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A CASE OF BLIND SPIDER'S BUFF?: PREY-CAPTURE BY JUMPING SPIDERS (ARANEAE, SALTICIDAE) IN THE ABSENCE OF VISUAL CUES

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ABSTRACT. Jumping spiders (Salticidae) are well known for their complex visual hunting behavior, but this is the first comparative study investigating their ability to catch prey in the absence of visual cues. When tested with vision occluded inside tubes, where spiders and prey (house flies, *Musca domestica*, and fruit flies, *Drosophila* spp.) could not easily evade each other, each of 42 salticid species tested caught prey in at least one of five different procedures used. Some salticids caught flies less frequently or were less aggressive when tested in petri dishes, where spiders and flies could easily evade each other. For both types of arena and prey, there were significant species differences in both success at prey-capture and tendency to respond aggressively when first contacted by flies. Additionally, there was significant positive correlation between success at catching prey and tendency to act aggressively when first contacted. Salticids resembled short-sighted spiders from other families by only attempting to catch flies when physically contacted, and by rapidly leaning forward ('lunging') to catch prey rather than leaping as they do when visual cues are available. We discuss circumstances in nature when an ability to catch prey in the absence of visual cues might be used by salticids.

Jumping spiders (Salticidae) have visual acuity that far exceeds the abilities of other spiders (Land 1985; Blest et al. 1990) and are well known for their use of vision when communicating (Crane 1949; Clark & Uetz 1994), navigating (Hill 1979; Tarsitano & Jackson 1997) and hunting (Forster 1977, 1979; Jackson & Pollard 1996; Bear & Hasson 1997; Li et al. 1997). Although members of some other spider families do use vision when hunting (e.g., Snelling 1983; Stratton 1984; Jackson et al. 1995), no non-salticid comes close to the refinement of vision-mediated hunting behavior used routinely by salticids. After orienting toward a target, a salticid relies mainly on visual cues when making decisions about whether and how a hunt should proceed (Forster 1977; Jackson & Pollard 1996; Li & Jackson 1996). For example, visual cues about prey identity, size, distance and orientation influence the salticid's speed and direction of approach (Dill 1974; Freed 1984; Jackson & van Olphen 1991; Bear & Hasson 1997). The salticid slowly creeps up on its prey until close enough for an attack, pauses, and then finally leaps at the prey (Heil 1936; Drees 1952; Forster 1977).

Despite their remarkable adaptation for diurnal activity, salticids appear able to coordinate some activities in darkness. For example, when in darkness, salticids can maintain straight courses by turn-alternation (Taylor 1995) and communicate by vibratory signals transmitted through nests (Richman & Jackson 1992). These non-visual abilities prompt speculation about whether salticids can also catch prey when visual cues are not available. Laboratory studies addressing this issue have yielded conflicting evidence; when tested in large arenas, *Phidippus johnsoni* (Peckham & Peckham 1883) failed to catch prey in the absence of visual cues (Jackson 1977), but *Trite planiceps* Simon 1899 was later found to catch prey when tested in smaller arenas (Forster 1982). *Trite planiceps* lives in dark recesses formed by rolled-up leaves, and adults usually do not build enclosing retreats (see Taylor 1997). Forster (1982) suggested that this species' ability to catch prey in the absence of visual cues is related to its lifestyle promoting frequent encounters with potential prey in darkness. Evaluation of whether *Trite*

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planiceps is unusual in its ability to catch prey in the absence of visual cues requires comparative data from a broad array of salticid species from this large and diverse spider family (see Coddington & Levi 1991).

In this paper we investigated the non-visual prey-catching abilities of salticids from 17 subfamilies, including representatives of diverse lifestyles (e.g., foliage-dwellers, ground-dwellers, active hunters, ambush hunters, web-invading araneophages, web-builders, ant-mimics, myrmecophages) and geographic regions (Table 1). For comparative purposes, we also investigated the non-visual prey-catching abilities of some non-salticid hunting spiders (i.e., spiders with comparatively poor eyesight) from the same habitat as *Trite planiceps.*

Because salticid eyes are not sensitive to infra-red light (Blest et al. 1981; Yamashita 1985; Peaslee & Wilson 1989), infra-red video was used to observe the behavior of spiders in the absence of visual cues. This is amongst the first studies to make use of this technology to study the behavior of salticids (see also Taylor 1995).

