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Natural diet and prey-choice behaviour of *Aelurillus muganicus* (Araneae: Salticidae), a myrmecophagic jumping spider from Azerbaijan

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Abstract

The distinctions between a predator's diet, its prey-choice behaviour and its preferences are illustrated in a study of *Aelurillus muganicus*, a salticid spider from the Apsheron Peninsula in Azerbaijan. Laboratory experiments showed that *A. muganicus* has an innate predisposition to choose ants as prey. The natural diet of this species was determined by sampling individuals seen feeding in the field ($n = 64$). Ten arthropod orders were represented. Seven were from the class Insecta (Coleoptera, Collembola, Diptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera) and three from the class Arachnida (Acari, Araneae, Pseudoscorpiones). Collectively, four orders accounted for > 70% of the prey records: Hymenoptera (20%), Lepidoptera (19%), Acari (19%) and Homoptera (14%). No other order accounted for > 10% of the prey records. Of the 45 insects among the prey, 13 (29%) were Hymenoptera, with ants (family Formicidae) alone accounting for 24% of the prey records. Although ants were the preferred prey of *A. muganicus*, as revealed by laboratory testing, and also the most common single category of prey from the field prey records, records of *A. muganicus* feeding on prey other than ants were actually more common than records of it feeding on ants, suggesting that, besides prey choice, other factors have a strong influence on the diet of this species.

Key words: spider, Salticidae, predation, diet, prey choice, preference, myrmecophagy

INTRODUCTION

One of the more interesting things about jumping spiders (Salticidae) is how they force us to examine the distinctions between a predator's diet, its prey-choice behaviour and its preferences. These terms, 'preference', 'choice' and 'diet', are useful for making particular distinctions that are often blurred in the ecological literature (see Morgan & Brown, 1996; Lockwood, 1998). A predator's natural diet is the prey the predator actually eats in nature, whereas preference is a cognitive attribute (i.e. the predator's attitude toward prey) that is revealed by the predator's prey-choice behaviour (Cross & Jackson, in press). A predator's prey-choice behaviour is only one potential influence on diet (Morse, 1971). For example, a predator's preferred prey might be scarce in a predator's diet simply because the preferred prey is scarce in the environment, or because it is difficult to locate or difficult to capture. Data on diet alone cannot simply reveal a predator's choices and preferences.

Salticids are unique spiders because of their large eyes, acute vision (Land & Nilsson, 2002) and intricate vision-based predatory strategies (Forster, 1982; Jackson & Pollard, 1996). Exceptional eyesight makes these spiders especially suitable for prey-choice testing (Li & Jackson, 1996) and ants have been especially interesting prey in these studies. The defences of ants (Blum, 1981; Holldobler & Wilson, 1990), including powerful mandibles, poison-injecting stings and formic acid sprays, may present formidable challenges to most salticid species. Although most salticids probably avoid ants (Richman & Jackson, 1992), ants are routine prey for a sizeable minority, the 'myrmecophagic salticids' (Li & Jackson, 1996). The special challenges ants present to salticids suggest that details about myrmecophagic salticids should be especially useful for clarifying the characteristics inherent in being a specialized predator.

Using three types of laboratory experiments (Jackson & van Olphen, 1991, 1992; Li, Jackson & Cutler, 1996; Jackson *et al*., 1998; Li, Jackson & Harland, 1999; Jackson & Li, 2001), consistent choice of ants instead of non-ant prey has been shown for species from nine genera of myrmecophagic salticids: *Aelurillus*, *Chalcotropis*, *Chrysilla*, *Corythalia*, *Habrocestum*, *Natta* (formerly *Cyllobelus*), *Siler*, *Xenocytaea* (formerly *Euophrys*)

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Table 1. Arthropods used in the laboratory as living prey and motionless lures

