



## Intense group selection selects for ideal group compositions, but selection within groups maintains them



Jonathan N. Pruitt<sup>a,\*</sup>, Charles J. Goodnight<sup>b</sup>, Susan E. Riechert<sup>c</sup>

<sup>a</sup> University of Pittsburgh, Department of Biological Sciences, Pittsburgh, PA, U.S.A.

<sup>b</sup> University of Vermont, Department of Biology, Burlington, VT, U.S.A.

<sup>c</sup> University of Tennessee Knoxville, Department of Ecology and Evolutionary Biology, Knoxville, TN, U.S.A.

### ARTICLE INFO

#### Article history:

Received 26 June 2016

Initial acceptance 10 August 2016

Final acceptance 3 October 2016

MS. number: A16-00565R

#### Keywords:

animal personality  
behavioural syndrome  
frequency-dependent selection  
green-beard nepotism  
multilevel selection  
temperament

A group's composition is important for its success. Colonies of the spider *Anelosimus studiosus* appear to have responded to this pressure by evolving the ability to maintain mixtures of docile versus aggressive individuals that help colonies avoid extinction. Here we demonstrate that colony extinction events unite the optimal group composition of all colony constituents, regardless of phenotype, with that of the colony as a whole. This is because colony extinction events explain the majority of individual mortality events in *A. studiosus*. Through within- and across-habitat colony manipulations, we further determined that reduction in reproductive output by individuals bearing overabundant phenotypes underlies the ability of colonies to adaptively regulate their compositions. When we experimentally created colonies with an overabundance of the docile or aggressive phenotype, individuals bearing the overabundant phenotype exhibited reduced reproductive output, which helped to move colony compositions back towards their site-specific optima. Colonies displaced from their native sites continued to recreate the patterns of reproductive output that characterized their site of origin, suggesting a genetic component to this trait. Individuals thus appear to adaptively cull their reproductive output depending on their phenotype and the composition of their colony. There is also considerable parent–offspring colony resemblance in the extent to which colonies can or do track their ideal compositions. This conveys a kind of collective heritability to this trait. Together, while group selection appears to be the principal driver of ongoing selection on group composition in *A. studiosus*, patterns of selection among individuals within groups appear to promote colonies' ability to track their ideal mixtures.

© 2016 Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour.

*Further, little evidence exists that selection on groups has promoted the evolution of any trait*

(Coyne, 2011)

Coyne's comment summarizes a view held by a surprisingly large number of evolutionary biologists. Proponents of multilevel selection argue that variation in the survival and reproductive output of groups can be a potent evolutionary force (Wade, 1978; Wilson, 1983). While there is some disagreement over the ideal definition of group selection (Gardner, 2015a, b; Goodnight, 2015), here we define group selection as selection caused by the differential performance of groups. While it was established long ago in laboratory studies that experimentally imposed group selection can lead to evolutionary changes (Wade, 1977, 1980), and that group

selection is regularly detectable in both laboratory (Eldakar, Dlugos, Pepper, & Wilson, 2009; Eldakar, Wilson, Dlugos, & Pepper, 2010; Shaffer et al., 2016) and natural populations (Goodnight & Stevens, 1997; Gordon, 2013), the ability of group selection to drive adaptations in nature is still doubted by many (Eldakar & Wilson, 2011). This is, in part, because there has been a tradition of viewing group selection and inclusive fitness as incompatible theories (Nowak, Tarnita, & Wilson, 2010; Wilson & Hölldobler, 2005). This is incorrect. Kin selection theory argues that indirect fitness can be an important contributor to evolutionary change (Hamilton, 1964a, b). Group selection argues that differences among groups in their collective performance can be a potent selective force (Wilson, 1975). There is nothing incompatible with these two notions. Both theoretical frameworks can converge on the same set of equations (Queller, 1991, 1992), however, the kinds of questions addressed by either framework are quite different (Birch & Okasha, 2015; Wilson, 2015). The frameworks are therefore compatible with each other, although they are not equivalent.

