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Ant and termite predation by the tropical blindsnake *Typhlops platycephalus*

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Summary. Dietary habits of the Puerto Rican blindsnake *Typhlops platycephalus* were studied by analysis of gastrointestinal tract contents and scats. Ant species (the principal prey taxon) were surveyed concurrently with the collection of the blindsnakes to determine what proportion of the species were used as prey. *Typhlops platycephalus* fed on 14 of 30 ant species found in the field and on two additional ant species that we did not find in the field. Individual snakes often feed on more than one prey species. Adult ants were most commonly found in the gastrointestinal tract and scats, although brood were occasionally encountered. However, laboratory feeding observations suggest that ant brood is more attractive to the snakes. Other prey taxa consumed included termites, mites, and sciarid fly larvae.

Key words: Ants, diet, snakes, termites, Puerto Rico.

Introduction

Many predators feed on insects, and colonies of eusocial insects can be treated as a factory within a fortress (Hölldobler and Wilson, 1990). Colonies of social insects represent a concentrated source of proteins, fats and carbohydrates for vertebrate and some invertebrate predators. The colonies are defended by an array of stings, mandibles and noxious secretions found mainly in the worker castes. Immatures generally do not have any defense against predators. One disadvantage to social insects is that their nests are mostly sessile, and although the members of the colony can flee or feign death, they leave behind a significant investment in immature stages and storage resources.

For a predator with vision many variables affect prey detection, but these are reduced in a blind predator like typhlopid snakes (e.g., prey motion and size are not important in prey detection). Blindsnakes seem to locate their prey by following odor trails (Webb and Shine, 1992), and probably have less ability to discriminate prey from non prey items than predators with vision. Blindsnakes of the family Typhlopidae are small, fossorial snakes with reduced eyes and a skull structure with non-expandable mandibles. In contrast to other snakes, which are noted for their adaptations for engulfing very large prey, typhlopids are limited to eating small-sized prey (Iordansky, 1981), principally ants and termites. Other invertebrates occasionally are noted as food, particularly centipedes and earthworms (Richter, 1955; Radovanovic, 1960; Sweeny, 1971; Pitman, 1974, Webb and Shine, 1993a). Although typhlopid snakes are virtually pantropical and often abundant, relatively little is known about their life history, presumably because of their small size and burrowing habits. Shine and Webb (1990) and Webb and Shine (1993a) reported dietary habits of Australian *Ramphotyphlops* based on examination of museum specimens, and White et al. (1992) studied the diet of the Hispaniolan *Typhlops syntherus*. However, none of the previous studies examined prey available at the sites where the snakes were collected.

Four species of typhlopids occur on mainland Puerto Rico (Schwartz and Henderson, 1990; Hedges and Thomas, 1991). *Typhlops platycephalus* is the largest, adults averaging 225 mm (Thomas and Gaa, 1996), and the most widely distributed occurring over most of the island, primarily in open or semi-open habitat, from sea level to around 650 m.

The objective of this study is to present prey diversity and prey size in *Typhlops platycephalus* and to compare these factors with the availability of different ant species (the main prey category) in the field. We also assess the possibility that the diet of *T. platycephalus* is limited by morphological constraints of the typhlopid feeding apparatus and/or prey defenses.

Materials and methods

Snakes were studied at three sites in the karst area of northern Puerto Rico. Site 1 was in western central Puerto Rico (18°20′N, 66°40′W) at an elevation of 100 m. Site 2 was 1.6 km by road on PR 651 E Dominguito (18°25′N, 66°45′W), elevation 130 m. Sites 1 and 2 were about 8 km apart. Site 3 was in Dorado (18°30′N, 66°15′W), elevation 25 m, and 22 km to the east of the first two sites. All sites contained pasture bordered by forested limestone hills and had numerous limestone rocks, which provided a ready means of searching for the snakes. In general we searched by lifting rocks along the edge between the limestone hills and the pasture.

