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The predatory strategy, natural diet, and life cycle of *Cyrba algerina*, an araneophagic jumping spider (Salticidae: Spartaeinae) from Azerbaijan

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Abstract The life cycle and natural diet of *Cyrba algerina* (Lucas) in the Apsheron Peninsula (Azerbaijan) was determined by sampling at frequent intervals throughout the year. Early-instar juveniles emerged in late July, grew to about half of adult size by winter, over-wintered and then, in the spring of the following year, grew to adult size and reached maturity. The primary mating season was in May, after which the number of adults in the population declined sharply. Ten arthropod orders were represented in the prey records from nature. Six of these were insects and four were arachnids. Spiders (order Araneae) were the dominant prey, accounting for 56% of the records. Half of these spiders were from one family, Oecobiidae. In laboratory prey-choice tests, *C. algerina* selected spiders in preference to insects and selected oecobiids in preference to other spiders. Video taping under infrared light confirmed that the Azerbaijan *C. algerina* captures prey in complete darkness.

Keywords spider; Salticidae; Spartaeinae; *Cyrba*; predation; Oecobiidae

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INTRODUCTION

Jumping spiders (Salticidae) have unique, complex eyes (Land 1969a,b; Blest et al. 1990), exceptionally acute vision (Land & Nilsson 2002), and intricate vision-guided predatory behaviour (Jackson & Pollard 1996). Most species in this large family of about 5000 described species (Platnick 2002) appear to be active hunters that prey primarily on insects (Richman & Jackson 1992), but some of the species in the subfamily Spartaeinae (Wanless 1984) are web-invading araneophagic predators (Jackson & Pollard 1996).

The literature on spartaeines is biased toward species from one genus, *Portia*, and from a particular kind of habitat, tropical rainforest. We redress this imbalance by investigating *Cyrba algerina* (Lucas), a spartaeine from a semi-desert habitat in Azerbaijan. This is the first detailed study of the biology of any salticid from Azerbaijan and the most extensive field-based study to date on any spartaeine. Our field data clarify this species' life cycle and natural diet. Typical predatory sequences are described and prey-preference hypotheses, suggested by the field data, are investigated in laboratory-based experiments. Our findings suggest that, besides being able to detect and identify prey by sight alone, the Azerbaijan *C. algerina* readily captures prey in the absence of light.

SURVEYS IN THE FIELD

Materials and methods

Cyrba algerina is a medium-size salticid (adult body length 6–7 mm), with adult males usually being slightly smaller than adult females. Juveniles and adult females are dull grey, whereas adult males are more richly coloured, having an orange cephalothorax and contrasting white patterns on a black abdomen.

The habitat in the Azerbaijan was an ephemeral semi-desert. Except for being drier, this habitat has general similarities to chaparral habitats of *C. algerina* in France, Spain, Portugal, and Israel (Legendre & Llinares 1970; Jackson 1990a; Jackson & Li 1998). Two primary study sites were chosen in the Apsheron Peninsula: 1) Bailov Park, situated on the south slope of Bailov Hill in Baku city; 2) Shagan Village, 25 km east of Baku. Pine trees, *Pinus eldaricus* (Medw.) (typical height 3–5 m), and short ephemeral grasses were the dominant vegetation at both sites. The most common grasses were *Calendula persica* (C.A.M.), *Senecio vernalis* (W. & K.), *Medicago denticulata* (W.), *Carduus arabicus* (Jaqu.), *Hirschfeldia incana* (L.), *Erodium cicutarium* (L.), *Hedypnois cretica* (W.), *Pterotheca marschalliana* (Rchb.), *Torularia contortuplicata* (Stapf.), *Ornithogalum gossonei* (Ten.), *Gagea tenuifolia* (Boiss.), *Poa bulbosa* (L.), *Anisanthea rubens* (L.), *Aegilops biuncialis* (Vis.), *Hordeum leporinum* (Link.), *Koeleria phleoides* (Vill.), *Bromopsis* sp. There were two secondary sites, one near Gala Village in the Apsheron Peninsula (15 km east of Baku) and the other on Boyuk-dash Hill in Gobustan (60 km south-west of Baku). The secondary sites were treeless, but had grass cover similar to that of the primary study sites. Stones were prevalent on the ground at all four sites, and *C. algerina* was especially common under these stones.

Field sampling ("surveys") began in the autumn of 1997, with one survey in September and two in November. After March 1998, 19 regular surveys were carried out once every 5 days between the beginning of March and the middle of June; 16 surveys were carried out once a week, between the beginning of August and the end of November; and another 24 were carried out every third day, between the beginning of March and the end of May 1999. There was an additional survey in late September 1999 and three more in April 2000. Total sampling time was about 90 h for the 66 surveys. All surveys were made in daylight hours (0900–1800 h), with 80% being between 1100 and 1600 h.

Surveys were made by overturning each stone encountered and taking every individual of *C. algerina* that was found into a glass vial. Using a magnifying lens, we immediately inspected the spider's mouthparts. Any individual found holding prey in its chelicerae was placed with the prey in a separate vial containing ethanol and then taken to the laboratory for measurement and for prey identification. Other individuals were released near the point of first sighting, after determining age and sex. Four age-sex categories were recognised: 1) small juvenile (<3 mm in body length); 2) subadult male (juvenile, >3 mm in body length, with enlarged pedipalp tips); 3) adult male (bright coloration made adult males readily distinguishable from subadult males; hereafter, the shorter expression "male" will be used specifically for adult males); 4) female (any specimen larger than 3 mm in body length, but without enlarged pedipalp tips). Distinguishing subadult from adult females in the field would have required closer examination of the spider's anterior ventral abdomen for the presence of an epigynum, which proved impracticable because field-collected individuals tended to be very active.

Results and discussion

Nests and egg sacs

Cyrba algerina was found occupying two types of nests. "Sparse nests" were small, flimsy silk sheets (more or less transparent). "Dense nests" were heavier silk sheets (translucent, if not opaque). Both types of nests were typically spun over slight concavities on the undersides of stones. Most individuals were found inside dense nests during the winter months. During the rest of the year, sparse nests were often found under the same stones, but *C. algerina* was only rarely found inside these nests. Sparse nests are known for all previously studied populations (Jackson 1990a; Jackson & Li 1998), but dense nests have never been encountered before.

