size $N$ is chosen accordingly. Each round consists of three steps (see Fig. 1). Firstly, each group is subjected to a behavioural assay of interest, which is evaluated to give a group performance score. Secondly, the groups are ranked from lowest to highest scoring. In the following analysis, the $j$th lowest score in each round will be referred to as $g_j(t)$. Finally, adjacent groups in this ranking exchange half of their members, chosen at random. That is, the exchange is between the 1st and 2nd ranked, between the 3rd and 4th ranked, all the way up to the pair of groups ranked $m-1$ and $m$.

The only labelling required is at the group-level, i.e. of the $m$ habitats. This presents an alternative to other combinatorial optimisation algorithms, such as for group testing problems and multi-armed bandits [32], which keep track of individuals as they are used in various combinations. In comparison, our algorithm is very straightforward to implement, and is also well-suited for animals that are difficult to distinguish or tag individually. The mixing stage makes it unlikely that the same exact combination of individuals appears twice, and allows the space of possible groups be explored efficiently.

A way of assessing whether the sorting has stabilised, independently of the distribution of group scores, is by comparing the rankings between rounds. The similarity of the rankings at round $t$ to those at round $t-1$ can be measured using the Spear-
Figure 1: The group sorting protocol. In each iteration, groups are evaluated and then sorted according to their performance, with the scores $g_1(t)$ to $g_m(t)$. Each pair of groups exchanges half of members, and the new groups are subject to the next round of evaluation.

A maximum equilibrium correlation close to one exists, corresponding to only adjacent pairs of groups swapping ranks. This correlation coefficient can therefore be useful for defining a criterion for stopping the sorting procedure.

The analytic treatment of the sorting protocol in this paper assumes a slight variation of the method presented above. In this variation, on alternate rounds the mixing pairs are shifted by one group. That is, in these rounds mixing occurs between groups 2 and 3, groups 4 and 5, and so on. This difference is not expected to significantly affect the method in practice.

2.2 Group performance and individual contributions

We assume that each individual has one underlying trait that determines its average contribution to the group’s performance, but that this contribution varies randomly between evaluations. For example, an individual contribution might be “attraction to conspecifics” while the overall group performance is “cohesiveness”. Mathematically, each individual is labelled $i \in 1, \ldots, N$ and has a trait value $\mu_i$. An individual’s contribution to its group when evaluated at time $t$ is then a random variable $X(i, t)$ drawn from a normal distribution with mean $\mu_i$ and standard deviation $\sigma$. We assume for now that $\sigma$ is the same for all individuals. For each group $j$, we denote the set of individuals that composes it as $A^j(t)$. We do not provide here an explicit representation on how $A^j(t)$ is updated between evaluations, but Figure 1 shows how group membership is updated.

We assume that it is unknown in advance how individual contributions determine group performance. Indeed, there are various ways that group-level performance can arise from individual traits [6, 2]. The simplest possibility is that the group is the sum of its parts. For example, the many wrongs hypothesis in group navigation [33] says that that the directional performance of a flock is determined by the average navigational ability of its members. In this case, we would have

\[ g_j(t) = m_j(t) = \frac{1}{n} \sum_{i \in A^j(t)} X(i, t) \]  

A similar averaging function also fits the observed group exploration of Argentine ants [34].

Another possibility is that a group’s performance is largely influenced by the most extreme individual contribution, which plays either a leading or inhibiting role in the group. For example, the most cautious member of a group may produce social cues to make the entire group more cautious. This type of model has been observed in fish, where bold individuals conform to shy conspecifics but not vice-versa [35], as well as in group activity levels [36]. The limiting case of this model is the group depending entirely on a single “weakest link”, in which case

\[ g_j(t) = \min_{i \in A^j(t)} X(i, t) \]  

Equivalently, the group could be limited by the ability of a single leader. Weighting in this direction has been observed in geese, where bolder individuals are
more likely to make decisions \cite{37}. In the limiting case the maximum contribution is the one of interest

\[ g_j(t) = \max_{i \in A_j(t)} X(i, t) \quad (3) \]

