

FORAGING BEHAVIOR OF *ODONTOMACHUS BAURI* ON
BARRO COLORADO ISLAND, PANAMA

BY BIRGIT EHMER AND BERT HÖLLDOBLER

Theodor-Boveri-Institut, Lehrstuhl für Verhaltensphysiologie
und Soziobiologie der Universität
(Zoologie II), Am Hubland, D-97074 Würzburg, Germany

ABSTRACT

Foraging behavior and partitioning of foraging areas of *Odontomachus bauri* were investigated on Barro Colorado Island in Panama. The activity of the ants did not show any daily pattern; foragers were active day and night. The type of prey captured by *O. bauri* supports the idea that in higher *Odontomachus* and *Anochetus* species, the high speed of mandible closure serves more for generating power than capturing elusive prey. Polydomous nests may enable *O. bauri* colonies to enlarge their foraging areas.

INTRODUCTION

The ponerine ant genus *Odontomachus* is distributed throughout the tropics and is especially abundant in the Neotropics. The most conspicuous feature of this genus is the trap-jaws, which the ants can open to an angle of 180° and close in less than 0.5 ms (Gronenberg, Tautz, and Hölldobler, 1993; Gronenberg, 1995). Convergenly evolved trap-jaws exist also in the dacetine ants (Myrmicinae) and in the formicine genus *Myrmoteras*, most species of which prey on springtails (Brown and Wilson, 1959; Moffett, 1986). Springtails have very fast escape responses (Christian, 1979), so it is likely that the trap-jaw mechanism in dacetines and *Myrmoteras* evolved to facilitate the capture of these arthropods. For *Odontomachus* species, however, very few field studies exist and surprisingly little is known about the nesting and foraging biology of most species. Even for *Odontomachus bauri*, a common and conspicuous species in the Neotropics, little is known about its foraging behavior and general biology. It is commonly regarded as a generalist predator (Brown, 1976; Levings and

Manuscript received 5 May 1996.

Franks, 1982). This assumption was examined during a study of foraging activity, choice of prey items, foraging range, and nesting habits on Barro Colorado Island in Panama.

MATERIALS AND METHODS

Ants were observed on Barro Colorado Island, Panama, during three months from April to June 1995. Ant colonies were collected on the nearby mainland at Gigante. To measure activity a nest was observed 25 minutes per hour for 5 to 6 hours, eventually covering an observation period from 6–23 h. All ants entering or leaving the observed nest were counted. The first 5 minutes of each 25 minute observation period were discarded, as the ants were usually disturbed by the observer when approaching the nest. Continuous observation of 1 nest for 3 hours showed, that an observation time of 20 minutes is sufficient to give a good representation of the activity of the colony. Foraging success was measured by noting whether or not the returning ants were carrying prey into the nest. The data were collected at the end of the dry season in May. Occasional rains had already occurred, but the soil was dry while recording. At the same time, air temperature above and below the leaf litter and humidity (above the leaf litter) was measured .

For assessing the foraging area, individual ants were followed out from the nest as far as possible. To facilitate following the ants the leaf litter was removed from the nest entrance area and in 10–15 cm wide strips in regular intervals around the nest. A marker was set where contact with the ant was lost or the ant turned back or captured prey. The distance and direction traveled from the major nest entrance was measured. All observed ants were unmarked, as marking was found to disturb the treated ants considerably and paint markings were not very durable.

Nests were studied mainly in one 200m² area in the east of the island where 23 nest sites were located. Most nests consisted of simple chambers between leaves in accumulations of leaf litter, preferentially next to dead wood.

RESULTS

Activity of *Odontomachus bauri*

The foraging activity of *Odontomachus bauri* colonies remained approximately the same during day and night (Fig. 1). The counts

varied from 2 to 44 ants entering or leaving the nest during a 20 minute observation period. There was no correlation between time of the day and activity of the ants (Fig. 1). Nor could a correlation be found between activity and air temperature, soil temperature, or humidity. These parameters did not vary much, air temperature ranging from 24°C to 30°C, the soil temperature from 24.2°C to 27.5°C and humidity from 78% to 97% (Fig. 2). The leaf litter buffers temperature and also probably humidity so that the conditions within it are even more constant.

