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DOI

[10.1016/j.tree.2015.04.005](https://doi.org/10.1016/j.tree.2015.04.005)

Publication date

2015

Document Version

Final published version

Published in

Trends in Ecology and Evolution

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[Link to publication](#)

Citation for published version (APA):

Smallegange, I. M., & Egas, M. (2015). Good for the group? Explaining apparent group-level selection. *Trends in Ecology and Evolution*, 30(7), 379-381.

<https://doi.org/10.1016/j.tree.2015.04.005>

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Good for the group? Explaining apparent group-level adaptation

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The idea that group selection can explain adaptive trait evolution is still controversial. Recent empirical work proposes evidence for group-level adaptation in a social spider, but the findings can also be explained from an individual-level perspective. The challenge remains to identify situations where one can separate group and individual selection.

An experimental system to study group selection

In evolutionary biology, group selection is well recognized but the existence of group-level adaptation, where natural selection acts to optimise group traits to maximise group fitness [1], is not. Recently, Pruitt and Goodnight [2] reported that the proportions of docile and aggressive individuals within single colonies of the social spider *Anelesimus studiosus* differ between high-resource and low-resource sites due to site-specific group selection, and that colony composition is optimised to promote long-term colony survival, thereby constituting a group-level adaptation. These findings are important because it is notoriously hard to study the effects of group selection in a natural setting.

The social spider *A. studiosus* forms an interesting system to study group selection. It lives in colonies of related individuals that share a web and cooperate in prey capture, but also suffer from egg cannibalism and social parasitism by heterospecific spiders. Individuals can be classified as docile or aggressive with a simple behavioural test, and this dimorphism is heritable [2]. In their study, Pruitt & Goodnight [2] collected spiders from six field sites (three high- and three low-resource sites), phenotyped them and constructed experimental colonies varying in the composition of docile and aggressive spiders. When reintroduced into the six sites, colonies with compositions mimicking the naturally occurring compositions survived, whereas colonies with deviating compositions disappeared. They also observed that experimental colonies with perturbed phenotype compositions that survived for two generations in a ‘foreign’ site had shifted their compositions towards their original one, not towards the

composition that would be locally optimal (see Figure 2 in [2]). They interpret this as compelling evidence for group-level adaptation and explain this as behavioural plasticity in response to the social environment within a colony. Evidence for this mechanism, however, is lacking.

Pruitt and Goodnight’s study presents exciting new insights, but can it help settle the debate on group-level adaptation? To judge this, we explore an alternative hypothesis based on individual-level selection and use a classic model for the evolution of dimorphism to explain Pruitt and Goodnight’s [2] observations.

The environmental threshold model to study trait evolution

Various evolutionary theories can explain the maintenance of phenotypic dimorphism in a population, including models on personality [3], but the environmental threshold (ET) model [4,5] specifically focuses on the evolution of dimorphic states in response to a cue that informs on the status of the environment. The ET model has been used to explain genetic variation in a wide range of threshold traits, including life cycle switches, disease resistance, trophic morphologies and alternative behavioural reproductive tactics [6]. It is assumed that threshold traits are based on [6]: (i) a continuously distributed, polygenic trait, called the ‘liability’, and (ii) a threshold of expression such that individuals that are above this threshold express one phenotype while those below the threshold express the alternative (e.g., [6]). Candidate traits for the liability are, for example, hormone profiles [6]. The position of the threshold depends on a cue that reliably correlates with the status of the (social) environment, which in many taxa represents population size [7,8]. The ET model assumes that, in response to environment-specific individual-level selection, alternative phenotypes have evolved different fitness functions, through which selection can affect the distribution of individual liabilities. Because phenotype frequency depends on the distribution of individual liabilities and the cue distribution, both are taken into account in determining how phenotype fitness influences the evolution of liabilities and hence the evolution of a threshold trait.

Applying the ET model to *A. studiosus*

We can fit the ET model to *A. studiosus* by assuming that the threshold relates to a cue that informs on the social environment, that is, colony size, and that fitness functions have evolved such that aggressive spiders have higher (lower) fitness at high (low) cue values at high-resource

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Keywords: adaptation; conditional strategy; environmental threshold model; group selection; multilevel selection; social spider.

