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Prey composition of three *Thanatus* species (Philodromidae, Araneae): indication of relationship between psammophily and myrmecophagy

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Abstract
The natural prey of three species of the genus *Thanatus* was studied in Absheron Peninsula, Azerbaijan. The percentage of feeding specimens in the sample of the studied *Thanatus* species was low: 1.7% in *Thanatus fabricii*, 7.1% in *Thanatus imbecillus*, and 7.2% in *Thanatus vulgaris*. The investigation has shown that all three species are polyphagous predators, feeding on a wide range of arthropods. They captured mainly small prey, not exceeding their own size. Arachnids (spiders and mites) were the dominant prey of two species, *T. imbecillus* and *T. vulgaris*, constituting over 50% of total prey in both species. In the diet of the third species, *T. fabricii*, arachnids constituted a large fraction (44.4%), but worker ants (Formicidae) were important, too (36.1%). Worker ants possessing effective defensive equipment are unusual prey for cursorial spiders. No philodromids are known to feed on this prey and both *T. imbecillus* and *T. vulgaris* tended to avoid attacking ants. Interestingly, unlike the two other species studied, which occur in dense grassy vegetation, *T. fabricii* is a psammophilous spider inhabiting open sandy ground with sparse vegetation. Sandy substrates are usually characterised by relatively poor arthropod fauna with the prevalence of ants. Thus the potential prey spectra of psammophilous spiders are biased towards ants that may favour evolving adaptations to catch this well-armed prey.

Key words: Philodromid spiders, natural diet, ant-eating

INTRODUCTION

Spiders of the family Philodromidae are typical cursorial hunters, which do not use silk for prey capture. Philodromidae is a large, worldwide distributed family, with over 500 species described (Platnick 2003). However, very few studies have addressed the biology of philodromids (Haynes & Sisojević 1966; Mikulska 1967; Putman 1967b; Anchipanova & Šternbergs 1984; Klein & Şengonca 1988; Şengonca & Klein 1988), and with the exception of Putman (1967a), who gave diet composition for *Philodromus* spp., no quantitative data on their natural diet are available.

The present paper concerns with natural prey of three species of the genus *Thanatus* C. L. Koch, 1837 inhabiting Absheron Peninsula, Azerbaijan. As is typical of *Thanatus*, all three species studied are found at ground level. Two of these, *Thanatus imbecillus* L. Koch, 1878 and *Thanatus vulgaris* Simon, 1870, occur in grass litter in dense vegetation, while the third species, *Thanatus fabricii* (Audouin, 1826), inhabits open sandy habitats with sparse vegetation. The three species have more or less similar size, with average body length of adult females of 5 mm in *T. fabricii*, 6 mm in *T. vulgaris*, and 7 mm in *T. imbecillus* (Guseinov, unpublished data). *T. fabricii* is brightly coloured, with yellow and brown markings on the opisthosoma, while *T. vulgaris* and *T. imbecillus* have grey coloration. However, the latter species are easily distinguishable from each other by having different abdominal patterns. Both

T. imbecillus and *T. vulgaris* are apparently univoltine species. Adults of *T. imbecillus* are found in early spring, from mid March to the end of April, while individuals of *T. vulgaris* reach maturity in the second half of April and occur until mid June. Adults of *T. fabricii* are found for a much longer period, from May through September. Moreover, a number of juvenile instars of different sizes occur together with adults, suggesting a complicated life cycle in *T. fabricii*, with overlapping generations (Guseinov unpublished data).

The three *Thanatus* species use sit-and-wait predatory strategy similar to that described for Lycosidae (Edgar 1969; Ford 1978; Stratton 1985). They wait for prey motionless in ambush, but frequently change their hunting locations. After the prey is detected, *Thanatus* attacks it by a sudden lunge.

