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Group selection versus group adaptation

ARISING FROM J. N. Pruitt & C. J. Goodnight *Nature* **514**, 359–362 (2014); doi:10.1038/nature13811

Pruitt and Goodnight¹ describe how the ratio of aggressive versus docile females varies among naturally occurring colonies of the social spider *Anelosimus studiosus*, with larger colonies exhibiting more aggression in high-resource environments and the reverse in low-resource environments. They experimentally manipulate this ratio to show that it influences a colony's reproductive success. Pruitt and Goodnight¹ conclude that this work demonstrates group-level adaptation and contradicts an earlier theoretical analysis². Here, I show that this conclusion is unfounded and arises from a conceptual misunderstanding. There is a Reply to this Brief Communication Arising by Pruitt, J. N. & Goodnight, C. J. *Nature* **524**, <http://dx.doi.org/10.1038/nature14597> (2015).

While Pruitt and Goodnight¹ provide evidence of group-level selection, they do not provide any evidence of group-level adaptation, as defined in the earlier analysis². A response to group-level selection occurs when there is heritable variation in group fitness and—along with selection acting within groups—this may contribute to evolutionary change^{3,4}. Owing to the mathematical equivalence of multilevel-selection and kin-selection analysis, this is entirely consistent with individuals being adapted to maximize their inclusive fitness³. In contrast, group-level adaptation is the stronger notion that phenotypes are optimized for the good of the group, a design objective that is typically in conflict with the individual's inclusive-fitness interests and which will rarely be favoured by natural selection^{2,5}. Other definitions of

group-level adaptation are possible, but this is the definition given in the earlier analysis² that Pruitt and Goodnight¹ claim to have refuted. Pruitt and Goodnight¹ present evidence that levels of aggression have been, at least in part, moulded by group-level selection, but they do not show that this ratio is optimized for the good of the group.

To illustrate this point, I adapt Frank's⁶ 'tragedy of the commons' model to study a scenario where aggressive individuals are competitively superior within groups but an intermediate level of aggression, depending on colony size and resource availability, is favoured at the group level (see Methods). The resulting level of aggression favoured by natural selection: (1) is that which balances within-group and between-group selection pressures and, accordingly, maximizes the individual's inclusive fitness; (2) increases with colony size in high-quality environments and decreases with colony size in low-quality environments, in line with the data of Pruitt and Goodnight¹; and (3) is generally higher than that which maximizes group fitness (Fig. 1). Accordingly, the data presented by Pruitt and Goodnight¹ neither invalidate the idea that individuals are adapted to maximize their inclusive fitness nor validate the idea that the colony is adapted to maximize its own fitness.

Pruitt and Goodnight¹ also claim that the earlier theoretical analysis² had suggested that group-level adaptation can occur only in the context of clonal groups. This is incorrect, as the analysis made clear that group-level adaptation can occur in genetically heterogeneous groups, as long as there is a mechanism for suppressing within-group conflict². Well-studied examples of such mechanisms are fair meiosis^{7,8} and worker policing in honeybees^{8,9}. Interestingly, Pruitt and Goodnight¹ suggest that policing may occur in *A. studiosus* colonies. If true, then there is scope for group-level adaptation, but further study would be needed to confirm this.

These points echo remarks made by Maynard Smith⁵, in connection with a different phenotypic polymorphism: females versus males. The sex ratio is perhaps the best-studied social-evolutionary trait, and provides some of the best quantitative evidence for Darwinian adaptation in the natural world¹⁰. Certain female-biased sex ratios are recognized to be driven, in part, by selection acting at the level of the group^{11,12}, and experimental manipulations have confirmed the impact of group sex ratio on group fitness¹³. But Maynard Smith⁵ cautioned that, because the sex ratio that evolves is not that which maximizes group fitness, but rather that which balances within-group and between-group selection pressures, it does not constitute a group-level adaptation. Instead, it represents the adaptation of individual organisms, for the purpose of maximizing their inclusive fitness.

Methods

A female's fitness is $w = fg$, where $f = x/y$ describes her within-group advantage if she is aggressive with probability x and the average female in her colony is aggressive with probability y ; and $g = y^b(1 - y)^{1-b}$ describes her colony's fitness.

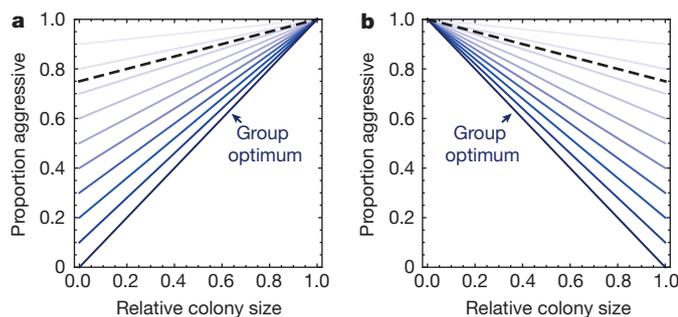


Figure 1 | Individual versus group optima. The proportion of aggressive individuals resulting from the maximization of the individual's inclusive fitness is plotted for a range of coefficients of relatedness, from $r = 0$ (lightest shading) to $r = 1$ (darkest shading), with the estimate of Pruitt and Goodnight¹ $r = 0.25$ marked as a dashed line. The group optimum corresponds to the $r = 1$ line; that is, when natural selection is acting only at the level of the colony. **a**, In high-resource environments, the level of aggression that maximizes the individual's inclusive fitness increases with colony size, in line with the data of Pruitt and Goodnight¹, and typically exceeds that which maximizes colony fitness. **b**, In low-resource environments, the level of aggression that maximizes the individual's inclusive fitness decreases with colony size, in line with the data of Pruitt and Goodnight¹, and typically exceeds that which maximizes colony fitness.