An additional possibility is that heterogeneity within a group is beneficial for performance. For example, foraging species may benefit from both bold and shy individuals to promote exploration and group cohesion, respectively \cite{38,39}. Variation in aggression levels may also be beneficial by reducing conflict \cite{40}. A simple performance function capturing this scenario is the standard deviation

\[ g_j(t) = \frac{1}{n} \sqrt{\sum_{i \in A_j(t)} (X(i, t) - m_j(t))^2} \quad (4) \]

where \( m_j(t) \) is the mean as defined above. Conversely, in other scenarios, homogeneity within a group may be beneficial for performance. This may occur when interactions with similar conspecifics are stronger or more frequent \cite{41}. A well-known benefit of group homogeneity is the “confusion effect” as a defence against predation \cite{42,43}. In this case, the negative of the above formula can be used

\[ g_j(t) = -\frac{1}{n} \sqrt{\sum_{i \in A_j(t)} (X(i, t) - m_j(t))^2} \quad (5) \]

All of these scenarios may be considered as special cases of a general group performance function

\[ g_j(t) = f(X(A^1_j, t), ..., X(A^n_j, t)) \quad (6) \]

where \( f \) is any function of the \( n \) contributions.

Simulations and subsequent analysis were run in MATLAB. Simulations were run for 50 rounds, generating two sets of data per time step. Statistics were built up by running each simulation 5000 times. Each round produces \( m \) ranked scores of the groups \( g_1 \) up to \( g_m \). These are used to quantify the between-group variation, given simply by the standard deviation of group scores.

\[ \sigma_g(t) = \sqrt{\sum_{j=1}^{m} (g_j(t) - \bar{g}(t))^2} \quad (7) \]

where \( \bar{g}(t) \) is the mean group score in round \( t \). The gain is defined by the ratio of this quantity to that in the first round

\[ \text{gain}(t) = \frac{\sigma_g(t)}{\sigma_g(0)} \quad (8) \]

This measures how much the between-group variation is increased compared to the initial random selection of groups. The group scores were transformed using the known distributions for random samples, so that initial distributions were normal.

A complementary set of useful data, less dependent on the distribution of traits, is the sequence of changes in group rank. The group ranked \( j \) in round \( t - 1 \) has a new rank in round \( t \) given by \( k_j(t) \). The overall probability of this transition, given by \( P_{jk}(t) \) was calculated by counting how many times this transition occurred over all simulations with identical parameters. For each simulation, the rank correlation used to track the sorting progress is calculated by

\[ \text{corr}(t) = 1 - 6 \frac{\sum_{j=1}^{m} (k_j(t) - j)^2}{m(m^2 - 1)} \quad \text{for } t > 0 \quad (9) \]

In addition, the asymmetry between upward and downward changes in rank is quantified by a cumulative skewness measure. This is calculated as

\[ \text{skew}(T) = \frac{\sum_{t=1}^{T} \sum_{j=1}^{m} (k_j(t) - j)^3}{m(m - 1)^3} \quad \text{for } T > 0 \quad (10) \]
3 Results

3.1 Sortability for monotonic increasing performance

Before we look at simulations of our sorting algorithm, we prove that a large range of group performance functions (equation 6) our sorting algorithm will be effective. Specifically, many of the biologically realistic performance functions are weakly monotonic, or non-decreasing on the individual contributions. These performance functions include the mean (equation 1) and other weighted averages, as well as the maximum (equation 2) and minimum (equation 3), and other functions based on quantiles or thresholds. The class does not include cases where performance depends on homogeneity, as in equations 4 and 5.

To make our analysis independent of the distribution of $\mu$, we use the global ranks of the individual traits. Let the global ranks of the individuals in group $j$ in round $t$ be $A^t_j(t)$ through $A^t_n(t)$ in ascending order, and let

$$S^t_j(t) = \sum_{i=1}^{n} A^t_j(t)$$

be the sum of ranks in group $j$ in round $t$. By our definition above, the group scores $g^t_j(t)$ are increasing with $j$. As the group scores diverge over time, we expect the rank-sums $S^t_j$ to be similarly diverging for monotonic functions $f$. To state this precisely, in the Supplementary Information we prove the following theorem for the case where $\sigma = 0$.