Description	Order	Family	Species	Body size (mm)	Origin
Ant worker	Hymenoptera	Formicidae	*Cataglyphis aenescens* Nylander	4–6	Azerbaijan
Ant worker	Hymenoptera	Formicidae	*Monomorium antarctica* (White)	3–4	New Zealand
Ant worker	Hymenoptera	Formicidae	*Messor denticulatus* Lepeletier	6	Azerbaijan
Caterpillar	Lepidoptera	Pyralidae	*Cnaphalocrosis medinalis* Guenee	6	Laboratory culture
Mosquito	Diptera	Culicidae	*Culex quinquefasciatus* Say	4–6	Kenya
Vinegar fly	Diptera	Drosophilidae	*Drosophila melanogaster* Meigen	3	Laboratory culture
Aphid	Hemiptera	Aphidae	*Macrosiphum euphorbiae* (C. Thomas)	3	New Zealand
Spider	Araneae	Philodromidae	*Thanatus fabricii* (Audouin)	3	Azerbaijan

and *Zenodorus* (formerly *Pystira*) (Edwards, Caroll & Whitcomb, 1974; Cutler, 1980; Jackson & van Olphen, 1991, 1992; Li, Jackson & Cutler, 1996; Jackson *et al*., 1998; Li, Jackson & Harland, 1999; Jackson & Li, 2001). Little quantitative information, however, is available concerning the prey of myrmecophagic salticids in nature. The primary exception is Wing's (1983) data for *Tutelina similis* Banks, a myrmecophagic salticid from North America. He summarized 43 sightings of this species feeding in the field. Each of these 43 individuals was feeding on an ant worker. These data are an ambiguous indication of this species' natural diet, however, because Wing (1983) introduced ants into the study site as part of his research procedure.

Here a previously unstudied myrmecophagic salticid, *Aelurillus muganicus* Dunin, is considered. This species is known only from Azerbaijan (Azarkina, 2002) and its typical habitats (cultivated areas, stands of pine trees on sandy hills and the bottom of dry ponds) seem to make it especially suitable for a study aimed at clarifying natural diet because, with vegetation being sparse in these habitats, it is feasible to locate active individuals by sight when walking slowly through the study site. Our objective in this paper is to provide data on diet from the field in conjunction with data from laboratory prey-choice experiments, and then to consider how these two types of data relate to each other.

METHODS

Surveys in the field

All surveys were near Baku in the Apsheron Peninsula (40.3°N, 49.8°E). The primary field site was at Bailov Hill, but there were 2 secondary sites, 1 near Bina and the other near Yeni-Surakhany. Bailov Hill was an open sandy area with a sparse covering of dwarf shrubs and low ephemeral grasses. Except for being more thickly vegetated, the Bina and Yeni-Surakhany sites were similar to Bailov Hill.

Adults of *Aelurillus muganicus* Dunin are common from April to June, and all surveys were carried out during these months. A total of 37 surveys (totalling *c*. 50 h) was carried out during 4 successive years (4 in 1997, 12 in 1998, 17 in 1999, 4 in 2000). All surveys were carried out between 12:00 and 17:00.

The ground surface was thoroughly searched during each survey. Whenever an individual of *A. muganicus* was found, it was placed in a transparent glass vial and then checked for prey by inspecting its mouthparts with a magnifying lens. The prey of any individual seen feeding was placed in a separate vial containing ethanol and taken to the laboratory for identification. All individuals of *A. muganicus* were released near the collecting site.

General methods for laboratory work

Maintenance procedures, cage design, basic testing methods and terminology were as in earlier salticid studies (Jackson & Hallas, 1986; Jackson & van Olphen, 1991) and included the convention that 'usually', 'sometimes', and 'rarely' indicate frequencies of occurrence of > 80%, 20–80% and < 20%, respectively. Description of predatory behaviour was based primarily on staging *c*. 600 encounters of *A. muganicus* with 3 types of prey (*c*. 200 each with *Monomorium antarctica*, *Drosophila melanogaster* and *Macrosiphum euphorbiae*), although a few encounters were staged with other prey. A variety of insect prey was used for rearing spiders, but the spiders used in preference tests had no prior experience with the ants or with the other prey types used in these tests (see Table 1).

Testing methods when using living prey

Tests were carried out using methods that have been described in detail elsewhere (Li, Jackson & Cutler, 1996). For all tests, an ant was paired with another prey because our objective was specifically to determine whether individuals of *A. muganicus* had a preference for ants. Hunger levels were always standardized by keeping each individual of *A. muganicus* without prey for 7 days before testing.