METHODS

Spiders from laboratory cultures were used (Table 1), excluding individuals that were missing appendages. Standard maintenance procedures were used (Jackson & Hallas 1986). Except during experiments, spiders had *ad libitum* access to adult house flies (*Musca domestica*) or adult fruit flies (*Drosophila melanogaster*) as prey, depending on the spider's size. *Portia* spp., which prefer spiders as prey, had their diets supplemented with various species of spiders, and *Corythalia canosa, Natta rufopicta* and *Zenodorus orbiculatus,* each of which prefers ants, had their diets supplemented with various species of ants. Voucher specimens of all spiders used have been deposited (by RRJ) at the Florida State Collection of Arthropods (Gainesville).

Five different testing procedures were used, but all had the six following elements in common: 1) All tests were carried out during the laboratory light phase (12L:12D), excluding the first and last 2 h. 2) Between tests, arenas were thoroughly washed with water and then ethanol to remove silk and chemical cues that may have accumulated during previous tests. 3) Prior to testing, spiders were kept without food for 6–8 days. 4) Spiders were tested only once per day. 5) Individual spiders were tested in the dark using only types of prey that they had been observed catching in the light. 6) Spiders were used only once with each prey type in any type of test.

Blinded spiders in horizontal tubes.—Two days after feeding and six days prior to testing, all eyes of the test spider were coated with two or three layers of opaque enamel paint while the spider was subdued under CO_2. A spider and an adult fly (*M. domestica* or vestigial-winged *D. melanogaster*) were placed at opposite ends of a 120 mm-long clear plastic tube plugged by a cork at each end. The spider and fly were separated by a partition placed in a slit at the tube mid-point. Spiders and flies were then left for 5 min to settle down before tests were started. To start a test, the partition was removed so that spiders and flies could move around the entire arena. Spiders were observed for 15 min or until predation occurred.

Spiders 6.0 mm or less in body length were tested in 6.4 mm diameter tubes, whereas spiders 6–8 mm in body length were tested in 7.9 mm diameter tubes. Adult females were used for tests of species in which adult body length was 8 mm or less. Juveniles 6–8 mm in body length were used for species in which adult body length was greater than 8 mm.

Blinded spiders in vertical tubes.—These tests were used primarily for species that failed to catch flies when blinded and in horizontal tubes. Tests using blinded spiders in horizontal tubes and in vertical tubes were identical except for tube orientation. Spiders were placed in the uppermost half of the tube. Because flies tend to move upwards when given the opportunity, this procedure was adopted as a means of promoting more frequent contact between spiders and flies than in tests using horizontal tubes.

Sighted spiders in tubes.—Tests with sighted spiders in tubes were the same as tests using blinded spiders in horizontal tubes except that the arena was made of glass rather than plastic and, instead of blinding the spiders, they were observed using infra-red (IR) video. Tests were staged inside a light-proof cabinet (800 mm high, 1200 mm long, 500 mm deep) illuminated by an infra-red light source (GTE Mini Kat narrow angle IR illuminator) and were observed using a video-camera that was sensitive to IR light (Burle TC300E CCD). The IR video camera was connected to a monitor positioned outside the cabinet so that behavior of spiders could be observed. Because the video field of view encompassed the whole arena there was no need to track the spiders and flies as they moved about during experiments. The light-proof cabinet had sleeves (500 mm long), consisting of a double layer of heavy black satin, attached to a 150 mm diameter hole in the wall so that the experimenter could reach in to remove the partition (i.e., begin tests) without allowing light to enter.

Rather than varying the tube diameter with spider size, only adult spiders were used and all spiders were tested in tubes that were 100 mm in length and 11 mm in internal diameter. Fruit flies used were fully winged *Drosophila immigrans* instead of vestigial winged *D. melanogaster. Drosophila immigrans* is larger and more active in darkness than is *D. melanogaster,* and the spiders and flies contacted each other more frequently when this species was used in preliminary tests. Instead of adjusting prey size to spider size, all spiders were tested using a 'standard fruit fly' 2.5–3 mm in body length or a 'standard house fly' 7–8 mm in body length. After placing a fly and a spider at opposite ends of the tube with the partition in place, the tube was placed horizontally in the light proof cabinet. The partition was removed in IR light after the spiders had been in IR light for a 5 min settling-down period. Each test lasted 15 min or until the spider caught the fly.

In preliminary tests, individual spiders responded to contact with the flies in one of several different ways. A spider might respond in an apparently aggressive manner; it might actually lunge at the fly (rapidly lean forward by extending Legs III and IV, tarsi of these legs remaining on the substrate) and attempt to grasp it with the front legs, or it might carry out apparent preliminaries to lunges, such as orienting toward the fly or raising its front legs. These responses were collectively termed 'confront'. Alternatively, a spider might respond in an apparently less aggressive manner; it might run, walk, or leap (all tarsi leave the substrate) away from the fly, turn away from the fly without stepping, or lean away from the fly by flexing legs on the side opposite to the fly. These responses were collectively termed 'avoid'. Whether spiders and flies physically contacted each other during the 15 min testing period was recorded and responses of spiders to first contact with the fly were recorded as either confront or avoid. The tendency to confront, rather than avoid, flies provided a general measure of 'aggressiveness'.

