

There is nothing wrong with inclusive fitness

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We thank Fletcher *et al.* [1] for their comments on our recent *TREE* article [2]. These can be condensed down to two key points. First, a change in the definition of altruism: to claim that altruism can evolve without relatedness, Fletcher *et al.* have simply changed and broadened the definition used by Wilson and Hölldobler [3] and ourselves [2] to include reciprocal altruism. Second, the authors argue that group selection preceded kin selection (i.e. inclusive fitness) theory as a theoretical tool to explain altruism in the social insects. We discuss both but note that neither point weakens our article [2], or rescues the problems in that by Wilson and Hölldobler [3].

Shifting semantics

Recent work by Fletcher and Zwick [4] showed that the altruism of insect workers, and reciprocal altruism, where one individual helps another and gains a delayed reproductive benefit, can both be modeled with a form of Hamilton's rule. We reached an identical conclusion in a recent model of mutualisms that is also based upon a direct-fitness version of Hamilton's rule [5]. The central point is that the delayed feedback benefit in reciprocal altruism can be captured with a phenotypic correlation term, which emerges in the same way as genetic relatedness. On this basis, Fletcher *et al.* claim that altruism can occur through a phenotypic correlation alone, without genetic relatedness. However, this is only true if one changes the definition of altruism used by Wilson and Hölldobler [3], and ourselves [2]: 'Altruism is defined as behavior that benefits others at the cost of the lifetime production of offspring by the altruist.' [3] Crucially, reciprocal altruism and the related phenomena that occur in mutualisms [5] cause a phenotypic feedback that benefits personal reproductive fitness. We appreciate that it is unfortunate that the nomenclature of both phenomena contain the word 'altruism', but we were careful to define our terms and, as with Wilson and Hölldobler [3], reciprocal altruism was not being discussed.

Where does this leave us? We are happy to accept that reciprocal altruism and mutualism can evolve without genetic relatedness between actor and recipient [5]. This much is obvious as partners in a mutualism need not even be of the same species. However, an altruistic act that decreases the lifetime reproduction of the actor will only be selected when it increases propagation of the causal genes through individuals that are related at one or more loci.

Which is the best: kin selection or group selection?

We view this as an empty question. There are three different ways of partitioning social selection: (i) the inclusive fitness extension of individual selection; (ii) the direct fitness model of individual selection; (iii) and the within-and-between group selection model [6,7]. Fletcher *et al.* spend most of their time advocating the second (a form of kin selection theory) but then conclude that group selection is best [1]. In reality, all three models are important and useful tools for investigating and modeling social evolution and, if applied carefully, will give the same answers [6–8].

What about our deliberate focus on the contemporary forms of these theories? Fletcher *et al.* emphasize that kin selection was historically considered an alternative to group selection [1]. This is fair enough, but there were problems with early group selection theory [9] that were not resolved until the models of D.S. Wilson [10] and Price and Hamilton [11].

As for kin selection only being correct in so far as it converges on group selection, it is revealing that no citations are offered for the latter. The reason is that group selection theory, so far at least, has done little for the study of social insects. If some hypotheses based on kin selection have failed, then that is the price of applying the theory. The positive side is that it has led to major insights on the origin of eusociality, sex ratio evolution, worker laying and policing, and caste conflict, many of which are supported by a wealth of empirical data [12,13].

Instead of these attacks on kin selection, we encourage group selection enthusiasts to provide new insights into social insect biology. However, given that the different theoretical approaches are compatible, we do not expect these insights to contradict kin selection findings. Indeed, it has long been known that group selection cannot explain the strong altruism of insect workers without invoking greater between-group genetic variance than can be achieved through random assortment [14,15]. And which ever way you slice it, this between-group variance means that group members are related [6].

References

- 1 Fletcher, J.A. *et al.* (2006) What's wrong with inclusive fitness? *Trends Ecol. Evol.* 21, 597–598
- 2 Foster, K.R. *et al.* (2006) Kin selection is the key to altruism. *Trends Ecol. Evol.* 21, 57–60
- 3 Wilson, E.O. and Hölldobler, B. (2005) Eusociality: origin and consequences. *Proc. Natl. Acad. Sci. U. S. A.* 102, 13367–13371
- 4 Fletcher, J.A. and Zwick, M. (2006) Unifying the theories of inclusive fitness and reciprocal altruism. *Am. Nat.* 168, 252–262
- 5 Foster, K.R. and Wenseleers, T. (2006) A general model for the evolution of mutualisms. *J. Evol. Biol.* 19, 1283–1293