Concurrently we sampled ants in the habitats from which snakes were collected to assess whether there was prey selectivity by the snakes. Ants were collected by searching beneath rocks (75 at sites 1 and 3, and 122 at site 2), using tuna fish as bait (32 at sites 1 and 3, and 17 at site 2), and pitfall traps (10 at sites 1 and 3, none at site 2). Tuna fish was placed as bait at intervals of 2 to 3 m and the ants species that came during a period of one hour were recorded. Pitfall traps were positioned at 3 m intervals and left for 24 hours. Bait transects and pitfall traps followed an edge between pasture and limestone hills. The number of times a given ant species was found under a rock, on a bait or in a pitfall trap was taken as a measure of abundance.

We determined prey consumed by analyzing the scats and the alimentary tracts of recently captured snakes. Freshly collected snakes (sites 1 and 3) were kept in plastic bags with a piece of white paper toweling for several days and the scats collected for examination. Snakes collected at site 2 were placed on ice at the time of collection and frozen after returning from the field. Later we dissected the snakes, and counted under a microscope the number of each prey. We classified prey by species, castes or developmental stage. For disarticulated ants and termites, only heads were counted. Prey numbers were underestimates, because in some instances only legs, antennae or other parts were found. Generally we did not count termites in the scat samples, although qualitative observations on the abundance of different castes were recorded. To see if the proportion of castes or immatures in nests was reflected in the alimentary tract contents or if prey discrimination occurred, we fed different castes and immatures of ants and termites to seven snakes in captivity. We offered each snake fifteen members of each caste or developmental stage and recorded the amount of each prey category eaten. In some instances numbers varied because of caste availability. Also, we measured with calipers the length of ten individuals (preserved in ethanol) of each ant caste found in the field to compare with the ant size distribution found in the snake intestinal tracts and scats.

Results

Ninety percent (N = 40) of the snakes contained food in their alimentary tracts ($\bar{X}$ = 20.5 prey, SE 7.4, range 0–222). Ants and termites were the main prey (Table 1). The snakes often ate a large number of prey (Table 1). Multiple prey taxa were found in 70% of the scats from 58 snakes and in 61% (N = 36) of the alimentary tracts that contained food. One snake scat contained ants from six species. Worker ants were most common, but larvae and pupae of *Wasmannia auropunctata*, *Pheidole fallax* and pupae of *Odontomachus ruginodis* were also found (Table 1). Adults of *W. auropunctata* and *P. fallax* were found together with their immatures in the same snakes, but only pupae of *O. ruginodis* were in the alimentary tracts or scats (the pupae in the scats were empty). Although we found, in four scats, parts of *O. ruginodis* which appear to be from adults, we did not know if they were remains from the contents of old pupae or were truly from adults. The scat from one snake contained 25 pupae from *O. ruginodis*, and it was common to find 10 or more *O. ruginodis* pupae in scats from a single snake. Compared with the size distribution of the other ant species (Table 2) these pupae were large, averaging 7 mm in length and 2.5 mm in width, and were ovoid, softer, and more compact than adult *O. ruginodis*. In addition, queens of *Paratrechina steinheili*, *Strumigenys rogeri*, and *Smithistruma margaritae*, and males of *P. fallax* were found in the scats and alimentary tracts.

Frequency of ant species found in the scats was significantly associated with their frequency in the field (Pearson correlation, r = 0.61, P < 0.05, N = 14) and the frequency of ant species in the alimentary tracts was also correlated with their frequency in the field (Pearson correlation, r = 0.84, P < 0.05, N = 6). *Wasmannia auropunctata,* the most common ant species under rocks at site 2, (Table 2) was the most frequent in the alimentary tracts. The fire ants *Solenopsis geminata* and *S. wagneri* were common under rocks, but were not found in the alimentary tracts of the snakes collected at site 2. Nonetheless, *S. geminata* minors were present in the scats from sites 1 and 3. Obligate soil-nesting ants, species of *Cardiocondyla* and *Mycocepurus smithi* (Smith, 1936), did not appear as prey. *Mycocepurus smithi* nests were common at site 2, but this species did not appear in our sampling schemes (this species usually does not nest under rocks and does not come to tuna fish baits). *Pheidole subarmata* was ingested in low numbers, considering that it is one of the most abundant ant species in pasture land (Table 2).