In the laboratory, only adult females built dense nests, sometimes spending a week or longer at a time inside these nests. Both sexes and all instars of *C. algerina* built sparse nests and used them as night-time shelters. Spiders left their sparse nests during the day and then either returned to the same nest or built a new one each evening.

Although *C. algerina* from other localities are known to oviposit in small crevices under stones (Jackson 1990a), no egg sacs were found in similar sites or anywhere else during our field study. If stone surfaces in Azerbaijan get too hot, *C. algerina* may use other oviposition sites that we did not find. In the laboratory, however, the egg sacs resembled those of *C. algerina* from other localities: two layers of silk, of which the outer layer is thin and has characteristic clusters of white spots embedded in structural silk (Jackson 1990a; Jackson & Li 1998).

Life cycle

Active juveniles began to appear outside nests by early spring (March and April). Mature individuals of both sexes were common by the end of April, and remained common until the end of May. May ap-

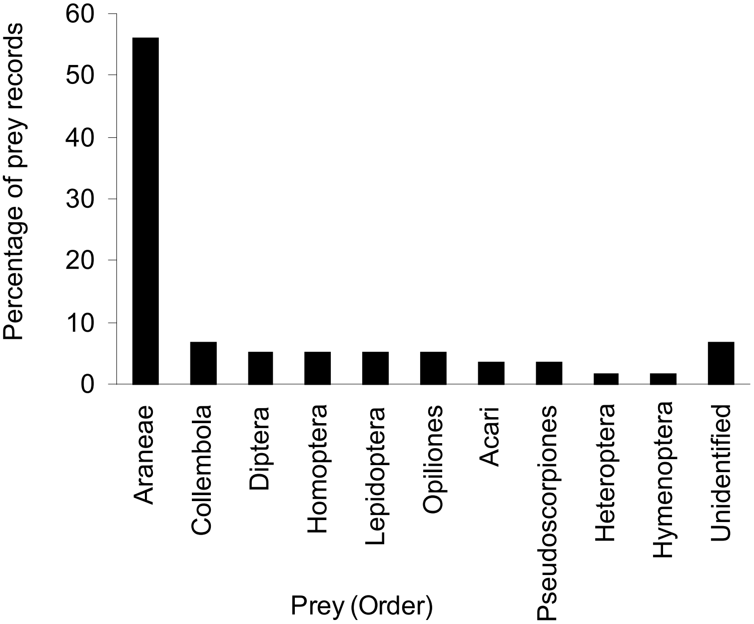

Fig. 1 Prey on which *Cyrba algerina* was seen feeding in the field in Azerbaijan. *N* = 59.

peared to be the primary mating season, after which there was a decline in the number of females, and an especially sharp decline in the number of males. Small juveniles appeared in late July and continued to feed, moult and grow until late autumn. However, only quiescent individuals (usually inside dense nests) were found in winter.

Prey records from the field

We recorded a total of 2223 sightings of *C. algerina* in the field, but *C. algerina* had prey in its chelicerae in only 59 (2.7%) of these sightings. All prey were arthropods, with spiders (order Araneae) being the most common prey, accounting for 56% of the records (Fig. 1; Appendix 1). No other arthropod order accounted for more than one-tenth of the prey records.

Five of the spiders on which *C. algerina* was found feeding in the field could not be identified to family level. Half (14 of 28) of the identified spiders belonged to one species, *Oecobius maculatus* Simon (Oecobiidae). Of the remaining 14 identified spiders, seven were more or less typical hunting (cursorial) spiders (Gnaphosidae, 2; Lycosidae, 2; Oonopidae, 1; Salticidae, 1; Zodariidae, 1). The other seven were more or less typical web-building spiders (Dictynidae, 3; Linyphiidae, 2; Theridiidae, 1; Titanoecidae, 1).

Whether *O. maculatus* is a web builder or a hunter may be debatable, but on the whole "hunting spider" appears to be the more accurate expression. Oecobiids typically build silken sheets under stones or on the walls of buildings, and there is no evidence that these silk sheets function as prey-capture devices (Glatz 1967). Moreover, individuals of *O. maculatus* in Azerbaijan were often observed away from their silken sheets.

Insects from six orders accounted for about a quarter of *C. algerina*'s identifiable prey in nature (Fig. 1): springtails (Collembola); aphids (Homoptera: Aphididae); leafhoppers (Homoptera: Cicadellidae); true-bug nymphs (Heteroptera); midges (Diptera: Cecydomiidae); flies (Diptera: Brachycera); moths and caterpillars (Lepidoptera); and ant eggs (Hymenoptera: Formicidae). We characterise these insects as "safe prey" because they are soft bodied and have limited ability to defend themselves once attacked. Comparable safe prey dominate the diets of many other salticids (Jackson 1977; Richman & Whitcomb 1981; Dean et al. 1987; Horner et al. 1988; Young 1989; Bartos 2002), suggesting that the Azerbaijan *C. algerina* is a spartaeine that frequently turns to typical salticid prey to supplement a primarily araneophagic diet.

The remaining identifiable prey (12% of the total) were arachnids other than spiders: harvestmen

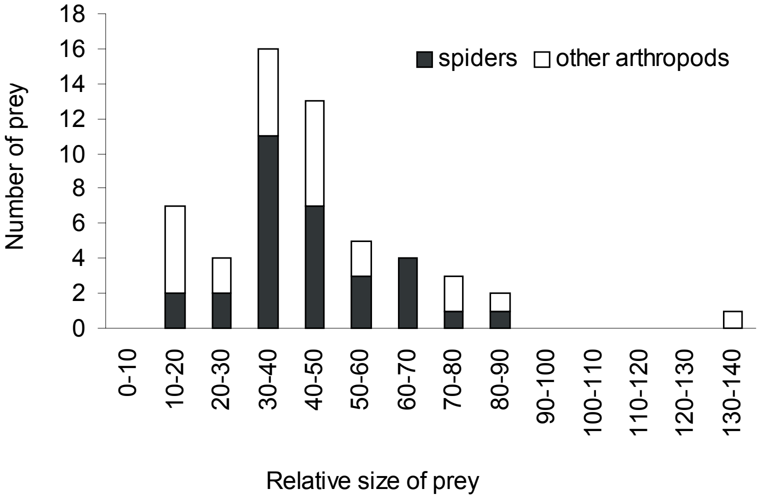

Fig. 2 Relative size of prey on which *Cyrba algerina* was seen feeding in the field in Azerbaijan. Relative size: prey body length divided by predator body length ×100. *N* = 55.