A test began when an individual of *A. muganicus* ('test spider') was introduced through a cork hole into a plastic cage already containing prey. The test ended when the test spider captured prey or 15 min elapsed, whichever came first. If the test spider was in the act of pursuing a prey individual when the 15-min period elapsed, however, observations continued until the end of the predatory sequence. Only adult females of *A. muganicus* were used.

No individual prey and no individual test spider was used more than once. The body length of the prey individual used in any given test was always about half of the body length of the individual of *A. muganicus* used as a test spider. The ant and the other prey used in any given test were, to the nearest mm, always of matching length.

Two kinds of testing, alternate-day and simultaneous-presentation, were carried out. In alternate-days testing, each test spider had access to 1 type of prey on 1 day and to the other type of prey on the following day. Half of the test spiders (group 1) were tested first with ants. The other half of the test spiders (group 2) were tested first with the other prey type. Test spiders were assigned to the 2 groups at random. In simultaneous-presentation testing, 1 ant and 1 other prey were put into the cage at the same time. The test ended when the test spider attacked 1 of the 2 prey individuals.

Testing methods when using motionless lures

Adopting methods from earlier studies (see Li, Jackson & Cutler, 1996), simultaneous-presentation tests were carried out using a Y-shaped ramp. A piece of brown wood glued to the top of each arm served as a background ('wall') against which the test spider saw a lure, with the lure centred on the horizontal ramp arm 10 mm from in front of the wall. The lure was made by using carbon dioxide to immobilize a prey individual, placing it in ethanol for 60 min, mounting it on the centre of one side of a disc-shaped piece of cork (diameter of the cork disc *c*. 1.25 times the body length of the prey) and then spraying it with an aerosol plastic adhesive for preservation.

Before testing began, the spider was kept until quiescent in a covered pit near the lower end of the ramp. Testing began by removing the cover, and testing was aborted whenever the spider failed to come out of the pit within 30 min or came out of the pit and then moved off the ramp before reaching the threshold. The threshold was a line just below where the 2 arms of the Y-shaped ramp joined. Successful tests ended when the spider moved past the threshold on an arm and stalked the lure, with the particular lure at the end of the arm on to which the spider walked being recorded as the choice of the spider.

Analysis of prey-choice data

For alternate-day testing, only those test-pairs in which the spider attacked 1 prey type (or stalked 1 type of mount) but not the other provided evidence of prey choice, and these data were analysed using McNemar tests for significance of changes. For simultaneous-presentation testing, a series of tests in which 1 prey type was consistently attacked (or 1 type of mount was consistently stalked) provided evidence of prey choice, and these data were analysed using tests of goodness-of-fit (null hypothesis 50/50).

RESULTS

Prey records from the field

There were 1531 sightings of *A. muganicus* at Bailov Hill, with 60 (3.9%) of these sightings being of individuals that were feeding. At Bina and Yeni-Surakhany, another four feeding individuals of *A. muganicus* were sighted (probably about the same percentage of total sightings as at Bailov Hill, but precise records were not kept at these two sites), making a total of 64 feeding records from the field. The 64 prey belonged to 10 arthropod orders (Fig. 1, Table 2), seven from the class