**Theorem 1:** If $f$ is non-decreasing on all arguments, and

$$Q^t_j(t) = P(S^t_j(t) > S^t_j(t+1))$$

then

$$Q^t_j(t + 2) \leq \lambda Q^t_j(t) \quad \forall j \in \{2, \ldots, m-2\}, t$$

for some $\lambda < 1$.

The theorem implies that over time the groups become more homogenous and the sorting algorithm increases between-group diversity. Therefore, for a broad class of realistic group behaviours, artificial selection can be efficiently performed by our method. If the monotonicity condition does not hold, then it is not guaranteed that within-group variation of traits will decrease, even if between-group variation increases.

3.2 Simulation results

The changes in group scores over time are shown in Fig. 2(a-c) for typical simulations of three group performance functions, based on the mean (equation 1), the max (equation 2) and the standard deviation (equation 3). The individuals with the most extreme and median hidden traits $\mu_i$ are tracked as they move between groups, indicating how they are sorted over time. Panels (d-f) show the corresponding rank correlations given by equation 5 and panels (g-i) show the average gain in between-group variation given by equation 8. Both of these measures, even for the non-monotonic, standard deviation performance function, increase up to an equilibrium value. Therefore, even when it is not known how group performance arises from the comprised individuals, our proposed sorting method can be used to substantially increase the between-group variation as compared to a random sampling strategy.

Both the global statistics and the sorting of hidden traits depend on the group performance function. When the group performance is the mean of contributions Fig. 2(a,d,g), the initial between-group standard deviation $\sigma^t_j(0) \approx 1/\sqrt{n}$. Over time, individuals will tend to become grouped according to their underlying rank. For all three group sizes the between-group variance increases towards the population-level variance of 1. For the maximum-based performance score Figure 2(b,e,h), the highest scoring group always contains the individual with the highest contribution in that round, and over time the individuals with highest trait values $\mu_i$ become clustered together. Under this scenario, the process is highly sensitive to individual variation, which slows down the overall sorting procedure. While the individuals with low $\mu_i$ are not well correlated with the groups they are associated with, those individuals with high $\mu_i$ (i.e. those that dominate group behaviour) are sorted together in higher performance groups. While not shown in Figure 2, the opposite case of minimum-
Figure 2: Typical simulations of the sorting procedure for three group performance functions. (a-c) Ranked group scores over 50 rounds of sorting using (a) the mean, (b) the maximum, and (c) the standard deviation of the individual performances as the group score, using $m = 16$ groups of $n = 10$ individuals. To show how the individual traits are sorted, we highlight the group that contains the individual with the highest (red), lowest (blue) and the two median (black) traits out of the entire population. (d-f) Spearman rank correlation coefficients between the set of group ranks before mixing and the set after mixing, corresponding to the simulations above. Grey areas represent the 95% confidence intervals. (g-i) Expected between-group variance, normalised to the initial variance, for $m = 10$ groups of $n = 16$ individuals (dotted lines), $m = 16$ groups of $n = 10$ individuals (full lines) and $m = 20$ groups of $n = 8$ individuals (dashed lines). In all simulations, the individual variation $\sigma = 0.2$.

Based or "weakest link" limited groups (equation 2) is identical to this, only with all group performances and individual traits changing sign. In both cases, the individuals that are most likely to determine group performance are the most efficient to select.

In the mean, min and max scenarios, the populations become approximately sorted according to their traits, as predicted by the result in section 3.1. When the group performance increases with heterogeneity in the group, i.e. performance is proportional to the standard deviation, this is no longer the case (Figure 2c,f,i)). While between-group variation still increases, this is due to both tails of the trait distribution becoming mixed in the same groups. Therefore, using the sorted groups with highest performance will result in artificial diversifying selection. Conversely, the lowest-scoring groups in this case can be used for artificial stabilising selection. In the opposite case, where group performance increases with within-group homogeneity (equation 5), the opposite is true. That is, the highest-scoring groups will contain intermediate traits and the lowest-scoring will contain the extremes.