MATERIAL AND METHODS

Investigations were carried out in Absheron Peninsula, Azerbaijan. The prey of *T. imbecillus* and *T. vulgaris* were sampled from 8 March to 21 June 1997 at three sites located near villages Bina, Mardakyan and Yeni-Surakhany. These areas were densely vegetated with short ephemeral grasses, predominantly *Calendula persica, Senecio vernalis, Medicago denticulata, Erodium cicutarium, Pterotheca marschalliana, Poa bulbosa, Anisanthea rubens, Aegilops biuncialis, Avena ventricosa.* The ground at these sites was entirely covered with litter consisting of bases of living plants, moss, dead grass stems and other plant debris. A total of 28 surveys were made at these sites, which amounts to more than 52 hours; 30.5 h at Mardakyan, 14 h at Yeni-Surakhany, and 7.5 h at Bina.

The prey of *T. fabricii* was observed near Dyubendy village from 3 May to 20 August 1998 and from 3 March to 8 August 1999. The plant composition at this site was similar to that in the three other areas, but vegetation cover was much more sparse with many patches of bare sandy ground. Thirty-three surveys were conducted at Dyubendy, which took about 50 hours in total.

All surveys were made in daylight hours between 10:00 and 17:00. During surveys, the ground at the study sites was thoroughly searched for *Thanatus* spiders, and each individual found was captured and put in a transparent glass vial. In the vial the spider mouthparts were inspected with a lens (×4) to prevent small prey being overlooked. Specimens with prey in their chelicerae were preserved in 75% ethyl alcohol and brought to the laboratory to take measurements of prey size (body length) and to identify it. The remaining spiders were released.

RESULTS

Prey composition

Altogether, 29 individuals of *T. imbecillus*, 40 individuals of *T. vulgaris*, and 36 individuals of *T. fabricii* were found with prey in their chelicerae. It constituted of 7.1%, 7.2% and 1.7% respectively of the total numbers of spiders observed.

All prey types were arthropods, represented by seven insect orders and three arachnid orders (Table 1). Eight orders were found in the diet of *T. imbecillus*, seven in *T. vulgaris*, and five in *T. fabricii.* Spiders were the only significant prey component of *T. imbecillus*, constituting over a half of its total diet (55.2%). They also predominated in the diet of *T. vulgaris* (35.0%), however, there mites were important, too (27.5%). Thus in the diet of *T. vulgaris* arachnids also made up over a half of the total prey. Similarly, arachnids contributed in a large portion to the diet of *T. fabricii.* Yet, in this species the dominant prey were mites (36.1%), whereas the proportion of spiders was lower (8.3%). Additionally, Hymenoptera composed a considerable part of the prey of *T. fabricii* (38.9%). Except for one parasitic wasp, all hymenopterans captured by this species were worker ants (Formicidae), represented by 11 individuals of *Messor denticulatus* Lepeletier and 2 individuals of *Tetramorium* sp. The only hymenopteran captured by another *Thanatus* was a halictid bee found in *T. imbecillus*.

Table 1. Composition of prey captured by the three *Thanatus* species.

Prey order	*Thanatus imbecillus*		*Thanatus vulgaris*		*Thanatus fabricii*	
	N	%	N	%	N	%
Araneae	16	55.2	14	35.0	3	8.3
Acari	—	—	11	27.5	13	36.1
Opiliones	1	3.4	—	—	—	—
Diptera	3	10.3	3	7.5	—	—
Orthoptera	1	3.4	3	7.5	—	—
Homoptera	4	13.8	4	10.0	2	5.6
Hemiptera	—	—	4	10.0	4	11.1
Hymenoptera	1	3.4	—	—	14	38.9
Coleoptera	1	3.4	—	—	—	—
Lepidoptera	2	6.9	1	2.5	—	—
Total	29	100.0	40	100.0	36	100.0

Predation on spiders

Members of six families of spiders were taken by *Thanatus* species (Table 2). Most of these (93.3%) were cursorial hunters (Philodromidae, Thomisidae, Salticidae, Gnaphosidae, and Lycosidae). Only two representatives of web-building family (Araneidae) were found among the prey of *Thanatus*. Moreover, one of these spiders was an adult male *Hypsosinga albovittata* (Westring, 1851). Another araneid was a juvenile of *Argiope lobata* (Pallas, 1772), which was consumed outside the web.

