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Research article

Colony structure and foraging behavior in the tropical formicine ant, *Gigantiops destructor*

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Summary. We present field and laboratory data on the Neotropical formicine ant *Gigantiops destructor* (Fabricius), the sole species of its genus and tribe. Monogynous and polydomous colonies of *G. destructor* from French Guiana are distributed along the rainforest edges or along streams with a nest density of about 300 nests/ha. The species presents rudimentary nesting habits, as most nests are found in pre-existing cavities in the ground, but some can be found in the hollowed internodes of *Cecropia* trees fallen onto the ground. A worker, sometimes hidden in a separate "sentry box", might guard the nest entrance. Colony size can reach several hundreds of workers. The foraging activity of the workers is strictly diurnal with a peak between 9:30 and 11:30. This largest-eyed of all known ant species has remarkable leaping abilities even more impressive than in other jumping ants. Workers are generalist solitary foragers. They collect extrafloral nectar from different plant species and prey on various small live arthropods that they detect visually before tracking and jumping on them. The same individual can forage both on prey and sugary sources during a single foraging trip. Foragers can eat their prey on site and never recruit nestmates in the field or even after a starvation period in the laboratory. They feed larvae with chewed prey. The complete lack of cooperation between foraging workers that can also fight for a prey with a nestmate, combined with the absence of any recruitment for large food sources, constitute a cluster of individualist traits rather unusual for an eusocial insect.

Key words: Gigantiops destructor, nest structure, nest distribution, foraging activity, food preferences.

Introduction

Firstly described as *Formica destructor* (Fabricius, 1804), the Formicinae *Gigantiops destructor* is noteworthy as it is the only species of its genus and of the Gigantiopini tribe (Ashmead, 1905). This species is confined to the rainforests distributed along a strip of South America east of the Andes, extending from about 10° north to 15° south of the equator (Wheeler, 1922; Kempf and Lenko, 1968; Tobin, 1989). Its life history is little known and limited to the following information. Workers forage solitarily on the ground, or sometimes among the branches of trees, leaping from twig to twig. They run and jump away when pursued by human observers (Smith 1858; Emery, 1893; Mann, 1916; Wheeler, 1922; Tobin, 1989; Hölldobler and Wilson, 1990). As a result, it is rather difficult to follow workers returning to their nests, so that early attempts to localize them were unsuccessful. Wheeler (1922) found only two queenless nests in British Guyana, Tobin (1989) found two nests, one queenless and the other queenright, in eastern Venezuela and a total of six nests in the Manu Biosphere Reserve in Peru. Other attempts to capture entire colonies were unsuccessful and, consequently, males were described only in the second half of the twentieth century (Kempf and Lenko, 1968). For all these reasons, this formicine ant species still merits investigation. In addition, because this species presents impressive forward jumping abilities and has the largest and most prominent eyes of all known ant species to date, it has recently attracted the interest of neuroanatomists (Jaffe and Perez, 1989; Tautz et al., 1994; Gronenberg and Hölldobler, 1999).

As foraging workers have been frequently observed in the Amazon basin, we hypothesized that *G. destructor* is not scarce, so that a systematic search would permit us to deduce the ecological conditions of nest site selection in this species and consequently to find nests for further study. We examine

here the colony structure and different biological and behavioral traits of this formicine ant.

Materials and methods

Field studies were carried out between June and August 1998 and 1999 in Sinnamary, French Guiana, on three sites close to the dam at Petit-Saut, after a systematic ant survey of the litter fauna was conducted in the forest (Durou, 2000). Two of the sites, situated 100m from each other at Base-vie, are located along the forest edge, and the third (PK 19) is situated along both sides of a 1m-wide stream, 8 km away. To locate the nests we scattered on the ground portions of termitaries, permitting us to track workers retrieving this easily found prey. After field observations we excavated 41 out of 56 localized nests, with individuals gathered manually or using smooth forceps; all homing foragers searching for their excavated nest entrances were collected during one hour after the excavation. Individuals from each nest were brought back to the field station in separate plastic bags.

In order to document the daily rhythm of activity of the species both in the field and in the laboratory, we recorded the number of workers that left and entered a nest during a continuous 24-hour period of observation.