If flies were grasped and then released, or if they broke free from spiders during tests, these spiders and flies were kept in IR light for a further 60 min after the 15 min testing period ended. This enabled us to investigate whether the flies died and, if the flies died, whether the spiders later picked up the dead flies and ate them. When flies died after being bitten, this was recorded as a capture.

Sighted spiders in petri dishes.—The arena used here was a plastic petri dish (85 mm diameter) with a plastic tube (30 mm long, 7 mm internal diameter) glued onto a hole in the wall. A standard house fly (i.e., 7–8 mm body length) was placed into the tube. A partition inserted into a slit at the petri dish end of the tube and a wooden plunger inserted into the other end of the tube prevented the fly's escape. Next, the test spider was placed in the petri dish and the arena was placed into the light-proof cabinet. After a 5 min settling-down period, the partition was removed. The entry of the fly into the dish defined the beginning of the test. As soon as the test began, the plunger was depressed so that neither the spider nor the fly could leave the petri dish. Tests lasted 15 min or until prey capture, and were observed using IR video (see above). These tests are the closest approximation in the present study to the procedures used by Jackson (1977) and Forster (1982) to investigate non-visual predation in the salticids *Phidippus johnsoni* and *Trite planiceps,* respectively, but with the improvement of being able to observe the behavior of the spiders.

Sighted spiders in darkness *vs.* light.—In these tests, we assessed differences in the frequency with which individual spiders caught flies in darkness *versus* light. The general procedure resembled tests using blinded spiders in horizontal tubes except that spiders were not blinded. Instead, each individual spider was tested once in the light and once in darkness on successive days (in random order). To begin tests in darkness, the tubes were placed horizontally in a light-proof cabinet as soon

Table 1.—Spiders tested for ability to catch prey in the absence of visual cues.

	Subfamily (Family[1])	Origin	Typical adult body length (mm)
Salticids			
Asemonea tenuipes O. P. Cambridge 1869	Lyssomaninae	Sri Lanka	4
Bavia aericeps Simon 1877	Thiodininae	Australia (Queensland)	12
Corythalia canosa (Walckenaer 1837)	Plexippinae	USA (Florida)	6
Cosmophasis bitaeniata (Keyserling 1882)	Heliophaninae	Australia (Queensland)	6
Cosmophasis micarioides (L. Koch 1880)	Heliophaninae	Australia (Queensland)	7
Cosmophasis sp.	Heliophaninae	Philippines	7
Cyrba ocellata (Kroneberg 1875)	Spartaeinae	Sri Lanka	5
Epeus sp. 1	Hyllinae	Singapore	8
Epeus sp. 2	Hyllinae	Philippines	8
Eris marginata (Walckenaer 1837)	Dendryphantinae	USA	6
Euophrys parvula Bryant 1905	Euophrynae	New Zealand	6
Euryattus sp.	Cytaeinae	Australia (Queensland)	8
Hasarius adansoni (Andouin 1827)	Hasariinae	Australia (Queensland)	6
Helpis minitabunda (L. Koch 1880)	Astianae	New Zealand	7
Hentzia mitrata (Hentz 1846)	Dendryphantinae	USA (North Carolina)	5
Holoplatys planissima (L. Koch 1879)	Marpissinae	New Zealand	8
Holoplatys sp.	Marpissinae	New Zealand	5
Jacksonoides queenslandicus Wanless 1988	Astianae	Australia (Queensland)	7
Lyssomanes viridis (Walckenaer 1837)	Lyssomaninae	USA (Florida)	6
Marpissa marina Goyen 1892	Marpissinae	New Zealand	8
Menemerus bivattatus (Dufour 1831)	Marpissinae	Australia (Queensland)	5
Mogrus dumicola (O. P. Cambridge 1872)	Dendryphantinae	Israel	8
Mopsus mormon Karsch 1878	Thyeninae	Australia (Queensland)	12
Myrmarachne lupata L. Koch 1879	Myrmarachninae	Australia (Queensland)	5
Natta rufopicta Simon 1901	Heliophaninae	Kenya	5
Phidippus johnsoni (Peckham & Peckham 1883)	Dendryphantinae	USA (California)	9
Phidippus sp. 1	Dendryphantinae	USA (Arizona)	9
Phidippus sp. 2	Dendryphantinae	USA (Texas)	9
Plexippus calcaratus Karsch 1880	Plexippinae	Australia (Queensland)	10
Portia africana (Simon 1886)	Spartaeinae	Kenya	8
Portia fimbriata (Doleschall 1859)	Spartaeinae	Australia (Queensland)	8
Portia labiata (Thorell 1882)	Spartaeinae	Sri Lanka, Philippines	8

Table 1.—Continued.

