# Questioning evidence of group selection in spiders

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

Any field study showing convincing evidence of group selection would be a significant contribution to the field of evolutionary biology. Pruitt and Goodnight[1] claim to provide such evidence in a 14–18-month field experiment on spiders. However, we contend that apparent flaws in their predictions, assumptions, methods and interpretations undermine this claim. We believe that the data presented are unreliable and are equally consistent with both group selection and individual-level selection; thus, we question the conclusion of Pruitt and Goodnight[1] that group selection has produced the observed patterns. 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).

Evaluating group selection involves, at a minimum, estimating and comparing both individual and group fitness, as stated by previous reviews[2,3] and performed by other studies[4,5]. However, Pruitt and Goodnight[1] did not estimate individual fitness, and so cannot evaluate the relative importance of group selection compared to individual-level selection. The chosen species, *Anelosimus studiosus*, is solitary, rarely forms groups[6], and shows no evidence of reproductive restraint or skew within groups[7]. Thus, individual and group fitness are not expected to conflict and are generally confounded, emphasizing how crucial it is, first, to formulate predictions capable of distinguishing individual-level selection and group selection explanations and, second, to estimate individual fitness.

Both predictions of Pruitt and Goodnight[1] could follow equally well from individual-level selection as from group selection. Their first prediction is "compositions that approximate the normal mixtures that characterize each site will enjoy greater success", where 'compositions' refers to within-group phenotypic frequencies. Merely demonstrating differential survival of groups does not allow the authors to distinguish successful groups from groups of successful individuals. The 'group trait' of Pruitt and Goodnight[1] is a group-size-dependent behavioural polymorphism. Experimental changes in this group trait (that is, manipulating group size and phenotype frequency) may directly affect within-group individual fitness just as well as whole-group fitness[8–11]. Specifically, creating experimental groups that deviate from locally stable polymorphisms may reduce mean individual fitness, rendering group extinction more likely. The prediction of

