Indirect genetic effects should make group size more evolvable than expected

David N. Fisher

School of Biological Sciences, University of Aberdeen, King's College, Aberdeen, AB243FX

david.fisher@abdn.ac.uk

Abstract

Group size is an important trait for many ecological and evolutionary processes. However, it is not a trait possessed by individuals but by social groups, and as many genomes contribute to group size understanding its genetic underpinnings and so predicting its evolution is a conceptual challenge. Here I suggest how group size can be modelled as a joint phenotype of multiple individuals, and so how models for evolution accounting for indirect genetic effects are essential for understanding the genetic variance of group size. This approach makes it clear that 1) group size should have a larger genetic variance than initially expected as indirect genetic effects always contribute exactly as much as direct genetic effects and 2) the response to selection of group size should be faster than expected based on direct genetic variance alone as the correlation between direct and indirect effects is always at the maximum positive limit of 1. Group size should therefore show relatively rapid evolved increases and decrease, the consequences of which and evidence for I discuss.

Key words: evolvability, group size, indirect genetic effects, joint phenotypes

Introduction

Understanding the evolution of traits that are jointly contributed to by multiple different organisms and genomes is difficult (Queller, 2014). For example, group size represents how many organisms are acting together within a limited space at a given time. Types of groups include shoals of fish and flocks of birds moving cohesively, offspring and their parent(s) associating prior to dispersal, and even long-term bonds in a monogamous pair can be thought of as groups of two individuals. Group size is an important trait as it impacts various ecological and evolutionary processes that are density dependent (e.g., sexual selection; Kokko & Rankin, 2006; McDonald, 2023). However, group size is not the property of one individual, and so its evolution cannot be modelled in the way we might model the trait of an individual such as its body mass e.g., by quantifying the narrow-sense heritability and measuring selection on it. Multiple, potentially 1000s, of individuals contribute to group size, with each individual contributing a small and equal amount to the overall size of the group. Further, individuals impact both their own group size and the group size of others when they join and leave groups. For instance, consider two groups of four. If one individual leaves one group and joins another, it changes its own group size from four to five, increases the group size of its four new groupmates from four to five, and decreases the group size of its old groupmates from four to three (Fig. 1a). An individual's underlying sociability therefore impacts both the group sizes it experiences and those of others in the population. Understanding the genetic variation underpinning the trait at the population level, and so being able to predict the evolutionary change of the sizes of animal groups (depending on the association with fitness), therefore represents an important but difficult task (see also: Radersma, 2020 for a similar problem for social network phenotypes).