All the harvested colonies were reared in artificial plaster-of-Paris nests, covered with a transparent plastic tap, and housed in darkened plastic detachable containers. Colonies were kept under a 12-hour light/dark cycle at 25 °C and provided with honey, small live cricket larvae (*Gryllus assimilis*) and adult *Drosophila melanogaster*.

We controlled, either by direct observation or through video recordings, if the colonies were polydomous thanks to confrontation tests between workers originating from the different nests harvested. Double-blind tests 3min long were conducted between five workers of a nest and an alien individual in a Petri dish 10cm in diameter (as a neutral territory). Tests between workers stemming from nests separated by a distance of 8km, so belonging to two different colonies, always triggered agonistic behavior, with the introduced alien individual being seized by its antennae and/or mandibles, but not always killed. The confrontations between workers from the same site were twofold. When the introduced individual was immediately sprayed with venom and killed, we deduced that it belonged to a different colony. When the introduced individual was licked, received trophallactic exchanges and was transported, which always occurred between ants from the same nest during control experiments, we deduced that the confronted individuals belonged to the same colony. We thus distinguished two opposite behavioral patterns: (1) trophallactic exchanges with or without mutual transport (assigned value 0); and (2) antennal contacts followed by mandibular bites with the traction of the opponent, or full attack including venom spraying possibly leading to death (assigned value 1). A Sorensen similarity index (Southwood, 1984), based on these two values was then calculated. The resultant dendogram, built with the single linkage method (nearest neighbour), shows the relative distribution of all the nests and their behavioral similarity.

Results

Nest distribution and structure

The habitat of *G. destructor* corresponds to partially sunny zones such as forest edges and the banks of streams. We have never found *G. destructor* nests in the undergrowth nor in open spaces, although we have conducted an ant survey on these areas (Durou, 2000). In the preferred areas, we recorded a density of about 300 nests/ha (11 nests out of 375m^2 = 293 nests/ha and 20 nests out of 700 m^2 = 286 nests/ha at first site of Base-vie, and 15 nests out of 560 m^2 = 268 nests/ha at PK 19). We found 21 epigean and 35 hypogean nests.

Epigean nests were installed in the internodal cavities of *Cecropia* spp. trees fallen onto the ground (n = 13), as already quoted by Kempf and Lenko (1968), the cavities of trunks of unidentified live trees (n = 2), and in rotten logs (n = 6), as also quoted by Tobin (1989). We also noted a nest in an "ant garden" occupied by two ponerine ant species: *Pachycondyla villosa* and *Odontomachus hastatus* living side by side. When installed in a *Cecropia* log or branch, the nests can occupy several internodes and we noted that workers built partitions using sand, leaf litter debris and vegetal fibers (Fig. 1a).

Hypogean nests were installed in crumbly soil (n = 18; one of them associated with a nest of *Paraponera clavata* at the base of a tree, as already described by Kempf and Lenko, 1968 and by Tobin, 1989), in muddy soil (n = 4), in a tangle of mixed compost and stones (n = 2), beneath a log (n = 1) or a stone (n = 1), and inside the dead cavities of live (n = 6) or decayed roots (n = 3). Nest entrances were composed of one to three small holes less than 4 mm in diameter. Some (5/35) included a so-called separate "sentry box" sheltering a worker acting as a guard (Fig. 1b). These entrances communicated with a single chamber by a 10 cm-long tunnel. Laboratory observations confirmed the existence of guards that stayed inside the plastic tubes connecting the artificial nests to the foraging arenas. Workers (and the queen of an incipient colony) also built partitions in the artificial plaster nests, using several kinds of vegetable detritus glued together.

Size and structure of the colonies

The populations of the 41 excavated nests ranged from 4 to 133 workers (44.7 ± 4.4 workers). We distinguished six nests with a queen, seven queenless nests with only workers and 28 queenless nests with workers plus brood. Alate females were noted six times, once in the presence of a queen; the presence of males was noted only three times.

In the laboratory, workers from queenless nests have laid eggs resulting in the continual production of males since October 1998. Both in the field and in the laboratory, the brood is found throughout the single nest chamber and inside the different internodal cavities of *Cecropia*.

While we searched for the nests in the field, we noted that after the main period of foraging activity some workers transported nestmates, pupae or larvae from one nest to another separated by a distance of up to 20 m. This argued the existence of polydomous colonies, but this behavior was fortuitously observed, so we conducted laboratory confrontation tests between workers originating from different nests in order to know which nests belonged to the same colony.

