

to the vicinity. In laboratory experiments, workers entering an arena simultaneously with workers from alien colonies always gained the initial advantage in the ensuing conflict if they had previously been allowed to mark the arena. When the arena was placed in a spatial position familiar to one colony but possessed a floor previously marked by the second colony, the second colony still won. To our knowledge these results represent the first demonstration of a true territorial pheromone in the social insects.

5. During foraging the *Oecophylla* workers move independently of one another and are distributed at random (Poisson distributed) or with slight temporary clumping of no more than two or three workers. Short-range recruitment of intruders causes the ants to shift to a more distinctly clumped pattern, involving as many as ten or more workers, at the same time that long-range recruitment brings more defenders into the vicinity. Together the two forms of response result in a more efficient capture of intruders that are too large to be immobilized by only one or two workers.

6. The complex recruitment and territorial behavior displayed by *O. longinoda* is considered to be part of the adaptation of these relatively large ants to a strongly arboreal existence. The similarity of four of the recruitment systems to each other (1a, b, c, and e above) is interpreted as an example of signal economy in the evolution of social insect communication systems. The parallel evolution has been enhanced by the lack of any strong functional distinction between territorial defense and predation (see Discussion).

7. Signal ritualization appears to have occurred in at least two contexts: the modification of body thrusting during territorial battles into the jerking signal used in long-range recruitment of nestmates to enemies; and the adoption of anal excrement in the chemical marking of territories.

Introduction

The study of recruitment systems in ants has begun to diversify during the past five years. In the 1950's and 1960's the straightforward identification of the glandular source of the trail pheromones was emphasized, with some attention being paid to the details of the trail-laying behavior and the nature of the accessory stimuli necessary to evoke the trail-following response in some species (Wilson, 1971; Maschwitz, 1975; Hölldobler, 1977). Now a new emphasis has begun to form: the analysis of the ecological significance of recruitment. The possession of one kind of recruitment system as opposed to another is seen to constitute adaptations by individual species to particular conditions in their environment. Indeed, the recruitment strategy appears to make little sense except with reference to the ecology of the species, while, conversely, the ecology of many species cannot be fully understood without a detailed knowledge of their recruitment procedures (Hölldobler, 1976a).

Ecologically dominant species are especially dependent on recruitment systems to control their environment. This is true, for example, of the African red weaver ant *Oecophylla longinoda*, the colonies of which spread their large territories over the canopies of forest trees and onto the surrounding ground.