Foraging behavior

Odontomachus bauri is a leaf litter ant and forages individually most of the time underneath the leaf litter. It probes narrow cranies for arthropods, and also readily takes dead insects. It was repeatedly observed that individual workers appear to return to locations where they had previously found food. This is apparently due to learning by the foragers, because Oliveira and Hölldobler (1989) failed to find evidence of sign posts for directing nestmates in *Odontomachus*. The foraging success of *Odontomachus bauri*, as determined by the proportion of workers returning with prey, is at least 28% (n=325). 41% of incoming workers were definitely unsuccessful as they entered the nest with opened mandibles, and the remaining 31% had either no prey or prey which was too small to be discerned.

The prey items taken from incoming workers are listed in Table 1. *O. bauri* accepts a wide range of invertebrates, but forages especially frequently on other ants and termites. The termites captured were mainly workers (22 of 25 caught were workers, 3 were soldiers). The termites all belonged to the family Termitidae: most were *Nasutitermes*; the rest were *Amitermes*. The ant prey consisted mainly of sexuals. The largest prey items are most likely found dead and then carried to the nest. The successful capture of larger insects was not observed, but the detection and retrieval of dead items was repeatedly witnessed. The size distribution of the prey specimens shows that items between 3 mm and 4 mm are the most common size class (Fig. 3) and the most frequent prey items, like termites and wood lice, are soft bodied.

Foraging area and polydomy

Mapping of the paths of foragers revealed that foraging areas of ants belonging to different colonies or to different nests belonging

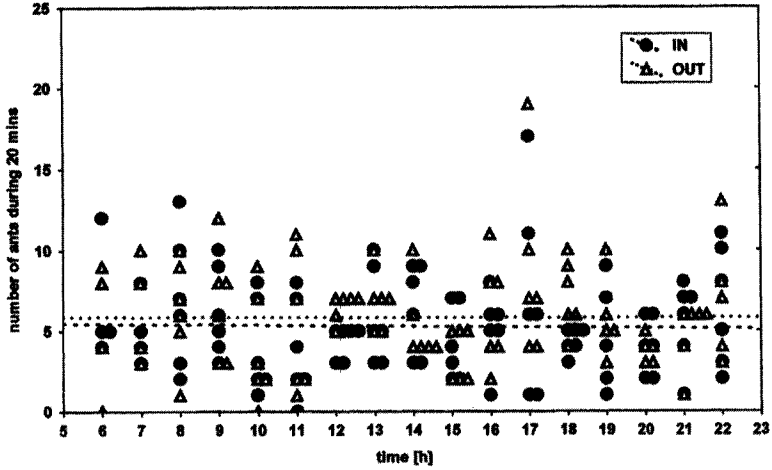


Fig. 1. Foraging activity of *Odontomachus bauri*. Each data point represents an observation period of 20 minutes. Open triangles show the number of ants leaving the nest, filled circles the number of ants entering the nest. A linear function is fitted to the data points and represented by a dotted (returning foragers; $y=5.55-0.018x$; $p=0.78$) or dashed (leaving foragers; $y=5.84-0.001x$; $p=0.98$) line. Data were collected from the observation of six colonies (except 6h,7h $n=4$; 19h $n=5$). The bar indicates the light/dark period.

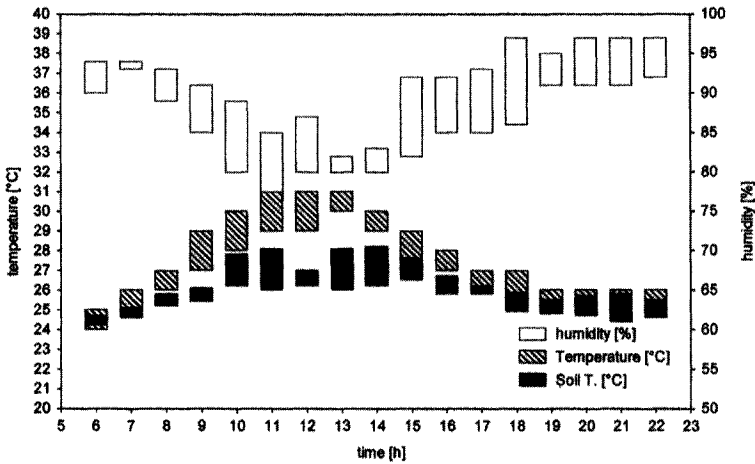


Fig. 2. Variation of air (hatched) and soil temperature (solid columns) and humidity (open columns) during the activity measurements. The range from minimum to maximum values measured is shown.

Table 1. Identity of prey items brought to the nest by *Odonotomachus bauri*.

