

THE EVOLUTION OF EUSOCIALITY IN TERMITES:  
A HAPLODIPLOID ANALOGY?

Since Hamilton (1964) first demonstrated that kin selection could act on the haplodiploid genetics of the Hymenoptera to lead to the evolution of sterile castes, the equally social termites (Isoptera) have posed a serious problem to the kin selection theory of insect eusociality. In the termites both males and females are diploid and follow a typical X-Y chromosomal sex determination, so that the unusual coefficients of relatedness that are found in the Hymenoptera would not seem to apply. The prevalent current hypothesis is that termite eusociality is a consequence of their dependence on symbiotic intestinal flagellates (Wilson 1971). As was first suggested by Cleveland (Cleveland et al. 1934), the symbiotic relationship between termites and their cellulose-digesting protozoans may necessitate colonial life. The protozoans are lost at each molt and reinoculation takes place via nutrient transfer among colony members. In itself, however, this requirement for coloniality would not predispose the termites to the evolution of sterile castes. Certainly many other colonial organisms exist that have not subsequently evolved separate castes for reproduction and offspring care.

Hamilton (1972) has suggested another possible evolutionary path to termite sociality. If inbreeding is common, then the high level of genetic relatedness within colonies might lead to a high degree of cooperativeness among colony members. It is difficult to see how Hamilton's inbreeding theory could lead to sterile castes, however, since inbreeding increases the genetic correlation between parents and progeny to the same extent as it increases the relationship between full siblings. (Both additive genetic correlations equal  $\frac{1}{2}(1 + F)$ , where  $F$  is the coefficient of inbreeding.) No amount of inbreeding will cause siblings to be closer genetically than are parents to their offspring, and thus inbreeding would not alter any evolutionary tendency for workers to forego reproduction in order to rear siblings. Dawkins (1978) has speculated that the genes of the symbiotic intestinal flagellates may have taken control over the physiology and behavior of their termite hosts, yet he offered no comment on how the protozoans might benefit from eusocial behavior in the termites. It appears that a mechanism for the evolution of sterile castes in termites still must be sought.

Whitney (1976) has pointed out that organisms with chromosomal sex determination are functionally haplodiploid with respect to the X chromosome. Therefore a tendency for like-sex sib directed altruism in the homogametic sex may be expected to evolve if a substantial fraction of the genome is sex linked. Recent cytogenetic studies of termites have revealed a system of translocations that effectively links much of the genome to the sex chromosomes. Syren and Luykx (1977) reported that males of the termite species *Incisitermes schwarzi* are heterozygous for a series of translocations in seven to eight of the 16 chromosome

pairs. This translocated set includes the sex chromosomes and forms a ring during meiotic pairing. Alternate disjunction from the ring prevents chromosomal imbalance in the gametes and assures that the translocated set of chromosomes is passed on to the male offspring along with the Y chromosome. The homologous set without the translocations is always transmitted to the female progeny with the X chromosome. Thus approximately half of the genome is maintained as a linkage group with the sex chromosomes. Syren and Luykx (1977) also observed translocation complexes of unspecified size during male meiosis in the species *Kaloterme approximatus* and *Neoterme castaneus*. More recently, Fontana and Amorelli (1978) found that translocation linkage chains often appear during meiosis in the termite *Reticuliterme lucifugus*. The chains involve less of the genome (two to four of the 21 chromosome pairs), but again the presence of the translocation heterozygote complex only in males suggests that a considerable fraction of the genome is sex linked.

These cytogenetic findings lead to genetic correlations among relatives that have some similarities to those in the Hymenoptera. Parents transmit half of their genes to each offspring regardless of sex. Thus the parent-offspring genetic correlation is .5 (in the absence of inbreeding). On the average sisters share 50% of their non-sex-linked genes and 50% of their maternal sex-linked genes, but receive identical sets of sex-linked genes from the father. In *I. schwarzi* where half of the genome is functionally sex linked, the genetic correlation between sisters is therefore .625 (.75 for the sex-linked genes and .50 for the non-sex-linked genes). Brothers similarly share half of the non-sex-linked and maternal sex-linked genes, and 100% of the paternal sex-linked translocation set. Thus they are related by .625 (unlike the haploid hymenopteran males that show genetic relationships of only .50). A brother-sister pair shares 50% of the non-sex-linked and maternal sex-linked genes, but have none of the paternal sex-linked genes in common, resulting in a genetic correlation of .375.

For termites such as *R. lucifugus* that have less of the genome involved in the translocation linkage group, the sister-sister and brother-brother correlations would be closer to .50. However, the pattern of relationships still holds: Individuals are more closely related to same-sex siblings than to their offspring, and genetically closer to their offspring than to opposite-sex siblings. A tendency to invest resources in same-sex sibs rather than in offspring would therefore increase inclusive fitness.

In the social Hymenoptera a skewed sex ratio in favor of females allows the female workers to take advantage of the genetic relationships by rearing sisters rather than offspring. The male drones, for whom all members of the immediate family are equally close genetically, do not forego reproduction and do not help to rear siblings. In termites the sterile worker and soldier castes are composed of both sexes, as would be predicted from the parallel coefficients of relatedness in the two sexes. Although males and females obviously cannot both skew the sex ratio of a termite colony in their favor, the investment of resources in young by a worker is not necessarily equally allotted to the two sexes. As long as nonreproductives preferentially invest in same-sex sibs within the colony, their inclusive fitness is greater than that of reproductives that rear equal numbers of progeny,

and an evolutionary advantage to sterile castes exists. I am unaware of any empirical data on the allotment of care to the sexes in termite broods by male and female workers; and indeed, until now, there would have been no reason to collect such data.

While the termites *I. schwarzi*, *K. approximatus*, *N. castaneus*, and *R. lucifugus* have been reported to contain heterozygous translocation complexes in males, no such rings or chains have been found in the species *Termopsis angusticollis*, *R. flavipes*, *Odontotermes redemanni*, and *N. jouteli* (Syren and Luykx 1977). Since *Incisitermes*, *Neotermes*, and *Kaloterme*s are in the relatively primitive family Kalotermitidae and the other genera in more advanced families (Wilson 1971), it would seem that the translocation complexes may represent the primitive termite genome that was present when eusociality with sterile castes first arose during termite evolution.

## ACKNOWLEDGMENTS

I thank Jan Salick for bringing the termite cytogenetic literature to my attention.

## LITERATURE CITED

- Cleveland, L. R., S. R. Hall, E. P. Sanders, and J. Collier. 1934. The wood-feeding roach *Cryptocerus*, its Protozoa, and the symbiosis between Protozoa and roach. Mem. Am. Acad. Arts Sci. 17:185-342.
- Dawkins, R. 1978. Replicator selection and the extended phenotype. Z. Tierpsychol. 47:61-76.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. I., II. J. Theor. Biol. 7:1-52.
- . 1972. Altruism and related phenomena, mainly in social insects. Annu. Rev. Ecol. Syst. 3:193-232.
- Syren, R. M., and P. Luykx. 1977. Permanent segmental interchange complex in the termite *Incisitermes schwarzi*. Nature (Lond.) 266:167-168.
- Whitney, G. 1976. Genetic substrates for the initial evolution of human sociality. I. Sex chromosome mechanisms. Am. Nat. 110:867-875.
- Wilson, E. O. 1971. The insect societies. Harvard University Press, Cambridge, Mass.

ROBERT C. LACY

SECTION OF ECOLOGY AND SYSTEMATICS  
CORNELL UNIVERSITY  
ITHACA, NEW YORK 14850

Submitted December 12, 1978; Accepted June 1, 1979