In all studied species, the most frequently captured spiders were philodromids. Each species caught either conspecifics (cannibalism) or individuals of other *Thanatus* species (intraguild predation). *T. imbecillus* exhibited especially high level of cannibalism; over 20% of the prey of this spider were conspecifics. It is remarkable that all conspecifics captured were adult spiders (four females and two males); the predators always being mature females. The two other *Thanatus* species fed on conspecifics less frequently (5.0% in *T. vulgaris* and 2.8% in *T. fabricii*). In all such cases larger spiders (probably older instars) captured smaller ones (probably younger instars).

Prey size

All species captured prey usually not exceeding the body size of the predator (Fig. 1). In the diet of *T. vulgaris* and *T. fabricii* small prey prevailed, not exceeding half the size of the spiders, whereas *T. imbecillus* preferred medium-sized prey (from 50 to 100% of its size). *T. fabricii* was the only species, which fed considerably on large prey, exceeding its own size. It is remarkable that all these large prey were workers of *Messor denticulatus*. All non-formicid prey of *T. fabricii* were smaller than their consumers.

DISCUSSION

As typical of cursorial spiders (Nentwig 1986; Nyffeler et al. 1994), the percentage of feeding specimens in the sample of the studied *Thanatus* species was low. However, the samples clearly indicate that the three species are polyphagous, feeding on a wide range of arthropods. The prevalence of arachnids in their diets is probably due to the abundance of this prey in the predators' habitats. Spiders and mites are among the dominant invertebrate groups inhabiting ground level (Nentwig 1982), and at least Araneae frequently constitutes a considerable part of prey of epigeic cursorial spiders (Edgar 1969; Hallander 1970; Schaefer 1974; Yeargan 1975; Jackson 1977; Gettmann 1978; Nyffeler & Benz 1979; Bardwell & Averill 1997). Mites appear to be uncommon prey of spiders, yet laboratory tests have shown that they are readily accepted by philodromids (Putman 1967a; Şengonca & Klein 1988).

Table 2. Spiders taken by the three *Thanatus* species.

Family	Species	*T. imbecillus*	*T. vulgaris*	*T. fabricii*
Philodromidae	*Thanatus imbecillus*	2 male, 4 female	2 juv.	1 juv.
	Thanatus vulgaris	1 juv.	2 juv.	—
	Thanatus fabricii	—	1 female	1 juv.
Salticidae	*Chalcoscirtus infimus*	1 male	—	—
	Heliophanus dunini	—	1 female	—
	Pellenes epularis	—	1 female	—
	Phlegra bresnieri	1 female	—	—
	unidentified	—	1 juv.	—
Gnaphosidae	*Micaria rossica*	—	1 juv.	—
	Nomisia ripariensis	1 juv.	—	—
	Zelotes longipes	1 juv.	—	—
	unidentified	—	1 male	—
Lycosidae	*Alopecosa* sp.	1 juv.	—	—
	Pardosa sp.	1 juv.	—	—
	unidentified	—	—	1 juv.
Thomisidae	*Xysticus kochi*	1 male, 1 juv.	—	—
	unidentified	—	1 juv.	—
Araneidae	*Argiope lobata*	—	1 juv.	—
	Hypsosinga albovittata	1 male	—	—
unidentified	unidentified	—	2 juv.	—

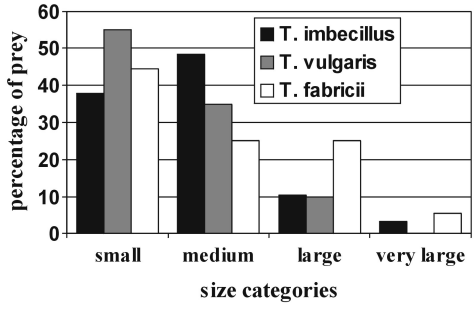

Fig. 1. Relative frequency of four size categories of prey of *T. imbecillus* (black), *T. vulgaris* (grey) and *T. fabricii* (white): small - less than 50% of spider body size; medium - between 50% and 100% of spider body size; large - between 100% and 200% of spider body size; very large - more than 200% of spider body size.