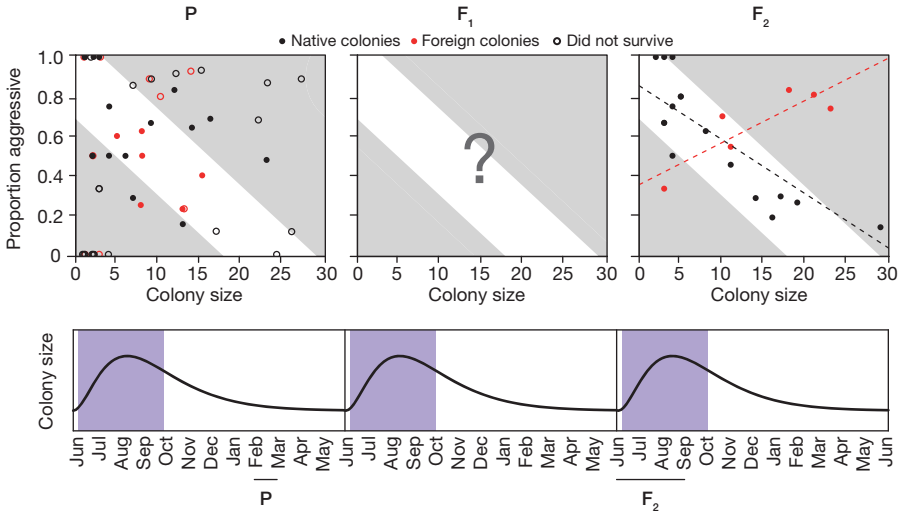


**Figure 1 | Overview of methods and results from Pruitt and Goodnight[1].** The top panel shows the distribution of experimental colonies placed in all six field sites in the parental (P) generation; the missing information of the next generation ($F_1$); and the distribution of final compositions of the grand-offspring generation ($F_2$). Phenotypic compositions, that is, proportions of aggressive individuals in each colony, are plotted against colony sizes. We present data only from one low-resource field site, Don Carter, to illustrate the setup. Black dots represent native colonies (created with spiders collected at Don Carter); red dots represent foreign colonies (spiders collected at high-resource field site Moccasin Creek). Filled circles of both colours in P are colonies that were still alive in $F_2$ (equal to figure 1c of Pruitt and Goodnight[1]); empty circles are colonies that had gone extinct by $F_2$. The white band represents the proposed selection pressure at that field site: a regression line fitted on phenotypic compositions and colony sizes of naturally occurring colonies at Don Carter (based here on colonies of sizes up to 30; its thickness chosen arbitrarily). Dotted lines in $F_2$ represent regressions of the final $F_2$ compositions of the surviving colonies: native (black) versus foreign (red). Surviving colonies had P compositions close to the white selection band, but $F_2$ compositions differed according to site of origin: Native $F_2$ compositions were close to the selection band while foreign $F_2$ compositions followed a positive regression, dissimilar to the selection band. Setup and results were similar in the two additional low-resource sites while the three high-resource sites showed opposite trends (that is, selection bands were positive regression lines while the foreign $F_2$ regressions showed negative correlations). Note that although foreign colonies end up opposite to the proposed selection pressure, Pruitt and Goodnight[1] still conclude that their proposed selection pressure was supported. The bottom panel shows how the size of an *A. studiosus* colony is expected to vary within years with a peak around egg hatching during summer. The period of maternal care is marked in purple. Black lines marked with 'P' and '$F_2$' indicate at which point in the life cycle Pruitt and Goodnight[1] performed the behavioural assays to determine the phenotypic compositions of colonies. Note that group sizes and phenotypic compositions of P and $F_2$ were measured at different points, apparently comparing sexually mature females (P) with juvenile grandchildren ($F_2$) during maternal care at a stage where offspring sex cannot be determined.



©2015 Macmillan Publishers Limited. All rights reserved

differential group extinction can therefore result from individual-level selection just as plausibly as from group selection. Similarly ambiguous is the second prediction that "colonies should only be able to adaptively hone compositions when composed of native individuals". If 'native colonies' can 'adaptively' change phenotype frequencies over time, this may occur via several mechanisms, as Pruitt and Goodnight[1] mention (plasticity, phenotype-biased dispersal, and so on). Yet, any of these mechanisms may evolve by individual-level selection, a possibility overlooked by Pruitt and Goodnight[1].

The conclusions of Pruitt and Goodnight[1] rest on the assumption that 'naturally occurring mixtures' (that is, field phenotypic frequencies; see figure 1a of Pruitt and Goodnight[1]) represent consistent selection pressures across years. Yet, the years of measurement were patchy (2007–14), differed among sites and often did not overlap (Table 1). Indeed, Pruitt and Goodnight[1] sampled significantly different phenotypic mixtures and group sizes among years at each site (mixtures: $P = 1.1 \times 10^{-5}$; group size: $P = 7.8 \times 10^{-14}$; Fisher's combined $P$ value across separate Kruskal–Wallis tests for each site) but overlooked this variation and pooled dissimilar data. In four out of nine samples taken at high resource sites, the selection pressure was no different from zero (non-significant correlations between mixtures and group size; separate *lm* for each year at each site), and in two out of the three low resource sites the relationship between mixture and group size differed significantly from year to year (Norris Dam: $P = 0.0074$; Don Carter: $P = 0.017$; interaction between log(group size) and year on phenotypic mixtures in linear models). Moreover, half of the sites had not been assessed for four to six years. These measurements cannot be assumed to represent consistent, current selection pressures.

Pruitt and Goodnight[1] infer group selection by comparing parental (P) and grand-offspring ($F_2$) generations based on parental traits alone: they compare P-phenotypic compositions of P colonies with P (not $F_2$) compositions of surviving $F_2$ colonies (figure 1c of Pruitt and Goodnight[1] is identical to their figure 1b, minus extinct colonies: $F_2$ colonies are depicted with their grandparents' compositions). We question the validity of assuming that past compositions are visible to selection but present compositions are not. Indeed, 'foreign colonies' changed to display $F_2$ compositions in a pattern opposite to the assumed selection pressure (Fig. 1; see figure 2 of Pruitt and Goodnight[1]). These changes mean that $F_1$ compositions presumably also differed from P compositions (and were visible to selection during that generation) but $F_1$ was not assessed (Fig. 1).