	Subfamily (Family[1])	Origin	Typical adult body length (mm)
Portia schultzi Karsch 1878	Spartaeinae	Kenya	7
Simaetha paetula (Keyserling 1882)	Simaetheae	Australia (Queensland)	8
Tauala lepidus Wanless 1988	Astianae	Australia (Queensland)	7
Thiania bhamoensis Thorell 1887	Itatinae	Singapore	5
Thorellia ensifera Thorell 1887	Spilarginae	Singapore	5
Trite auricoma Urquhart 1885	Cytaeinae	New Zealand	9
Trite planiceps Simon 1899	Cytaeinae	New Zealand	10
Tularosa plumosa de Lessert 1925	Hasariinae	Kenya	5
Viciria praemandibularis (Hasselt 1893)	Hyllinae	Singapore	10
Zenodorus orbiculatus (Keyserling 1881)	Euophrynae	Australia (Queensland)	4
Non-salticids			
Cheiracanthium stratioticum L. Koch 1873	Clubionidae[1]	New Zealand	8
Clubiona cambridgei L. Koch 1873	Clubionidae[1]	New Zealand	8
Dysdera crocata C. L. Koch 1838	Dysderidae[1]	New Zealand	10
Supunna picta (L. Koch 1873)	Clubionidae[1]	New Zealand	8
Taieria erebus (L. Koch 1873)	Gnaphosidae[1]	New Zealand	7

Table 2.—Number of individuals tested (*n*) and percentage that captured flies (C) during tests using blinded spiders in tubes. Species marked with a superscript 1 are non-salticids.

	Tubes horizontal		Tubes vertical	
	n	C	*n*	C
Tests using fruit flies				
Clubiona cambridgei[1]	9	66	6	66
Bavia aericeps	12	17	—	—
Corythalia canosa	9	22	—	—
Cosmophasis micarioides	6	17	—	—
Epeus sp. 1	7	14	—	—
Euophrys parvula	12	33	—	—
Hasarius adansoni	8	13	—	—
Helpis minitabunda	8	24	—	—
Holoplatys sp.	7	0	9	22
Jacksonoides queenslandicus	10	0	14	14
Lyssomanes viridis	10	0	11	9
Marpissa marina	7	0	7	14
Mopsus mormon	10	10	—	—
Myrmarachne lupata	6	0	5	20
Phidippus johnsoni	12	0	11	9
Plexippus calcarata	11	27	—	—
Portia labiata	7	0	8	13
Tauala lepidus	6	17	—	—
Thiania bhamoensis	7	14	—	—
Trite auricoma	15	20	—	—
Trite planiceps	10	40	7	43
Zenodorus orbiculatus	6	17	—	—
Tests using house flies				
Clubiona cambridgei[1]	4	100	—	—
Bavia aericeps	5	20	—	—
Euophrys parvula	5	20	—	—
Helpis minitabunda	4	0	5	20
Jacksonoides queenslandicus	9	0	10	20
Marpissa marina	8	38	7	14
Mopsus mormon	4	25	—	—
Phidippus johnsoni	5	0	10	10
Tauala lepidus	7	43	—	—
Trite auricoma	8	38	—	—
Trite planiceps	10	40	—	—

as the barrier was removed, and then left for 24 h. At the end of tests, dead flies were inspected for fang holes and mastication to confirm that they had been bitten by the spider.

Statistical methods.—Tests of independence in 2×2 contingency tables were carried out using Fisher's exact test, whereas tests in larger tables were carried out using χ^2 (excluding species for which $n < 10$). Tests of association were carried out using Spearman's rank correlations (excluding species for which $n < 10$). McNemar's test for significance of changes (Sokal & Rohlf 1981) was used to compare frequency data obtained from sequential testing of individuals in darkness and light.

RESULTS

Success at non-visual predation.—Each of the 47 species tested (42 salticids and 5 non-salticids) caught prey in the absence of visual cues in at least one type of test (Tables 2–4). There was no evidence of differences among salticid species in how frequently they caught prey in darkness when blinded (in horizontal or vertical tubes) or when sighted and tested for 24 h (for all test types, $P > 0.1$). However, there was significant variation among salticid species during tests using sighted spiders in tubes (fruit flies, $\chi^2 = 95.06$, 14 *df*, $P < 0.001$; house flies, $\chi^2 = 103.30$, 17 *df*, $P < 0.001$) and tests using sighted spiders in petri dishes (house flies, $\chi^2 = 154.80$, 13 *df*, $P < 0.001$). All species of non-salticids caught flies in all types of test, and there was no evidence that they differed in capture frequency in any type of test (for all test types, $P > 0.1$).

