

curves reconstructed for dinosaurs are realistic, because other types of curve might fit better, and few data at their lower ends are currently available.

A third crucial question is how birds and their immediate dinosaurian relatives became small. Erickson [1], we think, misstates our results [10,11] when he says: 'It was posited that selection favored reduced body size because it enabled decreases in wing loading and improved power-to-weight ratios.' Our general analysis of growth patterns in dinosaurs showed that adult size and absolute growth rate are usually correlated [12]. As bird ancestors became miniaturized, they retained similar adult body proportions as their larger ancestors. Once bird ancestors became small, regardless of selection pressures, a geometrically similar wing size at this smaller body size would have automatically lowered wing loading, and thus increased aerodynamic lift. Given the scaling of power requirements, we implied that this consideration might be useful in analyzing early flight evolution.

We agree on the potential value and use of bone histology in fossil (and living) vertebrates to understanding the growth strategies of extinct animals. However, the opening chapters of this book are just being written.

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What's wrong with inclusive fitness?

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In a recent issue of *TREE*, Foster *et al.* [1] defend inclusive fitness theory [2] from recent challenges [3,4]. The main author of these challenges, E.O. Wilson, argues that inclusive fitness (also called kin selection [5]) might not be the main explanation for the evolution of altruism and eusociality. By contrast, Foster *et al.* claim not only that inclusive fitness is the most prominent explanation for altruism, but also that genetic 'relatedness is always required for altruism to evolve' [1]. Here, we take issue with their claim about genetic relatedness and place the debate in a larger historical context.

The key finding of inclusive fitness theory is Hamilton's rule [2], which predicts that an altruistic trait will increase in frequency when the inequality $rb > c$ is satisfied. Here, b

is the average fitness benefit provided by the altruistic behaviour and c is its average cost. The claim by Foster *et al.* that genetic similarity between altruists and their recipients is always required stems from the r term, which is traditionally seen as a measure of relatedness, and which obviously must be >0 to satisfy Hamilton's rule. Ironically, in the form of Hamilton's rule [6] that is required to address conditional traits such as eusocial sterility, the 'relatedness coefficient', r , no longer depends on kinship or genetic similarity, and the indirect fitness concept of inclusive fitness theory is not used.

As Wilson and Hölldobler point out [4], traits for eusocial sterility must be phenotypically plastic. For such conditional behaviours, Queller [6] showed that r needs to be calculated using the assortment between the genotype of each individual and the phenotype (i.e. behaviours) of those with whom they interact. Queller's more general version of

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Hamilton's rule does not measure genetic similarity and it is thus not fundamental to Hamilton's rule [7]. Genetic similarity is just one way to create the necessary degree of genotype–phenotype assortment. Queller's version also calculates the average direct fitness benefits to carriers. This highlights the phenotypic effect that colony-level adaptations (e.g. sterile workers) [3,4,8] have on selection among reproductive individuals (e.g. queens), rather than on the indirect fitness of sterile workers themselves.

In the traditional view of inclusive fitness, rb measures the indirect fitness of an average altruist via its enhancement of direct fitness to its relatives. Alternatively, and more simply, Hamilton's rule can be interpreted in terms of the direct fitness of carriers of the altruistic genotype of interest, where rb measures how much the personal reproduction of an average carrier is enhanced by help from others, related or not. Although these alternative fitness accounting methods can yield the same result, the direct fitness approach used by Queller is more general; for example, it enables one to analyse interspecific mutualisms [7]. A preference for the indirect fitness accounting method (which requires genetic similarity) does not imply that genetic similarity is actually required either by Hamilton's rule or as a causal mechanism in the evolution of altruism and eusociality in general [9].

The debate between Foster *et al.* and Wilson and Hölldobler must also be viewed in its historical context [8,10]. Foster *et al.* list several 'fallacies' in their Table 1 as though these are simple mistakes that anyone should be able to avoid, when, in fact, they were discovered only after decades of research. There was a time when kin selection was regarded as an alternative to group selection, when 3/4 relatedness was thought to be the primary explanation of eusociality, when r meant genealogical relatedness, when the focus on r obscured the importance of ecological factors (encompassed by b and c), and so on. One by one, the predictions that appeared to issue from kin selection theory failed, leading to an expanded form in which 'relatedness' (r) can now be positive even in randomly formed groups.

Although we are not necessarily endorsing all their arguments, Wilson and Hölldobler's most important claim is that colony-level selection is necessary and sufficient to explain

the evolution of eusociality. This was the explanation that historically preceded kin selection theory, which Hamilton's focus on genetic relatedness appeared to replace. Colony-level selection for eusociality is made possible by colony-level adaptations that produce sufficient assortment between the genotype of reproductives and the phenotypic help from non-reproductives. The efficiency of these adaptations in delivering fitness benefits to reproductives matters, whereas the degree of relatedness to non-reproductives does not. This assortment produces heritable phenotypic variation at the colony level, which depends on genetic variation among colonies, but the amount of genetic variation need not be exceptional and can even be random, just as random genetic variation among individuals can be sufficient for individual-level selection. The expanded version of 'kin selection' described by Foster *et al.* is correct only insofar as it converges upon the theory that it appeared to replace.

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Free journals for developing countries

The WHO and six medical journal publishers have launched the Health InterNetwork Access to Research Initiative, which enables nearly 70 of the world's poorest countries to gain free access to biomedical literature through the internet.

The science publishers, Blackwell, Elsevier, Harcourt Worldwide STM group, Wolters Kluwer International Health and Science, Springer-Verlag and John Wiley, were approached by the WHO and the *British Medical Journal* in 2001. Initially, more than 1500 journals were made available for free or at significantly reduced prices to universities, medical schools, and research and public institutions in developing countries. In 2002, 22 additional publishers joined, and more than 2000 journals are now available. Currently more than 70 publishers are participating in the program.

Gro Harlem Brundtland, the former director-general of the WHO, said that this initiative was "perhaps the biggest step ever taken towards reducing the health information gap between rich and poor countries".

For more information, visit www.who.int/hinari

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].

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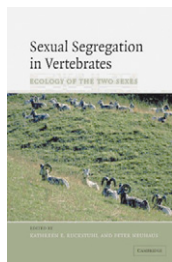
Book Review

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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