Generally, the small-sized ant species (Table 2) or the minors from larger species (*Solenopsis geminata*, *Pheidole fallax*, *P. megacephala*) were found in the scats and the alimentary tracts. The only ants of moderate to large size ingested were *Tetramorium bicarinatum*, *Camponotus sexguttatus*, and *Odontomachus ruginodis* (pupae). We ranked, by length (an indication of size), the different ant castes (N = 43) and found that the median caste length in the field was 2.29 mm corresponding to the minors of *S. geminata*. The snakes fed mostly on castes that fell below the median field caste length (binomial test: x = 11 castes, N = 15, P = 0.01). Also, the frequency of feeding on different castes is greater below the median field caste length (Fig. 1).

Termites were also common food items. Workers of *Nasutitermes costalis* and *Heterotermes* sp. were found in the alimentary tracts of *T. platycephalus* together with few soldiers. Twenty-six percent of the scats (representing 58 snakes) contained *N. costalis* (Table 1). The majority of the termites in the scats were alates, and workers were more common than soldiers. We found soldiers of *N. costalis* in only two (out of 15) scats containing termites. One snake scat contained 28 workers versus 8 soldiers of *N. costalis*. We found that large numbers of dipteran larvae (*Sciara* sp.) were found in scats of 4 snakes (Table 1); most of the larvae appeared to be undigested.

In the laboratory feeding trials, three snakes offered equal numbers of workers and soldiers of *Nasutitermes costalis* preferred the workers. In one feeding bout with the fire ant *Solenopsis wagneri* as prey the snake ate all the pupae (15), half (5) of the small workers and ignored the major workers (5).

Table 1. Frequency of occurrence of each prey type in *Typhlops platycephalus* individuals. Each scat corresponds to a different snake. Maximum number of prey individuals per snake for the common prey categories appears besides their frequency stage in parentheses.

	Site 2, alimentary tracts (N = 40)	Site 1 scats (N = 34)	Site 3 scats (N = 24)	Total scats (N = 58)
Ants				
Wasmannia auropunctata (M) (workers, larvae or pupae)	10 (19 W, 13 I)	9	9	18 (31 W)
Odontomachus ruginodis (M) (pupae)	1 (5 P)	11	6	17 (25 P)
Tetramorium bicarinatum (M)	3 (38 W)	13	1	14 (40 W)
Pheidole megacephala (workers)	–	–	8	8 (34 W)
Solenopsis geminata (minor workers)	–	4	4	8 (24 W)
Paratrechina steinheili (M) (workers or queens)	–	1	4	5 (72 W)
Pheidole exigua (workers)	–	2	2	4
Cyphomyrmex minutus (M)	3 (28 W)	–	–	0
Strumigenys louisianae (M)	–	2	1	3 (39 W)
Monomorium subcoecum (M)	–	1	1	2
Pheidole fallax (workers, males, pupae, larvae)	2 (38 W, 178 I)	–	–	0
Smithistruma margaritae (M) (workers or queens)	–	–	2	2
Strumigenys rogeri (M) (workers or queens)	–	2	–	2 (8 W)
Camponotus sexguttatus (media wokers)	–	1	–	1
Pheidole subarmata (workers)	–	1	–	1
Tapinoma melanocephalum (M)	1 (15 W)	–	1	1
Unidentified Formicidae	4	2	2	4
Unidentified ant larvae	–	1	1	2
Termites				
Nasutitermes costalis	2 (75 W, 11 S)	10	5	15
Heterotermes sp.	1 (41 W)	–	–	0
Others				
Mites	6	6	5	11 (30)
Insect parts	14	–	–	0
Coleoptera	–	4	5	9
Plant matter	3	–	2	2
Diptera (*Sciara* sp.)	–	2	2	4 (60 L)
Mollusk (gastropod)	–	–	1	1
Nematodes	1	–	–	0
Wasps (Diapriidae)	1	–	–	0
Unidentifiable	11	–	–	0
Empty	4	–	–	0

M indicates a monomorphic species, **I** immatures (larvae or pupae), **L** larvae, **P** pupae, **S** soldiers and **W** workers.