In experiments testing individual spider's success at catching flies in darkness and in light, all salticids caught fruit flies and house flies less frequently in the dark than in the light (Table 4). In contrast, there was no evidence that absence of light affected how often *Clubiona cambridgei*, the non-salticid tested, caught flies (Table 4).

Some sighted spiders caught flies immediately following the first physical contact with the flies ('immediate captures'). During tests in tubes using fruit flies as prey, immediate captures were made by the non-salticids *Clubiona cambridgei* (16 of 24 captures recorded), *Dysdera crocata* (2 of 10), *Supunna picta* (6 of 9) and *Taieria erebus* (4 of 8) as well as the salticids *Euophrys parvula* (1 of 10), *Helpis minitabunda* (1 of 7), *Mogrus dumicola* (1 of 4) and *Phidippus* sp. 1 (1 of 5); during tests in tubes using house flies as prey, they were made by the non-salticids *Cheiracanthium stratioticum* (3 of 11), *Clubiona cambridgei* (19 of 45), *Dysdera crocata* (2 of 13), and *Supunna picta* (6 of 16) as well as the salticids *Corythalia canosa* (1 of 5), *Euophrys parvula* (1 of 18), *Phidippus* sp. 2 (1 of 8), *Portia africana* (1 of 4) and *Trite planiceps* (5 of 18); during tests in petri dishes using house flies as prey, the non-salticids *Clubiona cambridgei* (8 of 20), *Dysdera crocata* (3 of 10), and *Supunna picta* (4 of 15) made immediate captures, whereas *Trite planiceps* (9 of 37) was the only salticid observed to make immediate captures in these tests.

Associations amongst spider size, aggressiveness and success at prey capture.—Salticid species varied in the frequency with which they confronted fruit flies and house flies when first contacted ('aggressiveness') during tests in tubes (fruit flies, $\chi^2 = 63.20$, 13 *df*, $P < 0.001$; house flies, $\chi^2 = 79.34$, 16 *df*, $P < 0.001$) and in petri dishes (house flies, $\chi^2 = 109.40$, 13 *df*, $P < 0.001$) (see Table 3). In contrast, all of the non-salticids were similar in that they usually confronted flies when first contacted (see Table 3), and there was no evidence of species variation in frequency of confrontation by non-salticids during any test type (for all test types, $P > 0.1$).

Salticid species that often confronted flies when first contacted tended to catch flies more frequently than species that rarely confronted flies during tests of sighted spiders in tubes (fruit flies, $r_s = 0.6677$, 13 *df*, $P < 0.01$; house flies, $r_s = 0.6779$, 16 *df*, $P < 0.01$) and tests of sighted spiders in petri dishes (house flies, $r_s = 0.5965$, 13 *df*, $P < 0.05$).

During tests with fruit flies in tubes, *Trite auricoma* individuals that confronted flies were more likely to catch the prey than were conspecifics that avoided flies when first contacted ($P < 0.05$). For all other species in all tests, there was no evidence that likelihood of catching flies was related to an individual spider's response when first contacted (for all species in all test types, $P > 0.1$). There was no evidence of relationship between size of salticid species (Table 1) and the proportion of individuals that confronted or caught flies in tests of sighted spiders in tubes or in petri dishes using either prey type (for all test types, $P > 0.1$).

Comparison of arenas used with sighted spiders.—For the following salticids, house flies were captured less frequently in the petri dish arena than in the tube arena (Table 3): *Cosmophasis* sp. ($P < 0.05$), *Euophrys parvula* ($P < 0.001$), *Helpis minitabunda* ($P < 0.001$), *Marpissa marina* ($P < 0.001$), *Mopsus mormon* ($P < 0.05$), *Portia labiata* ($P < 0.001$), *Portia shultzi* ($P < 0.05$), *Trite auricoma* ($P < 0.01$) and *Trite planiceps* ($P < 0.01$). However, there was no evidence for any non-salticid species that frequency of prey-capture by was different in these two types of tests (for all species, $P > 0.1$).

Some salticids confronted house flies less frequently when tested in petri dishes rather than in tubes (Table 3): *Corythalia canosa* ($P < 0.05$), *Euophrys parvula* ($P < 0.001$), *Marpissa marina* ($P < 0.001$) and *Portia labiata* ($P = 0.057$). However, there was no evidence for any non-salticid species that frequency of confrontation was different in these two types of test nor was there evidence that frequency of contact with house flies was different in these two types of test for any salticid or non-salticid (for all species, $P > 0.1$).

