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A SOCIAL ETHOGRAM OF THE NEOTROPICAL ARBOREAL ANT *ZACRYPTOCERUS VARIANS* (FR. SMITH)

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Abstract. An ethogram is presented of *Zacryptocerus varians*, a morphologically advanced member of the 'turtle ants' comprising the neotropical ant tribe Cephalotini. The species displays unusual and in one or two cases possibly even unique social behaviours, including the consumption and sharing of infrabuccal pellets, the apparent absence of adult transport, a primarily or exclusively mechanical form of colony defence, and a remarkable form of abdominal trophallaxis. All of these specializations seem to be associated with more primary adaptations by the species to arboreal nesting and scavenging. Among the additional results is the demonstration that the major worker is more specialized as a defensive caste than is the case in certain species of *Camponotus* and *Pheidole*.

The ethogram, or complete catalogue of the behavioural patterns of a species, is a far more practicable goal in the case of social insects than it is in vertebrates. Wilson & Fagen (1974), in an analysis of the ant *Leptothorax curvispinosus* Mayr, estimated that twenty-seven categories of interactions, which were obtained with only 1962 observations of behavioural acts spread over an accumulated period of 51 hr, covered no less than 77 per cent of the total social repertoire displayed within and in the immediate vicinity of the nest. More precisely, it was estimated that the total number of categories of interaction, examples of which include grooming larvae, carrying dead nestmates, stridulating, and so forth, is twenty-nine, with a 95 per cent confidence interval of [27, 35]. The sample coverage, which is the estimated probability that each new act will fall in a category already seen, was a much higher value, 0.9995. These levels were reached in *Leptothorax curvispinosus* much more quickly than in mammals because of two features of ant behaviour: the smaller repertoire of the ants and the smaller proportion of their behavioural categories that are relatively rare in occurrence.

Ant behaviour can thereby be encompassed more readily than vertebrate behaviour. Moreover, the colonies can be studied under laboratory conditions that facilitate experimentation and the recording of data. Entire colonies of many species can be placed on the stage of a dissecting microscope or within the field of a motion-picture camera and all their members monitored simultaneously. Myrmecologists are consequently in a position to proceed with comparative sociobiology at a quick pace. Why

they have not done so until now can be explained by two historical circumstances: the lack of understanding of the true basis of communication in ants, and the failure to appreciate the advantage intrinsic in the relatively sparse social repertoires of these insects. Both difficulties having recently been remedied (see reviews in Wilson 1971; Hölldobler 1976), we can proceed with the systematic exploration of the approximately 270 genera and 12 000 species of ants. Only through ethograms, organized in a way that permits species and even genera and tribes to be closely compared, will it be possible to trace social evolution efficiently within the ants as a whole. In ordinary reports valuable data can be and are presented within the contexts of narrow experimental design, but this format causes whole categories of behaviour to be overlooked, and other useful observations noted fortuitously outside the scope of the experiments are seldom recorded.

The present report comprises an example of social ethogram mapping in ants. Earlier efforts have included the analysis of *Leptothorax* just cited plus an earlier, non-quantitative study of *Daceton armigerum* (Wilson 1962). The importance of the species considered here, *Zacryptocerus varians*, is threefold. It is an advanced member of one of the least known major ant tribes, the Cephalotini; and it is extremely modified for an arboreal existence, offering the opportunity to study the influence of this adaptation in the modification of the basic ant social system. Finally, *Z. varians* has one of the most extreme and bizarre physical caste systems, and for this reason it was selected to be included in the author's current study of ant castes.