

THE EVOLUTION OF TERMITE EUSOCIALITY:
REPLY TO LEINAAS

I earlier suggested that an unusual system of chromosome transmission might have facilitated the evolution of sterile castes in the termites (Lacy 1980; Luykx and Syren [1979] independently raised the same possibility). Translocation complexes in the males of many termite species effectively link much of the genome to the sex chromosomes, leading to greater coefficients of relatedness among same-sex siblings than between parents and offspring. Because the coefficients of relatedness arising from the sex linkage are symmetrical in the two sexes of Isoptera, I predicted same-sex directed altruism by both sexes of termites. Sterile castes in termites are composed of both (genetical) males and females. This contrasts with the haplodiploid Hymenoptera, in which only females share a closer genetic relationship to siblings (sisters) than to offspring, and only females become sterile workers. The frequency and extent of the translocation complexes vary among termite taxa, leading Luykx and Syren (1979) to suggest a recent origin of the systems and, therefore, to view as unlikely a role for translocation complexes in the origins of eusociality. Translocation complexes have been found in the primitive families Kalotermitidae (Luykx and Syren 1979) and Rhinotermitidae (Fontana and Amorelli 1978), as well as in almost all members of the advanced family Termitidae that have been examined (Vincke and Tilquin 1978), however, and so either the translocation complexes have arisen multiple times in divergent taxa or they arose very early in the evolution of the Isoptera. Moreover, the largest complexes of sex-linked chromosomes (encompassing about half of the genomes) have been found in *Kalotermes* and *Incisitermes* (Luykx and Syren 1979), two of the more primitive of the living termite genera, suggesting that even more of the genome may have been linked to the sex chromosomes of the earliest termites.

Leinaas (1983) has questioned the efficacy of my hypothesis, first arguing that it is not biologically plausible for termites to invest preferentially in same-sex sibs, and then claiming that even if such behavior were possible, it would not increase the inclusive fitness of its performers. In discounting the possibility that nonreproductive termites could favor the production of same-sex reproductives, Leinaas points out that some functions (e.g., nest guarding) carried out by specialized castes (e.g., soldiers) cannot be biased toward a greater production of one sex of reproductives. At the early stages of the evolution of termite eusociality, however, there presumably were no castes that specialized on such functions to the exclusion of all others. In the more primitive living families, soldiers develop from nymphs and/or pseudergates that perform the worker tasks of the colony, such as tending immatures. Moreover, the inhibitory pheromones that determine which nymphs will develop into reproductives are sex-specific in their effects and are transferred through the colony by trophallaxis (Wilson 1971). It does not seem

at all implausible that workers could modify the sex ratio of new reproductives by selective transmission of the inhibitory pheromones. As pointed out by West-Eberhard (1975), once a worker caste has evolved sterility, selection on their efficiency in propagating genes via reproductive siblings will push them toward becoming "super donors." This might account for the subsequent diversification of primitive neuters into the highly specialized castes of the more advanced termites.

Leinaas claimed that a gene causing termites to invest preferentially in same-sex siblings rather than in offspring (if it could exist) would not be favored by natural selection: "The inclusive fitness of such a nonreproductive is not directly dependent on those individuals in which it has invested by itself. It refers to all receiving reproductives by which it shares genes identical by descent (Hamilton 1964), i.e., all receiving reproductives of the colony" (Leinaas 1983, p. 303). By including all genetically related reproductives in the determination of an individual's inclusive fitness, Leinaas uses an incorrect, but unfortunately common, interpretation of inclusive fitness theory. (See Grafen [1982] for further discussion of this type of error.) Inclusive fitness, as defined by Hamilton (1964, p. 8), is "the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit *which the individual himself* causes to the fitnesses of his neighbours." (Italics are mine.) Thus, the inclusive fitness of one individual is not dependent on the whole colony's investment, but rather on that individual's investment, in each sex. Although a worker may not benefit from the worker behavior of opposite-sex siblings, or even from the cumulative efforts of all other workers in the colony, this in no way changes the costs and benefits to an individual rearing siblings as opposed to offspring. A termite that forgoes the rearing of siblings because the efforts by the male and female workers of the colony seemingly cancel, will lose the genetic benefits it would have gained by rearing same-sex sibs, since the counterproductive (from its point of view) efforts by opposite-sex workers would continue. Natural selection will favor behavior by each individual that maximizes the number of copies of its genes transmitted to the next generation, even if such behavior does nothing to increase the fitness of the colony as a whole.

Two alternative impetuses toward the evolution of eusociality were suggested by Leinaas, though he unnecessarily links them and implies that I rejected both. First, I fully agree that if a termite would contribute more by assisting its mother's production of offspring than by reproducing at the natal nests despite inhibition by parents and sibs, or departing and attempting to found a new colony, then no asymmetries in genetic relatedness are necessary for the evolution of nonreproductive castes. Helpers at the nest in some bird species seem to altruistically delay reproduction for such reasons (Brown 1978).

Leinaas appears to tie this ecological hypothesis to an inbreeding hypothesis. The "specific conditions of inbreeding" under which siblings become more

closely related to each other than are parents to their offspring require an alternation of inbred and outbred generations (Bartz 1979), such that the choice made by potential workers is between inbred siblings and outbred offspring. The model requires that the first generation progeny of a colony newly established by an outcrossed pair remain at or near the natal nest and inbreed, though it is of no genetic advantage for them to do so. It is in the next generation, when Bartz finds an advantage to the inbred progeny of remaining in the nest as workers, that dispersal of reproductives must occur. Whether such an alternation of generations was common during the early evolution of the termites is presently open to speculation.

Notwithstanding early suggestions to the contrary (Hamilton 1964; Maynard Smith 1964), it is not generally the case that "inbreeding increases the likelihood that an altruistic trait will evolve also without any asymmetry in relationship" as Leinaas (1983, p. 304) claims. The evolution of altruism can be favored, or disfavored, by asymmetrical inbreeding coefficients (e.g., inbred siblings, but outbred offspring) or by inbreeding coupled with nonadditive effects of alleles (Michod 1979, 1982), but inbreeding in itself does not lead to the favoring of one relative over another when both have the same coefficient of relatedness to the altruist. Kin-directed altruism involves a loss in copies of the altruist genes carried by the altruist's own offspring in exchange for an increased number of the genes carried by other relatives in the next generation. Inbreeding increases the fractions of genes identical by descent with all relatives, including one's own offspring. Craig (1982) modeled the effect of inbreeding in haplodiploid systems and found that the ratio of (relatedness to siblings):(relatedness to offspring) remains near one. Uyenoyama and Bengtsson (1982) derived similar results in the diploid case: prolonged inbreeding increases sibling-sibling and parent-offspring relationships to the same degree, when sib matings occur at random with any constant probability over generations. Therefore, as the numbers of copies of an altruist's genes gained in the recipients of an altruistic trait are increased by any consistent frequency of inbreeding in the population, so proportionately is the cost in copies of genes lost by the reduction in offspring produced directly.

Thus, inbreeding probably does not account for the evolution of eusociality. Ecological circumstances that made sib-rearing behavior more efficient than offspring rearing could have favored the evolution of sterile castes in both the Isoptera and the Hymenoptera in the absence of any genetic predisposition. Eusociality, however, has evolved only in these two taxa (repeatedly in the Hymenoptera and presumably once in the Isoptera) which by virtue of sex linkage relationships have greater sib-sib than parent-offspring coefficients of genetic relatedness. This suggests that Hamilton's explanation of the evolution of sterile castes may apply not only to the Hymenoptera, but to the formerly exceptional Isoptera as well.

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