Class	Order	number n=68
Annelida	Oligochaeta	1
Crustacea	Isopoda	6
Myriapoda	Chilopoda	2
Arachnida	Aranea	2
	Opiliones	2
Insecta	Collembola	1
	Blattodea	1
	Isoptera	22
	Ensifera	3
	Hemiptera	2
	Coleoptera	2
	Hymenoptera	18
	Lepidoptera	1
	Diptera	1
unidentified		3

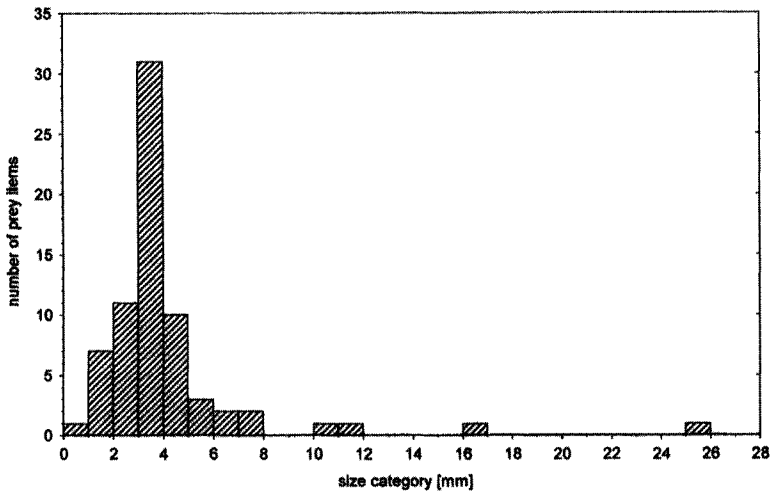


Fig. 3. Distribution of size classes of 71 prey items carried to the nest by *Odonotomachus bauri*.

to the same colony did not overlap. Even nests which were very close together appeared to have distinct foraging areas (Fig. 4A, B). The nests were generally not situated in the center of their foraging area and nests belonging to a single colony could be one to five meters apart. There was a preference for foragers to walk downslope after leaving the nest entrance, which helped to create asymmetric foraging areas. Neighboring nests appeared to have a strong influence on the shape of foraging areas, with foragers avoiding the foraging areas of neighboring colonies.

Odontomachus bauri appears to have a polydomous nest structure. This was initially suggested by the observation of a small number of workers travelling between nests during the measurements of colony foraging areas (Fig. 4B). Further evidence for polydomy was provided by observing that feeding a nest to saturation with termites led to a large number of ants (more than 10/minute for several minutes) transporting termites to a neighboring nest. In addition, ants from neighboring nests seldom fought, whereas encounters between ants from colonies 10 m apart were always aggressive.

No queens were found in 9 colonies excavated at Gigante, but all nests contained larvae and pupae. All of these nests did not extend into the soil, they consisted of gaps and cavities in leaf litter and under wood. Nests were also commonly found in the accumulated leaf litter in the tops of *Elaeis* palms more than 2 m tall. Five of 9 colonies in palms tops contained single queens. It seems that colonies of *O. bauri* are monogynous and sometimes polydomous in this habitat.

DISCUSSION

Activity of *Odontomachus bauri*

On Barro Colorado Island in Panama, the foraging of *Odontomachus bauri* is not limited by temperature and humidity. Their habit of foraging under leaf litter exposes them to little variation in weather conditions. In an arid Australian environment the activity of *Odontomachus sp.* was shown to depend on temperature by Briese and Macauley (1980), who found a shift from crepuscular activity in spring towards nocturnal activity in summer. Prior studies have demonstrated visual capabilities in *O. bauri* related to diurnal foraging: canopy orientation by Oliveira and Hölldobler

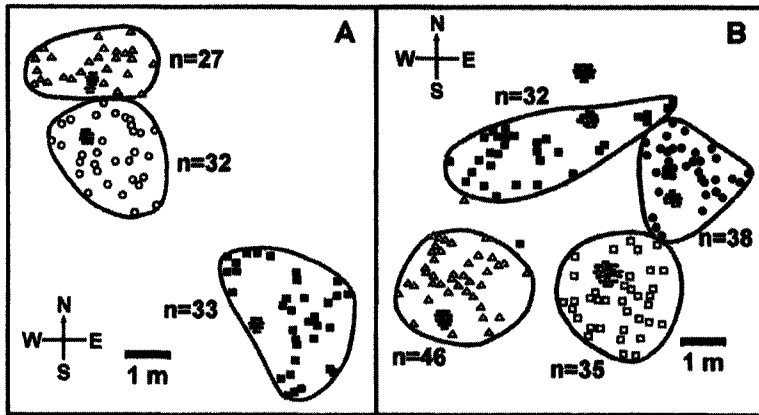


Fig. 4. Foraging areas at two different locations on Barro Colorado Island. Shaded areas indicate the locations of nests. Symbols depict the maximum distance of each worker from the nest. The number of workers followed from each nest is given (n). A The adjacent foraging areas belong to one colony, the third to a different colony. B All four nests belong to one colony. For a fifth nest no foraging area was established.