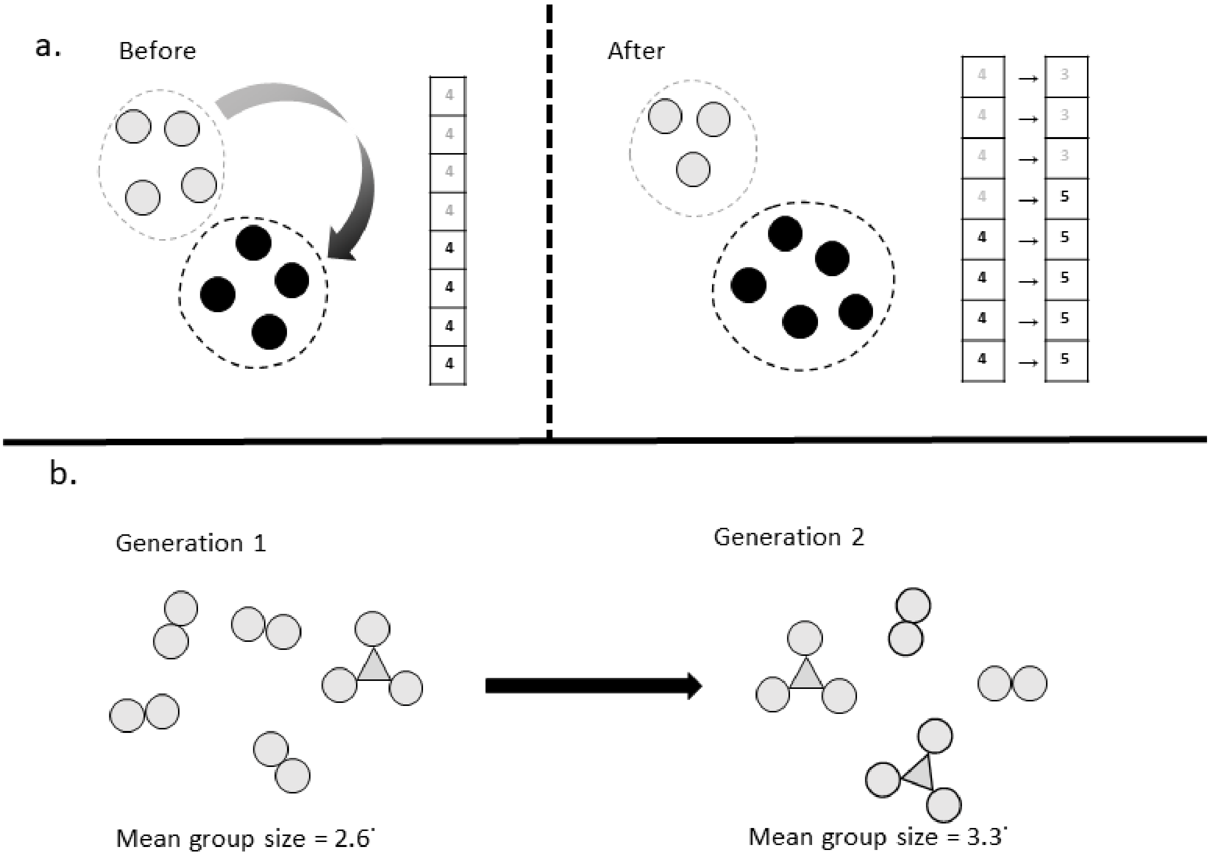
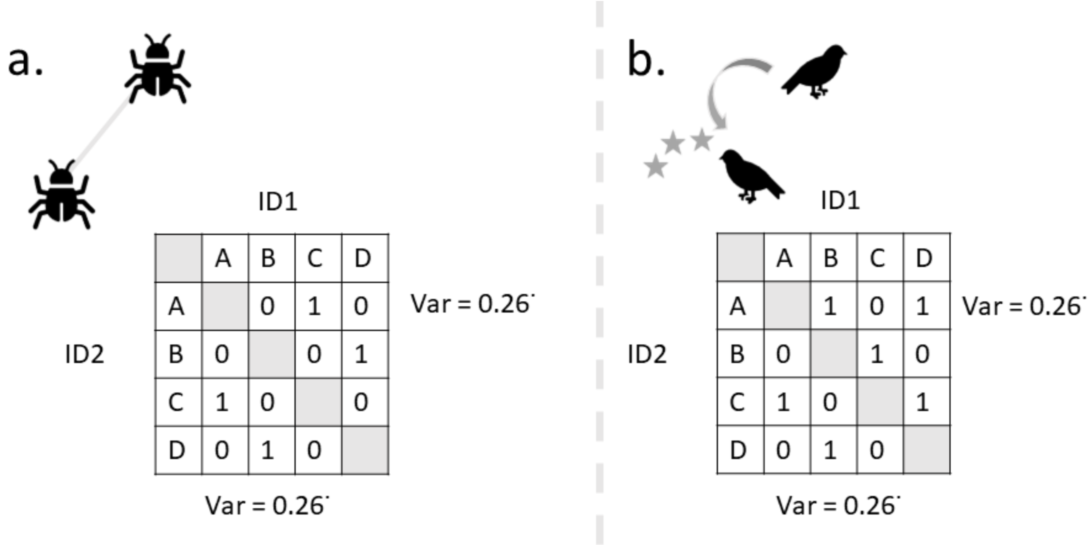


Figure 1. a. Plastic changes in group membership affect many individuals in the population, not just the focal individual. In "Before", we have two groups of four, coloured in grey and black. One of the grey individuals moves into the black group, changing colour as it does, giving the "After" situation. This single movement changes the group size of every individual in the two groups, demonstrating how individuals affect each other's group sizes. b. Evolved changes in sociability

can lead to a rapid evolved change in mean group size. In Generation 1 there is a single sociable individual (the triangle) who associates with three others, while the remaining eight unsociable individuals associate in pairs, giving a mean group size of $2.\dot{6}$. In Generation 2, one of the unsociable individuals has been replaced by a sociable individual, meaning there are ow two groups of four and two pairs, and a mean group size of $3.\dot{3}$; a rapid evolved increase. These two examples show how small changes in sociability can lead to large changes in group sizes.