(Opiliones: Phalangiidae), pseudoscorpions (Pseudoscorpiones: Olpiidae) and mites (Acari) (Fig. 1). Records of salticids eating arachnids other than spiders are scarce. Besides our data on *C. algerina*, we know of only two other reports: *Phidippus johnsoni* (Peckham & Peckham) feeding on two harvestmen (Jackson 1977) and *Phidippus rimator* (Walckenaer) feeding on a tick (Ault & Elliott 1979).

Prey size

Absolute prey length varied from 0.6 to 6.3 mm (mean ± SD: 2.1 ± 1.2 mm) and prey length relative to the predator length varied from 11 to 136% (mean ± SD: 44 ± 22%) (Fig. 2). Small arthropods (definition: body length not exceeding half the body length of the predator) were the most abundant prey category (73% of total prey) and medium-sized prey (prey with body length 50–100% of the predator's body length) accounted for 25% of records. There was only one instance of *C. algerina* feeding on a large prey item (i.e., prey's body length larger than predator's) (2% of the prey records). Although large, this prey (a moth) was probably not dangerous to the salticid. These findings suggest that *C. algerina* prefers prey considerably smaller than itself.

Web invasion

Even though *C. algerina* was found feeding on web-building spiders in the field, *C. algerina* was never found eating in a web. Perhaps *C. algerina* captured some or all of these web builders away from their webs. Alternatively *C. algerina* may have captured web builders while in or at the edges of their webs and then moved away from the webs to feed. In typical encounters with web-building spiders in the laboratory, the behaviour of the Azerbaijan *C. algerina* resembled that of all species and populations of *Cyrba* that have been studied (Jackson & Hallas 1986b; Jackson 1990a; Jackson 2002). *Cyrba* moved slowly onto the edge of web, but placed only its forelegs on the silk. With its rear legs firmly on the non-silk substrate at the web edge, *Cyrba* reached out and, by moving its palps on the silk, made signals. These signals sometimes lured the spider to the edge of the web. When the spider got close, *Cyrba* lunged out and captured it. *Cyrba* often moved away from the web to feed. Web-edge prey capture and away-from-the-web feeding appear to be part of a genus-wide strategy for *Cyrba*. However, in the field, *Cyrba algerina*, *C. ocellata* (Kroneberg), and *C. simoni* (Wijesinghe) from Portugal, Spain, Israel, Kenya, and Sri Lanka have all been seen feeding within the webs of other spiders (Jackson unpubl.), suggesting that away-from-the-web feeding is more strongly developed in the Azerbaijan *C. algerina*.

Only one instance of web invasion by *C. algerina* was actually witnessed in Azerbaijan. While walking about on the outside wall of a building, a juvenile of *C. algerina* repeatedly approached the funnel webs of *Filistata insidiatrix* (Forskal) (Filistatidae). These webs were common in crevices, with the outer edges typically extending 20–30 mm beyond the crevice on to the surrounding wall surface. The juvenile *C. algerina* only rarely went into the funnels, but it repeatedly walked on to the outer silk edges of these webs.

ENCOUNTERS WITH OECOBIIDS

Materials and methods

Test spiders were individuals of *C. algerina* reared from eggs using standard spider-laboratory procedures (Jackson & Hallas 1986a,b). As maintenance, rearing-cage design, terminology, and basic testing methods corresponded to those in the earlier studies, only modifications and critical details are given here. Lights came on in the laboratory at 0800 h (photoperiod 12L:12D), and each test began at 0900 h. The expressions "usually" or "often", "sometimes" or "occasionally", and "rarely" or "infrequently" are used, respectively, for frequencies of 80% or more, 20–80%, and 20% or less.

For a preliminary assessment of how *C. algerina* preys on oecobiids, we staged encounters between *C. algerina* and oecobiids both at and away from the oecobiid's nest. No cultures of living *Oecobius maculatus* were available, so we used cultures of *O. amboseli* Shear & Benoit, started from specimens collected in Kenya. This species builds silk sheets comparable to those of *O. maculatus*. A detailed study of the predatory tactics *C. algerina* uses when the prey is specifically *O. maculatus* is an objective for future research.

About 1 week before testing, adult *O. amboseli* females were put into petri-dish cages (one per cage, cage diameter 90 mm) and left without prey. During this time, most of the oecobiids built a typical silk nest at the edge of the cage. Testing was initiated by allowing an individual of *C. algerina* to enter a cage with a resident oecobiid. Entry was via a cork hole in the centre of the cage floor (diameter 20 mm). Observation continued until *C. algerina* captured the oecobiid or until 4 h had elapsed. All tests ($N = 400$) began at about 0900 h. About equal numbers were carried out with small juveniles (body length <3 mm, $N = 140$), adult males ($N = 120$), and adult females ($N = 140$) of *C. algerina*. However, data were pooled, as there were no significant differences across the different sex-age classes. Hunger level was standardised by keeping each individual of *C. algerina* without prey for 7 days before testing. No individual of *O. amboseli* or *C. algerina* was used in more than one test.

Results and discussion

During typical predatory sequences (Fig. 3), *C. algerina* walked in the cage, eventually oriented toward the oecobiid's nest, slowly approached until within a few millimetres and then became quiescent. The quiescent phase usually lasted several minutes, after which about half of the *C. algerina* individuals pulled their forelegs back and then, by leaping (i.e., their rear legs left the substrate) or lunging (i.e., their rear legs did not leave the substrate), forcefully contacted the silk. Individuals that did not leap or lunge began walking about near and on the nest, and eventually they probed the nest (i.e., they moved their palps forwards and backwards on the silk as described elsewhere) (Jackson & Hallas 1986b). Soon after *C. algerina* leapt, lunged or probed, about half of the oecobiids fled (i.e., they ran out of their nests). If the oecobiid remained in the nest, *C. algerina* intermittently probed again, but leaping or lunging again was rare. Most oecobiids eventually left the nest on which *C. algerina* continued to probe.