The dendrogram built from the core results of the confrontation tests shows that four nests have 100% behavioral similarity (Fig. 2), permitting us to deduce that the colonies of this species are polydomous. Three more nests that exchanged workers in the field can be added to this, resulting in a colony of seven nests composed of 1 queen, 6 alate females, 19 males, 576 workers, 88 pupae plus larvae and eggs. As a control, we connected these seven nests to the same experimental foraging area in the laboratory. After a

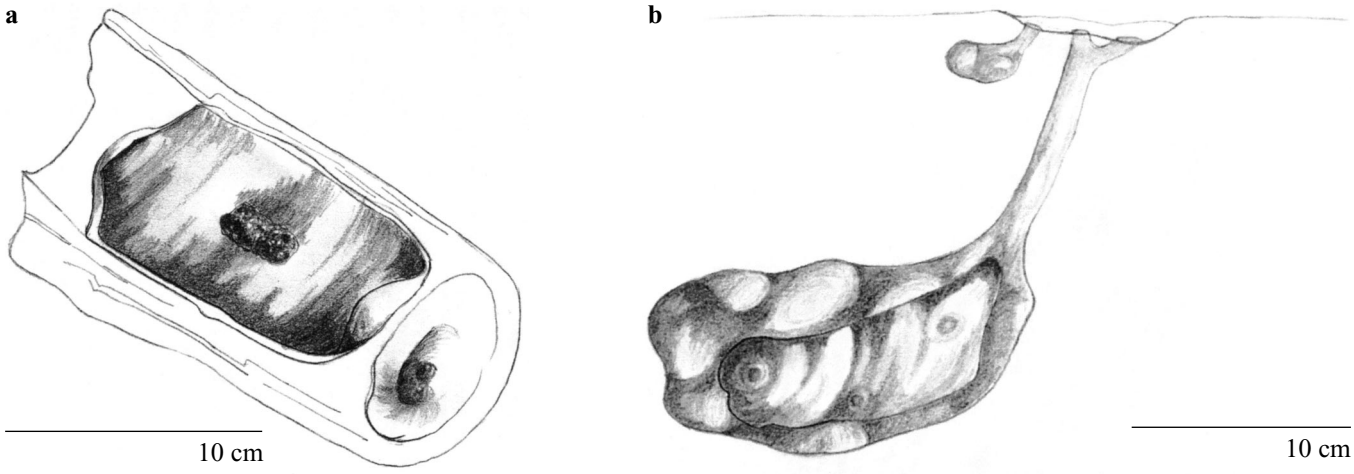

Figure 1. Drawing of the nests. a) Epigean nest found in a *Cecropia* log with, stuck to the wall, sand, litter debris and vegetal fibers deposited by ants for the building of a partition. b) Hypogean nest composed of two small entrances less than 4mm in diameter. A separate "sentry box" sheltering a worker acting as a guard is also represented. These entrances communicated with a single chamber by a 10 cm-long tunnel

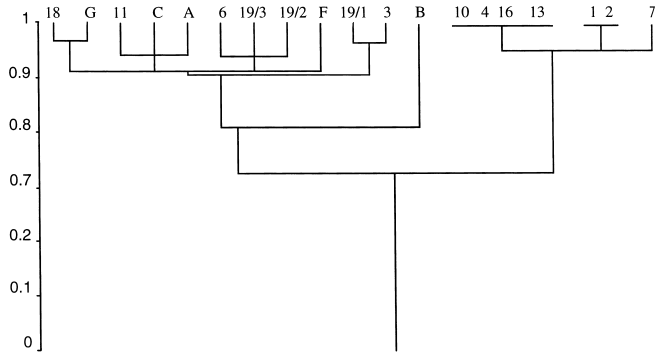

Figure 2. Dendrogram based on the calculation of the Sorensen similarity index (nearest neighbour). Nests numbered 4, 10, 13 and 16 share 100% similarity. Nests numbered 1 to 18 are from the first site at Base-vie; nests A to G are from the second site at Base-vie and nests 19/1, 2, 3 are from the site PK 19 (8 km away from Base-vie sites)

few days, we again observed the two-way transport of nestmates, pupae and larvae between the different nests, thus confirming the casual observations made in the field.