One approach is to consider group memberships at each time point that a population is surveyed. This assumes that groups can be strictly defined at a given moment in time or for a set period and does not apply to fleeting or ephemeral associations. For each possible pair of individuals in the population, the individuals are either in the same group as each other or not (hereafter “paired or not”, named distinctly to distinguish from the general concept of being in groups of any size). Being paired or not at a given point in time is therefore a binary trait under control of two individuals (even when overall groups are larger than two, paired or not always refers to two individuals). Note that we are not considering individual’s preferences for particular others here, just their general tendency to be with other individuals in the most general sense. We expect that an individual’s tendency to be paired or not will be influenced by its underlying sociability or gregariousness (Gartland *et al.*, 2022), a latent trait we cannot directly observe but through how often an individual is paired with others. Additionally, what is key is that, unlike traits that are completely under the control of the focal individual (such as eye colour), the phenotypic and genetic variance of traits influenced by two (or more) individuals, such as being paired or not, has both direct sources, stemming from the focal individual, but also indirect sources, stemming from the partner. In the case of being paired or not, an individual’s trait will be influenced by both its own sociability (and genetic variance for that) and the sociability of its partner (and the genetic variance for that; note that the designation of focal and partner is arbitrary). In fact, in this formulation both individuals contribute exactly equally to the trait of being paired or not, and therefore the variance attributable to focal and partner individuals is identical.

For a population of size *k* at a given point in time, it is instructive to represent the paired status as a binary and symmetrical matrix **K** of *k* x *k* dimensions, where cells *i, j* and *j, i* are coded as “1” if individuals *i* and *j* are paired in the same group and coded as “0” if they are not (the diagonal itself is left blank; Fig. 2a). Mean group size can be recovered from this matrix by $1 + [\frac{\sum \boldsymbol{K}}{k}]$, allowing comparison between the paired or not phenotype and groups size, a more common summary of population social structure. In Fig. 2a names of the columns indicate the (arbitrarily defined) focal, while names of the rows indicate the (arbitrarily defined) partner. Note how the matrix in Fig. 2a is symmetrical; there is exactly the same pattern of 0s and 1s on either side of the diagonal. Therefore, the variances of direct and indirect effects for the trait of paired or not are identical. This can be extended to cases where we have data on the number of times two individuals are paired. If there are *t* observations, we have a symmetrical matrix $\mathbf{K}_t$ where valued terms replace the 1s. Mean group size in this case is recovered through $1 + [\frac{\sum \boldsymbol{K_t}}{kt}]$. For both the binary and the valued cases, because an individual that is paired as a focal will also be paired as a partner, the correlation between a focal individual's scores and those of its partners must be exactly 1. The fact that we have exactly identical direct and indirect variances and a perfect, positive correlation between them has interesting consequences when we consider the evolutionary potential of the trait of paired or not, and therefore of group size.



a.

	A	B	C	D
A		0	1	0
B	0		0	1
C	1	0		0
D	0	1	0	

b.

	A	B	C	D
A		1	0	1
B	0		1	0
C	1	0		1
D	0	1	0	

Figure 2. a. When modelling group size using an indirect genetic effects model, individuals contribute both to their own values for being paired, and to the values of others. Their contributions as the focal (ID1) and partner (ID2) are identical, and so the variances are the same and their correlation is exactly 1. B. When modelling the outcome of dyadic contests for dominance in the same way, we see that individuals contribute to the outcome both as a focal and as a partner, but in this case their contributions are exactly opposite, and so, while the variances are equal, the correlation is exactly -1.

The evolutionary potential of a trait is defined by its additive genetic variance. Typically, we only consider the *direct* additive genetic variance, i.e., how the genes in a focal organism influence its own trait. However, when other individuals influence the trait value, then we must also account for *indirect* additive genetic variance i.e., how the genes in others influence the focal's trait value (Scott & Fuller, 1965; Griffing, 1967; Moore *et al.*, 1997). Indirect genetic effects can contribute substantial additional genetic variance to morphological, life history, physiological, and behavioural traits (Ellen *et al.*, 2014). Further, as I have argued above, indirect genetic effects must contribute exactly as much to the total genetic variance of the trait of paired or not as direct genetic effects do. In essence, individuals with genetic variants that increase their sociability will join groups more often, and therefore will increase the group sizes of other individuals in the population. This greatly increases the evolutionary potential of the trait, as a small increase (decrease) in sociability across generations will increase (decrease) the frequency at which individuals are with others, altering the group size of large portions of the population (Fig. 1b).