In high-resource environments $b = n$, where n denotes relative colony size, reflecting the finding of Pruitt and Goodnight¹ that aggression is relatively more important for colony survival in this setting; and in low-resource environments $b = 1 - n$, reflecting the finding of Pruitt and Goodnight¹ that the opposite is true in this setting. In both cases, the intermediate inclusive-fitness optimum z^* satisfies $((\partial w/\partial x) + r(\partial w/\partial y))|_{x=y=z^*} = 0$ (ref. 6).

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Pruitt & Goodnight reply

REPLYING TO L. Grinsted, T. Bilde & J. D. J. Gilbert *Nature* **524**, <http://dx.doi.org/10.1038/nature14595> (2015); A. Gardner *Nature* **524**, <http://dx.doi.org/10.1038/nature14596> (2015)

In Pruitt and Goodnight¹ we provided experimental evidence that group selection has contributed to a group-level adaptation in the social spider *Anelosimus studiosus*. Grinsted *et al.*² provide a wide diversity of system-specific critiques of our original study. In contrast, Gardner³ highlights differences between our definition of ‘group level adaptations’ and his own. He further describes a model that recreates some of the dynamics seen in *Anelosimus studiosus*. Below, we address the critiques of Grinsted *et al.*² first and Gardner³ second.

Grinsted *et al.*² claim that documenting group selection requires that one rule out evidence of individual selection; we believe that this is incorrect. Group selection occurs when there are differences among groups in their survival or reproductive output as a consequence of their traits^{4–6}, which is what we showed in our paper¹. It is widely agreed that individual selection, group selection and kin selection act simultaneously in most societies. The controversy is whether group selection contributes significantly to adaptations in the wild^{7,8}. We provided evidence that group selection has contributed to a group-level adaptation in *Anelosimus studiosus*¹. Our case study is clear because both the target and agent of selection are above the level of the individual: the target of selection (group composition) is a trait that an individual cannot have, and the agent of selection (extinction) is the textbook example of strong group selection^{9–11}. We showed that *A. studiosus* colonies live or die as a unit¹¹ because of their behavioural composition¹. None of the criticisms of Grinsted *et al.*² weakens this claim.

Grinsted *et al.*² argue that individual traits could underlie colony extinction events—we agree with this assertion. All collective traits can be decomposed into the traits of constituents. A group cannot perish unless the individuals within it die too. Grinsted *et al.*² merely want us to focus on a different, non-mutually exclusive, level of analysis. Following their logic, all behavioural studies would be flawed because behaviour can be decomposed into physiology, genetics, applied physics, and so on. Thus, the arguments of Grinsted *et al.*² aren’t against group selection per se, but instead it seems they take issue with the word ‘group’.

Grinsted *et al.*² argue that the interests of individuals and groups are united in *A. studiosus*, and we agree. This is because group selection (extinction) is the major force driving individual fitness. Grinsted

*et al.*² make reference to group selection requiring reproductive skew, and this would appear to suggest that they are conflating group selection with altruism⁷—these are different concepts. There is controversy whether group selection can beget altruism in the absence of relatedness¹², which our data don’t address. Yet, there is also interest in understanding the intensity of group selection acting in nature and how group selection varies across environments^{4,13}, which is the subject of our paper.

Grinsted *et al.*² demonstrate that the naturally occurring relationship between group composition and group size at each site differs across years. In particular, they note that the significance of the relationship between group size and composition vanishes in four out of our eighteen observations. Yet, with only one exception, the estimated relationships are always positive for high resource sites and negative for low resource sites. These trends are robust in spite of the inherent variability encountered by any field study. Grinsted *et al.*² fail to address the key issue of how our supposedly ‘weak’ baselines accurately predict colony survival. If these empirical relationships were truly unreliable then they would not accurately predict anything, thus the criticism of Grinsted *et al.*² is unfounded.

Grinsted *et al.*² claim that one must watch selection at each generation to document selection on group composition. However, that would disrupt the very processes that we were quantifying. Our results demonstrate unequivocally that the composition of the parental generation (P) predicts the number of grand-offspring (F₂) produced by colonies at all six sites. One rarely obtains a higher calibre field estimate of fitness than that.

Grinsted *et al.*² claim that we measured spiders at different developmental stages. In fact, we only measured mature females throughout our study. While our colonies had an accelerated phenology, we showed that this does not impact their performance¹. Aggressiveness varies with temperature¹⁴ and gravidity¹⁵ in *A. studiosus*, which could be problematic. Thankfully, rank order aggressiveness is maintained in spite of this plasticity¹⁴, thus allowing reliable assignment of either phenotype. The criticism of Grinsted *et al.*² that *A. studiosus* typically live solitarily is true but irrelevant. *Anelosimus studiosus* typically live in multi-female colonies at these sites¹⁶. Regardless, this wouldn’t compromise any of our findings.