Changes within generations were also not considered (Fig. 1). Around egg hatching[12], colonies peak in size, after which mortality and dispersal decrease colony size. Phenotypic composition cannot be considered a stable 'group trait' when its proposed selective advantage is a function of group size, and group size changes nonlinearly over time. Compounding this, compositions of P and $F_2$ were apparently measured at different developmental stages (Fig. 1): we believe that this is a serious flaw, as individual phenotypes are affected by reproductive status[13]. Pruitt and Goodnight[1] compared sexually mature females (P) with grandchildren ($F_2$) that, given the stated timescale, presumably were juvenile, mixed-gender and receiving maternal care (Fig. 1; mothers die off in October[12] and juvenile spiders are unsexable).

We believe that none of the findings of Pruitt and Goodnight[1] supports their claim to have demonstrated a "marked evolutionary response to group selection". Rather, after two generations, surviving foreign colonies failed to change phenotypic compositions in site-appropriate ways (instead changing to express compositions appropriate for their original site), suggesting a lack of genetic change over the experiment (Fig. 1). Pruitt and Goodnight[1] argue that this constitutes evidence that mechanisms for adjusting compositions are locally adapted due to historical group selection, but provide no justification for this claim: while they provide data suggesting phenotypes themselves may be partially heritable, there is no evidence that this 'adjustment mechanism' has undergone genetic change and, again, no attempt to reject individual-level selection as an explanation. Foreign colonies may revert to their native phenotype compositions without genetic change; for example, due to persistent maternal or epigenetic effects, either of which may respond to individual-level selection or group selection. The evolutionary mechanisms shaping population-level differences, whether in phenotype frequencies or the means by which these change over time, do not appear to have been addressed in this paper.

We would welcome any field study demonstrating that group selection causes genetic change over generations in ways inconsistent with individual-level selection. Given recent high-profile exchanges over the relative importance of group selection[14,15], such a paper would be a significant contribution to the field. Unfortunately, we do not believe that the paper of Pruitt and Goodnight[1] is such a study.

**Table 1 | Collection years for each field site**

| | Collection years | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 |
| High resource sites | | | | | | | | |
| Melton Hill | X | X | X | E | E X | X | | |
| Little River | X | X | | | | | E | E |
| Moccasin Creek | | | | | | | E X | E X |
| Low resource sites | | | | | | | | |
| Norris Dam | X | X | X | E | E X | X | | |
| Clinch River | | X | | X | | | E | E |
| Don Carter | | | X | X | | | E | E |

Data from years marked with 'X' were pooled within sites to create the naturally occurring mixtures (figure 1a in Pruitt and Goodnight[1]) used to infer site-specific selection pressures. 'E' indicates the years during which the experiment took place.

**Lena Grinsted[1], Trine Bilde[2] & James D. J. Gilbert[1,3]**
[1]School of Life Sciences, University of Sussex, John Maynard Smith Building, Brighton BN1 9QG, UK.
email: l.grinsted@sussex.ac.uk
[2]Department of Bioscience, Aarhus University, Ny Munkegade 116, building 1540, 8000 Aarhus C, Denmark.
[3]School of Biological, Biomedical and Environmental Sciences, University of Hull, Cottingham Road, Hull HU6 7RX, UK.

**Received 1 January; accepted 7 May 2015.**

1. Pruitt, J. N. & Goodnight, C. J. Site-specific group selection drives locally adapted group compositions. *Nature* **514,** 359–362 (2014).
2. Eldakar, O. T. & Wilson, D. S. Eight criticisms not to make about group selection. *Evolution* **65,** 1523–1526 (2011).
3. Marshall, J. A. R. Group selection and kin selection: formally equivalent approaches. *Trends Ecol. Evol.* **26,** 325–332 (2011).
4. Rainey, P. B. & Rainey, K. Evolution of cooperation and conflict in experimental bacterial populations. *Nature* **425,** 72–74 (2003).
5. Kerr, B., Neuhauser, C., Bohannan, B. J. M. & Dean, A. M. Local migration promotes competitive restraint in a host-pathogen 'tragedy of the commons'. *Nature* **442,** 75–78 (2006).
6. Grinsted, L. & Bacon, J. P. Animal behaviour: task differentiation by personality in spider groups. *Curr. Biol.* **24,** R749–R751 (2014).
7. Jones, T. C., Pruitt, J. N. & Riechert, S. E. Reproductive success in a socially polymorphic spider: social individuals experience depressed reproductive success in isolation. *Ecol. Entomol.* **35,** 684–690 (2010).
8. Moczek, A. P., Hunt, J., Emlen, D. J. & Simmons, L. W. Threshold evolution in exotic populations of a polyphenic beetle. *Evol. Ecol. Res.* **4,** 587–601 (2002).
9. Culumber, Z. W., Bautista-Hernandez, C. E., Monks, S., Arias-Rodriguez, L. & Tobler, M. Variation in melanism and female preference in proximate but ecologically distinct environments. *Ethology* **120,** 1090–1100 (2014).
10. Weider, L. J. *et al.* Genotype × environment interactions, stoichiometric food quality effects, and clonal coexistence in *Daphnia pulex*. *Oecologia* **143,** 537–547 (2005).



©2015 Macmillan Publishers Limited. All rights reserved

11. Fitzpatrick, M. J., Feder, E., Rowe, L. & Sokolowski, M. B. Maintaining a behaviour polymorphism by frequency-dependent selection on a single gene. *Nature* **447,** 210–212 (2007).
12. Furey, F. E. Two cooperatively social populations of the theridiid spider Anelosimus studiosus in a temperate region. *Anim. Behav.* **55,** 727–735 (1998).
13. Watts, J. C., Ross, C. R. & Jones, T. C. Diel and life-history characteristics of personality: consistency versus flexibility in relation to ecological change. *Anim. Behav.* **101,** 43–49 (2015).
14. Abbot, P. *et al.* Inclusive fitness theory and eusociality. *Nature* **471,** E1–E4 (2011).
15. West, S. A., Griffin, A. S. & Gardner, A. Social semantics: how useful has group selection been? *J. Evol. Biol.* **21,** 374–385 (2007).

**Author Contributions** L.G., J.D.J.G. and T.B. authored this paper; L.G. performed statistical analyses.

**Competing Financial Interests** Declared none.

**doi:**10.1038/nature14595

# Group selection versus group adaptation

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

Pruitt and Goodnight[1] 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 Goodnight[1] conclude that this work demonstrates group-level adaptation and contradicts an earlier theoretical analysis[2]. 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 Goodnight[1] provide evidence of group-level selection, they do not provide any evidence of group-level adaptation, as defined in the earlier analysis[2]. 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 fitness[3]. 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 analysis[2] that Pruitt and Goodnight[1] claim to have refuted. Pruitt and Goodnight[1] 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's[6] '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 Goodnight[1]; and (3) is generally higher than that which maximizes group fitness (Fig. 1). Accordingly, the data presented by Pruitt and Goodnight[1] 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 Goodnight[1] also claim that the earlier theoretical analysis[2] 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 conflict[2]. Well-studied examples of such mechanisms are fair meiosis[7,8] and worker policing in honeybees[8,9]. Interestingly, Pruitt and Goodnight[1] 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 Smith[5], 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 world[10]. 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 fitness[13]. But Maynard Smith[5] 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.

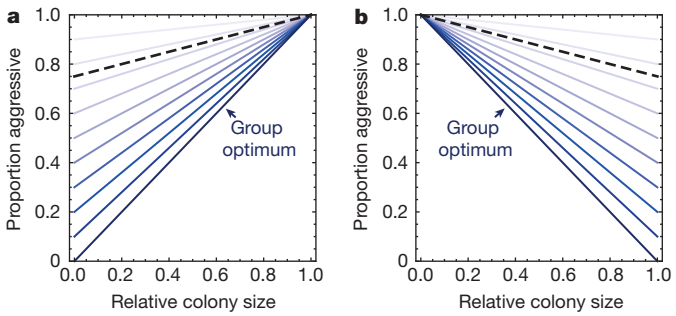


**Figure 1 | Individual versus group optima.** The proportion of aggressive individuals resulting from the maximization of the individual's inclusive fitness is plotted for a range of coefficients of relatedness, from $r = 0$ (lightest shading) to $r = 1$ (darkest shading), with the estimate of Pruitt and Goodnight[1] $r = 0.25$ 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 Goodnight[1], 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 Goodnight[1], and typically exceeds that which maximizes colony 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.



©2015 Macmillan Publishers Limited. All rights reserved

In high-resource environments $b = n$, where $n$ denotes relative colony size, reflecting the finding of Pruitt and Goodnight[1] 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 Goodnight[1] 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).