To quantify the change in evolutionary potential brought about by indirect genetic effects, we can consider the total heritable variance in a trait with and without indirect genetic effects. The trait we are considering here is whether an individual is paired or not with each other individual in the population (giving $k(k-1)$ measures), rather than mean group size or total number of individuals in the group. The total heritable variance ($\hat{\sigma}_H^2$) reflects the amount of variation of a trait in a population which is underpinned by genetic variation, rather than environmental or stochastic variation. $\hat{\sigma}_H^2$ in the absence and presence of indirect genetic effects is shown in *eqs. 1* & *2* respectively (Bijma, 2011). In *eq. 1* it is simply equal to the direct additive genetic variance ($\sigma_{A_D}^2$).

$$\hat{\sigma}_H^2 = \sigma_{A_D}^2 \qquad \textit{eq. 1}$$

In *eq. 2* (including indirect genetic effects) $\hat{\sigma}_H^2$ includes $\sigma_{A_D}^2$, the indirect additive genetic variance ($\sigma_{A_I}^2$), and twice the covariance between direct and indirect effects ($\sigma_{A_{DS}}$).

$$\hat{\sigma}_H^2 = \sigma_{A_D}^2 + 2\,\sigma_{A_{DS}} + \sigma_{A_I}^2 \qquad \textit{eq. 2}$$

Note that this is the same calculation as for the more familiar maternal genetic effects model (Mousseau & Fox, 1998). Note also that in models where more than two individuals interact the number of interacting individuals (or the group size, *n*) minus one is included in the calculation (Bijma & Wade, 2008), but since we are modelling our phenotype as a product of only and always exactly two individuals interacting, *n*-1 always equals 1 and so does not affect the sum. What is clear in the case of being paired or not is that, as $\sigma_{A_{DS}}$ is guaranteed to be positive, *eq. 2* will always be larger, and potentially much larger, than *eq. 1*. Therefore, being paired or not, and so group size, will have a larger total heritable variance than initially expected based on $\sigma_{A_D}^2$ alone and therefore could have substantial potential for evolution.

Further, when predicting the response to selection, the covariance between direct and indirect genetic effects can radically alter our estimates (Moore *et al.*, 1997). The response to selection (change in mean phenotype across a single generation; $\Delta\bar{P}$) in the absence of indirect genetic effects is given in *eq. 3*; it is simply the product of the selection gradient (β) and the direct additive genetic variance (Muir, 2005; Bijma & Wade, 2008):

$$\Delta\bar{P} = \beta\sigma_{A_D}^2 \qquad \textit{eq. 3}$$

Meanwhile, the response to selection in the presence of indirect genetic effects includes the direct indirect genetic covariance:

$$\Delta\bar{P} = \beta[\sigma_{A_D}^2 + \sigma_{A_{DS}}] \qquad \textit{eq. 4}$$

Positive values of $\sigma_{A_{DS}}$ greatly enhance the response to selection, speeding evolution, while negative values can reduce, remove, or even reverse the response to selection (Bijma *et al.*, 2007; Bijma & Wade, 2008), potentially causing evolutionary change to move in the opposite direction to selection (Fisher & Pruitt, 2019). In the case of being paired or not, as I have argued above, we must have a strong (the strongest possible) positive covariance between direct and indirect genetic effects. Individuals with genes that predispose them to join others and so make groups larger also cause other individuals to be with others and so be in larger groups (or be in a group at all). Therefore, group size has a larger evolutionary potential than initially expected, as both direct and indirect genetic effects must contribute to its total genetic variation, and evolutionary responses will be especially rapid as these direct and indirect effects are also perfectly positively correlated.