Table 3.—Behavior and prey-capture success of sighted spiders in tubes and in petri dishes. Species marked with a superscript 1 are non-salticids. 'Contact' is the percentage of *n* that contacted the fly (see text). 'Confront' is the percentage of individuals that confronted, rather than avoided, the fly (see text) immediately after first contact and 'Capture' is the percentage of *n* that captured the fly.

	n	Contact	Confront	Capture
Tests in tubes using fruit flies as prey				
Cheiracanthium stratioticum[1]	28	50	86	50
Clubiona cambridgei[1]	33	73	92	73
Dysdera crocata[1]	18	72	62	56
Supunna picta[1]	15	73	82	60
Taieria erebus[1]	16	63	70	50
Bavia aericeps	15	73	9	0
Corythalia canosa	17	53	0	12
Cosmophasis bitaeniata	4	75	33	50
Cosmophasis sp.	12	83	0	42
Epeus sp. 2	3	67	0	0
Eris marginata	5	100	0	0
Euophrys parvula	22	64	57	45
Helpis minitabunda	46	87	8	15
Holoplatys planissima	8	50	25	0
Jacksonoides queenslandicus	20	80	0	0
Lyssomanes viridis	33	70	0	12
Marpissa marina	28	93	23	46
Mogrus dumicola	26	42	9	15
Mopsus mormon	8	88	14	0
Phidippus sp. 1	13	85	45	38
Phidippus sp. 2	9	89	13	33
Portia fimbriata	22	64	0	5
Portia labiata	64	53	3	5
Tauala lepidus	13	77	40	46
Trite auricoma	38	53	25	18
Trite planiceps	43	72	43	63
Zenodorus orbiculatus	2	50	100	0
Tests in tubes using house flies as prey				
Cheiracanthium stratioticum[1]	13	85	90	85
Clubiona cambridgei[1]	54	93	89	83
Dysdera crocata[1]	15	100	85	87
Supunna picta[1]	18	100	88	89
Bavia aericeps	15	100	7	13
Corythalia canosa	17	94	38	29
Cosmophasis sp.	16	88	14	38
Epeus sp. 2	7	100	0	57
Eris marginata	5	100	0	0
Euophrys parvula	22	95	43	82
Helpis minitabunda	50	100	6	34
Holoplatys planissima	12	92	20	25
Jacksonoides queenslandicus	16	94	7	0
Lyssomanes viridis	42	98	3	14
Marpissa marina	32	94	50	56
Mogrus dumicola	26	96	28	46
Mopsus mormon	10	80	0	40
Phidippus sp. 1	14	100	38	100
Phidippus sp. 2	9	100	13	89
Portia africana	7	86	17	57
Portia fimbriata	26	100	0	12
Portia labiata	24	83	11	33
Portia shultzi	10	100	20	50

Table 3.—Continued.

	n	Contact	Confront	Capture
Tauala lepidus	16	100	19	25
Trite auricoma	33	91	21	27
Trite planiceps	21	100	70	86
Tests in petri dishes using house flies as prey				
Clubiona cambridgei[1]	22	91	85	91
Dysdera crocata[1]	12	100	67	83
Supunna picta[1]	16	94	87	94
Bavia aericeps	15	93	0	0
Corythalia canosa	15	87	0	7
Cosmophasis sp.	14	86	8	0
Epeus sp.	9	89	0	11
Euophrys parvula	46	85	0	0
Helpis minitabunda	39	95	5	3
Holoplatys planissima	4	100	0	0
Jacksonoides queenslandicus	20	85	0	0
Lyssomanes viridis	35	94	0	9
Marpissa marina	26	100	4	4
Mopsus mormon	12	83	0	0
Portia africana	5	100	0	0
Portia labiata	66	89	0	0
Portia shultzi	10	100	0	0
Tauala lepidus	12	83	20	17
Trite auricoma	36	92	9	3
Trite planiceps	70	90	44	53

Prey-capture behavior in the absence of visual cues.—Salticids always lunged to catch prey, and were never observed to leap onto prey as they commonly do in light. No spider, salticid or non-salticid, ever lunged at the flies prior to being touched. *Cheiracanthium stratioticum* and *Clubiona cambridgei,* non-salticids, sometimes chased after flies that moved away following contact, but no salticid ever did this.