The diets of *T. imbecillus* and *T. vulgaris* are typical of cursorial spiders in that these species feed primarily on soft-bodied, safe prey. In contrast, significant part of *T. fabricii* diet consisted of worker ants, which possess effective defenses and are not palatable prey to most cursorial spiders (Nentwig 1986). Further investigation is required to clarify whether *T. fabricii* uses a specialised predatory technique to catch ants, and whether it prefers ants to other prey, as some other myrmecophagic spiders do (Harkness & Harkness 1992; Li & Jackson 1996; Castanho & Oliveira 1997). However, the fact that *T. fabricii* regularly feeds on ants larger or even twice as large than the spider, suggests that it is quite a competent ant feeder. This is an unusual habit for philodromids. Laboratory tests with *Tibellus oblongus* (Walckenaer, 1802) and *Philodromus praelustris* Keyserling, 1880 have shown that these philodromids refused worker ants as prey (Putman 1967b; Nentwig 1986). The present observations indicate that both *T. imbecillus* and *T. vulgaris* avoid attacking ant workers. Nonetheless, at two occasions in the previous years (in 1991 and 1992) I found *T. imbecil-*

lus eating worker ants in the field, although this might be a rather rare event, as *T. imbecillus* consistently rejected worker ants in the laboratory (Guseinov, unpublished data). Similar ant-avoiding behaviour was exhibited by individuals of *T. vulgaris* in captivity. In the field, *T. vulgaris* has never been observed to feed on ants, except for one observation: in 1995 a specimen was found consuming a queen of *Messor denticulatus*. Unlike workers, reproductive individuals of ants are virtually defenseless and readily captured by many cursorial spiders. Interestingly, one of the prey of *T. vulgaris* was the ant-mimicking spider *Micaria rossica* Thorell, 1875. Further observation of *M. rossica* predation by *T. vulgaris* was recorded in 1996. Thus it appears that *T. vulgaris* does catch prey similar in general appearance to worker ants, if they do not possess the ant defences. These observations suggest that during prey capture *T. vulgaris* may rely primarily on vibratory and/or chemical stimuli in distinguishing prey, rather than on vision.

The question arises why has *T. fabricii* adapted to catching prey (i.e. worker ants) that is not palatable to other congenerics and probably to most other philodromids? Unlike two other species studied, *T. fabricii* is a psammophilous spider inhabiting bare sandy ground with sparse vegetation. Sandy substrates are usually characterised by relatively poor arthropod fauna with the exception of ants which constitute a major part of the prey of web-building spiders occurring here (e.g. Nørgaard 1956; Henschel & Lubin 1992). Thus the potential prey spectra of psammophilous cursorial spiders are probably biased towards ants, and that may favour evolving adaptations to catch this well-armed prey. It is remarkable that other psammophilous cursorial spiders occurring in Absheron Peninsula are also myrmecophagic. Laboratory experiments and field observations have shown that gnaphosid spiders of the tribe Pterotrichini (*Berlandina, Nomisia, Pterotricha*) are competent ant-eaters, too (Guseinov, unpublished data). Likewise, worker ants constitute a considerable part of the prey of two psammophilous salticids of the genus *Aelurillus*: *A. muganicus* Dunin, 1984 and *A. m*-nigr*um* (Kulczynski, 1891) (Guseinov 1999). Other psammophilous salticids occurring in Absheron are two species of the genus *Yllenus*. The samples of prey of one of these species yielded several ants in its diet. The above data indicate that psammophily is apparently among the factors influencing the evolution of myrmecophagy within certain families of cursorial spiders. Further investigations of the prey of psammophilous spiders are needed to evaluate this hypothesis.

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