Interestingly, this is the exact inverse situation to that of another trait expressed jointly: outcomes in dyadic contests for dominance. In the case of dyadic contests, each contest must have one winner and one loser. These outcomes are therefore perfectly *negatively* correlated, as if the focal individual wins its partner always loses, and vice versa. As Wilson *et al.* (2011) have highlighted, the indirect genetic variance for outcomes in dyadic contests must equal the direct genetic variance, as designation of focal and partner is again arbitrary and so both contribute equally to the outcome. Further, the direct-indirect genetic correlation must be -1, as individuals with genes that predispose them to win contests cause other individuals to lose contests. Another way of thinking about this is to consider the matrix in Fig 2b, which shows the outcomes of dyadic contests in a population. This matrix is asymmetrical; if there is a “1” in a cell in the top right half, there is a “0” in the corresponding cell on the opposite side of the diagonal in the bottom left half, and vice versa. The consequences for the predicted evolution of average dyadic contest outcome are stark: evolutionary change in the trait mean becomes *impossible* as predicted increases through direct effects are always exactly cancelled out by changes in the opposite direction in indirect effects (this appeals to our common sense, half of all in the individuals participating in dyadic contests must lose [trait value of 0], while half win [trait value 1], and so the mean trait value can never differ from 0.5, and so should never be able to evolve; Wilson *et al.*, 2011).

The cases of paired or not and the outcomes of dyadic contests are exact mirrors of each other; in both cases the direct genetic variance must equal the indirect genetic variance, and for both we expect perfect correlations between direct and indirect genetic effects. However, for paired or not this is a perfect positive correlation (Fig. 2a), while for outcomes of dyadic contests it is perfectly negative (Fig. 2b). Therefore, while for dyadic contest outcome we never expect evolution, for paired or not (and so group size) we expect relatively rapid evolutionary changes (which could be increases or decreases in mean group size).

While the result for paired or not might seem esoteric, it is actually quite intuitive. If an individual starts off alone, and then joins a group (of size n), they increase not only their own group size (from 1 to $n + 1$) but also the group size of all those already in the group (from n to $n + 1$). If this initially lone individual and the group they join are the only animals in the population, the mean group size in the population goes from $(1 + n*n)/ (n+ 1)$ to $n + 1$, a rapid increase at the population level given only one individual changed its behaviour (if n was 30 this is an increase from 29.06 to 31). If we imagine the same process, but instead of plastic change within a generation, evolved change across generations, it is easy to see how rapid changes in group size can occur (see also Fig. 1). Even small increases in sociability will give a rapid increase in mean group size as not only are the more sociable individuals in larger groups, but even those with the same underlying tendency to be sociable as the previous generation have a higher mean group size, as they are more often being joined by the more sociable individuals (Fig. 1b). This is true independently of the conceptual framework used to understand it; my use of indirect genetic effects is merely a tool to make accurate predictions about change across generations. It might seem more straightforward to measure sociability directly, and to estimate its heritability and selection on it, but sociability is a latent trait that can only be inferred from observations of individuals interacting with others, and so it always needs untangling from indirect effects (Fisher, 2023). When we observe individuals forming groups, the phenotypes we are observing are inherently a product of at least two genomes, a phenomenon that evolutionary models incorporating indirect genetic effects, which I highlight here, are specifically designed to account for (see also: Queller, 2014).

Consequences of the higher evolvability of group size

The primary consequence of the increased total heritable variance in group size is that we expect to see relatively rapid increases (decreases) across generations in mean group size when selection favours (disfavours) larger groups. Note that the initial genetic variation in being paired or not may still be quite small, especially if environmental variation strongly influences grouping, and so the total heritable variation in group size may not be large in the absolute sense, but it should always be larger than that expected from direct genetic effects alone. Group size is commonly linked to fitness, as it can provide protection for predators and access to mates and other resources, but also be associated with increased food competition and exposure to disease. Variation in group size may therefore often be linked to variation in fitness, and so individual sociability may be under selection in a range of systems (Snyder-Mackler *et al.*, 2020; Gartland *et al.*, 2022; selection on group size is discussed more below). Given we now expect a higher degree of genetic variation in group size, evolved changes should be common, albeit I have no general expectations about a direction (i.e., I do not expect animals to be typically evolving to live in larger or smaller groups). In the presence of consistent directional selection, we expect group sizes to rapidly evolve in line with selection (*eq. 4*). Even if selection was weak and highly variable in direction, we would still expect relatively rapid changes in group size across generations as there is large amounts of genetic variation, but these will be both increases and decreases, and so mean group sizes should be highly variable around a mean value over evolutionary time. However, as noted above, the trait of paired or not could have exceptionally low direct genetic variance if the tendency to be paired is strongly influenced by environmental effects such as current resource availability or predation risk. In this case, even the addition of indirect effects may not raise the total heritable variance to a particularly high level, keeping the rate of evolutionary change low. Directly estimating the direct and indirect genetic variance in the tendency to be in pairs in wild populations is key for understanding the trait's evolutionary potential, and therefore the evolutionary potential of group size.