Once out of the nest, about half of the oecobiids were captured by *C. algerina* using one of four tactics. In 16 tests (8%), *C. algerina* chased after, overtook, and captured the fleeing oecobiid. In another 31 tests (15%), *C. algerina* watched the fleeing oecobiid, then stalked and captured it. *Cyrba algerina* lunged and captured the oecobiid as it left the nest in 29 tests (14%). The fourth tactic was the most common: 99 (48%) of the *C. algerina* individuals remained quiescent at the nest and captured the oecobiid when it returned to the nest. This tactic worked because, after a period ranging from a few minutes to more than an hour, oecobiids that fled usually returned to their nests. The waiting *C. algerina* slowly oriented toward the approaching oecobiid and, when the oecobiid got close, *C. algerina* lunged and captured it at the nest's threshold. However, *C. algerina* was not always successful: in ten (5%) tests, *C. algerina* chased after, but failed to capture the fleeing oecobiid; in 11 (5%) tests, *C. algerina* lunged but missed; and in another 12 (6%) tests, the oecobiid failed to return while *C. algerina* waited at the nest.

PREDATION IN THE DARK

Using an infrared light source and an infrared-sensitive video camera, we viewed encounters of *C. algerina* with oecobiids, lycosids, and various web-building spiders in the absence of visible light. Only a brief summary of these observations is provided, and full details of this ongoing work will be reported elsewhere.

While walking, whether in the light or in the dark, *C. algerina* made characteristic sweeping movements (called "swim-waving") with legs I and II (Jackson & Hallas 1986b). While swim-waving in

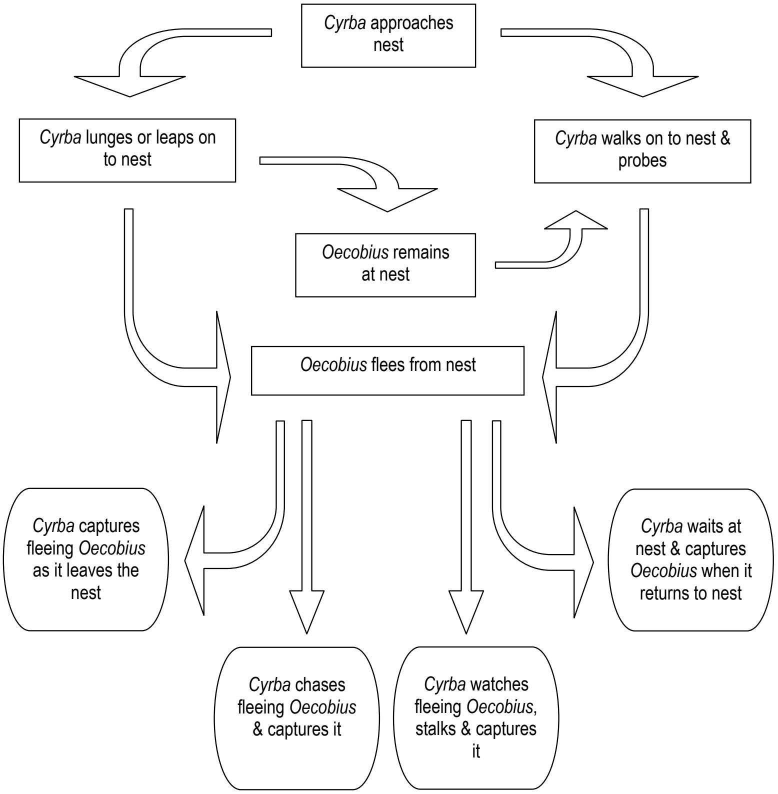

Fig. 3 Typical successful prey-capture sequences following encounters by *Cyrba algerina* with *Oecobius amboseli.*

the dark, sometimes *C. algerina*, with one of its legs, made contact with a prey that was not in a web or nest. When this happened, *C. algerina* usually made a sudden lunge forward and, with its chelicerae, grabbed hold of the prey. When contacting a web while swim waving, *C. algerina* initially became quiescent and then, several minutes later, began probing with its palps and walking slowly on the silk. Sometimes a spider was lured to the edge of the web, where *C. algerina* lunged and captured it.

When *C. algerina* contacted an oecobiid nest while swim waving, it initially became quiescent. Several minutes later, *C. algerina* either probed or lunged at the silk. As during encounters with oecobiids in nests in the light, *C. algerina* sometimes captured oecobiids as they ran out of their nests, but most oecobiids got away. When the oecobiid fled, *C. algerina* waited at the nest and sometimes captured the oecobiid when it returned to the nest.

PREY-CHOICE BEHAVIOUR

Methods

The methods used for making lures (dead prey mounted on cork disks) and for testing preference corresponded to those used in other salticid studies (Li & Jackson 1996; Li et al. 1997; Jackson & Li 1998; Jackson 2000). However, we adopted only one of the feeding regimes (well fed: pre-test fast of only 5 days) from earlier studies. This was because our goal was limited to investigating basic preference, not the stability of preference under fasting.

In a series of tests, we investigated *C. algerina*'s choice between spiders and insects and between oecobiids and other spiders. Two types of prey-choice testing were carried out: alternate-day (one prey presented at a time, on two successive days) and simultaneous-presentation (two prey presented at the same time). However, when living spiders are used as prey, simultaneous-presentation testing introduces a potential problem: one of the prey may eat the other prey before *C. algerina* makes a choice. We avoided this problem by doing all simultaneous-presentation testing with lures. For alternate-day testing we used living prey and lures. Only juveniles of *C. algerina* were used as test spiders (body length 4–6 mm). The body length of the test spider was always about twice that of the prey.

Alternate-day testing for prey preference using living prey

Each test was carried out in a petri dish-cage (diameter 90 mm). Testing began when *C. algerina* entered the cage and ended when either *C. algerina* attacked a prey or 15 min elapsed, whichever came first. However, if *C. algerina* was still stalking a prey when the time limit (15 min) elapsed, observation continued until the predatory sequence ended (Jackson & van Olphen 1991).

Each *C. algerina* individual was used in a pair of tests (given access to one individual of one type of prey on one day and to an individual of another type of prey on the following day): half was tested first with one prey type (Group A) and the other half was tested first with the other prey type (Group B). Individuals of *C. algerina* were assigned to Groups A or B at random.

Only those test-pairs in which the *C. algerina* chose one prey type but not the other provided evidence of preference. Data were analysed using McNemar tests for significance of changes (Sokal & Rohlf 1995). The prey that *C. algerina* attacked was recorded as *C. algerina*'s choice, but analysing data separately for eating the prey, instead of simply attacking the prey, did not alter the stated *P* values. This was because *C. algerina* only rarely failed to eat a prey immediately after attacking it.