- 6 Queller, D.C. (1992) Quantitative genetics, inclusive fitness, and group selection. *Am. Nat.* 139, 540–558
- 7 Queller, D.C. (1985) Kinship, reciprocity and synergism in the evolution of social behavior. *Nature* 318, 366–367
- 8 Foster, K.R. (2006) Balancing synthesis with pluralism in sociobiology. *J. Evol. Biol.* 19, 1394–1396
- 9 Wynne-Edwards, V.C. (1962) *Animal Dispersal in Relation to Social Behaviour*. Oliver & Boyd
- 10 Wilson, D.S. (1975) A theory of group selection. *Proc. Natl. Acad. Sci. U. S. A.* 72, 143–146
- 11 Hamilton, W.D. (1975) Innate social aptitudes in man: an approach from evolutionary genetics. In *Biosocial Anthropology* (Fox, R., ed.), pp. 133–155, John Wiley & Sons
- 12 Ratnieks, F.L.W. *et al.* (2006) Conflict resolution in insect societies. *Annu. Rev. Entomol.* 51, 581–608
- 13 Bourke, A.F.G. (2005) Genetics, relatedness and social behaviour in insect societies. In *Insect Evolutionary Ecology* (Fellowes, M. *et al.*, eds), pp. 1–30, CABI Publishing
- 14 Grafen, A. (1980) Models of *r* and *d*. *Nature* 284, 494–495
- 15 Lehmann, L. and Keller, L. (2006) The evolution of cooperation and altruism – a general framework and a classification of models. *J. Evol. Biol.* 19, 1365–1376

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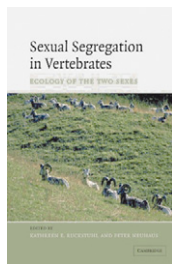
Book Review

When opposites don't attract

Sexual Segregation in Vertebrates edited by Kathreen Ruckstuhl and Peter Neuhaus. Cambridge University Press, 2006. £65.00, hbk (488 pages) ISBN-10: 0521835224, ISBN-13: 9780521835220

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The concept of sexual segregation has gained prominence in recent years, particularly in the literature on social ungulates [1–5]. It derives from the common observation that adult males and females tend to aggregate assortatively or, more formally, tend to be found in same-sex groups more often than is predicted by chance. Over the past decade, Kathreen Ruckstuhl and Peter Neuhaus have been instrumental in documenting this pattern and establishing a formal, conceptual framework for assessing its prevalence and functional significance [4,5]. In September 2002, they organized a three-day workshop at the University of Cambridge with the aim of consolidating information on sexual segregation across all vertebrates and integrating this knowledge into a common conceptual framework. *Sexual Segregation in Vertebrates* represents the culmination of these efforts and serves to establish this area of research as a productive focus for population biologists, behavioral ecologists and wildlife managers.

The book consists of 20 contributed chapters, most of which can stand alone as independent reviews. Non-specialists might be content with reading only the first two and the last two chapters, which together provide a concise overview of the key concepts and empirical evidence for sexual segregation, as well as its implications for conservation and wildlife management. However, the real meat of the volume lies in the 16 taxon-based chapters that describe what is currently known and surmised about sexual segregation in various vertebrate groups. These chapters firmly establish that sexual segregation is very common not only in sexually dimorphic, social ungulates, where it has been most extensively studied, but also in every other vertebrate group described. The general

concepts developed for ungulates work well as a framework for other taxa, albeit with some notable differences in the details. For example, thermal regime emerges as an important variable for habitat segregation in both sharks and reptiles, suggesting that it is generally important for ectotherms. Primates, including humans, also diverge somewhat from the ungulate model in that sexual segregation appears to depend much more on social factors than on factors related to the habitat per se. These and other deviations from the ungulate model enrich and extend the concept of sexual segregation and open new avenues for future research and hypothesis testing.

A bewildering array of hypotheses is advanced to explain sexual segregation and, in the second chapter, Larissa Conrath tries valiantly to organize these into a standard conceptual framework. This proves to be a difficult task, as many of the hypotheses are not mutually exclusive and several make similar, or even identical, predictions. Furthermore, many of the proposed causes of sexual segregation can be secondary effects of sexual dimorphism in body size. Body size differences lead inevitably to differences in metabolic rate, gut capacity, forage availability (e.g. browse height for ungulates), sensitivity to extreme weather, risk of predation, and even movement and activity patterns (e.g. differences in stride length and metabolic costs of transport). Body size differences can also underlie dominance relationships and the outcome of competitive interactions between the sexes. The key question is whether sexual segregation evolves in response to selection acting directly on these variables, which form the functional basis of many of the hypotheses, or is an indirect effect of divergent selection acting on body size. The authors are aware of the importance of body size and, indeed, determining to what extent sexual segregation is independent of sexual size dimorphism is one of the secondary goals of the volume. However, although the book contains several examples of sexual segregation in the absence of sexual size dimorphism (e.g. thermal niche

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