A high variability of group size over evolutionary timescales would mean that other ecological and evolutionary processes that depend on group size should also be highly variable. For instance, the spread of an infection through a population can depend on the typical group size, if transmission is fast within groups and not between them (Nunn *et al.*, 2015). Fewer, larger groups will then allow a faster spread than many small groups. If group sizes are variable across generations, then the speed of disease spread, or indeed any processes that is influenced by group size, will also be highly variable. This high degree of variability means that making predictions for timescales encompassing multiple generations will be difficult.

In the presence of direct selection for larger groups, we would expect to see a rapid increase in group size. For short-lived species such as some insects, multiple generations can occur in a year or even season, and so evolved changes in group size might be observably on those timescales. We already are aware that large aggregations of pest insects such as desert locust (*Schistocerca gregaria*) can appear seemingly from nowhere, with plastic changes in aggregative behaviour assumed to be behind this (Uvarov, 1921; recently reviewed in: Simpson, 2022). However, evolved changes in sociability and therefore group size might also contribute if selection for larger groups emerged, given that those changes could be very rapid. The importance of evolved changes for outbreaks in desert locust is likely limited due to their generation times (although changes in social behaviour across generations do appear possible; Roessingh *et al.*, 1993) but in short-lived species such as *Drosophila spp.* the importance of evolved changes is more plausible (Behrman *et al.*, 2018).

The evolution of group size as discussed here may also apply to the evolution of multicellularity. In a population of unicellular organisms, a mutant cell that adheres to or joins other individuals forms a multicellular aggregation not just for itself, but for the other individual(s) it has joined (Fig. 1b). Change in mean phenotype (the number of cells grouped together) could then change relatively quickly as more “sociable” cells (such as those *Saccharomyces cerevisiae* that express flocculin proteins that bind cells together; Belpaire *et al.*, 2022) would lead to many cells being involved in multicellular aggregations, whether the other cells have an innate tendency to group or not. Further work on facultatively multicellular organisms such as *S. cerevisiae* under artificial selection for “floc” formation (Fisher & Regenberg, 2019) could test whether the evolution of multicellularity is faster than that expected based on direct genetic variance for production of flocculin proteins alone.

Selection on group size

While this article is focused on the total heritable variation in group size, when considering the evolution of this trait we must also consider selection on group size, and how that depends on the type of genetic variation available. For species that form groups, we often expect the relationship between group size and fitness to be humped, such that fitness for individuals within a group increases with increasing group size up to an optimum, and then declines (Sibly, 1983). The shape of this relationship might be due to initial benefits such as detection of predators with increased group sizes, and but increased costs of group size after a point such as risk of transmission of diseases at especially high group sizes. In standard models for phenotypic selection, this could be captured through the use of linear and quadratic selection gradients, where we would expect a positive linear gradient and a negative quadratic one (Phillips & Arnold, 1989). Note that for group size to have fitness consequences the associations need to be more than simply ephemeral co-locations in space and time, which fits within my general definition of groups given above.

As group co-membership is a joint phenotype, it is partly under control of both current group members and those other individuals who may be alone or in other groups who wish to join another group. This means there can be a conflict of interest (in terms of fitness outcome) for individuals joining an existing group (Giraldeau & Caraco, 1993; Higashi & Yamamura, 1993). If a group is at the optimum size, additional individuals joining would imply fitness costs for the current group members, as they are now in a group larger than the optimum. In contrast, from the perspective of the joining individual, their fitness is likely to be increased by joining, as they transition from being alone into a group that will give them higher fitness, even if it is above the optimum group size (Sibly, 1983). The resolution of this conflict depends on both who controls group membership (current group members or joining individuals) and the relatedness between interacting individuals (Giraldeau & Caraco, 1993; Higashi & Yamamura, 1993). The fact that joining individuals can reduce the fitness of current group members indicates that a form of negative social selection is acting on group membership, when the trait of one individual reduces the fitness of others (Wolf *et al.*, 1999), which could lead to mean fitness in the population being below the maximum possible (“maladaptation”; McGlothlin & Fisher, 2021). Further, social selection interacts with indirect genetic effects (which we expect to be ubiquitous for group co-membership) to influence the phenotypic response to selection (along with relatedness; Bijma & Wade, 2008). As we now always expect a positive correlation between direct and indirect effects, the additional effect of indirect genetic effects should be to accelerate the response to selection, in whichever direction the combination of relatedness and direct and social selection suggests (Bijma & Wade, 2008; see also: McGlothlin *et al.*, 2014).