Testing for prey preference using motionless lures

A single-arm (linear) and a two-arm (Y-shaped) wooden ramp was used during alternate-day and simultaneous-presentation testing, respectively (Li et al. 1997). The arms were 40 mm wide and angled upwards at 20°. The single arm of the linear ramp was 100 mm long. The two arms (ends of the Y) of the two-arm ramp, and the stem of the Y, were all 50 mm long. Arms ended at a perpendicular wooden wall (55 mm high, 40 mm wide, and 15 mm thick) that held a petri dish. Lures were positioned in the centre of each petri dish.

Prey used as lures (Table 1) were first killed by asphyxiation with CO_2. The dead prey was placed in alcohol for 60 min and then the lure was made by mounting the dead prey in a lifelike posture in the centre of one side of a cork disk (diameter 1–2 times the body length of the prey). For preservation, the prey and cork were sprayed with an aerosol plastic adhesive and then left to dry in the air for 24 h before use. *C. algerina* was never allowed to contact the lures.

The test spider was placed in a covered pit near the lower end of the ramp. Once it became quiescent, the cover was removed and testing began. Successful

Table 1 Spiders and insects used for making lures.

Order and Family	Species	Origin
Araneae, Clubionidae	*Clubiona* sp.[1]	Kenya
Araneae, Eresidae	*Stegodyphus mimosarum*[2]	Kenya
Araneae, Hersiliidae	*Hersilia* sp.[1]	Kenya
Araneae, Heteropodidae	*Olios* sp.[1]	Kenya
Araneae, Lycosidae	Unidentified lycosid[1]	Kenya
Araneae, Oecobiidae	*Oecobius amboseli*[1]	Kenya
Araneae, Palpimanidae	*Palpimanus* sp.[1]	Kenya
Araneae, Philodromidae	*Thanatus* sp.[1]	Azerbaijan
Araneae, Salticidae	*Aelurillus azerbaijanicus*[1]	Azerbaijan
Araneae, Uloboridae	*Zosis geniculatus*[2]	Kenya
Diptera, Psycodidae	*Psychoda* sp.[3]	Kenya
Homoptera, Aphidae	*Brevicayne brassicca*[3]	Kenya
Lepidoptera, Noctuidae	*Busseola fusca*[4]	Kenya

[1]Hunting spider; [2]web spider; [3]adult insect; [4]insect larva.

tests ended when the test spider did one of the following: 1) reached the end of the ramp and contacted the petri dish; 2) walked or leapt off the ramp before reaching the end of the arm; 3) remained on the ramp for 30 min, but failed to contact the petri dish. Result 1, but not 2 and 3, was recorded as an instance of a test spider choosing a particular lure. Tests were aborted if test spiders failed to come out of the pit within 30 min, or if they moved off the ramp before reaching the arm's threshold (a line 40 mm up from the centre of the pit). When a test was aborted, the same individual of *C. algerina* was tested again (up to four times a day), then on subsequent days, until a successful test was completed or 4 days of unsuccessful testing elapsed.

Testing for preferred location of prey

The importance of the presence of a web or nest was investigated in a series of simultaneous-presentation tests. In tests using oecobiids, a lure made from *Oecobius* was positioned in the centre of each dish, facing down. Silk from an oecobiid's nest was positioned over one of the two lures. Other tests were carried out with one lure inside and another outside a web. The particular arm that held the web or nest was decided at random.

Results and discussion

During alternate-day and simultaneous-presentation testing, *C. algerina* chose spiders more often than insects and oecobiids more often than other

Table 2 Results from alternate-day testing of *Cyrba algerina* juveniles with living prey. Prey: two individuals of comparable size, each a different species. NS, not significant.

Prey 1	Prey 2	Chose prey 1 only	Chose prey 2 only	Chose both	McNemar test*
Brevicayne brassicca[2]	*Busseola fusca*[2]	9	10	20	NS
Brevicayne brassicca[2]	*Psychoda* sp.[2]	13	8	19	NS
Busseola fusca[2]	*Psychoda* sp.[2]	12	9	19	NS
Hersilia sp.[1]	*Brevicayne brassicca*[2]	22	1	29	$x^2 = 19.17$, $P < 0.001$
Hersilia sp.[1]	*Psychoda* sp.[2]	20	2	12	$x^2 = 14.73$, $P < 0.001$
Lycosid[1]	*Brevicayne brassicca*[2]	26	3	19	$x^2 = 18.24$, $P < 0.001$
Lycosid[1]	*Hersilia* sp.[1]	20	18	24	NS
Lycosid[1]	*Psychoda* sp.[2]	16	0	4	$x^2 = 16.00$, $P < 0.001$
Oecobius amboseli[1]	*Brevicayne brassicca*[2]	21	1	14	$x^2 = 18.18$, $P < 0.001$
Oecobius amboseli[1]	*Busseola fusca*[2]	25	3	7	$x^2 = 17.29$, $P < 0.001$
Oecobius amboseli[1]	*Hersilia* sp.[1]	35	13	25	$x^2 = 10.08$, $P < 0.01$
Oecobius amboseli[1]	Lycosid[1]	29	10	30	$x^2 = 9.26$, $P < 0.01$
Oecobius amboseli[1]	*Psychoda* sp.[2]	28	4	8	$x^2 = 18.00$, $P < 0.001$

[1]Spider; [2]insect; *only test-pairs in which the *C. algerina* chose one prey type but not the other were used. Null hypothesis: P (chose prey 1) = P (chose prey 2).

Table 3 Results from alternate-day testing of *Cyrba algerina* juveniles with lures. Prey: two individuals of comparable size, each a different species. NS, not significant.

Prey 1	Prey 2	Chose prey 1 only	Chose prey 2 only	Chose both	McNemar test*
Oecobius amboseli[1]	Lycosid[1]	27	8	27	$x^2 = 10.31$, $P < 0.01$
Oecobius amboseli[1]	*Hersilia* sp.[1]	21	5	23	$x^2 = 9.85$, $P < 0.01$
Oecobius amboseli[1]	*Psychoda* sp.[2]	17	2	14	$x^2 = 11.84$, $P < 0.001$
Lycosid[1]	*Hersilia* sp.[1]	9	10	17	NS
Lycosid[1]	*Psychoda* sp.[2]	19	5	17	$x^2 = 8.167$, $P < 0.01$
Psychoda sp.[2]	*Brevicayne brassicca*[2]	12	9	12	NS

[1]Spider; [2]insect; *only test-pairs in which the *C. algerina* chose one prey type but not the other were used. Null hypothesis: P (chose prey 1) = P (chose prey 2).

spiders. However, when neither of two spiders was an oecobiid, *C. algerina* did not choose either prey type significantly more often than the other. Likewise, when both prey were insects, no prey type was chosen significantly more often than the other (Tables 2–4). These basic findings held when testing with living prey and when testing with lures.

There was no evidence that the presence of a web or nest influenced *C. algerina*'s prey-choice decisions. Regardless of whether or not a web or a nest was present, spiders were chosen significantly more often than insects and oecobiids were chosen significantly more often than other spiders (Table 5).

GENERAL DISCUSSION

Salticids are generally characterised as hunting spiders that do not rely on webs or other silk devices for prey capture (Richman & Jackson 1992). Yet,

Table 4 Results from simultaneous-presentation testing of *Cyrba algerina* juveniles with lures. Prey: two individuals of comparable size, each a different species. NS, not significant.

Prey 1	Prey 2	Chose prey 1	Chose prey 2	Chose neither	Test of goodness of fit*
Lycosid[1]	*Hersilia* sp.[1]	8	14	33	NS
Lycosid[1]	*Palpimanus* sp.[1]	9	9	31	NS
Lycosid[1]	*Thanatus* sp.[1]	13	14	37	NS
Oecobius amboseli[1]	*Aelurillus azerbaijanicus*[1]	24	2	41	$x^2 = 18.62$, $P < 0.001$
Oecobius amboseli[1]	*Clubiona* sp.[1]	18	2	27	$x^2 = 12.80$, $P < 0.001$
Oecobius amboseli[1]	*Hersilia* sp.[1]	25	3	32	$x^2 = 17.29$, $P < 0.001$
Oecobius amboseli[1]	Lycosid[1]	27	6	43	$x^2 = 13.36$, $P < 0.01$
Oecobius amboseli[1]	*Olios* sp.[1]	21	4	28	$x^2 = 11.56$, $P < 0.001$
Oecobius amboseli[1]	*Palpimanus* sp.[1]	22	2	29	$x^2 = 16.67$, $P < 0.001$
Oecobius amboseli[1]	*Thanatus* sp.[1]	24	7	38	$x^2 = 9.32$, $P < 0.01$
Psychoda sp.[2]	*Aelurillus azerbaijanicus*[1]	6	25	35	$x^2 = 11.65$, $P < 0.001$
Psychoda sp.[2]	*Brevicayne brassicca*[2]	9	13	54	NS
Psychoda sp.[2]	*Hersilia* sp.[1]	2	19	38	$x^2 = 13.76$, $P < 0.001$
Psychoda sp.[2]	Lycosid[1]	5	22	39	$x^2 = 10.70$, $P < 0.01$
Psychoda sp.[2]	*Oecobius amboseli*[1]	8	25	35	$x^2 = 8.76$, $P < 0.01$
Psychoda sp.[2]	*Palpimanus* sp.[1]	5	20	33	$x^2 = 9.00$, $P < 0.01$
Psychoda sp.[2]	*Thanatus* sp.[1]	1	11	25	$x^2 = 8.33$, $P < 0.01$

[1]Spider; [2]insect; *null hypothesis: P (chose prey 1) = P (chose prey 2).

Table 5 Results from simultaneous-presentation testing of *Cyrba algerina* juveniles with spider and insect lures. Prey 1: no nest or web. Prey 2 in nest (oecobiids) or web (all others). NS, not significant.

Prey 1	Prey 2	Chose prey 1	Chose prey 2	Chose neither	Test of goodness of fit*
Oecobius amboseli[1]	*Oecobius amboseli*[1]	14	17	25	NS
Oecobius amboseli[1]	*Stegodyphus mimosarum*[1]	16	2	24	$x^2 = 10.89$, $P < 0.001$
Oecobius amboseli[1]	*Zosis geniculatus*[1]	23	4	37	$x^2 = 13.37$, $P < 0.001$
Psychoda sp.[2]	*Psychoda* sp.[2]	8	5	30	NS
Psychoda sp.[2]	*Stegodyphus mimosarum*[1]	3	20	27	$x^2 = 12.56$, $P < 0.001$
Psychoda sp.[2]	*Zosis geniculatus*[1]	2	18	26	$x^2 = 12.80$, $P < 0.001$
Stegodyphus mimosarum[1]	*Oecobius amboseli*[1]	2	19	30	$x^2 = 13.76$, $P < 0.001$
Stegodyphus mimosarum[1]	*Psychoda* sp.[2]	23	4	42	$x^2 = 13.37$, $P < 0.001$
Stegodyphus mimosarum[1]	*Stegodyphus mimosarum*[1]	14	12	51	NS
Zosis geniculatus[1]	*Oecobius amboseli*[1]	2	17	21	$x^2 = 11.84$, $P < 0.001$
Zosis geniculatus[1]	*Psychoda* sp.[2]	15	1	35	$x^2 = 12.25$, $P < 0.001$
Zosis geniculatus[1]	*Zosis geniculatus*[1]	13	12	32	NS

[1]Spider; [2]insect; *null hypothesis: P (chose prey 1) = P (chose prey 2).

like all spiders (Foelix 1996), salticids routinely use silk in a variety of ways. For most salticids, silk use includes the spinning of densely woven tubular nests. These nests typically have no role in prey capture (Hallas & Jackson 1986), serving instead as shelters for resting, moulting, and oviposition (Jackson 1979). Spartaeines, in general, are different because no sparteines are known to spin dense enclosing (tubular) nests (Jackson & Hallas 1986a; Jackson 1990b–d; Jackson & Pollard 1990). The nests of adult females and overwintering juveniles of the Azerbaijan *C. algerina* are not tubular in shape, but they have silk density approaching that of more typical salticid nests.

Preference is a behavioural trait of an animal and cannot be inferred simply from knowing its diet in nature. Preference implies the ability to distinguish between different types of prey and choose to take one rather than the other. Diet, however, is an ecological attribute (Morse 1980), and the terms "stenophagy" (narrow diet) and "euryphagy" (wide diet) simply indicate the ends of a continuum.

Spiders were the most common prey in the natural diet of the Azerbaijan *C. algerina*, despite the prevalence of other prey types in the habitat. Laboratory experiments confirmed that the Azerbaijan *C. algerina* actively selects spiders in preference to insects. Furthermore, a particular spider, *Oecobius maculatus* (Oecobiidae), was the dominant prey in *C. algerina*'s natural diet, and laboratory experiments confirmed that the Azerbaijan *C. algerina* actively selected oecobiids in preference to other spiders.

Although the prey-choice behaviour of spartaeines has been extensively studied before (Li & Jackson 1996; Li et al. 1997; Jackson & Li 1998; Jackson 2000; Li 2000), almost all previously published information on spartaeine diet in nature has come from two studies (Jackson & Blest 1982; Clark & Jackson 2000) showing that *Portia fimbriata* from Queensland *(*Australia) feeds primarily on spiders.

One of the most striking findings from the present study is the wide range of arthropods other than spiders found in the prey records for *C. algerina* in Azerbaijan. Most spartaeines have a distribution limited primarily to the tropical regions of Africa, Asia, and Australasia, especially in rainforest (Jackson & Hallas 1986a,b). *Cyrba algerina* is, however, widely distributed at higher latitudes, ranging from the Canary Islands in the west through North Africa, Southern Europe, the Near East, the Caucasus and Central Asia to the Himalayas in the east (Wanless 1984; Logunov & Rakov 1998). Over much of this range, the habitat of *C. algerina* is considerably more xeric than rainforest, but more mesic than the habitat studied in Azerbaijan. If araneophagy is the ancestral feeding strategy of spartaeines (Jackson & Blest 1982; Jackson 1986), then our findings for the Azerbaijan *C. algerina* suggest that evolution in a xeric habitat in a high-latitude region has favoured the evolution of higher levels of euryphagy. For araneophagic spartaeines, supplementing a primarily spider diet with insects and other arthropods may be especially important in xeric habitats at high latitude, where the diversity and availability of prey may be especially limited.

Laboratory experiments using lures demonstrated that, by eyesight alone and in the absence of movement cues from the prey, the Azerbaijan *C. algerina* discriminates between spiders and insects and between oecobiids and other spiders. Only naïve laboratory-reared individuals were used, implying that the Azerbaijan *C. algerina*'s preference for spiders in general and oecobiids in particular is innate.

The microhabitat in which feeding individuals of *C. algerina* were found (spaces beneath stones) suggests that, in the field, this species might often hunt in dim light. Laboratory tests confirmed that the Azerbaijan *C. algerina* can perform the complete predatory sequence and capture spiders even in complete darkness. A goal for future work will be a fuller understanding of how low light levels typical of this species' microhabitat may constrain its predatory behaviour.

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REFERENCES

Ault, S. K.; Elliott, K. D. 1979: Spider predation (Araneae: Salticidae) on *Ornithodorus coriaceus* (Acarina: Argasidae), with survey of the predators of the genus *Ornithodorus*. *Journal of Medical Entomology 15*: 570–571.

Bartos, M. 2002: The prey of *Yllenus arenarius* (Araneae, Salticidae). *In*: Samu, F. *ed*. Abstracts of 20th European Colloquium of Arachnology. Szombathely: Balogh es Tarza Nyomda. P. 25.

Blest, A. D.; O'Carrol, D. C.; Carter, M. 1990: Comparative ultrastructure of layer I receptor mosaics in principal eyes of jumping spiders: the evolution of regular arrays of light guides. *Cell and Tissue Research 262*: 445–460.

Clark, R. J.; Jackson, R. R. 2000: Web use during predatory encounters between *Portia fimbriata*, an araneophagic jumping spider, and its preferred prey, other jumping spiders. *New Zealand Journal of Zoology 27*: 129–136.

Dean, D. A.; Sterling, W. L.; Nyffeler, M.; Breene, R. G. 1987: Foraging by selected spider predators on the cotton fleahopper and other prey. *Southwestern Entomology 12*: 263–270.

Foelix, R. F. 1996: Biology of spiders. Harvard University Press, Cambridge, Massachusetts.

Glatz, L. 1967: Zur biologie und Morphologie von *Oecobius annulipes* Lucas (Araneae, Oecobiidae). *Zeitschrift für Morphologie der Tiere 61*: 185–214.

Hallas, S. E. A.; Jackson, R. R. 1986: Prey-holding abilities of the nests and webs of jumping spiders (Araneae, Salticidae). *Journal of Natural History 20*: 881–894.

Horner, N. V.; Stangl, F. B.; Fuller, G. K. 1988: Natural history observations of *Salticus austinensis* (Araneae, Salticidae) in north-central Texas. *Journal of Arachnology 16*: 260–262.

Jackson, R. R. 1977: Prey of the jumping spider *Phidippus johnsoni* (Araneae: Salticidae). *Journal of Arachnology 5*: 145–149.

Jackson, R. R. 1979: Nests of *Phidippus johnsoni* (Araneae, Salticidae): characteristics, pattern of occupation, and function. *Journal of Arachnology 7*: 47–58.

Jackson, R. R. 1986: Web building, predatory versatility, and the evolution of the Salticidae. *In*: Spiders: webs, behavior, and evolution. *ed*. Shear, W. A. Stanford University Press. Pp. 232–268.

Jackson, R. R. 1990a: Predatory versatility and intraspecific interactions of *Cyrba algerina* and *C. ocellata*, web-invading spartaeine jumping spiders (Araneae, Salticidae). *New Zealand Journal of Zoology 17*: 157–168.

Jackson, R. R. 1990b: Predatory and silk utilisation behaviour of *Gelotia* sp. indet. (Araneae: Salticidae: Spartaeinae), a web-invading aggressive mimic from Sri Lanka. *New Zealand Journal of Zoology 17*: 475–482.

Jackson, R. R. 1990c: Predatory and nesting behaviour of *Cocalus gibbosus*, a spartaeine jumping spider (Araneae: Salticidae) from Queensland. *New Zealand Journal of Zoology 17*: 483–490.

Jackson, R. R. 1990d: Ambush predatory behaviour of *Phaeacius malayensis* and *Phaeacius* sp. indet., spartaeine jumping spiders (Araneae: Salticidae) from tropical Asia. *New Zealand Journal of Zoology 17*: 491–498.

Jackson, R. R. 2000: Prey preferences and visual discrimination ability of *Brettus*, *Cocalus* and *Cyrba*, araneophagic jumping spiders (Araneae: Salticidae) from Australia, Kenya and Sri Lanka. *New Zealand Journal of Zoology 27*: 29–39.