(1989) and use of vision in prey capture by Carlin and Gladstein (1989). However, the activity pattern found in the present study suggests that prey can successfully be located, captured, and returned to the nest in the dark.

Transient variations in activity could be caused by varying availability of prey. It is a common phenomenon in ants that the foraging activity rises after prey is brought into the nest. In this primitive kind of recruitment no apparent directional information is transmitted; only the rate at which foragers emerge is influenced. This type of recruitment was demonstrated in *O. bauri* by Oliveira and Hölldobler (1989), and is known from several additional ant species: *Formica* spp. (Carroll and Janzen, 1973), *Paltothyreus tarsatus* (Hölldobler, 1984), *Ectatomma ruidum* (Pratt, 1989), *Odontomachus chelifer* (Fowler, 1980), and *O. ruginodis* (Carlin and Gladstein, 1989).

Significance of the trap-jaws

In *O. bauri*, the trap-jaws appear to be designed to stun or kill prey, usually small, soft-bodied insects. This is suggested by the fact that *O. bauri* has short, broad mandibles with blunt instead of

sharp teeth (Brown, 1976). The function of the mandibles is especially evident when the ants were observed catching termites. The ants snapped at individual termites and either stunned or squashed the insects. Even though the prey was usually stunned by the first strike, often the ant administered repeated blows before carrying the prey to the nest. *O. bauri* never stung termite prey, as was regularly observed in *Ectatomma ruidum*. Use of the high speed mandible strike may also be an effective mechanism for avoiding the chemical defenses by arthropods like the termite *Nasutitermes*. The very high speed of closure of the mandibles, and the fast release of the reflex via range finding trigger hairs (Gronenberg et al., 1993; Gronenberg, 1995), as well as the "strike and recoil" behavior, should be very well suited to handle chemically protected prey (Brown, 1976). Indeed, Traniello (1981) found that *O. bauri* was the most efficient ant species tested at successfully attacking *Nasutitermes* soldiers, which squirt a secretion that entangles and irritates an aggressor and can physically block sensilla and spiracles (Prestwich, 1979). The presence of *Nasutitermes* workers among prey items retrieved by *O. bauri* workers in this study shows that *O. bauri* can exploit a food resource largely unavailable to other ants.

Polydomy

The polydomous colony structure revealed in this study may be an adaptation for maximizing the foraging area, while minimizing predation risk or desiccation while foraging. A polydomous nest allows a more effective use of an area (Hölldobler and Lumsden, 1980). This also could explain why the foraging areas of different subnests hardly overlap. How partitioning between subnests is accomplished is not known, one possibility would be route fidelity by foragers as found, for example, in the ponerine *Pachycondyla apicalis* (Fresneau, 1985).

Another ecological factor supporting polydomy is the instability of nest sites in the leaf litter. Most nest sites did not extend into soil, but were confined to spaces in the leaf litter, so that they are not protected from accidental disruption. According to Hölldobler and Wilson (1977, 1990) unstable nest sites favor polydomy and polygyny to ensure colony persistence even if subnests are lost. For *O. troglodytes*, which inhabits nests very similar to those of *O.*

bauri, a polydomous and polygynous organization was shown for colonies exceeding 300 workers (Colombel, 1970). No evidence, however, exists that *O. bauri* is polygynous, and according to Frumhoff and Ward (1992) the genus *Odontomachus* is predominantly monogynous. Polydomy could also facilitate escape emigration during army ant attacks (Droual and Toppoff, 1981), but during one observed *Eciton* raid the *O. bauri* nest was not evacuated. So the primary function of polydomy may be to increase the foraging area of *O. bauri* colonies.