**Andy Gardner[1]**
[1]School of Biology, University of St Andrews, Dyers Brae, St Andrews KY16 9TH, UK.
email: andy.gardner@st-andrews.ac.uk

**Received 24 October 2014; accepted 7 May 2015.**

1. Pruitt, J. N. & Goodnight, C. J. Site-specific group selection drives locally adapted group compositions. *Nature* **514,** 359–362 (2014).
2. Gardner, A. & Grafen, A. Capturing the superorganism: a formal theory of group adaptation. *J. Evol. Biol.* **22,** 659–671 (2009).
3. Hamilton, W. D. In *Biosocial Anthropology* (ed. Fox, R.) 133–155 (Wiley, 1975).
4. Okasha, S. *Evolution and the Levels of Selection* (Oxford Univ. Press, 2006).
5. Maynard Smith, J. In *The Latest on the Best: Essays on Evolution and Optimality* (ed. Dupré, J.) 147–149 (MIT, 1987).
6. Frank, S. A. *Foundations of Social Evolution* (Princeton Univ. Press, 1998).
7. Leigh, E. G. How does selection reconcile individual advantage with the good of the group? *Proc. Natl Acad. Sci. USA* **74,** 4542–4546 (1977).
8. Frank, S. A. Repression of competition and the evolution of cooperation. *Evolution* **57,** 693–705 (2003).
9. Wenseleers, T. & Ratnieks, F. L. W. Enforced altruism in insect societies. *Nature* **444,** 50 (2006).
10. West, S. A. *Sex Allocation* (Princeton Univ. Press, 2009).
11. Hamilton, W. D. Extraordinary sex ratios. *Science* **156,** 477–488 (1967).
12. Frank, S. A. Hierarchical selection theory and sex ratios. I. General solutions for structured populations. *Theor. Popul. Biol.* **29,** 312–342 (1986).
13. Reece, S. E., Drew, D. R. & Gardner, A. Sex ratio adjustment and kin discrimination in malaria parasites. *Nature* **453,** 609–614 (2008).

**Competing Financial Interests** Declared none.

**doi:**10.1038/nature14596

# 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 Goodnight[1] 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, Gardner[3] 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 Gardner[3] 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 paper[1]. 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 unit[11] because of their behavioural composition[1]. 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 altruism[7]—these are different concepts. There is controversy whether group selection can beget altruism in the absence of relatedness[12], 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 ($F_2$) 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 performance[1]. Aggressiveness varies with temperature[14] and gravidity[15] in *A. studiosus*, which could be problematic. Thankfully, rank order aggressiveness is maintained in spite of this plasticity[14], 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 sites[16]. Regardless, this wouldn't compromise any of our findings.



©2015 Macmillan Publishers Limited. All rights reserved

Grinsted *et al.*[2] assert that we did not provide any evidence of genetic change as a consequence of group selection. We argue that we provided evidence that the mechanisms used by colonies to adjust their compositions are site specific, genetically influenced, and locally adapted because of group selection. First, we showed that the behaviour of colonies is adaptive: colonies always hone their compositions in ways that would evade extinction at their home sites, which cannot be purely coincidental. Second, we showed that these regulatory mechanisms are genetically influenced: after two generations displaced colonies still exhibited the same regulatory behaviour that they would at their home site. This conveys that the differences in the regulatory behaviour of native/foreign colonies are unlikely to be plastic. Such was the case at every site: six two-generation common garden experiments. Common garden experiments are the gold standard for verifying a genetic component to any phenotype[17].

Grinsted *et al.*[2] claim that they await a study that demonstrates that group selection has caused genetic change in a way that is inconsistent with individual selection; however, those papers have already been published[4,18]. The novelty of our study is that we showed that the nature of group selection changes across environments, and we provide evidence that historic group selection has caused local adaption in a collective trait.

We define 'group-level adaptions' as adaptations in group-level traits that evolve via a combination of individual selection and group selection. Group composition in *A. studiosus* meets these criteria[1,3]. Gardner[3] adds the requirement that 'group-level adaptations' must evolve because of the advantages they confer to the group, at the cost of the individual[3,19]. This definition is problematic not only because it confounds adaptions in group-level traits with the concept of altruism, but also mandates that a trait can only be considered a group-level adaptation if it is optimized solely for the group. However, no trait in the real world is ever the result of adaptation to a single selection pressure. We expect no different from group traits. Group traits are inevitably a compromise among competing selection pressures at the individual and group level. We argue that if one demands that traits can only be counted as adaptations if they are subject to a single selective pressure, then it is almost certainly true that there are no such things as adaptations.