Table 2. Relative abundance of ants. Ant mean size (mm) and SE (N = 10) follow the species (first number corresponds to minors and second to majors of polymorphic species). Members of the genus *Strumigenys* were not found in the field samples, but were recorded in the scats of *Typhlops platycephalus*.

	Under rocks			Baits			Pitfalls		Total
	site 1 N = 75	site 2 N = 122	site 3 N = 75	site 1 N = 32	site 2 N = 17	site 3 N = 32	site 1 N = 10	site 3 N = 10	
Wasmannia auropunctata (1.50 ± 0.02)	18	18	4	20	–	12	10	4	86
Pheidole subarmata (1.95 ± 0.05, 4.23 ± 0.13)	7	–	–	21	2	7	3	4	44
Solenopsis geminata (2.29 ± 0.05, 5.03 ± 0.04)	6	16	5	5	3	6	–	–	41
Odontomachus ruginodis (8.94 ± 0.20)	18	5	11	1	–	3	1	1	40
Brachymyrmex obscurior (1.59 ± 0.09)	5	6	1	6	7	8	–	–	33
Cyphomyrmex minutus (2.03 ± 0.04)	9	8	2	–	–	–	1	2	22
Monomorium ebeninum (1.84 ± 0.04)	–	–	–	2	–	16	–	4	22
Cardiocondyla emeryi (1.77 ± 0.06)	2	3	2	2	4	5	–	1	19
Pheidole fallax (3.37 ± 0.08, 5.23 ± 0.18)	–	1	–	5	11	–	–	2	19
Solenopsis wagneri (2.62 ± 0.07, 5.93 ± 0.11)	–	15	–	–	1	–	–	–	16
Pheidole megacephala (2.02 ± 0.02, 3.57 ± 0.10)	–	–	7	–	–	5	–	2	14
Paratrechina steinheili (1.96 ± 0.04)	1	–	4	–	–	8	–	1	14
Tapinoma melanocephalum (1.93 ± 0.08)	–	3	2	–	–	7	1	–	13
Tetramorium bicarinatum (3.81 ± 0.10)	–	1	–	5	3	–	–	–	9
Brachymyrmex heeri (1.32 ± 0.04)	4	–	1	–	–	1	–	–	6
Monomorium floricola (1.60 ± 0.05)	–	–	–	–	1	4	–	1	6
Anochetus mayri (3.75 ± 0.12)	3	–	1	–	–	–	–	–	4
Mycocepurus smithi (2.29 ± 0.02)	–	–	–	–	–	–	–	3	3
Pheidole exigua (1.53 ± 0.04, 2.46 ± 0.05)	1	–	2	–	–	–	–	–	3
Hypoponera opaciceps (2.47 ± 0.03)	–	2	–	–	–	–	–	–	2
Leptogenys pubiceps (6.20 ± 0.08)	1	1	–	–	–	–	–	–	2
Pheidole sculptior (1.46 ± 0.03, 2.60 ± 0.06)	–	1	–	–	–	–	–	1	2
Rogeria foreli (2.18 ± 0.08)	1	1	–	–	–	–	–	–	2
Smithistruma margaritae (1.74 ± 0.05)	–	2	–	–	–	–	–	–	2
Camponotus sexguttatus (4.68 ± 0.17, 6.62 ± 0.06)	–	–	–	–	–	1	–	–	1
Solenopsis azteca (1.22 ± 0.03)	–	–	–	–	–	1	–	–	1
Solenopsis pygmaea (1.03 ± 0.02)	1	–	–	–	–	–	–	–	1
Cardiocondyla nuda (1.95 ± 0.07)	–	–	–	–	–	–	–	1	1
Monomorium subcoecum (1.63 ± 0.07)	–	–	–	–	–	–	1	–	1
Myrmelachista ramulorum (2.37 ± 0.10)	–	–	–	–	–	1	–	–	1
Strumigenys louisianae (1.62 ± 0.04)	–	–	–	–	–	–	–	–	0
Strumigenys rogeri (1.94 ± 0.04)	–	–	–	–	–	–	–	–	0

