Observations on the prey and prey capture behaviour of the funnelweb mygalomorph spider genus *Ischnothele* (Araneae, Dipluridae)

Frederick A. Coyle and Nancy D. Ketner

Department of Biology,
Western Carolina University,
Cullowhee, NC 28723, USA

Summary

The diet and prey capture behaviour of five morphs of *Ischnothele* funnelweb spiders from northern Argentina, the Peruvian Andes, the Peruvian Amazon Basin, and Jamaica were investigated. All morphs construct exposed, adhesive space webs which entangle prey (at least temporarily). Field collected prey remains indicate that ants and beetles and lesser quantities of other ambulatory invertebrates comprise 95% or more of the prey intake of these morphs. Capture sequences recorded on videotape reveal that these spiders approach prey in a series of short rapid advances alternating with pauses. During the capture, the pedipalps and anterior legs reach beyond, pull, and position the prey under the extended chelicerae, which then strike downwards in typical mygalomorph fashion. The prey is held only by the chelicerae and fangs as it is carried to the retreat. Observations indicate that prey detection and approach orientation depend primarily, if not completely, upon prey-generated web vibrations and that the approach pauses function as information gathering periods. Jamaican spiders, with proportionally longer appendages than the Peruvian morphs, tend to approach and capture prey faster than do the Peruvian morphs. Immobilisation wrapping, previously observed in Panamanian *Ischnothele*, did not occur in this study. When provided with a superabundance of prey, *Ischnothele* spiders exhibit an unlimited functional response (the over-kill phenomenon).

Introduction

In spite of the justifiable interest in understanding the prey capture behaviour of spiders (Riechert & Luczak, 1982), relatively little effort has been devoted to studying prey capture behaviour in mygalomorph spiders, especially sheetweb and funnelweb mygalomorphs (Mecicobothriidae, Hexathelidae and Dipluridae), which, unlike other mygalomorphs, construct capture webs (Coyle, 1986).

Virtually nothing is known about the prey capture behaviour of mecicobothriids (Coyle, 1986). Although Laing (1973, 1975, 1978, 1979) has learned much about certain aspects of prey capture in *Porrhothele antipodiana* (Walck.), only a few brief notes have been published on the prey capture behaviour of other hexathelids (McKeown, 1952; Levitt, 1961; Hickman, 1964; Darchen, 1967). Excluding records of prey remains (Vollrath, 1979; Raven, 1984; Coyle, 1986, 1988; Paz, 1988), we are aware of only four published prey capture observations for diplurid genera other than *Ischnothele*: (1) Stern & Kullmann (1975) noted that some diplurids practice immobilisation wrapping, (2) Vollrath (1979) gave a brief general description of prey capture in *Diplura* (probably = *Linothele*), (3) Coyle (1986, 1988) described some aspects of prey capture in *Euagrus*, and (4) Paz (1988) described how a

Linothele species captures wasps, cockroaches, crickets and polydesmid millipedes.

We have found only three references to the prey capture behaviour of *Ischnothele*, a genus of common tropical American diplurid spiders: (1) Petrunkevitch (1911) noted the rapidity of prey capture by *Ischnothele digitata* (O. P.-Cambr.) in southern Mexico; (2) Nentwig & Wissel (1986) observed that Panamanian *Ischnothele guyanensis* (Walck.) spiders could capture prey as large as twice their own body length; and (3) Strohmenger & Nentwig (1987) tested the adhesiveness and prey retention ability of webs of the latter species.

Recent field work associated with the first author's study of ischnotheline systematics provided us with the opportunity to study *Ischnothele* prey capture behaviour. The primary objectives of this project were (1) to begin characterising the diets of *Ischnothele* species, (2) to describe their prey capture behaviour in detail, and (3) to develop hypotheses to guide future investigations of *Ischnothele* prey capture.

Material and methods

Field data were collected from eight *Ischnothele* populations representing from three to five species. Since the taxonomic status of these populations is currently under investigation (Coyle, in prep.) and since most of the species are undescribed, we will refer to each putative species as a "morph" and give the collection data for each morph. Morphs A and B are closely related and may prove to be conspecific; likewise morphs D and E might be conspecific.