After lunging at flies, salticids sometimes held the flies for 1–5 sec with their fangs whilst appearing to make little or no attempt at using their legs to grasp the fly. In these instances, flies broke free or were released by the spiders but always stopped moving within 10 min of being bitten. During tests using sighted spiders in tubes, the following salticids made bite-then-release attacks on house flies: *Bavia aericeps* (1 of 2 captures recorded), *Corythalia canosa* (1 of 5), *Helpis minitabunda* (1 of 17), *Mogrus dumicola* (2 of 12), *Mopsus mormon* (1 of 4), *Phidippus* sp. 1 (2 of 14), *Portia labiata* (1 of 8), *Trite auricoma* (3 of 9) and *Trite planiceps* (2 of 18). After these attacks, spiders usually later picked up the immobilized fly and ate it, the only exception being *Bavia aericeps. Trite planiceps* was the only salticid observed to kill a fruit fly by a bite-then-release attack (3 of 27). During tests in petri-dish arenas using house flies as prey, spiders that grasped flies always held onto them until they died.

DISCUSSION

Salticids are conventionally thought of as strictly diurnal hunters that shelter overnight, and this general impression is supported by observations of spider activity patterns in nature and in the laboratory (e.g., Jackson 1976; Givens 1978; Taylor 1997). Nonetheless, the present study finds that, as well as being extraordinarily adept visual predators (Forster 1977, 1979; Jackson & Pollard 1996; Bear & Hasson 1997), salticids are able to coordinate attacks using other senses when visual cues are unavailable. This finding in a laboratory context establishes a need for research investigating naturally occurring situations during which salticids might depend primarily or solely on cues other than vision to coordinate attacks.

Table 4.—Number of spiders that caught flies in light *vs.* dark. Species marked with a superscript 1 are non-salticids. Only columns 'Light only' and 'Dark only' are relevant for McNemar tests for significance of changes (Sokal & Rohlf 1981).

	Light only	Dark only	Both	Neither	McNemar test
Tests using fruit flies					
Clubiona cambridgei[1]	2	3	10	3	NS
Asemonea tenuipes	7	0	2	1	$P < 0.01$
Bavia aericeps	15	0	1	2	$P < 0.001$
Corythalia canosa	10	0	1	4	$P < 0.005$
Cosmophasis micarioides	14	0	2	3	$P < 0.001$
Cosmophasis bitaeniata	5	0	2	4	$P < 0.05$
Cyrba ocellata	6	0	1	3	$P < 0.025$
Euophrys parvula	17	0	3	5	$P < 0.001$
Epeus sp. 2	18	0	1	2	$P < 0.001$
Eris marginata	11	0	4	0	$P < 0.001$
Euryattus sp.	9	0	3	4	$P < 0.005$
Hasarius adansoni	13	1	3	3	$P < 0.005$
Helpis minitabunda	17	1	2	2	$P < 0.001$
Hentzia mitrata	5	0	2	1	$P < 0.05$
Holoplatys sp.	19	0	4	3	$P < 0.001$
Jacksonoides queenslandicus	20	0	4	4	$P < 0.001$
Lyssomanes viridis	15	0	0	4	$P < 0.001$
Marpissa marina	18	1	2	3	$P < 0.001$
Menemerus bivattatus	12	0	3	5	$P < 0.001$
Mopsus mormon	13	0	2	5	$P < 0.001$
Myrmarachne lupata	19	1	3	2	$P < 0.001$
Natta rufopicta	14	1	2	3	$P < 0.001$
Phidippus johnsoni	18	0	0	3	$P < 0.001$
Plexippus calcarata	17	0	3	1	$P < 0.001$
Portia labiata	9	2	0	11	$P < 0.05$
Simaetha paetula	19	0	3	1	$P < 0.001$
Tauala lepidus	12	1	3	1	$P < 0.005$
Thiania bhamoensis	22	1	2	2	$P < 0.001$
Thorellia ensifera	11	1	2	2	$P < 0.005$
Trite auricoma	19	0	6	1	$P < 0.001$
Trite planiceps	16	0	8	1	$P < 0.001$
Tularosa plumosa	5	0	2	2	$P < 0.05$
Viciria praemandibularis	13	0	3	4	$P < 0.001$
Zenodorus orbiculatus	15	0	1	3	$P < 0.001$
Tests using house flies					
Clubiona cambridgei[1]	0	2	5	1	NS
Bavia aericeps	8	0	2	0	$P < 0.005$
Euophrys parvula	5	0	2	1	$P < 0.05$
Helpis minitabunda	7	1	0	6	$P < 0.05$
Jacksonoides queenslandicus	8	0	1	1	$P < 0.005$
Marpissa marina	9	0	2	0	$P < 0.005$
Mopsus mormon	5	0	2	0	$P < 0.05$
Phidippus johnsoni	8	0	2	1	$P < 0.005$
Plexippus calcarata	6	0	1	1	$P < 0.025$
Tauala lepidus	5	0	2	0	$P < 0.05$
Trite auricoma	4	0	1	3	$P < 0.05$
Trite planiceps	8	0	4	0	$P < 0.005$