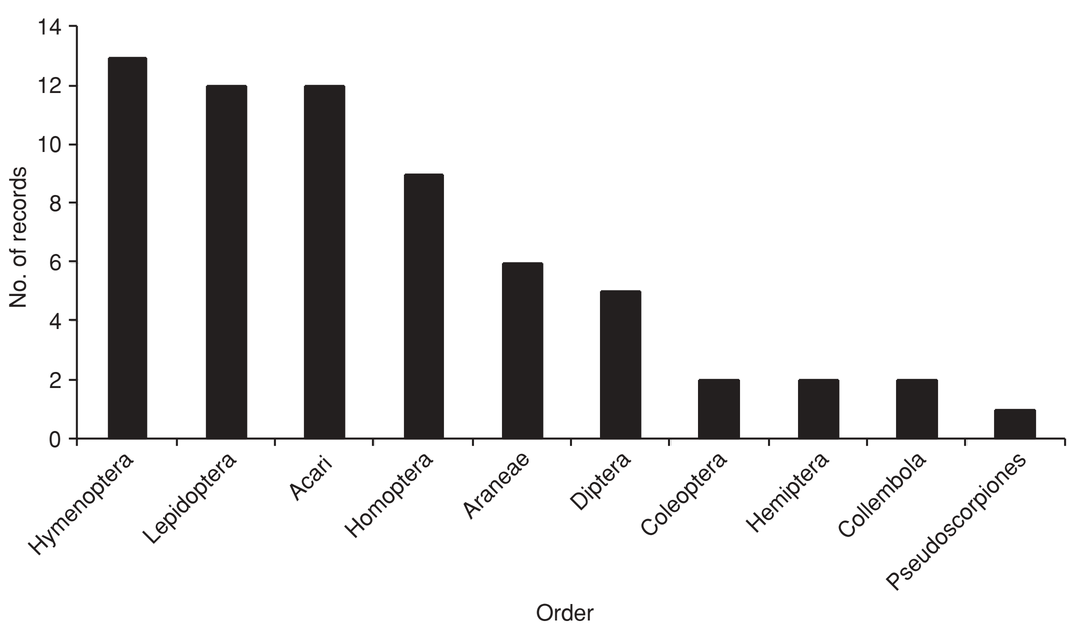

Fig. 1. Prey on which individuals of *Aelurillus muganicus* were seen feeding in the field.

Table 2. Records of prey *Aelurillus muganicus* was seen feeding on in the field

Order	Suborder or family	Species	No.
Hymenoptera[a]	Formicidae	*Cataglyphis aenescens*	3
		Messor denticulatus	2
		Leptothorax sp.	3
		Pheidole sp.	1
		Diploroptrum sp.	2
	Bethyloidea	Unidentified	1
	Chalcidoidea	Unidentified	1
Lepidoptera[a]		Unidentified moth	1
		Unidentified larvae	11
Homoptera[a]	Cicadinea	Unidentified	5
	Aphidinea	Unidentified	3
	Coccinea	Unidentified	1
Diptera[a]	Bombyliidae	Unidentified	1
	Cecidomiidae	Unidentified	3
	Chironomidae	Unidentified	1
Coleoptera[a]	Anthribidae	Unidentified	1
	Unknown	Unidentified	1
Heteroptera[a]	Miridae	Unidentified	1
	Unknown	Unidentified	1
Collembola[a]	Unknown	Unidentified	2
Acari[b]	Unknown	Unidentified	12
Araneae[b]	Philodromidae	*Thanatus* sp.	2
	Thomisidae	*Xysticus* sp.	2
	Gnaphosidae	*Nomisia ripariensis*	1
	Oecobiidae	*Thalamia maculata*	1
Pseudoscorpiones[b]	Olpiidae	*Calocheiridius nataliae*	1

[a] Insecta.
[b] Arachnida.

Insecta (Coleoptera, Collembola, Diptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera) and three from the class Arachnida (Acari, Araneae, Pseudoscorpiones). Collectively, four orders accounted for > 70% of the prey records: Hymenoptera (20.3%), Lepidoptera (18.8%), Acari (18.8%) and Homoptera (14.1%). No other arthropod order accounted for > 10% of the prey records. Of the 45 recorded prey organisms that were insects, 11 were ants (order Hymenoptera, family Formicidae). Two of the ants were winged reproductive females (*Diploroptrum* sp., 2), but the other nine were workers (*Cataglyphis aenescens* Nylander, 3; *Leptothorax* sp., 3; *Messor denticulatus* Lepeletier, 2; and *Pheidole* sp., 1). Hymenopteran prey also included two wasps that could not be identified beyond superfamily (one from the superfamily Bethyloidea and the other from the superfamily Chalcidoidea).

One of the lepidopterans was an unidentified adult moth, and the remainder (11) were unidentified caterpillars. Homopterans were identified to suborder: Cicadinea, 5; Aphidinea, 3; Coccinea, 1. One of the dipterans was a bombyliid. The remainder (4) were nematocerans (families Chironomidae, 1 & Cecidomyidae, 3). There were two beetles (Coleoptera), one unidentified anthribiid and the other not being identifiable to family. There were two true bugs (Heteroptera), one being a mirid and the other not being identifiable to family. There were also two unidentified springtails (Collembola).