Morph A: population A1 – Argentina, Cordoba Prov., 2 km N.E. Villa Carlos Paz, scrub savanna, 15 March 1988; population A2 – Argentina, Santiago del Estero Prov., S. edge Ojo de Agua, rock road bank, 22 March 1988. Morph B: population B1 – Peru, Dept. Madre de Dios, Puerto Maldonado, about 300 m elev., palm trunks and board fence, 31 March 1988. Morph C: population C1 – Peru, Dept. Junin, S. edge Santa Rosa de Sacco, 3900 m elev., rock outcrops, 27 and 29 March 1988; population C2 – Peru, Dept. Junin, Cochas Bajo, 11 km W. Tarma, 3600 m elev., rock outcrop, 28 March 1988. Morph D: population D1 – Jamaica, St. Andrew Parish, Newcastle to Hardwar Gap, 1160-1280 m elev., roadbanks in or near moist montane forest, 8 April 1988. Morph E: population E1 – Jamaica, St. Catherine Parish, Fort Clarence and Hellshire Hills near Seafort, 10-50 m elev., cactus thorn scrub, 9 April 1988; population E2 – St. Thomas Parish, rt. A4, 23 km E. Kingston, about 100 m elev., dry limestone forest, 10 April 1988.

In the field, arthropods were occasionally dropped into webs or webs were vibrated artificially to elicit prey capture responses in order to observe, photograph (35 mm Minolta X-700 with 50/3.5 macro lens and electronic flash), or capture the spiders. The retreat portions of some webs were collected and all exoskeletal remains of consumed prey were carefully sorted under a stereomicroscope. Using primarily skeletal parts that were seldom fragmented (heads, beetle elytra, snail shells), we obtained a reasonably

accurate record of the number and identity of prey in these web samples, although it is important to note that especially soft-bodied prey are probably under-represented by this type of sampling procedure.

The spiders used in the laboratory study of prey capture (May and June 1988, in Cullowhee, North Carolina) were adult females (except for perhaps a few subadults), 13-22 mm long (body length plus chelicerae). They were kept in covered, clear plastic shoe boxes (29 cm long, 15 cm wide, 8.5 cm high) at room temperature (20-24°C) and a photoperiod of approximately 14 hours. A vial taped to the floor of the box against the middle of the box end served as a retreat. Each spider constructed a capture web out from the open end of this vial. Webs were misted with water every 2-3 days. Prey used in the laboratory observations included both larval (11-17 mm long) and adult (13-15 mm long) mealworm beetles (*Tenebrio*), house cricket nymphs (*Acheta domestica*) (6-11 mm long), *Formica* worker ants (5-8 mm long), and (rarely) other arthropods. Prey capture responses were elicited by dropping these prey on to the capture web. The distance from retreat mouth to prey (approach distance) varied from 15 to 120 mm and was measured (to the nearest 5 mm) for 36 captures. All prey types were offered to all spider morphs, although not in equal numbers. Eighty-three complete or partial prey capture sequences were recorded on videotape with a Panasonic WV-D5000 video-recorder with a Micro-Nikkor 50 mm close-up lens. The clear plastic boxes allowed filming from virtually any angle, even from below. During playback, 1 s of action could be subdivided into 30 individual stop-action frames. Approach duration was recorded as the time interval between when the spider's anteriormost appendages emerged from the retreat opening and when they contacted the prey. Capture duration was recorded as the interval between this first contact with the prey and the onset of the carry. Left tibia I and carapace lengths of morph B, C and D females were measured with a Wild M-5 stereomicroscope with 20x eyepiece lenses and an eyepiece micrometer scale, and are accurate to 0.038 mm.