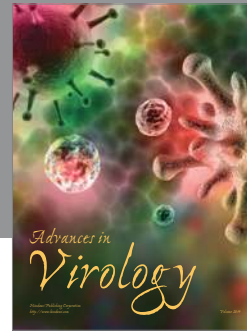
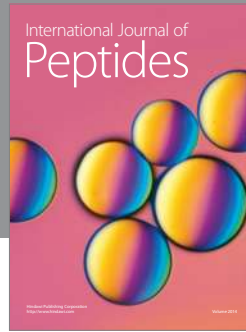
ACKNOWLEDGEMENTS

The Smithsonian Tropical Research Institute generously provided facilities and resources. Many thanks to Wulfilia Gronenberg, Stefan Cover and anonymous referees for helpful comments on the manuscript. The Deutsche Forschungsgemeinschaft (Graduiertenkolleg "Arthropodenverhalten" and Gr 933/3-2) supported funding.

LITERATURE CITED

- Briese, D.T., and B.J. Macauley. 1980. Temporal structure of an ant community in semi-arid Australia. *Australian J. of Ecol.* 5:121-134.
- Brown, W.L. Jr. 1976. Contributions toward a reclassification of the Formicidae, Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters, genus *Odontomachus*. *Studia Ent.* 19 (1-4):67-171.
- Brown, W.L., and E.O. Wilson. 1959. The evolution of the dacetine ants. *The Quarterly Rev. of Biology* 34(4):278-294.
- Carlin, N.F., and D.S. Gladstein. 1989. The "bouncer" defense of *Odontomachus ruginodis* and other odontomachine ants (Hymenoptera: Formicidae). *Psyche* 96(1-2):1-19.
- Carroll, C.R., and D.H. Janzen. 1973. Ecology of foraging by ants. *Ann. Rev. of Ecol. and Systematics* 4:231-257.
- Christian, E. 1979. Der Sprung der Collembolen. *Zool. Jb. Physiol.* 83:457-490.
- Colombel, P. 1970. Recherches sur la biologie et l'éthologie d'*Odontomachus haematodes* L.: Étude des populations dans leur milieu naturel. *Ins. Soc.* 17(3):183-198.
- Droual, R., and H. Topoff. 1981. The emigration behavior of two species of the genus *Pheidole* (Hymenoptera: Formicidae). *Psyche* 88(1-2):135-150.
- Fowler, H.G. 1980. Populations, prey capture and sharing, and foraging of the Paraguayan ponerine *Odontomachus chelifer* Latreille. *J. of Nat. History* 14:79-84.
- Fresneau, D. 1985. Individual foraging and path fidelity in a ponerine ant. *Insectes Sociaux* 32(2):109-116.

- Frumhoff, P.C., and P.S. Ward. 1992. Individual-level selection, colony-level selection, and the association between polygyny and worker monomorphism in ants. *The Am. Nat.* 139(3):559-590.
- Gronenberg, W. 1995. The fast mandible strike in the trap-jaw ant *Odontomachus* I. Temporal properties and morphological characteristics. *J. Comp. Physiol. A* 176:391-398.
- Gronenberg, W., J. Tautz, and B. Hölldobler. 1993. Fast trap-jaws and giant neurons in the ant *Odontomachus*. *Science* 262:561-563.
- Hölldobler, B. 1984. Communication during foraging and nest-relocation in the African stink ant *Paltothyreus tarsatus* Fabr. (Hymenoptera, Formicidae, Ponerinae). *Z. Tierpsychol.* 65:40-52
- Hölldobler, B., and C.J. Lumsden. 1980. Territorial strategies in ants. *Science* 210:732-739.
- Hölldobler, B., and E.O. Wilson. 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64:8-15.
- Hölldobler, B., and E.O. Wilson. 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Mass. 732 p.
- Levings, S.C., and N.R. Franks. 1982. Patterns of nest dispersion in a tropical ground ant community. *Ecology* 63(2):338-344.
- Moffett, M.W. 1986. Trap-jaw predation and other observations on two species of *Myrmoteras* (Hymenoptera: Formicidae). *Ins. Soc.* 33(1):85-99.
- Oliveira, P.S., and B. Hölldobler. 1989. Orientation and communication in the Neotropical ant *Odontomachus bauri* Emery (Hymenoptera, Formicidae, Ponerinae). *Ethology* 83:154-166.
- Pratt, S.C. 1989. Recruitment and other communication behavior in the ponerine ant *Ectatomma ruidum*. *Ethology* 81:313-331.
- Prestwich, G.D. 1979. Chemical defense by termite soldiers. *J. of Chem. Ecol.* 5(3):459-480.
- Traniello, J.F.A. 1981. Enemy deterrence in the recruitment strategy of a termite: soldier-organized foraging in *Nasutitermes costalis*. *Proc. Natl. Acad. Sci. USA* 78(3):1976-1979.



Hindawi

Submit your manuscripts at
<http://www.hindawi.com>