Keeping the total population constant and using a different group size has little effect on the between-group variation over 50 rounds (Figure 2g-i)). An exception to this is the standard deviation case, where there is a slight increase in between-group vari-
Figure 3: Probabilities of transitions in group rank due to mixing. (a-e) Transition probabilities on the first round of mixing using (a) the mean, (b) the maximum, (c) the minimum, (d) the standard deviation and (e) the negative standard deviation of the individual performances as the group score. (f-j) show the probabilities after 50 rounds of sorting for the same group scoring functions. Probabilities are calculated using 5000 simulations of the sorting procedure, with \( m = 16 \) groups and \( \sigma = 0.2 \).

3.3 Inference of the group performance function

If it is unknown how group trait composition affects collective behaviour, this can be inferred from the data produced during the sorting procedure. We can see how this might be done by looking at the distribution of group performance scores, shown in Figure 2. In each round, the expected between-group variation increases by different amounts depending on whether the performance function is based on the mean, the maximum or the standard deviation of individual contributions.

Differences in the simulated data between the group performance functions can also be seen in the transitions in rank. The probability matrices for these transitions are shown in Figure 3 for the three performance functions considered above, as well as the minimum and negative standard deviation. Here, we see that if the group performance function increases with the standard deviation of contributions, or is weighted towards the maximum, large downward shifts in rank are more likely than large upward shifts. The opposite is true if the group performance increases with homogeneity (equation 5) or is weighted towards the minimum individual performance (equation 2).

Using two simple statistics, derived from the group scores and rank transitions respectively, it is possible to distinguish between five candidate group performance functions. The first statistic is the gain in between-group deviation as defined in equation 8. Figure 4(a) shows the expected between-group variation for the mean, maximum and standard deviation functions as a function of round \( T \). These three functions diverge over time for both \( \sigma = 0 \) and \( \sigma = 0.2 \), while the minimum and negative standard deviation have the same gain as the maximum and standard deviation, respectively. The second statistic is the cumulative skewness as given by equation 10. The expected values of this statistic are shown in Figure 4(b) as a function of time. This measure diverges over time for all five functions considered.

Combining these two statistics, the five perfor-
Figure 4: Statistics for inference of group function with $m = 16$. (a) Evolution of expected values of (a) gain in between-group variation, and (b) cumulative skewness of rank changes. Solid lines indicate $\sigma = 0$ and dashed lines indicate $\sigma = 0.2$. In (a) the curves for minimum and negative standard deviation are identical to those for the maximum and standard deviation, respectively. (c) 95% confidence intervals of the two test statistics after 20 rounds. Areas indicate $\sigma = 0$ and lines indicate $\sigma = 0.2$.

performance functions can be distinguished using the experimental data. Figure 4(c) gives 95% confidence intervals from 5000 simulations of the five group performance functions over 50 rounds. With no individual variation between rounds, the functions are nearly separated after 20 rounds of sorting. The five confidence intervals have a similar arrangement when the individual variation $\sigma = 0.2$, but are slightly larger in area.

Measurements of group repeatability in behaviour over time are beneficial for this model selection. For each model considered here, there is a one-to-one mapping between $\sigma$ and the variation of a group’s performance over multiple evaluations. By estimating $\sigma$, one can then construct confidence intervals for the sorting data as shown in Figure 4.

4 Discussion

We have proposed a general framework for creating and studying variation in social behaviour at the group level. Our sorting protocol can be used to increase between-group variation for a wide variety of models of group behaviour. Our approach is especially useful for animals that aggregate in self-organised groups such as fish shoals or bird flocks, since it does not require individual labelling or individual behavioural tests. We now highlight five areas of application where we believe our method can be particularly useful.

Our method of increasing group-level variation in behaviour can be used to confirm and quantify consistent individual-level differences in social behaviour [6, 2]. For a wide variety of group performance functions, the variation in group behaviour can be increased by a significant amount compared to a randomised approach, adding statistical power to tests of personality. By sorting groups and then identifying whether or not there are clear differences between the new groups, we can identify whether individuals vary in their tendency to, for example, aggregate, align or detect predators.

The ability to sort groups based on aspects of social behaviour also makes it possible to test hypotheses about interactions between groups of different behavioural properties [44]. Despite the abundance of cooperative behaviour and group conflict in the wild, empirical testing of the related theory is currently limited to only a few species outside of primates [26, 45, 46]. Other applications may involve comparing the ability of different groups to attract new members [47] or remain cohesive [48].