Among the arachnids, there were 12 unidentified mites (order Acari). Another arachnid was a pseudoscorpion (order Pseudoscorpiones), *Calocheiridius nataliae* Dashdamirov (family Olpiidae). All of the spiders (order Araneae) were identified at least to genus: two juveniles of *Thanatus fabricii* (Audouin) (Philodromidae), two juveniles of *Xysticus* sp. (Thomisidae), an adult male of *Nomisia ripariensis* (O.P.-Cambridge) (Gnaphosidae) and an adult male of *Thalamia maculata* Simon (Oecobiidae).

Routine behaviour

In the absence of prey, *A. muganicus* usually walked in a rapid stop-and-go gait (step for 0.5 s, pause for 0.5 s, etc.), waving its palps up and down while stepping and during pauses between steps. All leg tarsi stayed on the ground except when stepping. When *A. muganicus* encountered prey, it used one of two prey-capture methods (see below).

Methods used to capture ants

Aelurillus muganicus usually ignored or avoided ants *Monomorium antarctica* for at least several seconds, and sometimes for some minutes, before becoming 'suddenly activated' (i.e. after a period of passively ignoring an ant, avoiding it or simply watching it, the spider suddenly switched to active pursuit without any obvious prelude). *Aelurillus muganicus* usually avoided ants that were moving rapidly, however, and was slow to respond to inactive ants. If *A. muganicus* became suddenly activated at all, this was generally within the first 5 min of a test. Once activated, *A. muganicus* almost always attacked and ate the ant.

In a typical ant-capture sequence, *A. muganicus* moved rapidly in spurts to get head on with the ant and then lunged or made a short leap on to the ant from about a body length away. At the end of the lunge or leap, *A. muganicus* usually stabbed the ant, released it immediately, stabbed it again and so forth until eventually it held on.

If the ant was stationary or moving especially slowly, however, *A. muganicus* often approached it by moving more slowly than during normal locomotion. Slow moving or stationary ants were usually attacked head on.

Methods used to capture prey other than ants

Sudden activation was not routine when the prey *A. muganicus* encountered was not an ant. Predatory sequences usually began with *A. muganicus* repeatedly orienting briefly towards the prey before approaching. *Aelurillus muganicus* occasionally approached more or less directly and, when close, leapt with or without a preceding pause. Stalk-and-leap sequences were more usual, however (i.e. *A. muganicus* usually approached slowly with its body lowered, paused when close, fastened a dragline and then leapt on to the prey). Similar sequences have been described for other salticids (Forster, 1977, 1982). *Aelurillus muganicus* only rarely attacked by lunging instead of leaping, and leaps were rarely from more than a body length away. *Aelurillus muganicus* seemed to make no effort to orient attacks on prey other than ants in any particular direction (i.e. attacks from the side, in front and behind were all about equally common when preying on insects other than ants).

Findings from prey-choice testing

Aelurillus muganicus attacked ants more often (Figs 2 & 3) than other prey during alternate-day (vinegar fly *Drosophila melanogaster*, $\chi^2 = 12.448$, $P < 0.001$; aphid *Macrosiphum euphorbiae*, $\chi^2 = 10.667$, $P < 0.001$) and simultaneous-presentation (*D. melanogaster*, $\chi^2 = 7.143$, $P < 0.001$; *M. euphorbiae*, $\chi^2 = 7.364$, $P < 0.001$) testing with living prey. *Aelurillus muganicus* always ate the living prey it attacked. When tested with lures (Fig. 4), *A. muganicus* chose the lure made from an ant more often than a lure made from non-ant prey regardless of whether the ant was *Messor denticulatus* (Fig. 4a: caterpillar *Cnaphalocrosis medinalis*, $\chi^2 = 8.067$, $P < 0.001$; mosquito *Culex quinquefasciatus*, $\chi^2 = 11.267$, $P < 0.001$),