Results and discussion

Web structure

Webs of all the morphs in this study are generally similar and also resemble those described for *Ischnothele* species living in Mexico and Costa Rica (Coyle, 1986). Many of the web-fibres are remarkably fine and closely spaced (Figs. 1, 2), perhaps the result of a fibrillation process like that which Palmer (1985) has discovered in the diplurid genus *Euagrus*. The retreat portion of the web is a silk tube, often flattened and irregular and sometimes branching, which is constructed in some concealed space, e.g. under a rock or fallen *Opuntia* pad, in the soil, in a fissure in a rock outcrop, under the base of a palm frond, etc. The retreat opens out (Fig. 1) on to a rather complex, asymmetrical, three-dimensional, exposed capture web consisting of irregular, interconnected, suspended silk sheets (most are roughly horizontal but some may be

oblique or nearly vertical) attached to surrounding substrates. Often there is a primary horizontal sheet plus numerous accessory sheets occupying different planes above and beside it. The web frequently contains one to three tubular access passageways leading from the retreat entrance to different portions of the capture web. The approximate horizontal area (cm²) covered by the natural, capture web of a large adult female of each morph is 900 (morph A), 1300 (B), 250 (C), 1200 (D), and 900 (E). Sometimes a few to many silk strands extend from the main part of the capture web as far as 30 cm to substrates above the web. Whether these serve to intercept aerial prey, to support the web, or other functions is not known.

A typical capture web constructed in the laboratory began as a single roughly horizontal sheet extending out from the retreat, but as days passed auxiliary sheets and access passageways were added. Just as they did in nature, morph C spiders constructed smaller capture webs than the other morphs in the lab. Even after five months in shoe boxes, morph C capture webs never developed beyond the single horizontal sheet stage, even though their webs in nature were three-dimensional.
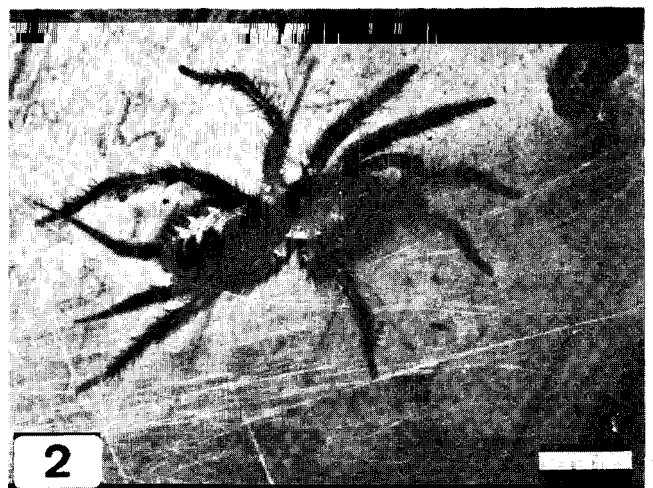
Figs. 1, 2: *Ischnothele* approach pause posture. Photos taken in the field. **1** Morph D female in mouth of retreat at beginning of approach; **2** Morph B female on capture web close to isopod prey. Scale bars = 5 mm.

Natural diet

The prey remains data in Table 1 indicate that non-flying and non-saltatory invertebrates may comprise 95% or more of the prey of the *Ischnothele* populations we sampled, although it should be noted that prey remains data may be biased against soft-skeletoned (and therefore flying) insects, because such insects may be highly fragmented during feeding. Worker ants and adult beetles were the most common prey, comprising 75% or more of the prey in every population sampled. In all populations except C1 and C2 many more ants than beetles were captured, but since the great majority of the ants were much smaller (90% had head widths of 0.4-0.7 mm) than the beetles, beetles formed a greater percentage of prey biomass than their numbers indicate. We estimate that beetles comprised at least 70% of the prey biomass observed in populations C1 and C2. Termites, millipedes, spiders, isopods and land snails occasionally constituted a noteworthy (but still minor) proportion (5-13%) of the prey taken by a population. The presence of two bees and two vespid wasps in two of the prey samples indicates that *Ischnothele* spiders are at least occasionally able to capture and consume relatively large active fliers.

Observations of other diplurid funnelweb spiders (Raven, 1984; Coyle, 1986, 1988; Paz, 1988) indicate that they also capture mostly non-flying prey. Raven's (1984) data suggest that Australian euagrines may capture a higher proportion of millipedes and snails than does *Ischnothele*, and Paz's (1988) observations indicate that *Linothele* commonly capture adult Orthoptera (especially cockroaches and crickets), adult Hemiptera, and larval Lepidoptera in addition to the kinds of prey that have been most commonly found in the webs of *Ischnothele* and other diplurids.