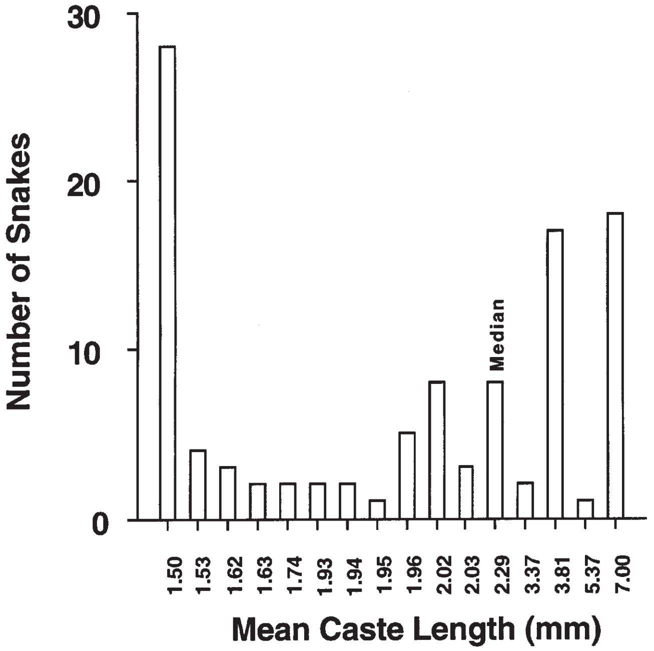

Figure 1. Ant castes or developmental stage, ranked by length, found in the alimentary tracts or scats of *Typhlops platycephalus*. The largest prey corresponded to *Odontomachus ruginodis* pupae. Median caste length in the field is indicated.

Another snake ate only pupae of *Odontomachus ruginodis* and ignored workers and reproductives. When workers and pupae of the fungus-growing ant *Cyphomyrmex minutus* were presented, the snake ate all the pupae (10) and only four of the 39 workers. The last snake individual was presented *Pheidole fallax* soldiers and workers and fed on five of the 19 workers and ignored the 15 soldiers.

Discussion

The results indicate that *Typhlops platycephalus* is a generalist predator, feeding on 16 ant species in the field and on the fire ant, *Solenopsis wagneri*, in laboratory tests. Also this snake fed on the most abundant termite species. There is an association between frequency of feeding on an ant species and its abundance. However, a few species that rank low in abundance were fed upon, and a few that ranked high in abundance were not fed upon. The finding that *T. platycephalus* ate male ants, queens, larvae and pupae indicates that it enters ant colonies. We do not know to what extent these snakes feed on ants or termites outside of the colonies, where these insects are less concentrated. In addition *T. platycephalus* feeds sporadically on mites, fly larvae, diapriid wasps, beetles, and snails. Some of these invertebrates might have been symbionts of ant nests (e.g. diapriid wasps are parasites of ants) and may have been accidentally ingested.

We found more worker ants and less often larvae and pupae in the alimentary tracts. However, it is possible that snakes prefer to eat the more nutritious immature stages, because many of the prey, including adult ants, were undigested in the scats. The laboratory feeding bouts suggest preference for the brood. Ant larvae and pupae neither move, do not seem to have chemical defenses, lack morphological defenses, and contain more digestable body parts compare to adult ants. This apparent lack of defenses facilitates predation over the immatures of holometabolous insects (Gotwald, 1995). In contrast, Webb and Shine (1993 a) found mostly ant immatures in Australian blindsnakes, although they did find ant workers in 43% of the tropical *Ramphotyphlops polygrammicus*. The proportion of immatures eaten by *T. platycephalus* could be higher than observed, because immature stages may be digested faster than workers and remain identifiable for shorter periods of time. Also, we found a higher percentage of snakes with food items in their alimentary tracts than Shine and Webb (1990) found in Australian blindsnakes. This difference could be related to the fact that our snakes were either kept alive until they defecated (scats examined) or immediately frozen to stop digestion. Also, we examined the content of the whole gastrointestinal tract, and Webb and Shine (1993 a) only reported items found in the stomach.