Daily rhythm of activity

The foraging activity of *G. destructor* ranges from 7:00 to 18:00 (sunrise at 6:00; sunset at 19:00) with a main peak occurring between 9:30 and 11:30 (Fig. 3a). At the end of the morning we noted, as cited above, workers transporting nestmates or brood from nest to nest. More foragers were observed in the field on sunny days than on cloudy days. A similar peak of activity occurred about three hours after the beginning of illumination in the laboratory according to a 12/12 h light/dark cycle starting at 8:00 (Fig. 3b). Both foraging activity and activity inside the nest are exclusively diurnal as indicated by a continuous 24 h-period of observation, that was conducted under red light during the dark cycle.

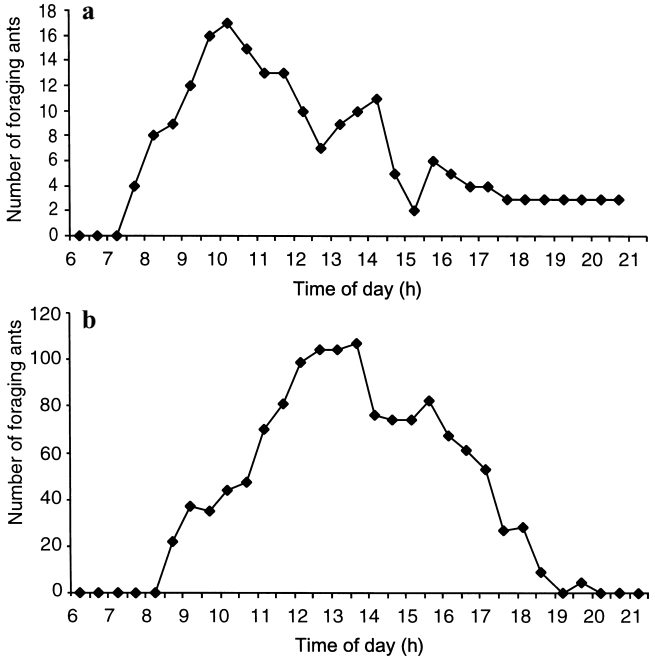

Figure 3. Rhythms of foraging activity of *G. destructor.* **a**) – Activity rhythm observed in the field (sunrise at 6:00; sunset at 19:00). The number of foraging ants is a cumulated number of outgoing minus ingoing ants all day. The three workers observed after 17:30 went into another nest belonging to the same colony before sunset. **b**) – Activity rhythm observed under laboratory conditions (with a 12-hour light/dark cycle starting at 8:00). The number of foraging ants is the exact number of ants observed outside their nest all day

Food preferences

Both in the field and in laboratory breeding, workers foraged individually to exploit sugary sources and to capture various live insects. A worker can exploit different food sources during a single foraging trip, gathering nectar then capturing a

prey, for example. We never observed any kind of recruitment for large sugary food sources nor for groups of prey, even after five days of starvation in the laboratory.

In nature, workers foraged along the forest edges for extrafloral nectar on different low plants, mostly Mimosaceae and Passifloraceae, and on small trees (up to 10m in height). They were even noted in the canopy of a *Virola melinonii* (Myristicaceae) at a height of more than 30 m. Also workers preyed on spiders, flies, mosquitoes, caterpillars, earth-worms, and other ants (*Pseudomyrmex* spp., *Crematogaster* spp.), but termites (mostly *Nasutitermes* spp. and *Microcerotermes indistinctus*) seemed to be particularly prized. A worker can successively capture up to eight small termites that it retrieves together between its mandibles. We noted that the hunting workers visually tracked their prey from behind, then jumped and caught them with their mandibles, sometimes spraying them with venom. Workers can also jump vertically to catch small flying prey. Frequently two hunting workers fought for a prey rather than cooperating or remaining neutral.

After prey capture or nectar collecting, foragers returned in a rather direct manner to their nest from distances of up to 20 m. Obstacles such as fallen trees were bypassed and the ants resumed their former direction, jumping over small obstacles such as blades of grass, dead branches or stones, either already present on the ground or deliberately placed there by the experimenter. Jumping abilities, as a normal means of locomotion either on the ground or from leaf to leaf, were very impressive. Even when loaded with small termites between their mandibles, workers are able to jump horizontally over distances up to 30 cm. This leaping ability renders difficult or impossible the following of eventual chemical trails between the nest and a given foraging site, resulting in a very probable strict visual orientation in this species.