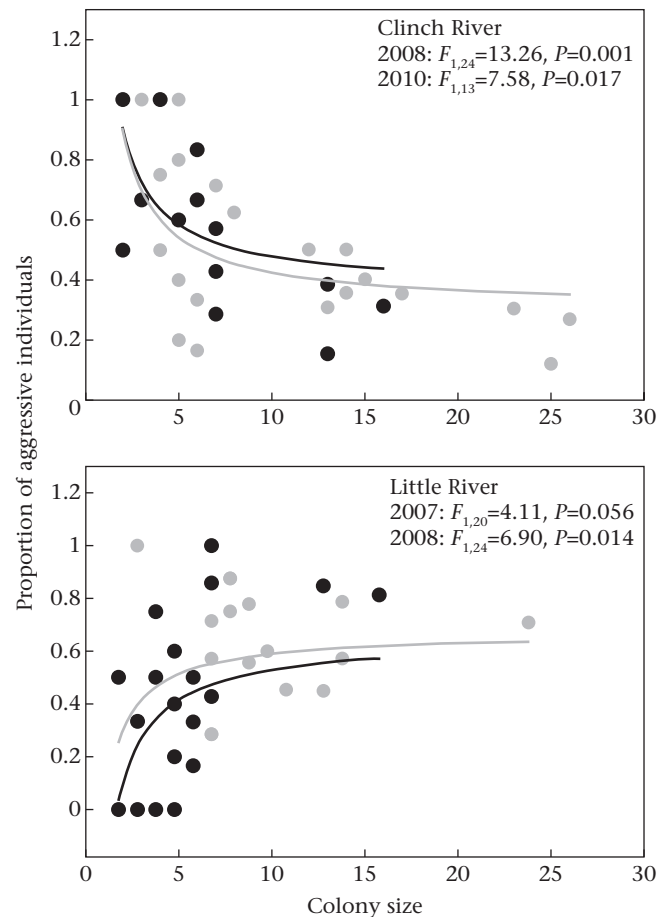
\* Correspondence: J. N. Pruitt, University of Pittsburgh, Department of Biological Sciences, Pittsburgh, PA 15260, U.S.A.

E-mail address: [Agelenopsis@gmail.com](mailto:Agelenopsis@gmail.com) (J. N. Pruitt).

The efficacy of group selection is further doubted because few experimental studies have been able to demonstrate that group selection is the force responsible for the evolution of adaptations seen in natural populations (e.g. local adaptation in colony traits; Pruitt & Goodnight, 2014; Shaffer et al., 2016). For most systems, demonstrating that an adaptation is due to group selection would be a daunting and possibly impossible task, due to the intractable experimental time spans required for tracking colony life history (e.g. decades; Gordon, 2013), and the difficulty of generating and tracking large numbers of experimental groups in situ. A rigorous test of group selection would require that one be able to manipulate the trait or traits that are thought to be under group selection, to deploy experimentally manipulated groups into the field, and then to track group's long-term survival and reproductive output. This is simply impossible for most systems. Social spiders, on the other hand, are a practical model system for the study of group selection because group longevity is short (Aviles, 1986, 1993a; Henschel, 1998), group extinction rates are high (Negron, Rodriguez, & Aviles, 1991; Pruitt, 2012; Pruitt & Modlmeier, 2015), the number of offspring colonies produced by focal colonies can be estimated (Aviles, 1993b; Pruitt, 2013) and groups rarely mix (Agnarsson, Aviles, & Maddison, 2013; Johannesen, Wickler, Seibt, & Moritz, 2009). As a result, it is feasible to manipulate collective traits that are thought to be under group selection in the wild.