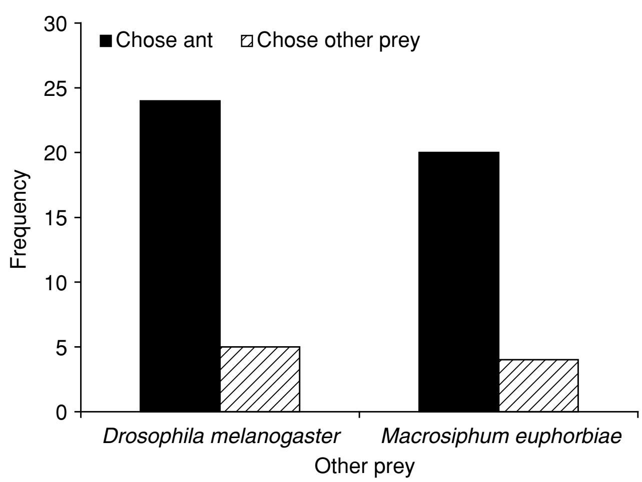

Fig. 2. Findings from simultaneous-presentation testing of *Aelurillus muganicus*. Living prey. Ant: *Monomorium antarctica*. Chose ants more often than chose other prey.

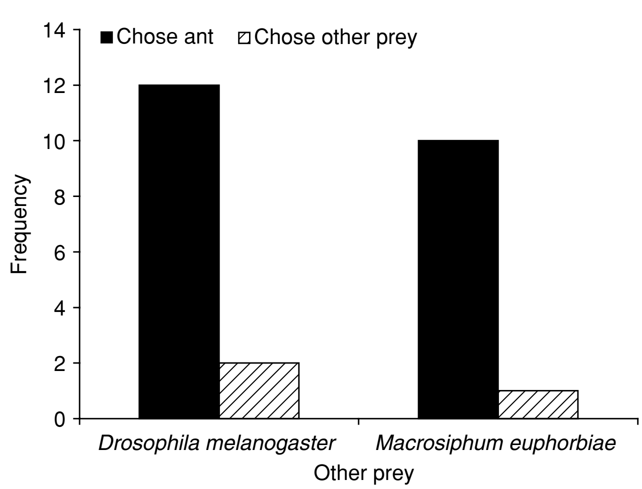

Fig. 3. Findings from alternate-day testing of *Aelurillus muganicus*. Living prey. Ant: *Monomorium antarctica*. Chose ants more often than chose other prey.