Foragers from the same colony can fight for the same prey, performing cleptobiosis ($n > 200$ observations) by snatching up a prey from the mandibles of a nestmate. Both in the field ($n = 5$ observations) and in the laboratory ($n > 50$ observations) the foraging workers can eat their prey just after capture, after having chewed it for several minutes (range 5–15 min), then continue to forage, capturing and eating other prey before homing. We cannot say if this behavior corresponds only to self provisioning or if the workers later regurgitate all the chewed prey. The latter hypothesis could be valid as in this species scraps are extremely rare and even dead nestmates are always crushed to form a "mushy paste" that is eaten by workers and larvae.

Discussion

Gigantiops destructor nests in the forest edges and the banks of streams with a relatively high nest density, about 300 nests/ha, that permitted us to study the basic biology of the species. We noted rudimentary opportunistic nesting habits, with colonies (17 to 133 workers) sheltering in pre-existing cavities in the ground or in rotting vegetation with sometimes a worker guarding the nest entrance. Neither hypogeous nor epigeous nests are at all elaborate and the diversity of the places in which they were found suggests that availability, architecture, and concealing features of the substratum are the primary determinants of the nest site selection. We also noted cases of parabiosis, i.e. the sharing of the same nest with no direct interaction between morphologically and behaviorally different ant species (Hölldobler and Wilson, 1990), between *G. destructor* and three ponerine ant species (see also Kempf and Lenko, 1968; Tobin, 1989). Thanks to confrontation tests between workers originating from the different nests harvested, we have provided evidence that the monogynous *G. destructor* colonies are polydomous. The two-way transport of workers and brood between *G. destructor* nests seems similar to that described in polycalic colonies of the monogynous ant *Cataglyphis iberica* (Dahbi et al., 1997).

Although *Gigantiops* workers hunt for a large spectrum of prey, they capture mostly termites that they can retrieve several at a time. They feed larvae with the chewed pellets of insects. As prey can be eaten on the spot, a foraging worker can alternatively collect proteinic and sugary sources during the same foraging trip. As far as we know, such behavior has never been previously reported in ants. The collection of sugary substances is opportunistic (see also Kempf and Lenko, 1968) and we never observed the workers attending trophobionts. Thus, workers are not specialized in any particular type of prey and recruitment to food sources or coordinated foraging are totally absent in this eusocial insect: there is no tandem running, no group recruitment, no recruitment trail. The extreme category of solitary hunting combined with solitary retrieval described in ants (Hölldobler and Wilson, 1990) is extended here to the notion of solitary prey feeding. In addition, homocolonial workers can even fight for the same prey. All these patterns constitute an important cluster of non-cooperative traits that could explain why this unusual 'individualist' formicine ant was once described as *Formica solitaria* (Smith, 1858).

As its genus name implies, workers of *Gigantiops* have huge eyes, the number of ommatidia per eye in workers being the highest number reported in ants (Gronenberg and Liebig, 1999). Consequently, vision is very important in this species and infers a diurnal rhythm of activity. Jumping abilities, as a normal means of locomotion either at ground level or from leaf to leaf, are very impressive. Such forward jumping abilities, that require no mid- leap sensory feedback in this species (Tautz et al., 1994), allow the ants to home very rapidly even on the cluttered forest-floor of the tropical rain forest. Well developed vision associated with the ability to jump is also used in catching prey, so that even flying insects are captured as appears in ponerine ants of the genus *Harpegnathos* and in Myrmeciinae (Gray 1971a, b, 1974; Hölldobler and Wilson, 1990; Musthak Ali et al., 1992; Baroni Urbani et al., 1994; Crosland, 1995).

These overdeveloped jumping and visual abilities should enable *G. destructor* to display higher visual information processing properties. Indeed, Gronenberg and Hölldobler (1999) indicated that the volume ratio of optic lobes to antennal lobes in *G. destructor* is about 1.5 times higher than in the

visual jumping predator ant *Harpegnathos* and 4.75 times higher than in the formicine *Cataglyphis bicolor*. For all these reasons, by integrating theory and data from behavioral ecology and cognitive science (Beugnon et al., 1996; Chameron et al., 1998), we can hypothesize that the 'individualist' ant *G. destructor* should provide a very good model for deeper investigations into the field of cognitive ecology in insects.

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References

Ashmead, W.H., 1905. A skeleton of a new arrangement of the families, subfamilies, tribes and genera of the ants, or the superfamily Formicoidea. *Can. Entomol. 37*: 381–384.

Baroni Urbani, C., G.S. Boyan, A. Blarer, J. Billen and T.M. Musthak Ali, 1994. A novel mechanism for jumping in the Indian ant *Harpegnathos saltator* (Jerdon) (Formicidae, Ponerinae). *Experientia 50*: 63–71.

Beugnon, G., I. Pastergue, B. Schatz and J.-P. Lachaud, 1996. Cognitive approach of spatial and temporal information processing in insects. *Behav. Proc. 35*: 55–62.

Chameron, S., B. Schatz, I. Pastergue-Ruiz, G. Beugnon and T.S. Collett, 1998. The learning of a sequence of visual patterns by the ant *Cataglyphis cursor*. *Proc. R. Soc. Lond. B 265*: 2309–2313.

Crosland, M.W.J., 1995. Foraging in *Harpegnathos venator*, the jumping ant from Hong Kong. *Mem. Hong Kong Nat. Hist. Soc. 20*: 233–234.

Dahbi, A., X. Cerdà, A. Hefetz and A. Lenoir, 1997. Adult transport in the ant *Cataglyphis iberica*: a means to maintain a uniform colonial odour in a species with multiple nests. *Physiol. Entomol. 22*: 13–19.

Durou, S., 2000. Etude sur la biodiversité des Formicidae de la litière en forêt tropicale guyanaise. Diplôme d'Etudes Supérieurs Universitaires, Toulouse. 62 pp. Unpublished ms.

Emery, C, 1893. Zirpende und springende Ameisen. *Biol. Centralbl. 13*: 189–190.

Fabricius, J.C. 1804. *Systema Piezatorum*. Carolum Reichard, Brunsvigae. 439 pp.

Gray, B., 1971a. Notes on the biology of the ant *Myrmecia dispar* (Clark) (Hymenoptera: Formicidae). *Insectes soc. 18*: 71–80.

Gray, B., 1971b. Notes on the field behaviour of two ant species *Myrmecia sertorum* Wheeler and *Myrmecia dispar* (Clark) (Hymenoptera: Formicidae). *Insectes soc. 18*: 81–94.

Gray, B., 1974. Nest structure and population of *Myrmecia* (Hymenoptera: Formicidae), with observations on the capture of prey. *Insectes soc. 21*: 107–120.

Gronenberg, W. and B. Hölldobler, 1999. Morphologic representation of visual and antennal information in the ant brain. *J. Comp. Neurol. 412*: 229–240.

Gronenberg, W. and J. Liebig, 1999. Smaller brains and optic lobes in reproductive workers of the ant *Harpegnathos*. *Naturwissenschaften 86*: 343–345.

Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Harvard University Press, Cambridge Mass. 732 pp.

Jaffe, K. and E. Perez, 1989. Comparative study of brain morphology in ants. *Brain Behav. Evol. 33*: 25–33.

Kempf, W.W. and K. Lenko, 1968. Novas observações e estudos sôbre *Gigantiops destructor* (Fabricius)(Hymenoptera: Formicidae). *Pap. Avuls. Zool. São Paulo 21*: 209–230.

Mann, W.M., 1916. The ants of Brazil. *Bull. Mus. Compar. Zool. 60*: 339–490.

Musthak Ali, T.M., C. Baroni Urbani and J. Billen, 1992. Multiple jumping behaviors in the ant *Harpegnathos saltator*. *Naturwissenschaften 79*: 374–376.

Smith, F., 1858. Catalogue of hymenopterous insects in the collection of the British Museum, *Formicidae 6*: 45–46.

Southwood, T.R.E., 1984. *Ecological Methods with Particular Reference to the Study of Insect Populations.* London; Chapman and Hall. 526 pp.

Tautz, J., B. Hölldobler and T. Danker, 1994. The ants that jump: different techniques to take off. *Zoology 98*: 1–6.

Tobin, J.E., 1989. On the association between *Gigantiops destructor* and *Paraponera clavata*: an unlikely symbiosis. *Notes from Underground 3*: 3–6.

Wheeler, W.M., 1922. Observations on *Gigantiops destructor* Fabricius and other leaping ants. *Biol. Bull. 42*: 185–201.