The facultatively social spider *Anelosimus studiosus* forms multifemale societies in northern portions of its range (Furey, 1998; Jones & Riechert, 2008; Jones, Riechert, Dalrymple, & Parker, 2007). These colder climates slow the development of offspring and increase the chance that spiderling groups will be orphaned before they can fledge (Jones & Parker, 2002). This landscape is therefore thought to select for cooperative alloparental care, where females adopt the orphaned offspring of their neighbours (Jones et al., 2007; Riechert & Jones, 2008). This species also exhibits a behavioural polymorphism, where females exhibit one of two relatively discrete (Pruitt & Riechert, 2009a) temporally stable, heritable ( $h^2 = 0.66$ ) behavioural phenotypes: 'docile' or 'aggressive' (Pruitt & Goodnight, 2014; Pruitt, Riechert, & Jones, 2008). In *A. studiosus*, as in other social *Anelosimus*, aggressiveness is bimodally distributed and individual differences in aggressiveness are repeatable over individuals' adult lifetimes (Pruitt, Iturralde, Aviles, & Riechert, 2011; Pruitt, Oufiero, Aviles, & Riechert, 2012). Although neither phenotype breeds true in *A. studiosus*, broods produced by docile dams mated with docile sires are predominantly of the docile phenotype, and the same is true of the aggressive phenotype (Pruitt & Goodnight, 2014; Pruitt & Riechert, 2009b).

Populations of *A. studiosus* at higher latitudes also exhibit characteristic differences in their docile:aggressive ratios that vary based on a site's resource levels and as colonies grow (Fig. 1) (Pruitt & Goodnight, 2014). These site-specific colony compositions are, at least in part, maintained by colony extinction events. The phenotypic compositions that beget success at high-resource sites cause colony extinction at low-resource sites and vice versa. Experimental colonies that exhibit mixtures unlike those of natural colonies at each site quickly go extinct. *Anelosimus studiosus* colonies appear to have responded to this selection pressure by evolving the ability to adjust suboptimal phenotypic ratios in ways that promote colony success (Pruitt & Goodnight, 2014). When colonies' compositions are experimentally altered, colonies are able to shift their behavioural compositions back towards those that characterize their site of origin and facilitate group success. This tendency is maintained even when colonies are reared in contrasting environments for multiple generations, suggesting a genetic component to the mechanisms that allow colonies to adjust their compositions. Thus, group selection appears to have played a role in driving adaptive population-level differences in group composition



**Figure 1.** The naturally occurring relationship between colony size and composition (ratio of aggressive:docile phenotypes) of *A. studiosus* at the two study sites: Clinch River (2008: ●; 2010: ●); Little River (2007: ●; 2008: ●).

and the mechanisms that govern it. The mechanism(s) by which these alterations are achieved in *A. studiosus* colonies is (are) presently unknown (Grinsted, Bilde, & Gilbert, 2015; Smallegange & Egas, 2015). Although group selection has been detected in several systems (Chang & Sih, 2013; Gordon, 2013), experiments with *A. studiosus* were the first to show that group selection differs across sites and that colonies appear to have responded to this selection.

The first paper on group selection in this system (Pruitt & Goodnight, 2014) received considerable attention but was critiqued for three primary reasons (summarized in Table 1). (1) In the original paper we failed to account for selection within colonies and the role that it might play in guiding the dynamics of the system. This oversight is arguably problematic because some researchers have suggested that simultaneously accounting for individual selection and group selection is required in order to implicate group selection as a guiding evolutionary force. Although we disagree with this assertion, we feel it valuable to address this critique (Grinsted et al., 2015). (2) In our first paper (Pruitt & Goodnight, 2014), we referred to local adaptation in colonies' phenotypic ratios and the mechanisms that guide them as 'group-level adaptations'. Following Gardner's (2014) definition, this implies that the optimal phenotypic ratio for colonies is different from that for the individuals within them and, to be deemed a 'group-level adaptation', the compositions seen in nature would need to match the optimum for colonies (Gardner, 2014; Gardner & Grafen, 2009). We did not rigorously evaluate this possibility in our prior

Download English Version:

<https://daneshyari.com/en/article/5538622>

Download Persian Version:

<https://daneshyari.com/article/5538622>

[Daneshyari.com](https://daneshyari.com)