Prey retention ability of the web

As Strohmenger & Nentwig (1987) have demonstrated, the *Ischnothele* capture web is adhesive and impedes or entraps many arthropods which encounter it. Of the arthropods we dropped on to *Ischnothele* webs, ants were the least likely to become entrapped. However, even though some ants escaped easily, others became hopelessly entrapped or escaped only after a considerable struggle. Similarly, Strohmenger & Nentwig (1987) found that only 25% of the *Formica* ants they dropped on to Panamanian *Ischnothele guyanensis* webs became hopelessly entrapped (100 s in webs from which the spiders had been removed). We found that grasshoppers, in spite of their powerful hind leg thrusts, were sometimes entrapped for a few minutes.

Three properties of *Ischnothele* webs may be especially important in prey entanglement: (1) The high fibre density increases the chances that setae and other exoskeletal irregularities will become entangled; (2) The extremely small diameter of many fibres may foster electrostatic adhesive forces (Palmer, 1985); (3) The three-dimensional nature of the web tends to increase the probability that a prey will encounter additional web surface as it struggles. We observed that prey dropped on *Ischnothele* webs were more likely to escape from simple webs consisting of one horizontal capture sheet than from more complex three-dimensional webs. Strohmenger & Nentwig (1987) found that, although *Tegenaria* silk is more adhesive than *Ischnothele* silk, *Tegenaria* webs, unlike *Ischnothele* webs, were unable to entrap *Formica* ants and *Calliphora* flies, in part, they felt, because the *Tegenaria* webs consist only of a single horizontal sheet.

Description of prey capture behaviour

We observed no clear qualitative differences in prey capture behaviour among the four *Ischnothele* morphs (A-D) we studied in detail. The following is a composite description, based upon all of the capture sequences observed, of the three phases — approach, capture and carry — of a complete prey capture sequence.

Approach

When an *Ischnothele* spider detects prey from within its retreat, it turns to face out of the mouth of the retreat (if not already doing so) and adopts the standard pause posture (Fig. 1). The approach consists of one (rarely) or more (usually) rapid advances towards the prey, each followed by a pause. Depending

Prey taxon	*Ischnothele* morph and population						
	A1	B1	C1	C2	D1	E1	E2
Formicidae	65(83)	474(72)	29(50)	14(26)	234(95)	12(67)	201(93)
Other Hymenoptera		2(0.3)					2(0.9)
Coleoptera	11(14)	88(13)	26(45)	27(51)	8(3)	3(17)	8(4)
Hemiptera	1(1)	6(0.9)					
Homoptera		4(0.6)	2(3)		1(0.4)		
Isoptera		31(5)					
Orthoptera		1(0.2)					
Psocoptera		1(0.2)					
Diplopoda		5(0.7)		3(6)			2(0.9)
Araneae	1(1)		1(2)	2(4)		2(11)	
Acarina					2(0.8)		
Pseudoscorpionida					1(0.4)		1(0.5)
Isopoda		36(6)					
Pulmonata		6(0.9)		7(13)	1(0.4)	1(6)	2(0.9)

Table 1:   Prey remains found in *Ischnothele* webs collected in the field. Number of webs sampled in each population is unknown. Number of prey and percentage of total prey (in parentheses) given for each prey taxon for each *Ischnothele* web sample.

on the location of the prey and the topography of the web, the spider runs on horizontal, inclined, or vertical planes [and either upright (usually) or upside-down], with nearly equal facility.

In the pause posture (Figs. 1-3) the pedipalps are usually half flexed (never greatly extended); the first legs extend forwards with tarsi resting on the web; the second legs also extend forwards and somewhat to the side; the third legs are directed at approximately right angles to the body axis; and the fourth legs extend backwards and slightly to the side. Except for relatively minor variation in the flexion and relative position of the pedipalps and legs, this bilaterally symmetrical pattern was consistently observed throughout the hundreds of pauses recorded.

