

an area of approximately half the size of the daily foraging area of *E. burchelli*.

Comparison with other *Leptogenys* species

We began our studies on this genus with *Leptogenys processionalis* (*L. ocellifera*) from Sri Lanka (Maschwitz and Mühlenberg 1973, 1975). This species as well has many army-ant-like habits, but also some distinct specialized characteristics. The colony size is similar to that of *Leptogenys* sp. 1. The ants may change their nest frequently; however one colony was observed at the same site for at least ten weeks. In contrast to the characterization of army ant behavior already mentioned, the raiding ants leave the temporary nest to deepened trunk trails that may be used for several weeks.

In the area where our studies on *Leptogenys* sp. 1 were conducted, we found a total of twelve *Leptogenys* species, five of which have army ant characteristics. Besides *Leptogenys* sp. 1, these species are *L. mutabilis*, *L. birmana*, *L. crassicornis*, and *Leptogenys* sp. 2 (unidentified and possibly undescribed species resembling *L. borneensis*). Though we have not yet finished our studies on the behavior of these species, differences in their ecology are obvious. *L. mutabilis* is an epigaeic mass raider, but contrary to *Leptogenys* sp. 1, the workers forage mainly beneath the leaf litter. *L. crassicornis* is hypogaeic, but parts of the raid columns of this small species sometimes were discovered above ground, at night.

The seven species that are not army ants in the sense already mentioned search for prey solitarily. After encountering the prey, they either recruit a group of nestmates, e.g., *L. diminuta*, or even attack and retrieve their prey solitarily, e.g., *L. pequeti*.

Acknowledgements. The authors wish to express their gratitude to the Deutsche Forschungsgemeinschaft and the Studienstiftung des Deutschen Volkes, which supported this project with grants. We also thank the University of Malaya for allowing us to stay at the Ulu Gombak Field Studies Centre. For the identification of the ants we are grateful to B. Bolton (London). The ant-guests were determined by R.H.L. Disney (Cambridge, U.K.), S. Taiti and F. Ferrara (Florence). The statistical analysis of the emigration pattern was done by W. and R. Wiltshko (Frankfurt). Figure 5 was taken by D. Kovac. We are grateful to K. Fiedler, R.W. Klein, and W.A. Nässig for their critical comments on the manuscript.

References

- Attygalle AB, Vostrowsky O, Bestmann HJ, Steghaus-Kovac S, Maschwitz U (1988) (3R,4S)-4-Methyl-3-heptanol, the trail pheromone of the ant *Leptogenys diminuta*. *Naturwissenschaften* 75:315-317
- Batschelet E (1981) Circular statistics in biology. Academic Press, London
- Bishop JE (1973) Limnology of a small Malayan river Sungai Gombak. Junk, The Hague
- Chadab R, Rettenmeyer CW (1975) Mass recruitment by army ants. *Science* 188:1124-1125
- Disney RHL (1988) Biology and taxonomy of Old world *Puliciphora* (Diptera: Phoridae) with descriptions of nine new species. *Orient Insects* 22:267-286
- Ferrara F, Maschwitz U, Steghaus-Kovac S, Taiti S (1987) The genus *Exalloniscus* Stebbing, 1911 (Crustacea, Oniscoidea) and its relationship with social insects. *Publ Inst Entomol Univ Pavia* 36:43-46
- Fletcher DJC (1973) "Army ant" behaviour in the Ponerinae: a re-assessment. Proc VII Congr IUSSI, London
- Franks NR (1982) A new method for censusing animal populations: the number of *Eciton burchelli* army ant colonies Barro Colorado Island, Panama. *Oecologia* 52:266-268
- Franks NR, Fletcher CR (1983) Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behav Ecol Sociobiol* 12:261-270
- Gotwald WH Jr (1978) Emigration behavior of the East African driver ant, *Dorylus (Anomma) molesta* Gerstaecker (Hymenoptera: Formicidae: Dorylinae). *J NY Entomol Soc* 86:290
- Gotwald WH Jr (1979) Phylogenetic implications of army ant zoogeography (Hymenoptera: Formicidae). *Ann Entomol Soc Am* 72:462-467
- Maschwitz U, Hänel H (1985) The migrating herdsman *Dolichoderus (Diabolus) cuspidatus*: an ant with a novel mode of life. *Behav Ecol Sociobiol* 17:171-184
- Maschwitz U, Mühlenberg M (1973) *Leptogenys ocellifera* (Form.). Verhalten auf Dauerspuren. Alarmierung und Beuteeintragen (Freilandaufnahmen). *Encyclop Cinemat, Göttingen*, pp 3-10
- Maschwitz U, Mühlenberg M (1975) Zur Jagdstrategie einiger orientalischer *Leptogenys*-Arten (Formicidae: Ponerinae). *Oecologia* 20:65-83
- Maschwitz U, Schönegge P (1983) Forage communication, nest moving recruitment, and prey specialization in the oriental ponerine *Leptogenys chinensis*. *Oecologia* 57:175-182
- Masuko K (1987) *Leptanilla japonica*: the first bionomic information on the enigmatic ant subfamily Leptanillinae. In: Eder J, Rembold H (eds) Chemistry and biology of social insects. Proc 10th Int Congr IUSSI, Peperny, Munich, pp 597-598
- Moffett MW (1984) Swarm raiding in a myrmicine ant. *Naturwissenschaften* 71:588-590
- Raignier A, van Boven J (1955) Etude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera Formicidae). *Ann Mus R Congo Belge Sci Zool* 2:1-359
- Rettenmeyer CW (1963) Behavioral studies of army ants. *Univ Kans Sci Bull* 44:281-465
- Sachs L (1974) *Angewandte Statistik*. Springer, Berlin
- Schneirla TC (1971) Army ants. In: Topoff HR (ed) A study in social organization. Freeman, San Francisco
- Schneirla TC, Reyes A (1966) Raiding and related behaviour in two surface-adapted species of the Old World doryline ant, *Aenictus*. *Anim Behav* 14:132-148
- Smallwood J (1982) Nest relocations in ants. *Insectes Soc* 29:138-147
- Smallwood J, Culver DC (1979) Colony movements of some North American ants. *J Anim Ecol* 48:373-382
- Topoff H, Miranda J (1980) Army ants do not eat and run: