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Driver Ants Invading a Termite Nest: Why Do the Most Catholic Predators of All Seldom Take This Abundant Prey?

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ABSTRACT

Driver ants (*i.e.*, epigaeic species in the army ant genus *Dorylus*, subgenus *Anomma*) are among the most extreme polyphagous predators, but termites appear to be conspicuously absent from their prey spectrum and attacks by driver ants on termite nests have not yet been described. Here, we report a *Dorylus* (*Anomma*) *rubellus* attack on a colony of the fungus-growing termite *Macrotermes subhyalinus* that was observed during the dry season in a savannah habitat in Nigeria's Gashaka National Park. It was estimated that several hundred thousand termites (probably more than 2.4 kg dry mass) were retrieved. The apparent rarity of driver ant predation on *Macrotermes* nests may be explained by different habitat requirements, by the fact that these ants mostly forage aboveground, by efficient termite defense behavior and nest architecture that make entry into the nest difficult, and finally by driver ant worker morphology, which differs remarkably from that of subterranean *Dorylus* species that regularly invade and destroy termite colonies.

Key words: army ants; *Dorylus (Anomma) rubellus*; fungus-growing termites; Lanchester battles; *Macrotermes subhyalinus*.

SWARM-RAIDING ARMY ANTS, NAMELY THE EPIGAEIC *DORYLUS* (SUBGENUS *ANOMMA*) SPECIES IN TROPICAL AFRICA (the "classic" African driver ants of legend and lore) and the Neotropical *Eciton burchellii*, *Labidus coecus*, and *L. praedator*, have a generalist diet (Gotwald 1974, 1995; Rettenmeyer *et al.* 1983; Vieira & Höfer 1994). Because driver ants attack, fragment, and retrieve any animal that is incapable of escaping the approaching swarm and lacks effective defensive mechanisms, it has been speculated that they might be the most polyphagous of all predators on earth (Franks 2001). In spite of their reputation as voracious generalist carnivores, and particularly their proficiency at raiding the nests of other social insects like ants and bees (Gotwald 1995, Hepburn & Radloff 1998), there has been one striking gap in the records of their prey spectrum: termites are known to be taken only as alates and scattered foragers, while attacks on termite nests have not been recorded (Gotwald 1974, 1995). This is remarkable because primarily subterranean *Dorylus* species in other subgenera are known to raid and destroy termite nests in Africa (Bodot 1961, 1967; Abe & Darlington 1985; Darlington 1985). Here, we present the first documentation of a raid by a driver ant species directly on a termite nest.

The raid was observed in the dry season (23–24 January 2005) at the Kwano field station (7°19′46.1″ N, 11°35′1.9″ E; 560 m asl) in the Gashaka-Gumti National Park in eastern Nigeria (see Sommer *et al.* 2004). The park contains a mosaic of savannah and gallery forests spread along streams and rivers. A *Dorylus* (*Anomma*) *rubellus* colony was nesting at the base of a tree at the edge of the field station that faces an open savannah habitat with low *Macrotermes* mounds. The colony usually foraged from soon after sunset at 1800 h until 1000 h and thereby avoided the dry and hot conditions during the day. Voucher specimens of the driver ant predators and their termite prey are deposited in the collection of the Zoological Museum of the University of Copenhagen.

The *D. rubellus* workers were first noticed carrying *Macrotermes subhyalinus* termites along an exposed segment of trail near the nest at 1945 h on 23 January 2005. In the beginning, the ants almost all transported termite workers of about their own body size. About 3 percent of the termites were small soldiers about the size of a medium sized *D. rubellus* worker. About every 5–10 min, one much larger soldier was transported on the trail, with the head and body carried separately by different ants. By midnight, the soldiers were notably less frequent and the termites of the reproductive brood began to appear. The next morning, far fewer worker termites were carried on the trail and most of the retrieved booty were the much larger, flaccid reproductives. Throughout this time, even callow ant workers were running on the trail, indicating that the recruitment to the raid was very intense (callow workers are usually only seen on emigration trails, since workers participate in raids only when they are older). At intervals, we counted the numbers of termites carried by in 20 sec. Multiplying these counts by three produced estimates of burden/min of (beginning at 2000 h on the 23rd): 2000 h (300), 2100 h (360), 2200 h (270), 2300 h (330), 0300 h (350), 0500 h (120), 0600 h (78), 0700 h (42), 0800 h (12), 1200 h (78), 1500 h (6), 1600 h (12), 1700 h (42), 2100 h (15). Presuming each estimate was representative of the period until the following measurement (traffic patterns seldom fluctuated rapidly),

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we estimate that in total about 220,000 termites or termite pieces were transported along this trail.

While looking for the nest of raided termite colony on the morning of 24 January 2005, we discovered two more columns heading to the same *D. rubellus* nest. These seemed to be independent foraging trails, because the workers on them carried a much higher proportion of termite workers and soldiers than those on the trail we had been watching. We conclude that these columns either led to a different part of the termite nest or to different termite nests, and that these raids had not progressed as far in their attack. Indeed, over the course of that day (the 24th), the ants on these columns likewise began to carry more reproductives. Because there was a similar termite prey flow on the two other trails, we believe the *D. rubellus* colony could have taken in a half million termites in total from all three trails, and perhaps many more. The average dry mass of these items (determined by weighing items preserved in 80% ethanol after oven-drying for 48 h at 55°C) was 4.88 mg (± 9.51 SD, range 0.84–37.48 mg, $N = 13$). We therefore estimate that the driver ant colony may have gathered 2440 g dry mass or more of termite prey. Although this estimate should be viewed with caution due to the low number of termite pieces weighed, our sample contained fewer reproductives than would be representative for the entire prey intake, so this figure is probably an underestimate. Mature *M. subhyalinus* colonies (including reproductives) have a mean dry mass of about 9 kg (Darlington 1990), so the estimate seems realistic. According to Leroux (1982), the dry mass of entire *D. nigricans* colonies (including workers, larvae and pupae) ranges from 9.1 kg to 14.8 kg at Lamto, Ivory Coast. If *D. rubellus* at Gashaka has similar colony sizes as *D. nigricans* at Lamto, the termite prey would thus have equaled about a quarter to a sixth of the colony's dry mass.

Unfortunately, we did not succeed in locating the attacked mound (or mounds). Low and eroded *Macrotermes* nests were scattered throughout the savannah area, but no raiding activity was visible on the surface. We followed one of the trails for 54 m until it entered a hole. We then excavated about a meter deep in a termite mound located beyond the trail's end point, uncovering dozens of fungus garden chambers with many workers and reproductives also belonging to *M. subhyalinus*, but there was no sign of driver ants. It is possible that the ants were raiding from far underground in a part of the nest we had not touched. Alternatively, this and other trails could have extended much further elsewhere through cracks in the soil or in belowground termite foraging galleries.

Termite reproductives were often carried by two workers in tandem. In contrast to the expectation of efficient cooperative transport with additional "team" members helping to lift the item (Franks *et al.* 1999, 2001), inspection through a camera macro lens showed that often the second "porter" (and sometimes a third ant) would partially or entirely climb on the prey and gnaw or explore it rather than aiding in its transport in any apparently useful way (Fig. 1).

FIGURE 1. Transport of termite prey. Media worker carrying a developing termite reproductive. Notice a smaller worker rides on the prey: often riding ants dragged one or more legs but did not seem to assist in transport.

The traffic flow on two of the trails ceased entirely on the night of 24 January 2005. In contrast, on the first trail, the retrieval of termite prey to the nest continued at a low rate throughout that night, with worker traffic flow remaining intense in both directions and an increasing number of workers accumulating in a defensive position alongside the trail. From about 1800 h on the 24th, we saw ants on the trail carry termites in both directions. Soon after, the first ant brood items were transported out of the nest and this emigration continued until 0900 h on the 26th. During the emigration, many thousands of termite prey were also transported to the new nest, indicating that only a small fraction of them had been consumed. During the morning of the 25th, we located the new nest site 67 m away from the old one. The ants had taken advantage of a 25 cm wide cavity in the ground covered partly by a large rock. Upon removing the rock we found a 15-cm wide mass of termite bodies in the center of the cavity. To our knowledge, this kind of large food stash has not been observed previously within the nests of *Dorylus* colonies. We had guessed that the colony might emigrate to the nest of their termite victims, but it seems unlikely that such a large, open chamber had initially been part of a termite nest.

When we checked the old driver ant nest during the emigration in the morning of the 25th, there was an unpleasant smell emanating from the nest openings. Moreover, *Crematogaster* ants were collecting termites discarded onto the nest's refuse piles. Because these were whole termites and substantial termite pieces and not just exoskeleton parts, we concluded that the driver ant colony had harvested more food than it could consume, so that termite pieces were starting to rot in the nest. While workers of specialized termite-hunting ant species like *Pachycondyla marginata* can sting their termite prey and thus keep the termites paralyzed as a live food store in their nest (Leal & Oliveira 1995), driver ants apparently have no way of preserving excess food stocks for later consumption.

In the raid attack we observed, the driver ant colony must have succeeded in entering a *Macrotermes* nest because reproductive brood was retrieved, but we do not know whether the termite colony was eventually killed by the ants. During inspections of prey retrieved by more than 10 *D. rubellus* colonies throughout our three weeks of fieldwork in the Gashaka National Park (including examination of hundreds of photographs of prey transport) we never saw termite workers being transported on the trails. Different species of driver ants certainly encounter termite nests regularly

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during their raids in various habitats—but why have such raids not been observed more frequently?

One possible answer is that the analysis of driver ant prey spectra has not been thorough enough and that such attacks happen more often than generally thought. In spite of the presumed importance of swarm-raiding army ants as keystone predators in many tropical ecosystems (Franks & Bossert 1983, Boswell *et al.* 1998), our knowledge of driver ant prey spectrum is still based mostly on anecdotal reports and only very few systematic studies with extensive longer-term sampling (Raignier & van Boven 1955; Gotwald 1974, 1995). Through the coordinated behavior of millions of workers, driver ants can conduct efficient, up to 20-m wide raids that sweep through the forest like a dragnet and thus gain access to an enormous prey type spectrum and prey size range (from mammal carcasses down to insect eggs). In order to determine the relative importance of evenly distributed small prey (such as caterpillars) and fortuitous findings of huge prey (such as a dead mammal), one certainly has to analyze vast numbers of prey samples from many colonies.

The other more convincing explanation for the lack of observations of successful driver ant raids of termite mounds is that they are, in contrast to those by subterranean *Dorylus* species, indeed very rare. Driver ants may attempt to raid termite colonies on a regular basis (*i.e.*, whenever they encounter a mound during their swarm raid), but apparently usually fail to breach the termite defenses. Bodot (1967) found that, during a 4-yr observation period, the subterranean *D. (Typhlopone) dentifrons* (according to Bolton 1995, the status of this and all other *D. (Typhlopone)* taxa mentioned in this publication is that of subspecies of *D. fulvus*) killed 60 young *Macrotermes bellicosus* colonies on a 24-ha site in Ivory Coast. Darlington (1985) directly observed raids by the subterranean *D. (Typhlopone) juvenculus* on a *Microtermes* sp. nest and a *Macrotermes michaelseni* mound and found numerous signs of other attacks in dead mounds of the latter species in a savannah habitat in Kenya. Korb and Linsenmair (2001) concluded that predation by subterranean *Dorylus* spp. was a key factor in regulating population dynamics of fungus-cultivating termites in Africa. Berghoff *et al.* (2002) reported that the subterranean *D.* (*Dichthadia*) *laevigatus* often attacks termite mounds of *Globitermes sulphureus* and two *Macrotermes* species in Malaysia, although the ants only took small numbers of workers at a time. Why do attacks by subterranean *Dorylus* species take place much more often and why would these be so much better at harvesting *Macrotermes* termites? We propose four complementary explanations.

1. In savannah/forest mosaic landscapes such as Gashaka, driver ants and *Macrotermes* species have different habitat requirements. While *Macrotermes* colonies are almost absent from closed-canopy forest in such landscapes (Korb & Linsenmair 1999), driver ants are apparently very susceptible to desiccation and occur at four times higher densities in gallery forests than in savannah (Leroux 1982, Schöning *et al.* 2007).
2. The encounter rate of foraging termites and termite colony entrances may be lower for driver ants that forage largely on the surface. Therefore, the paucity of termites in driver ant prey samples may reflect niche differences in foraging stratum rather than an exception from these ants' generalist diet (Gotwald 1974, Schöning *et al.* 2005).
3. Breaching a termite entrance from the surface will probably be much more difficult than gaining access belowground. During a swarm raid, surface-foraging workers can probably only enter a termite mound either through ventilation passages or the termites' foraging galleries. But *Macrotermes* spp. can quickly plug the connections between the ventilation passages and the nest chambers (Darlington 1985) and thereby prevent a successful invasion. Also, running in the termites' foraging galleries is more difficult for driver ant workers than for the workers of subterranean *Dorylus* species, because driver ants have longer legs and thus a much larger cross-sectional area (Kaspari & Weiser 1999, Schöning *et al.* 2005). Therefore, breaching the termites' defense seems to be a hard task for driver ants—unless the mound has been opened for them, *e.g.*, by an aardvark.
4. Whenever the driver ant workers do manage to proceed through termite foraging tunnels, they are morphologically less well adapted for belowground fights than the subterranean *Dorylus*. There are some interesting parallels between the attacks of subterranean *Dorylus* species on the mounds of fungus-growing termites and the attacks of the subterranean army ant *Nomamyrmex esenbeckii* on the colonies of fungus-growing ants in the Neotropics. Following the argument of Powell and Clark (2004), who analyzed battles between *N. esenbeckii* and the leaf-cutting ants *Atta cephalotes* and *A. colombica*, one can expect that, during fighting between *Dorylus* workers and termites in tunnels, Lanchester's linear law of combat (Franks & Partridge 1993) will apply. The linear law predicts that when individuals are forced to engage in a parallel series of duels, as might be expected in belowground attacks on termite (or *Atta*) nests, the fighting abilities of combatants become relatively more important for victory than the size of the army due to a restricted combat arena. Accordingly, *N. esenbeckii* and *Atta* colonies deploy their largest workers at the frontline of battles (Powell & Clark 2004). One of us (C. S.) observed and collected *D.* (*Typhlopone*) *obscurior* workers hunting *Macrotermes* termites in their foraging tunnels at Wamba, Samburu District, Kenya, during the rainy season in April 2002. A comparison of their sizes with those of foraging workers from three other colonies of the same species attracted to oil/fat baits (collected also at Wamba during the same field trip) suggests that *D. obscurior* also employs disproportionally many large workers when hunting termites (Fig. 2). Based on the assumption that *Macrotermes* colonies also deploy their largest and strongest individuals (*i.e.*, the soldiers) for the defense of the mound, we can conclude that the outcome of the fight is likely to depend on the relative fighting strengths of the termite soldiers and largest *Dorylus* workers. While the largest *D.* (*Typhlopone*) and driver ant workers do not differ significantly in overall size (C. Schöning, pers. obs.), *D.* (*Typhlopone*) workers resemble *N. esenbeckii* workers in having short and highly sclerotized antennae and legs, while the largest driver ant workers have very long and relatively thin antennae and legs (Schöning

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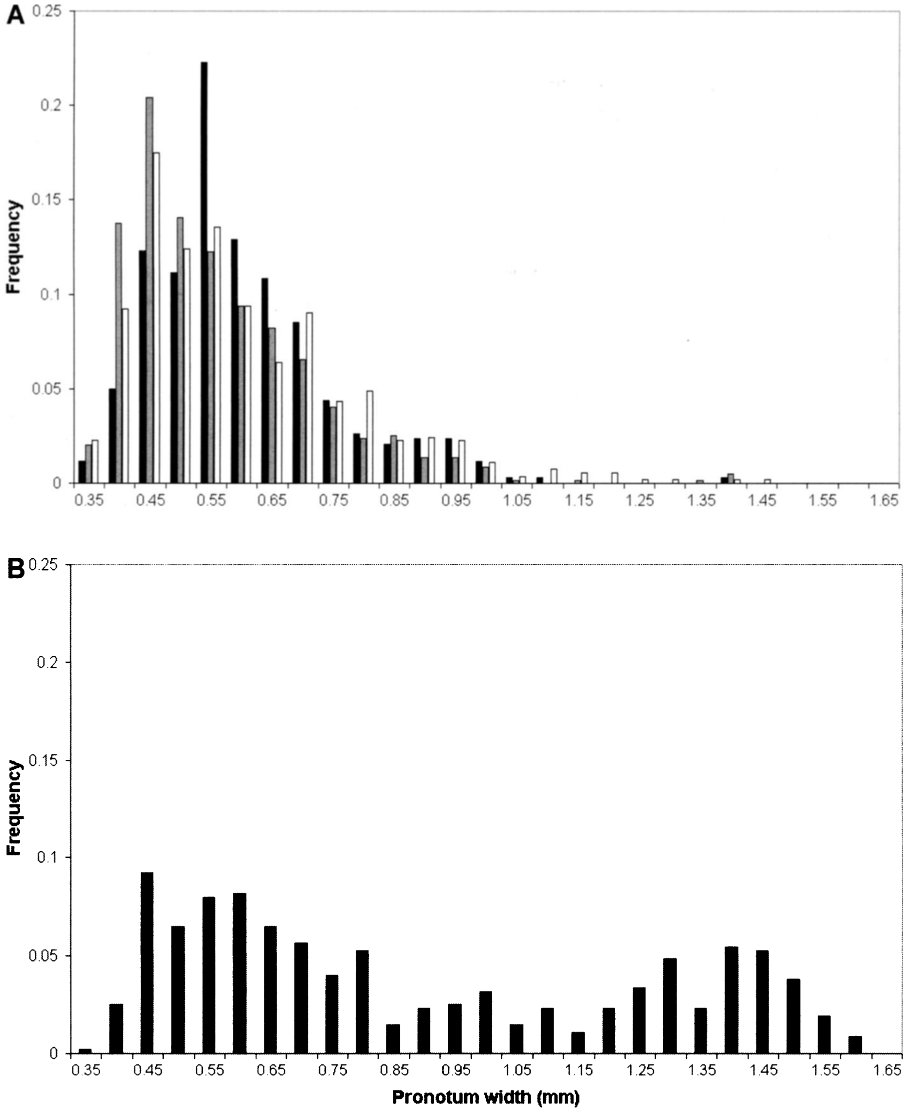

FIGURE 2. Size-frequency distribution of *Dorylus* (*Typhlopone*) *obscurior* worker samples. The x-axis shows the upper limit of the respective worker size class (as pronotum width, in mm), with the limit being excluded. (A) These three samples ($N = 341$, 597, and 532, respectively) were collected at combined oil/fat baits during fieldwork at Wamba, Samburu District, Kenya, April 2002, and most probably came from different colonies (> 300 m distance between sampling points). (B) This sample ($N = 478$) consists of workers hunting *Macrotermes* sp. in foraging galleries taken also at Wamba during the same field trip. The hunting workers were significantly larger than the workers of the other three samples (Mann–Whitney *U*-test, $P < 0.01$ in all pairwise comparisons between oil bait and fighting workers).

et al. 2005). We therefore propose that driver ant workers are more vulnerable in belowground fights with termites. Interestingly, *D.* (*Typhlopone*) colonies regularly attack and sometimes destroy driver ant colonies in their nests (Leroux 1982) and these fights should in principle be similar to *Dorylus* attacks on termite mounds. Hence, *D.* (*Typhlopone*) species seem to be morphologically better adapted for one-to-one battles belowground than driver ants.

In conclusion, we describe the hitherto unreported predation by driver ants on a *Macrotermes* nest and propose hypotheses why this widely and abundantly available prey is apparently so rare in the food spectrum of these polyphagous predators. Long-term studies will be necessary to determine the exact frequency of such successful attacks by driver ants and to understand the effect of predation by *Dorylus* species that use different foraging strata on the population dynamics of termites in the Old World tropics. Moreover, this study system offers an opportunity to test theoretical predictions concerning fights between large social insect societies experimentally.

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