By using the experimental data to infer which group performance functions are most likely, we can also test how group-level behaviour is related to
individual-level personality. This provides a new route to analysing how individuals react to different social environments, and their consistency over time [6]. Such analysis is common in social psychology and operations research, where individual personalities are determined through tests and compared to group performance [7]. In a similar way, linking group composition to social behaviour in animals has been achieved by individual testing on related traits [5, 18, 20]. However, behaviours that emerge only in group activity are difficult to quantify at an individual level. Testing in the space of group performance functions, as we have done here, can give experimental insight into how group trait composition affects group behaviour. For example, it can be determined whether an emergent behaviour of a group can be attributed to a small minority of leaders, or to a sum of contributions from all members. This latter question is central to the study of how animal groups make decisions [49, 50, 51, 52].

This investigation of group composition can also be used to test mechanistic models of collective behaviour. The basic parameters of these models, such as the size and weighting of alignment and attraction zones, are often quantified via detailed analysis of micro-level interactions over time [53, 54, 55]. These models often further predict certain relationships between group composition of traits and macroscopic group-level behaviour [56, 19], but these individual differences are hard to identify in large groups. As the dependence of group behaviour on trait composition can be inferred from the large amount of data produced, these more detailed predictions can be validated.

Identification of other traits that are associated with social behaviour has also been difficult due to the earlier identified problems with detecting individual qualities in a collective setting. Our method now allows for high throughput analysis of individual aspects of social behaviour and sorting of individuals for later analysis on other traits that might be of interest. Such traits include for instance morphological traits [57, 58] and life-history traits [59]. As we have shown, individual traits can be sorted as long as the group performance is a monotonic function of all member traits.

Our method provides the basis for the experimental design of artificial selection experiments on generic social behaviours. To our knowledge, such experiments have not been attempted to date. This is likely due to the time and resource investment required, and the assumption that the behaviour is subject to confounding inter-individual influence. Our method solves both of these problems. Depending on how the group performance is related to individual performance, it can be used for efficient directional, stabilising or diversifying selection on groups. Selection on social behaviour opens up an experimental route to studying the evolution of social traits.

As an example of how our method could be implemented in practice, a selection experiment for social cohesion (i.e. small inter-individual distance) would start by randomly placing, for instance, eight individuals each in 20 different subpopulations. Each of those groups is then assessed for cohesiveness by means of video cameras and tracking software and they are ranked according to their cohesiveness-score. In the next round new groups are composed by swapping half of the individuals of each group with half of the groups immediately adjacent to them (above and below) on the scoreboard. Here a good catching protocol is essential, because the most daring/proactive/least-stressed individuals will often otherwise be caught first [60], thereby biasing group composition in the next round. To further avoid experimenter bias, the person handling the animals should be unaware of the score of the groups; also the sequence of testing the groups should be randomized. This procedure is repeated until a predefined criterion is reached i.e. a certain number of rounds, or until the ranking of the groups remains stable. The individuals in the top and bottom groups could then be directly compared to determine which traits are associated with group-cohesiveness, or they are used to start an artificial selection experiment. To up- and down-select on group cohesiveness over several generations should elucidate the processes involved in the evolution of sociality.

Various extensions can be made to the models and analysis presented in this paper. A more detailed model selection can be done using the full set of transition probabilities $P_{jk}$, using a Markovian approxi-
mation that the transitions at time $t$ are independent of those at previous times. Moreover, since our method is quite general, the analysis we have presented can be extended to include other models of group performance. For animals which learn to recognise individual conspecifics, a time-dependence may be added to the modelled group behaviour \[61, 62\], although the randomised exchange of group members in each round is expected to mitigate this effect. The analysis can also be extended to multiple traits with different influences on group-level behaviour.

To conclude, we have demonstrated a general and efficient experimental method for enhancing the diversity between groups. Not only does this algorithm produce data useful for inference, but it also leads to many otherwise elusive experiments in collective behaviour, making it possible to bridge the empirical gap between individual properties and collective outcomes.

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Supporting Information

Proof of sortability result

We consider $N$ individuals being sorted in $m$ groups of $n$. The $N$ hidden individual traits are constant in time, and are written in increasing order as \{X(1), ..., X(N)\} $\in \mathbb{R}$.

