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EVOLUTIONARY BIOLOGY

Survival of the fittest group

Experiments with social spiders find that colony size and composition affect colony survival in a site-specific manner, indicating that natural selection on group-level traits contributes to local adaptation.

TIMOTHY LINKSVAYER

Organisms often seem remarkably well adapted to their environment, as a result of evolution by natural selection. Natural selection is usually thought to act at the individual level — when the survival or reproduction of individuals depends on their own traits — but it can also act at other levels, from genes to social groups to populations[1]. For example, the survival and reproduction of individuals or groups of individuals may also depend on group-level traits, resulting in group selection. In a paper published on *Nature*'s website today, Pruitt and Goodnight[2] present a rare experimental study from a group-selection perspective in natural populations, providing evidence that strong group selection on the colony traits of social spiders may drive adaptation to local conditions.

The idea that natural selection at the group level is evolutionarily important and can produce group-level adaptations has been contentious and associated with semantic debate and confusion[1]. This debate has been especially heated regarding the relationship between group selection and kin selection — another form of natural selection. The concept of kin selection was originally formulated by evolutionary biologist W. D. Hamilton to explain the evolution of altruism[3], which seems paradoxical from an individual's perspective, because, by definition, it involves fitness costs to the individual and benefits to the group. Yet from a gene's perspective, altruism can be thought of as being selfish when beneficiaries are relatives (and thus share genes), because the gene experiences a net benefit by effectively helping itself to spread in the population. Subsequently, Hamilton and others showed that the evolution of social traits such as altruism can equivalently be understood as being driven by the balance between group selection and individual selection[4].

Kin selection and group selection are now broadly understood to describe the same evolutionary process from complementary perspectives[5]. However, although it is clear that iconic altruistic traits, such as the sterile worker castes of social insects, have been shaped by selection between kin groups, actually studying how selection on group-level traits influences the evolutionary process in natural populations has proved difficult.

Pruitt and Goodnight have done this by studying *Anelosimus studiosus* spiders, which live in social colonies containing related individuals (Fig. 1). Female spiders consistently display either docile or aggressive behaviour, and colonies vary in the proportion of aggressive individuals in a site-specific way. To test whether these differences in colony composition between sites may be shaped by group selection on colony composition, the authors constructed spider colonies containing different proportions of aggressive and docile females and different group sizes at field sites that were either high resource or low resource. Each experimental colony was constructed from a single source colony. Some colonies were composed of 'native' individuals (the colonies were formed at the same site from which the spiders were taken) and others were composed of 'foreign' individuals (the spiders were transplanted from a different site).

The authors then tracked colony survival, composition and reproductive output over the next two generations, and found that the relationship between colony size and group composition strongly affects colony survival and reproductive success, and that sites with high or low resources consistently favour different relationships. Furthermore, they found that, after two generations, surviving colonies had shifted their size and composition to be more similar to their home site. These results suggest that the relationship between group size and composition is both heritable and locally adapted. Because whole colonies of these spiders survive or die depending on group traits, group selection is probably playing a central part in driving this local adaptation. Although the causative agents of selection are not known, the authors identify two likely culprits for colony extinction: egg cannibalism at low-resource sites and an abundance of parasitic spiders of other species at high-resource sites.

This spider system bears many similarities to colonies of social insects. Group selection, which in these species translates to colony-level selection and in some cases involves direct warfare between colonies, is thought to shape social insect traits[6]. Like social spider colonies, social insect colonies are composed of close kin, which probably explains why group selection has seemingly had such strong evolutionary impacts. Although actually quantifying selection on colony-level traits of social insects has been elusive[7], the social mechanisms that regulate some such traits, referred to as social physiology, are well

ALEX WILD

Figure 1 | Social spiders. Several species of the spider genus *Anelosimus* live in kin groups and cooperate in web construction, care of young and prey capture, as shown here in *Anelosimus eximius*.

studied in social insects and are understood to be colony-level adaptations[8] that are shaped by colony-level selection[9].

This highlights a key remaining challenge in understanding the social spider system. The precise social and developmental mechanisms that enable spider colonies to adaptively adjust their colony composition must be characterized. Pruitt and Goodnight suggest that within-colony conflict or the collective cessation of reproduction are involved, which emphasizes another crucial issue: although the authors present a compelling case for a strong evolutionary role of group selection, it is important to determine whether individual selection also operates within colonies. That is, does the survival and reproduction of individuals within groups depend on whether the individual is aggressive or docile?

Another line of future research will be to study the genetic basis of group traits. Adaptation can occur only when selection acts on heritable traits, so researchers need to understand the nature of the genetic architecture of specific traits together with patterns of selection on these traits. Some of the most persuasive evidence for the potential evolutionary strength of group selection comes from animal-breeding studies demonstrating that artificial selection at the group level can increase traits associated with productivity, even when these traits have long been the target of artificial individual-level selection[10]. The intuitive explanation for this is that an unintended side effect of individual-level selection for productivity is the evolution of highly aggressive individuals that monopolize resources to the detriment of group members. By contrast, group selection acts more efficiently on heritable traits underlying positive social interactions, leading to the evolution of groups of amiable animals with high overall reproductive success [11]. The ability of group selection to more effectively act on heritable social traits may also underlie the seemingly strong evolutionary influence of group selection in Pruitt and Goodnight's study and earlier studies. ■

Timothy Linksvayer *is in the Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104, USA.*
e-mail: tlinks@sas.upenn.edu

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