At the end of the approach phase, when the spider first contacts the prey, it may continue to advance briefly, immediately pause, or immediately manipulate the prey. Usually (53 of 62 interpretable encounters) one of the first legs makes the initial contact; only rarely is a second leg (5 of 62) or a pedipalp (4 of 62) the first appendage to touch the prey.
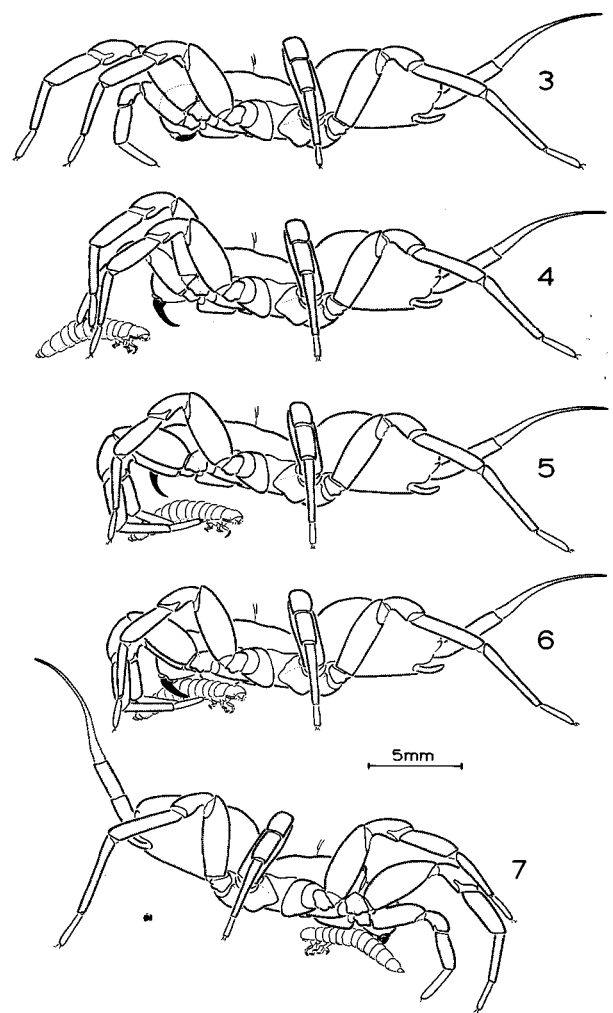
Capture

Prey manipulation is usually the first action in the capture phase. During manipulation (Fig. 4) the cephalothorax may be raised a little, the pedipalps and first legs (and sometimes the second legs) touch and often move the prey, and often the chelicerae and fangs are partly extended. Typically, the principal and most obvious act of manipulation is the extension of the pedipalps and often the first and sometimes second legs beyond the prey and the subsequent flexion of these appendages which begin to pull and/or lift the prey into a position under the chelicerae.

The initial manipulation is followed by a pause or a strike or, more rarely, a brief advance or shift in posture. There may be a series of manipulations alternating with pauses before a strike occurs. During a capture pause, the spider remains motionless, either with or without the pedipalps and/or first legs touching the prey. Just before a strike (Fig. 5), the cephalothorax is elevated, the chelicerae and fangs are fully extended and spread apart, and the prey is swept under the chelicerae by the flexion of the pedipalps and/or first (and sometimes second) legs. During the strike (Fig. 6) the cephalothorax is lowered to meet the prey as the prey is lifted by the pedipalps and first legs, and the chelicerae and fangs flex so that part of the prey is pierced and/or clamped between the fangs and chelicerae. Sometimes (Table 2) the spider may strike a second, third, or fourth time, with a pause and/or manipulation preceding each strike.

Carry

The carry phase (when the spider carries the prey back to the retreat) is more variable than the approach phase. Immediately after the (final) strike, the spider either pauses or begins the carry. During the initial movement towards the retreat the spider either backs up or performs a 180° turn. Occasionally, if the prey is

captured close to the retreat, the spider backs up for most or all of the carry, but more commonly the spider turns 180° during the early part of the carry so that most of the carry is a forward advance. Invariably, during both forward and backward carry modes, the pedipalps are held away from the prey (Fig. 7), which is held only by the fangs (rarely one or both pedipalps remained flexed and touching the prey for a fraction of a second at the start of a carry). During the typical forward carry (Fig. 7), the body is tilted forwards with the abdomen elevated. If the spider encounters silk barriers on its return to the retreat (a common occurrence if the web is complex), it lunges and almost "swims" through the silk, and this tilted body and the pedipalps and front legs appear to shield the prey from contact with the web.