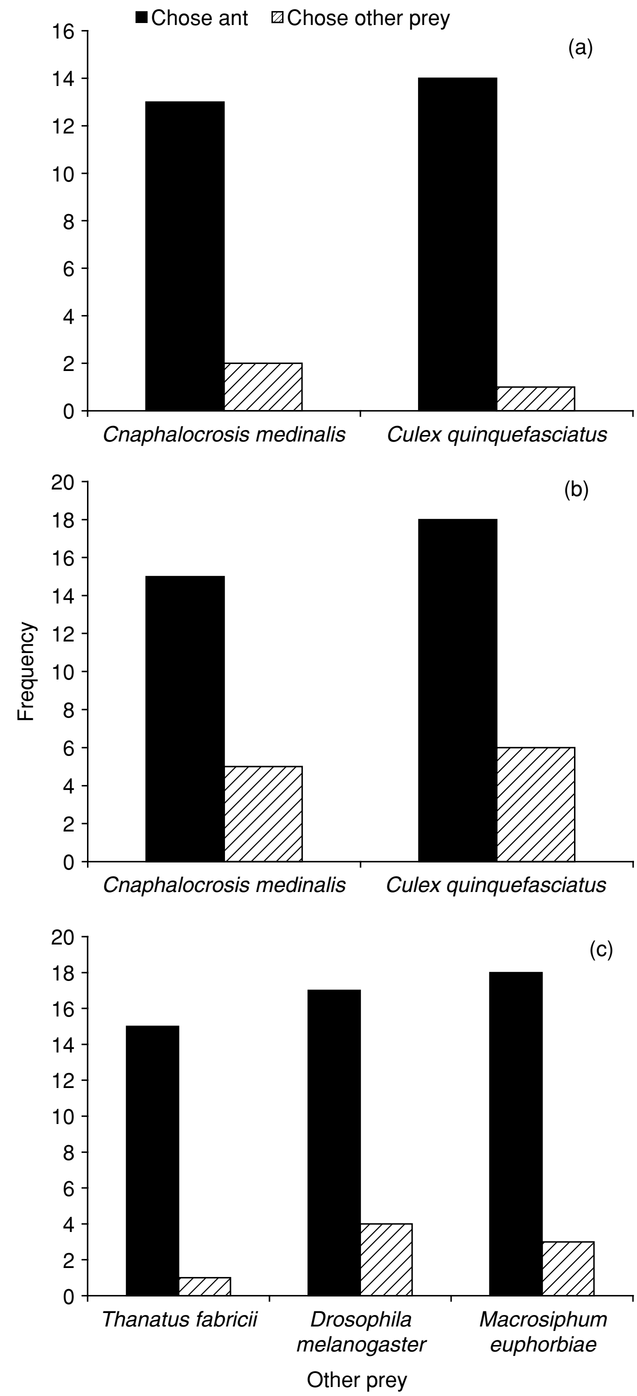

Fig. 4. Findings from simultaneous-presentation testing of *Aelurillus muganicus*. Motionless lures. Ants: *Messor denticulatus* (a), *Cataglyphis aenescens* (b), *Monomorium antarctica* (c). Chose lures made from ants more often than lures made from other prey.

Cataglyphis aenescens (Fig. 4b: *Cnaphalocrosis medinalis*, $\chi^2 = 5.000$, $P < 0.001$; *C. quinquefasciatus*, $\chi^2 = 6.000$, $P < 0.001$) or *Monomorium antarctica* (Fig. 4c: spider *Thanatus fabricii*, $\chi^2 = 12.250$, $P < 0.001$; *D. melanogaster*, $\chi^2 = 8.048$, $P < 0.001$; *M. euphorbiae*, $\chi^2 = 10.714$, $P < 0.001$).

DISCUSSION

Besides this study, the most extensive published data on salticid diet in the field have come from *Cyrba algerina* (Lucas), *Evarcha culicivora* Wesolowska & Jackson, *Menemerus semilimbatus* (Hahn), *Metaphidippus galathea* (Walckenaer), *Phidippus audax* (Hentz), *Paracyrba wanlessi* Zabka & Kovac, *Phidippus johnsoni* (Peckham et Peckham), *Portia fimbriata* (Doleschall), *Salticus austinensis* Gertsch and *Yllenus arenarius* Menge (Jackson, 1977; Jackson & Blest, 1982; Dean *et al*., 1987; Horner, Stangl & Fuller, 1988; Young, 1989; Zabka & Kovac, 1996; Clark & Jackson, 2000; Bartos, 2002; Wesolowska & Jackson, 2003; Guseinov, 2004; Guseinov, Cerveira & Jackson, 2004), none of which are ant specialists. As with *A. muganicus*, most individuals of these species were not feeding when sighted in nature. Because our total number of sightings of *A. muganicus* was large (1531), however, we have 64 prey records. These 64 records suggest that *A. muganicus* normally feeds on a wide variety of arthropods.

By family, ants (family Formicidae) accounted for the largest percentage (20%) recorded for any one type of prey. This is a striking finding because ants are unusual prey for a salticid (Richman & Jackson, 1992). Yet 80% of the prey of this salticid was not ants. In order to call this species an 'ant specialist', the precise way in which it is specialized needs to be considered. The term 'ant specialist' on its own is ambiguous.

When the behavioural attributes are considered, there is a stronger justification for characterizing this salticid as an 'ant specialist'. *Aelurillus muganicus* adopts ant-specific prey-capture behaviour similar to that of three previously studied species of *Aelurillus* (Li, Jackson & Harland, 1999), and a strong preference for ants as prey is implied by the findings from prey-choice experiments. Moreover, the ant-specific prey-capture behaviour of *A. muganicus* and its preference for ants both seem to be innate because the individuals used in the laboratory study had no prior experience with ants.

Aelurillus muganicus seems to be a particularly striking illustration of the distinctions between diet, choice and preference. Contrary to much of the ecological literature (e.g. Manly, 1974; Morgan & Brown, 1996; Lockwood, 1998), preference is usefully defined as a cognitive attribute that cannot, in principle, be determined simply from recording a predator's diet or from how its diet might deviate from the relative availability of different types of prey. Preference is revealed instead by the behaviour of the predator in prey-choice experiments. Evidently, *A. muganicus* has a strong preference for ants as prey, with the strength of this preference not being evident from the percentage of feeding individuals of *A. muganicus* for which the prey was an ant.

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