Indirect genetic effects should make group size highly evolvable

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Abstract

Group size is an important trait is 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 present a suggestion for 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 large genetic variance as indirect effects always contribute exactly as much as direct genetic effects and 2) the response to selection of group size should be rapid as the correlation between direct and indirect effects is always at the maximum positive limit of 1. Group size should therefore show 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

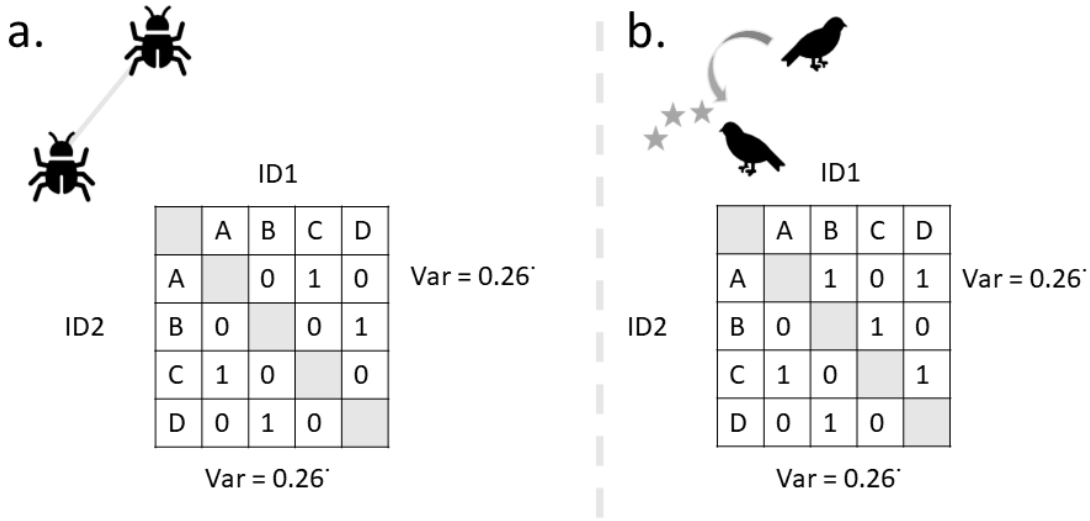
Understanding the evolution of traits that are jointly contributed to by multiple different organisms and genomes is difficult (Queller, 2014). For example, group size is an important trait as it impacts various ecological and evolutionary processes that are density dependent (e.g., sexual selection; Kokko and 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 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. 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, therefore represents an important but difficult task (see also: Radersma, 2020 for a similar problem for social network phenotypes).

One approach is to consider group memberships at each time point that a population is surveyed. 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 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 left blank; Fig. 1a). 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. 1a 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, giving a symmetrical matrix where valued terms replace the 1s. Further, 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	B	C	D
A		0	1	0
B	0		0	1
C	1	0		0
D	0	1	0	

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

Figure 1. 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 trait value (Griffing, 1967; Moore et al., 1997; Scott and Fuller, 1965). Indirect genetic effects can contribute substantial additional genetic variance to morphological, life history, physiological, and behavioural traits (Ellen et al., 2014), and as I have argued above 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 join groups, altering the group size of large portions of the population.

To quantify this change in evolutionary potential we can consider the total heritable variance in a trait with and without indirect genetic effects. Total heritable variance ($\hat{\sigma}_H^2$) in the absence and presence of indirect genetic effects are 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 and 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 and 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 should 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. The response to selection (change in mean phenotype across a single generation; ΔP) 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 (Bijma and Wade, 2008; Muir, 2005):

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

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

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

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 and Wade, 2008), potentially causing evolutionary change to move in the opposite direction to selection (Fisher and 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 large evolutionary potential, 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 1b, which shows the outcomes of dyadic contests in a population. This matrix is asymmetrical, where 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 direct 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. 1b), while for outcomes of dyadic contests it is perfectly negative (Fig. 1c). Therefore, while for dyadic contest outcome we never expect evolution, for paired or not (and so group size) we expect rapid evolutionary changes (which could be increases or decreases in mean group size).

While the above might seem esoteric, the result 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, this means 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. Even small increases in sociability can lead to 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. 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 directly studying it is often not possible. When we observe individuals forming groups, the phenotypes we are observing are inherently a product of at least two genomes, a phenomenon evolutionary the models incorporating indirect genetic effects I highlight here are specifically designed to account for.

Consequences of the high evolvability of group size

The primary consequence of the large total heritable variance in group size is that we expect to see rapid increases (decreases) across generations in mean group size when selection favours (disfavours) larger groups. 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 (Gartland et al., 2022; Snyder-Mackler et al., 2020). Given we now except a high 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. A caveat to this is that 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. Therefore, 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 traits 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 can appear seemingly from nowhere, with plastic changes in aggregative behaviour assumed to be behind this (Simpson et al., 1999). However, evolved changes in sociability and therefore group size might also contribute, given that those changes could be very rapid.

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 arenas containing 16 flies to form groups, and so was analogous to being paired or not and also mean group size (Scott et al., 2022). They 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-selection lines) sociable flies in each of 12 groups for 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. 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 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 especially rapid.

Indirect effects on sociability itself

A final consideration is that the sociability itself of an individual is 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 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 large genetic variance and

so should respond very 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.

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