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0169-5347/

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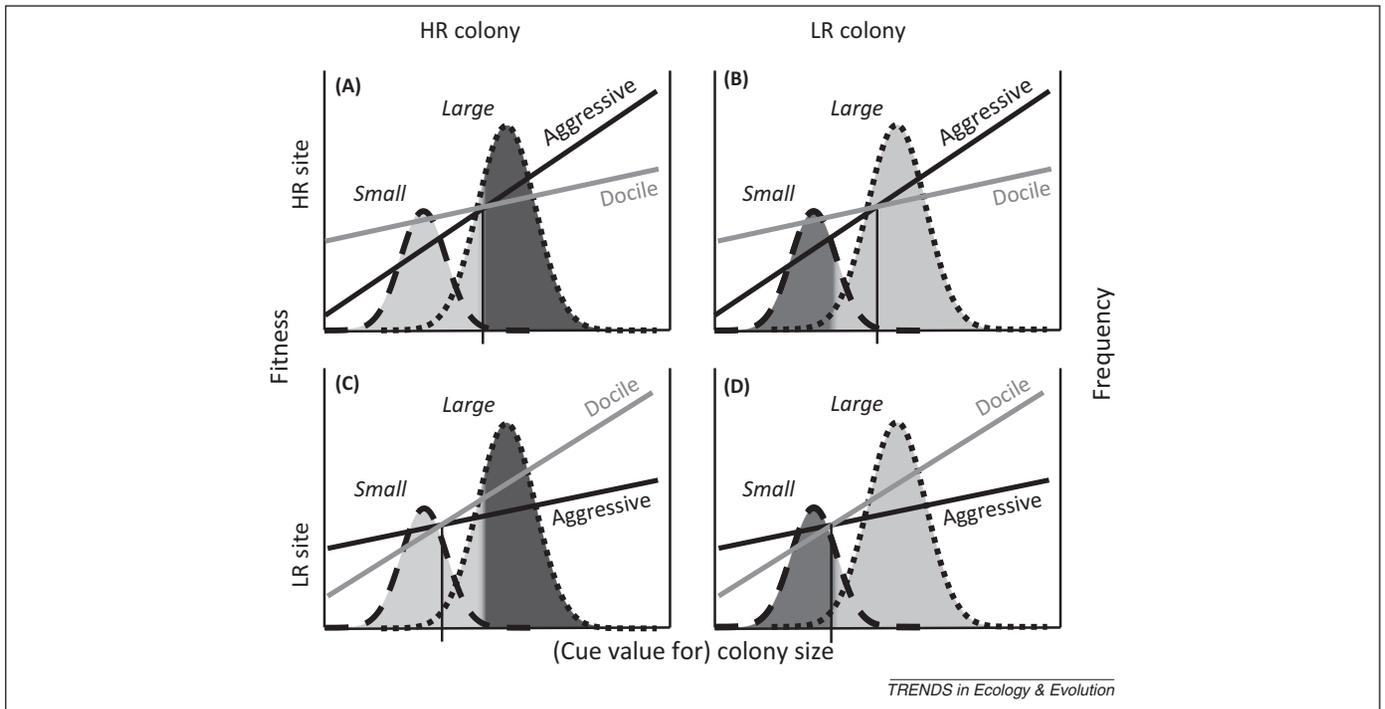


Figure 1. Social environment-specific individual-level selection explains colony composition. Panels (A) and (D) illustrate predictions according to the ET model [4,5] for single colonies of spiders adapted to a high-resource (HR) site or a low-resource (LR) site, respectively, using hypothesized fitness functions (unbroken lines) for docile (grey) and aggressive (black) individuals and hypothesized frequency distributions of cue values within a small colony (broken curves) and a large colony (dotted curves); the area under the curve represents colony size. The proportion of individuals adopting alternative phenotypes in each colony (contrastingly shaded areas under the curves: light grey for docile and dark grey for aggressive) is then determined by the threshold cue value at the intersection of the fitness functions (indicated by vertical line). We assume that at HR sites (top panels), aggressive individuals have higher fitness at higher cue values than docile individuals and vice versa; the opposite pattern is assumed to occur at LR sites (bottom panels). As a result of local adaptation, the genetically determined response to colony size will result in contrasting colony compositions between HR and LR sites. Hence, second-generation offspring in experimental colonies at a HR site display a mismatch with locally adapted phenotype proportions if individuals originated from a LR site (B) because the spiders respond genetically to colony size and not to a site-specific cue. Similarly, an experimental colony at a LR site displays a mismatch if individuals originated from a HR site (C). For ease of presentation we assume in this figure that the fitness functions are independent of colony size; the predictions do not change qualitatively if this assumption is discarded, as long as the intersection point does not change too much.

sites, and lower (higher) fitness values at high (low) cue values at low-resource sites (Figure 1A,D). The location of the threshold cue value (positioned where fitness functions cross) within the cue value frequency distribution determines the proportion of each phenotype within a colony (illustrated by the contrastingly shaded parts of the frequency distributions in Figure 1). Thus, as colony size increases, aggressive phenotype expression increases at high-resource sites but decreases at low-resource sites (Figure 1A,D). This is the pattern that Pruitt and Goodnight [2] observed among natural colonies.

The second observation of Pruitt & Goodnight [2] is that experimental colonies surviving in a ‘foreign’ site shifted their phenotype composition towards the one found in their ‘native’ site. Importantly, our alternative explanation for colony composition in terms of the ET model predicts this observation: phenotype composition in perturbed colonies changes in response to a cue related to colony size – not in response to a site-specific cue. *A. studiosus* females in perturbed colonies in a ‘foreign’ site, therefore, produce offspring in the ‘native’ ratio of phenotype expression, because their response to the cue is largely genetically determined and locally adapted to their ‘native’ site. Over many generations we do expect colony composition to change adaptively in the ‘foreign’ sites, as natural selection shifts the fitness functions to match local environmental conditions; experimental evolution provides an excellent framework for testing this prediction [9].

Outlook on disentangling individual from group selection

Our analysis using the ET model provides a mechanistic, individual-level explanation for the apparent group-level adaptation of colony composition in *A. studiosus*. The ET model can incorporate frequency-dependence [4] (as found for *A. studiosus* [2]) and social context [5] (as proposed for *A. studiosus* [2]). The ET model can also be used to explore multilevel liability selection on a threshold trait and analyse when individual or group selection dominates if these levels of selection are in conflict, e.g. as described by Hamilton’s rule if groups consist of kin [10]. Our analysis suggests that individual and group selection are probably aligned in the colonies studied by Pruitt and Goodnight [2]. Applying these insights can aid in identifying situations where the two are opposing, which is crucial for understanding when group selection drives group composition.

Acknowledgements

IMS is funded by a MacGillavry Fellowship from the University of Amsterdam, and a MEERVOUD grant no. 836.13.001 and a VIDI grant no. 864.13.005 from the Netherlands Organisation for Scientific Research (NWO). This paper is dedicated to the memory of Professor Maus Sabelis (†7 January 2015).

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