Jackson, R. R. 2002: Trial-and-error derivation of aggressive-mimicry signals by *Brettus* and *Cyrba*, jumping spiders (Araneae: Salticidae) from Australia, Kenya and Sri Lanka. *New Zealand Journal of Zoology 29*: 95–117.

Jackson, R. R.; Blest, A. D. 1982: The biology of *Portia fimbriata*, a web-building jumping spider (Araneae: Salticidae) from Queensland: utilization of webs and predatory versatility. *Journal of Zoology, London 196*: 255–293.

Jackson, R. R.; Hallas, S. E. A. 1986a: Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. schultzi*, araneophagic web-building jumping spiders (Araneae: Salticidae): utilisation of silk, predatory versatility, and intraspecific interactions. *New Zealand Journal of Zoology 13*: 423–489.

Jackson, R. R.; Hallas, S. E. A. 1986b: Predatory versatility and intraspecific interactions of spartaeine jumping spiders (Araneae: Salticidae): *Brettus adonis*, *B. cingulatus*, *Cyrba algerina*, and *Phaeacius* sp. indet. *New Zealand Journal of Zoology 13*: 491–520.

Jackson, R. R.; Li, D. 1998: Prey preferences and visual discrimination ability of *Cyrba algerina*, an araneophagic jumping spider (Araneae: Salticidae) with primitive retinae. *Israel Journal of Zoology 44*: 227–242.

Jackson, R. R.; Pollard, S. D. 1990: Web-building and predatory behaviour of *Spartaeus spinimanus* and *Spartaeus thailandicus*, primitive jumping spiders (Araneae: Salticidae) from Southeast Asia. *Journal of Zoology, London 220*: 561–567.

Jackson, R. R.; Pollard, S. D. 1996: Predatory behavior of jumping spiders. *Annual Review of Entomology 41*: 287–308.

Jackson, R. R.; van Olphen, A. 1991: Prey-capture techniques and prey-preferences of *Corythalia canosa* and *Pystira orbiculata*, ant-eating jumping spiders (Araneae, Salticidae). *Journal of Zoology, London 223*: 577–591.

Land, M. F. 1969a: Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *Journal of Experimental Biology 51*: 443–470.

Land, M. F. 1969b: Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *Journal of Experimental Biology 51*: 471–493.

Land, M. F.; Nilsson, D-E. 2002: Animal eyes. Oxford University Press.

Legendre, R.; Llinares, D. 1970: L'accouplement de l'araignee salticide *Cyrba algerina* (Lucas, 1846). *Annales de la Societe d'Horticulture et d'Histoire Naturelle de l'Herault 110*: 169–174.

Li, D. 2000: Prey preference of *Phaeacius malayensis*, a spartaeine jumping spider (Araneae: Salticidae) from Singapore. *Canadian Journal of Zoology 78*: 2218–2226.

Li, D.; Jackson, R. R. 1996: Prey preferences of *Portia fimbriata*, an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland. *Journal of Insect Behavior 9*: 613–642.

Li, D.; Jackson, R. R.; Barrion, A. 1997: Prey preferences of *Portia labiata*, *P. africana*, and *P. schultzi*, araneophagic jumping spiders (Araneae: Salticidae) from Philippines, Sri Lanka, Kenya, and Uganda. *New Zealand Journal of Zoology 24*: 333–349.

Logunov, D. V.; Rakov, S. Y. 1998: Miscellaneous notes on Middle Asian jumping spiders (Araneae: Salticidae). *Arthropoda Selecta 7*: 117–144.

Morse, D. H. 1980: Behavioral mechanisms in ecology. Cambridge, Massachusetts, Harvard University Press.

Platnick, N. I. 2002: The world spider catalog. Version 4.5. http://research.amnh.org/entomology/spiders/catalog/

Richman, D.; Jackson, R. R. 1992: A review of the ethology of jumping spiders (Araneae, Salticidae). *Bulletin of the British Arachnology Society 9*: 33–37.

Richman, D. B.; Whitcomb, W. H. 1981: The ontogeny of *Lyssomanes viridis* (Walckenaer) (Araneae: Salticidae) on *Magnolia grandiflora* L. *Psyche 88*: 127–133.

Sokal, R. R, Rohlf, F. J. 1995: Biometry: the principles of statistics in biological research. 3rd ed. New York, W. H. Freeman & Co.

Wanless, F. R. 1984: A review of the spider subfamily Spartaeinae nom.n. (Araneae: Salticidae) with descriptions of six new genera. *Bulletin of the British Museum of Natural History (Zoology) 46*: 135–205.

Young, O. P. 1989: Field observations of predation by *Phidippus audax* (Araneae: Salticidae) on arthropods associated with cotton. *Journal of Entomological Science 24*: 266–273.

Appendix 1 Prey records for *Cyrba algerina* in the field in Azerbaijan. Number of records given in parentheses.

Acari	
1.	Oribatid mite (1)
2.	Unidentified mite (1)
Araneae	
1.	Dictynidae: *Lathys stigmatisata* (3)
2.	Gnaphosidae: *Drassylus* sp. (1); *Nomisia* sp. (1)
3.	Linyphiidae: *Agyneta* sp. (2)
4.	Lycosidae (wolf spiders): unidentified (2)
5.	Oecobiidae: *Oecobius maculatus* (14)
6.	Oonopidae: *Oonops pulcher* (1)
7.	Salticidae (jumping spider): unidentified (1)
8.	Theridiidae: *Enoplognatha gemina* (1)
9.	Titanoecidae: *Titanoeca veteranica* (1)
10.	Zodariidae: *Zodarion cyprium* (1)
11.	Unidentified spiders (5)
Collembola	
1.	Springtails (4)
Diptera	
1.	Brachycera (fly) (1)
2.	Cecydomiidae (midges) (2)
Heteroptera	
1.	True-bug nymphs (1)
Homoptera	
1.	Aphididae (aphids) (2)
2.	Cicadellidae (leafhopper) (1)
Hymenoptera	
1.	Formicidae (ant egg) (1)
Lepidoptera	
1.	Unidentified caterpillars (2)
2.	Unidentified moth (1)
Opiliones	
1.	Phalangidae (harvestmen): *Opilio* sp. (3)
Pseudoscorpiones	
1.	Olpiidae (pseudoscorpions): *Calocheiridius libanoticus* (2)
Unidentified	(4)