Gardner's model[3] recreates a subset of the patterns seen in *A. studiosus*, although it invokes group selection to do so. While there is nothing wrong with Gardner's interesting model, it's not grounded in the biology of our system. For instance, aggressive individuals are not competitively superior to docile individuals in *A. studiosus*[20], but Gardner's model relies on this assumption[3]. Gardner's model also fails to predict key findings. For example, his model does not explain why displaced colonies recreate the ideal mixtures of their home sites after generations at a new site. In short, an accomplished theorist like Gardner could devise many models that capture some of the patterns seen in our system. We devised one such model ourselves. The difference is that we then vetted our model with arguably the most comprehensive field assessment of group selection ever conducted[1]. Our findings yielded strong support for our model, providing a high standard of scientific evidence.

**Jonathan N. Pruitt[1] & Charles J. Goodnight[1]**
[1]Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15216, USA.
email: pruittj@pitt.edu

1. Pruitt, J. N. & Goodnight, C. J. Site-specific group selection drives locally adapted colony compositions. *Nature* **514,** 359–362 (2014).
2. Grinsted, L., Bilde, T. & Gilbert, J. D. J. Questioning evidence of group selection in spiders. *Nature* **524,** http://dx.doi.org/10.1038/nature14595 (2015).
3. Gardner, A. Group selection versus group adaptation. *Nature* **524,** http://dx.doi.org/10.1038/nature14596 (2015).
4. Goodnight, C. J. & Stevens, L. Experimental studies of group selection: What do they tell us about group selection in nature? *Am. Nat.* **150,** S59–S79 (1997).
5. Goodnight, C. On multilevel selection and kin selection: Contextual analysis meets direct fitness. *Evolution* **67,** 1539–1548 (2013).
6. Eldakar, O. T. & Wilson, D. S. Eight criticisms not to make about group selection. *Evolution* **65,** 1523–1526 (2011).
7. West, S. A., Griffin, A. S. & Gardner, A. Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20,** 415–432 (2007).
8. West, S. A., Griffin, A. S. & Gardner, A. Social semantics: How useful has group selection been? *J. Evol. Biol.* **21,** 374–385 (2008).
9. Wade, M. J. Critical-review of models of group selection. *Q. Rev. Biol.* **53,** 101–114 (1978).
10. Maynard Smith, J. Group selection. *Q. Rev. Biol.* **51,** 277–283 (1976).
11. Lewontin, R. C. The units of selection. *Annu. Rev. Ecol. Syst.* **1,** 1–18 (1970).
12. Abbot, P. *et al.* Inclusive fitness theory and eusociality. *Nature* **471,** E1–E4 (2011).
13. Sumpter, D. J. T. The principles of collective animal behaviour. *Phil. Trans. R. Soc. Lond. B* **361,** 5–22 (2006).
14. Pruitt, J. N., Demes, K. W. & Dittrich-Reed, D. R. Temperature mediates shifts in individual aggressiveness, activity level, and social behavior in a spider. *Ethology* **117,** 318–325 (2011).
15. Watts, J. C., Ross, C. R. & Jones, T. C. Diel and life-history characteristics of personality: Consistency versus flexibility in relation to ecological change. *Anim. Behav.* **101,** 43–49 (2015).
16. Pruitt, J. N. Behavioural traits of colony founders affect the life history of their colonies. *Ecol. Lett.* **15,** 1026–1032 (2012).
17. Falconer, D. S. & McKay, T. F. *Introduction to Quantitative Genetics* (Prentice Hall, 1996).
18. Gordon, D. M. The rewards of restraint in the collective regulation of foraging by harvester ant colonies. *Nature* **498,** 91–93 (2013).
19. Gardner, A. & Grafen, A. Capturing the superorganism: A formal theory of group adaptation. *J. Evol. Biol.* **22,** 659–671 (2009).
20. Pruitt, J. N. & Riechert, S. E. How within-group behavioral variation and task efficiency enhance fitness in a social group. *Proc. R. Soc. Biol. B* **278,** 1209–1215 (2011).

**doi:**10.1038/nature14597



©2015 Macmillan Publishers Limited. All rights reserved