

The Epigenetical Origins of Insect Sociality

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Evolutionary theories of insect sociality deal extensively with the problem of explaining the spread and stable persistence of genes promoting the helping (or "altruistic") behavior of workers (for a review of genetic models, see Michod, 1982). It is now desirable to take full account of the fact that worker and reproductive phenotypes are usually facultative in nature: they are alternative expressions of a single genotype, with the phenotype adopted depending on developmental and/or behavioral circumstances (long referred to by students of social insects as "caste determination"). This lecture addresses the question of how such facultative adaptive responses are constructed during evolution.

Consideration of the reproductive cycles of solitary, primitively social (group-living but casteless), and eusocial (worker containing) wasps indicates that the facultative expression of a worker phenotype is derived from two condition-sensitive responses evidently widespread in solitary species, namely, broodcare in the presence of larvae and oosorption when oviposition is blocked (see Flanders, 1962; Bell and Bohm, 1975). Observations of the primitively social eumenid wasp *Zethus miniatus* Saussure showed that individual females usually behaved like solitary wasps, independently building cells, laying eggs, and provisioning and defending their own larvae one at a time. However, temporarily sterile individuals (broodless females lacking a mature ovarian egg) adopted the orphaned larvae of other females if any were available. This suggests that worker behavior can originate as misplaced parental care by an eggless female in the presence of orphans, and might occur with little or no genetic change in groups which have evolved under selection in other contexts (e.g., reuse of cells under selection for economy of construction activity, or mutualistic defense). Intragroup reproductive competition, likewise expected to be a common result of life in groups (see West-Eberhard, 1981), has evidently produced permanently sterile workers via the evolution of effective devices (including parental manipulation) for monopolizing oviposition ("queen control"). Control of nestmate oviposition by filling and defending cells may have been sufficient cause for the advent of worker sterility, since oosorption when oviposition is blocked is a widespread response in the Hymenoptera and other insects (Flanders, 1961; Bell and Bohm, 1971). At the same time, aggressive queen control could generate, as a side effect, a supply of orphaned larvae, the product of a negligent (non-foraging) dominant female ("queen") preoccupied with territorial domination of the nest. The hypothesis that a worker caste is readily derived from a solitary phenotype given life and competition in groups is supported by the finding that a worker phenotype can be produced in solitary bees (*Ceratina* species) experimentally forced to live in groups

(Sakagami and Maeta, 1986). Even if some worker traits in such species were to prove vestiges of an ancestral social state, these studies are important demonstrations of the ease of passing back and forth across the border between solitary and eusocial life (see also, Michener, 1985).

Kin selection (the genetic profit associated with aid to kin) undoubtedly plays an important role in the evolution of a sterile worker caste, which in all known cases occurs in kin groups. However, given the above considerations kin selection is not necessary to explain the origin of sterile workers, which can occur without positive selection of alleles for helping non-offspring. Rather, kin selection may act primarily to maintain facultative aid by affecting the evolution of regulatory mechanisms assuring that worker behavior is expressed only when likely to be adaptive. Other behaviors (such as surreptitious egg-laying, waiting for a future opportunity to reproduce, independent nest initiation, or fighting to the death) expressed as alternative patterns when more advantageous than worker behavior (West-Eberhard, 1981). Kin selection would thus play a role, not in the spread of "altruistic" alleles, but in the evolution of the regulation of the worker phenotype once it has originated as a side effect of selection in other contexts (e.g. favoring cell reuse or mutualistic defense, and control of nestmate oviposition).

By this "epigenetic" interpretation Hamilton's Rule for the operation of kin selection describes the switch point for the expression of the worker phenotype in subordinate individuals (West, 1967; West-Eberhard, 1975). Hamilton's Rule-- $K > 1/r$ --states that there is positive selection for helping behavior when the ratio of benefit to cost of aid (K) in terms of individual fitness is greater than the reciprocal of a coefficient of relatedness between donor and recipient (r). The epigenetic interpretation predicts the evolution of mechanisms permitting the evaluation of K and r , including use of cues indicating expected reproductive success and relatedness, as well as the setting (under neutral selection) of threshold states of those cues likely to yield profitable worker behavior in particular species and situations. Such cues exist, e.g. in the form of dominance relations (proposed as an evaluator of K --see West-Eberhard, 1967), and kin recognition devices (evaluators of r --reviewed in Gadagkar, 1985). And there is some evidence (e.g., West, 1967; Noonan, 1981; Metcalf and Whitt, 1977 a and b; Strassman, 1981) that Hamilton's Rule is satisfied in nature.

Thus far, all of these field studies using social insects to test kin selection theory have examined the results of facultative alternative patterns and confirm the importance of kin selection in the evolutionary fine-tuning of a caste-determining switch mechanism. That is, they are tests of an epigenetic model concerned with expression of alternative phenotypes rather than of a genetic model concerned with competition among alternative alleles.

Evolutionary epigenetics calls for a synthesis of information and theory on development, genetics, phylogeny, and comparative behavior. It would aim to describe the likely phenotype transitions from ancestral to derived phenotypic states. Such an approach, in the tradition of Roubaud (1916) and Wheeler (1920), is not new to students of social insects. But incorporation of a developmental viewpoint (e.g., see Kennedy, 1966) has been neglected because of emphasis on genetic issues and failure to see precisely how the

insights of genetic theory should be related to information on development and ancestral phenotypes (see discussion following Kennedy, 1966; Craig, 1983 is a recent attempt at synthesis).

An epigenetic approach leads to a revised view of how major transitions occur during the evolution of social behavior, for example, suggesting that novel phenotypes such as eusociality and social parasitism can originate and be elaborated as facultative intraspecific alternatives rather than new branches on a phylogenetic tree (see West-Eberhard, 1986; and in press b for general discussions; Michener, 1985 on bees). Studies of social insects may help to illuminate the evolution of flexible behavior in general, especially given the wealth of information now available on the physiology, behavior, and environmental correlates of caste determination in species having different degrees of behavioral and morphological specialization (Nijhout and Wheeler, 1982).

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