Some ants eaten by the snakes were not completely disarticulated; mites found in scats were almost entire (some were alive) and sciarid larvae, which are soft-bodied, were remarkably entire in the scats. The energetic gain from ingesting adult, well, sclerotized animals might not be nearly as great as ingestion of larvae or pupae. Laboratory observations (unpublished data) show rapid feeding-frenzy behavior in *Typhlops platycephalus* when feeding on termites. The snakes seize their prey on any part of the body and swallow them. Possibly these snakes enter a colony of ants in search of the brood and their feeding-frenzy behavior results in that they eat everything they can seize, larvae, pupae or adults.

Current data regarding the effects of ant defenses on *Typhlops platycephalus* prey choice is lacking. However, our experience with these ants indicates that *T. platycephalus* preyed on species with painful stings (*Solenopsis geminata*, *Wasmannia auropunctata*) as well as species with mild stings (*Strumigenys* spp., *Pheidole* spp., *Cyphomyrmex minutus*). Also, *Odontomachus ruginodis*, (pupae only eaten) possess one of the most painful stings among Puerto Rican ants. *Solenopsis geminata* attacks any intruder very rapidly but *W. auropunctata* moves and stings slowly. Along with small size, the slow movements of *W. auropunctata* probably explain the high proportion of snakes that fed on this ant.

Gape limitation has been found to be an important factor limiting the diet of snakes (Webb and Shine, 1993b) and may play a role in the diet of *Typhlops platycephalus*. The absence of *Pheidole* spp. soldiers and *Solenopsis* spp. majors as prey could be the result of the stinging or biting ant defenses, but these castes are also large and may be at the limits of the gape of these blindsnakes. Probably the adults of *O. ruginodis* and the majors of *C. sexguttatus* fall outside of the gape size of these snakes. However, due to the highly specialized skull morphology, which includes edentulous mandibles and small, highly kinetic, toothed maxillas and non-expandable mandibular symphyses, obtaining confident measures of the gape size of *T. platycephalus* was not possible.

Skatole produced by army ants repels several species of blindsnakes (Watkins et al., 1969, Gotwald, 1995). *Pheidole fallax* soldiers synthesizes skatole in their hypertrophied poison gland (Blum, 1985) and perhaps this chemical functions as a defense against *Typhlops platycephalus*. Workers of *Nasutitermes costalis* were found in greater numbers than soldiers of *Heterotermes*, even though the workers are larger than the soldiers, which could point to the defense provided by the mandibles of *Heterotermes* soldiers. The spraying of gummy repugnatorial fluids from the heads of *N. costalis* soldiers could explain the avoidance of them by the snakes.

The fungus-growing ant, *Mycocepurus smithi,* was not eaten by the snakes. *Mycocepurus smithi* is mostly a ground nesting species, in contrast to the other fungus-growing ant *Cyphomyrmex minutus*, which frequently nests under rocks (Torres and Snelling, 1997). The difference in nesting sites could explain the presence of *C. minutus* and the absence of *M. smithi* from the diet of the snakes. Perhaps the snakes fed mostly under rocks and avoided open areas or were better at foraging in crevices than penetrating the soil.

Even among West Indies *Typhlops* there are notable differences in prey items. White et al. (1992) examined stomach contents of *Typhlops syntherus* (a species smaller than *T. platycephalus*) from Hispaniola. They found 302 food items in 22 specimens of *T. syntherus*, most were termites and beetles, no ants were found. Compared to our results, the number of items found per snake was low.

Our study demonstrates that *Typhlops platycephalus* feeds on a variety of species of ants and termites including ant species that defend their colonies with potent stings. We do not know how the snakes neutralize the ant defenses. Unanswered is whether some ant castes are not part of the diet due to gape limitation or because of prey defense. Perhaps a combination of large size and potent stings prevent some of the ant castes from being eaten. Another critical question is the amount of nutritional gain that the snakes get from the food. Our observations revealed that some prey eaten is not well digested; perhaps some of these prey represent incidental ingestion (Wright et al., 1983).

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