Let the global ranks in group $j$ in round $t$ be $A_j^1(t)$ through $A_j^n(t)$ in ascending order.

The groups in each round are sorted by their group score

$$g_j(t) = f(X(A_j^1(t)), ..., X(A_j^n(t)))$$ (14)

such that $g_j(t) < g_{j+1}(t)$ for all $j < m$ and $t$.

In odd rounds, mixing occurs between groups $2k - 1$ and $2k$ for all $1 \leq k \leq m/2$, while in even rounds, mixing occurs between groups $2k$ and $2k + 1$ for all $1 \leq k < m/2$. This is assumed to be done by combining into a group of size $2n$ then randomly partitioning back into groups of size $n$.

Let

$$S_j(t) = \sum_{i=1}^{n} A_j^i(t)$$ (15)

be the sum of ranks in group $j$ in round $t$. We expect these to be increasing with $j$ along with $g_j$ if the groups are well sorted. Let

$$Q_j(t) = P(S_j(t) > S_j(t+1)) \forall j < m$$ (16)

be the probability that groups $j$ and $j + 1$ are in the wrong order in terms of the rank sum.

**Proposition 1:** When there is mixing of groups $j$ and $k$ and there is no rearranging between pairs of groups, the sum $S_j + S_k$ is conserved.

**Proposition 2:** Furthermore, if $f$ is monotonic we know $E[S_j(t+1)]$ and $E[S_k(t+1)]$ are both monotonically increasing functions of $S_j(t) + S_k(t)$.

**Proposition 3:** When $f$ is monotonic

$$\forall j, k, t : g_j(t) < g_k(t) \exists r : A_j^r(t) < A_k^r(t)$$ (17)

If $A_j^t(t)$ and $A_j^{t+1}(t)$ are random partitions of the same set at time $t$, this implies the upper bound

$$Q_j(t) \leq \frac{1 - 1/n}{2}$$ (18)

This therefore applies to all groups at $t = 0$ i.e.

$$E[S_j(0)] < E[S_j(t+1)] \forall j < m$$ (19)

since the starting groups are randomly sampled from the population. This observation also applies to each pair of groups upon mixing.

**Theorem 1:** If $f$ is nontrivial and non-decreasing on all arguments, then

$$Q_j(t+2) \leq \lambda Q_j(t) \forall j \in \{2, ..., m-2\}, t$$ (20)

for some $\lambda < 1$ and therefore on average the groups become more homogenous over time.
**Proof:** Consider $m = 4$ groups. At round $t$, groups 2 and 3 are mixed. We know from proposition 3 that $E[S_2(t-1)] < E[S_3(t-1)]$ and $E[S_2(t)] < E[S_3(t)]$. If the pair is anomalous at time $t - 1$, that is, $S_2(t - 1) > S_3(t - 1)$ (which has probability $Q_2(t - 1)$) invoking proposition 1 leaves us with

$$E[S_2(t) - S_2(t - 1)] < 0 \quad (21)$$

and

$$E[S_3(t) - S_3(t - 1)] > 0 \quad (22)$$

In round $t + 1$, groups 1 and 2 are mixed, and groups 3 and 4 are mixed. In this anomalous case, the sum $S_1 + S_2$ is expected to decrease, and the sum $S_3 + S_4$ is expected to increase, since $S_1$ and $S_4$ were unchanged. Using proposition 2, we know that $S_2(t + 1)$ is expected to decrease, and $S_3(t + 1)$ is expected to increase. Therefore

$$P[S_2(t + 1) > S_3(t + 1)|S_2(t - 1) > S_3(t - 1)] < P[S_2(t - 1) > S_3(t - 1)] \quad (23)$$

In the other case at $t - 1$, there is no expected change to $S_2$ and $S_3$.

$$P[S_2(t + 1) > S_3(t + 1)|S_2(t - 1) < S_3(t - 1)] = P[S_2(t - 1) < S_3(t - 1)] \quad (24)$$

By the law of total probability, when $Q_2$ is nonzero, it must decrease by a nonzero amount every two rounds. This proof is easily expanded to $m > 4$ groups.