Finally, a note on group-level (or among-group) selection gradients (Goodnight *et al.*, 1992; Okasha, 2004a). Within a single observation, all individuals within a group have the same group size. Therefore, at this temporal scale there can be no within-group selection gradient for this trait, and all selection must manifest itself at the among-group level (if taking a Price covariance approach, partitioned to the among-group covariance rather than the within-group covariance; Okasha, 2004b). Across multiple observations, individuals can be part of many groups, and so fitness due to group size can vary both within and among groups. This would imply that selection can indeed act at multiple levels. Care therefore should be taken when estimating and interpreting selection gradients; understanding what they mean both in isolation and what can be inferred from the combination of within- and among-group selection (Goodnight *et al.*, 1992).

Evidence for the evolvability of group size

Above I have outlined that we expect group size to be highly evolvable, given that there should be genetic variance from indirect and well as direct sources in the tendency to be paired with other individuals, and the covariance between these will always be positive. Is there any empirical evidence that allows us to evaluate whether this is the case or not? The one case study I am aware of indicated that sociability does indeed have genetic variance, and responds to selection, but we cannot evaluate whether it is at the pace expected. Scott *et al*. have determined that sociability is heritable in both male (h^2 = 0.24) and female (h^2 = 0.21) fruit flies *Drosophila melanogaster* (Scott *et al.*, 2018), and that it increases (decrease) in response to artificial selection for higher (lower) sociability (Scott *et al.*, 2022). In their study, sociability was measured by allowing 16 flies in an arena to form groups (Scott *et al.*, 2022), and so was analogous to being paired or not and also mean group size; the formulation of grouping using in the current article. Scott and colleagues have therefore effectively assessed whether mean group size responds to artificial selection. They found it did, with an increase of 40% in females and 54% in males over 25 generations. Scott *et al*. (2022) performed within-group selection, taking the four most (or least for the down-selected lines) sociable flies in each of 12 groups, for both males and females, per generation. This mode of selection does not take advantage of any genetic variation among groups (Muir, 2005; Muir *et al.*, 2013), and so it is not clear whether the observed response is faster or slower than that expected by the narrow sense heritabilities found in their earlier work, and therefore if it is as fast as that predicted by the model of evolution accounting for indirect genetic effects I present here. Nevertheless, this study does at least show that group size responds to artificial selection, and so must possess some genetic variance. Further work would need to select for the most sociable animals across all individuals within a population, not just within each group, and measure the increase of group size across generations, in order to test the prediction that the evolution of group size should be relatively rapid.

Indirect effects on sociability itself

A final consideration is that an individual's sociability itself may be influenced by indirect genetic effects. An individual's decision to join or leave groups may be influenced by the traits of the other individuals already in those groups. If those traits are partly genetically determined, then there will be indirect genetic effects on sociability (Fisher, 2023). Therefore, an individual's *willingness* to join a group will be influenced by the genes of others (Fisher, 2023), but also its *realised* group size will be influenced by the genes of others (this article). The overall heritability of group size may therefore be influenced by direct genetic effects for sociability (individuals' have an underlying preference to be with others that is partly genetically determined), indirect genetic effects for sociability (an individual's preference to be with others depends on their traits and therefore also their genes), and indirect genetic effects for group size (the sociability of others, and therefore their genes, influences the realised group size of an individual), plus the covariances among these components. Predicting the outcome of this is complicated, but parallels may be drawn with models for the heritability of social phenotypes in social networks using latent variables representing the tendency to be social and the contribution to social associations (Radersma, 2020).

Conclusions

In summary, I have suggested that the evolution of group size can be understood using an indirect genetic effects model. This model predicts that group size should have a relatively large genetic variance and so should respond surprisingly rapidly to selection. This high evolvability will increase the variability in demographic, ecological, and evolutionary processes that depend on group size. Testing whether this prediction is true or not is the next step.

Acknowledgements

I am grateful to Alastair Wilson and Ben Jarrett for comments and suggestions on an earlier draft, and to the two anonymous reviewers whose critique improved the initial submission. I have no conflicts of interest.

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