Acute vision is not a prerequisite for successful cursorial hunters. Many spiders from other families (i.e., non-salticids) are successful cursorial hunters despite lacking acute vision (e.g., Ctenidae, Pisauridae, Clubionidae, Gnaphosidae) and there is no obvious reason to presume that salticids could not also sometimes hunt cursorially when visual cues are not available. There is even anecdotal evidence that at least one salticid, *Phidippus otiosus* (Hentz 1846) [= *Phidippus pulcher* (Walckenaer 1837)], does sometimes hunt after nightfall (Reiskind 1982). Web-building spiders from other families lack acute vision, and instead use their webs as extensions of their tactile sense organs to hunt both during the day and at night (Witt 1975; Suter 1978; Jarman & Jackson 1986). Web-building salticids have at their disposal all of the prey-catching facilities used by web-builders from other families but whether salticids make use of these facilities when visual cues are absent is not known. Salticids that build webs (Jackson & Hallas 1986; Jackson & Pollard 1990) or web-like nests (Hallas & Jackson 1986a, b; Jackson & McNab 1989a) are prime candidates for investigation of nocturnal predation.

Although predation is conventionally envisaged as a means of gaining food, it may also function as defense (Curio 1976; Archer 1988). Salticids may commonly find themselves in situations that demand immediate responses to attacks in the absence of visual cues from the attacker. For example, salticids may be suddenly attacked by fast-moving predators in light (Jackson 1980; Young & Lockley 1987; Jackson & McNab 1989b; Jackson et al. 1990), in darkness when in their nests at night (Jackson 1976; Jackson & Griswold 1979; Jarman & Jackson 1986; Taylor 1997) or in dark places during the day. Additionally, salticids attacked in their nests during the day may be denied visual cues by the opaque walls of their nest (see Hallas & Jackson 1986b). How salticids mediate anti-predator behavior in these contexts has not yet been studied specifically, but immediate orientation and attack (similar to confrontation and 'immediate captures' in our experiments) might be an appropriate defense against an unidentified intruder.

The poorly known natural histories of most salticid species cause difficulty in interpreting the observed species differences in predation success and aggressiveness toward flies in the absence of visual cues. Nonetheless, results of this laboratory study do suggest certain hypotheses about how salticids might respond in nature. For example, tendency to respond aggressively when touched by flies in darkness was not strongly associated with size, a measure of physical ability. Instead, we may consider each species' relationships with prey and enemies to understand why salticids varied in aggressiveness. Most likely, success in nature depends not only on a salticid's size or strength, but also on the types of predators and prey encountered and the situations in which encounters take place. For example, some large salticids may have responded timidly because their nocturnal predators are especially ferocious or encounters take place at sites where escape is easy, whereas some smaller salticids may have responded aggressively because their nocturnal intruders are less dangerous or because encounters with enemies in nature are difficult to escape.

Some salticids (e.g., *Euophrys parvula, Marpissa marina*), adjusted their tendency to confront and later catch flies in darkness depending on ease of avoidance. These species made greater use of the comparatively easy avoidance option when tested in expansive petri dishes, but they responded more aggressively when in tubes with few options for escape. If prey-capture was based on feeding considerations, then we would not have expected these differences. Instead, evasion of potential enemies, rather than hunting, seems a better explanation of non-visual predation by these salticids in our experiments.

Trite planiceps, the salticid for which non-visual predation was first reported by Forster (1982), appears to be a special case. Although other salticids often caught house flies when tested in tubes, *T. planiceps* was unusually aggressive and successful at prey-capture when tested in the more spacious petri-dishes. Perhaps, as was suggested by Forster (1982), *T. planiceps'* unusual aggressiveness is an adaptation related to frequent encounters with potential prey, dangerous intruders, or both in the restrictive dark recesses within rolled-up leaves where this species normally lives. *Trite planiceps* used in the present study share their habitat with each of the non-salticids tested. Of these, *Clubiona cambridgei, Cheiracanthium stratioticum* and *Taieria erebus* have been observed eating *Trite planiceps* adults, juveniles and eggs in nature (PWT unpubl. data). Of course, other salticids tested also encounter enemies in darkness (Jackson 1976; Jarman & Jackson 1986), but the abundance of nocturnal hunting spiders and confining microhabitat inside rolled-up leaves may make encounters with predators unusually frequent and unusually difficult to escape.

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