Figs. 3-7: Important segments of a typical *Ischnothele* prey capture sequence. Side view drawings based upon videotape sequences, photographs of prey capture, and a preserved female specimen of morph B. **3** Approach pause posture; **4** Manipulation of prey with pedipalps and first legs; chelicerae and fangs partly extended; **5** Just before strike; cephalothorax lifts, chelicerae and fangs extend fully, and pedipalps and first legs position prey under chelicerae; **6** Strike; cephalothorax drops, pedipalps and first legs lift prey, and chelicerae and fangs flex around prey; **7** Forward carry towards retreat.

Prey detection and orientation

The following evidence strongly suggests that *Ischnothele* spiders detect and locate their prey primarily, if not solely, by means of prey-generated web vibrations, rather than by vision or olfaction: (1) A prolonged, open-mouthed, low pitched "whooo" sound (with expired air) directed at a·capture web from several cm distance sometimes lured a spider out of its retreat towards the appropriate part of the web; (2) Spiders were sometimes lured from their retreats when we touched the web with a vibrating brush, twig, or leaf, and sometimes these spiders attempted to manipulate and strike the vibrating object; (3) Spiders that were facing into the closed end of the retreat vial (so that they could not possibly see the capture web) were able to detect prey moving in the capture web; (4) Five spiders offered prey (beetle larvae and crickets) at night in dim red light all detected and captured prey normally; (5) When freshly killed prey were placed in the webs of four spiders, the spiders did not respond, even though they had each captured a live prey placed in the same part of the web less than 3 minutes earlier and subsequently captured another live prey placed in the same part of the web 3-4 minutes after the dead prey was presented.

As described above, *Ischnothele* spiders, like *Euagrus* (Coyle, 1986) and at least some agelenids (Krafft, 1969; Foelix, 1982), typically approach their prey in a series of short dashes separated by pauses. On average, *Ischnothele* spiders spend one-half or more of their total approach time pausing (Table 2). Since this pause time significantly increases the time required for the spider to reach the prey, it presumably increases the prey's chances of escaping and the exposed spider's chances of being captured by predators. In view of these costs of pauses, it is reasonable to suppose that they serve an important function. We postulate that the primary function of these pauses is to gather tactile information about the location and nature of the vibration source, information essential for effective orientation and for predicting the consequences of completing the approach/capture sequence. On a priori grounds this hypothesis seems reasonable, because it is likely to be very difficult for a running spider to separate prey-generated vibration information from vibration noise generated by its own movement. Moreover, the observation that an *Ischnothele* prey capture approach typically involves two or more pauses (Table 2) is what one would predict if these pauses serve to gather directional information, because such information would be more difficult to extract from vibrations in a three-dimensional capture web composed of irregular sheets than from the hub of an orb web.

Three casual observations further support the hypothesis that the approach pauses of *Ischnothele* serve to gather information: (1) Pause duration was extremely variable (Table 2), even within many individual approach sequences, suggesting that it is dependent

	Ischnothele morphs			
	A	**B**	**C**	**D**
Approach duration	0.7-14.5(7) 3.6±5.1	0.7-19.6(19) 4.6±5.4	0.4-67.8(11) 9.7±19.8	0.1-24.8(26) 2.6±4.9
Pause duration*	0.2-5.0(6) 1.2±1.9	0.2-18.8(19) 3.6±5.3	0.2-66.3(11) 9.1±19.5	0.1-23.6(25) 2.1±4.7
Pause/Approach[a]	0.25-0.89(6) 0.48±0.22	0.25-0.97(19) 0.65±0.18	0.57-0.99(11) 0.75±0.17	0.15-0.96(25) 0.59±0.22
Number pauses (per approach)	2-5(6) 3.7±1.0	2-7(20) 4.2±1.3	1-6(11) 3.2±1.7	1-6(25) 2.5±1.6
Approach speed[b]	48.0(1)	1.5-36.6(6) 18.2±12.7	0.6-50.0(9) 18.1±19.1	1.0-126.9(16) 51.8±37.8
Advance speed[c]	80.0(1)	34.3-78.3(6) 58.5±20.4	37.5-120.0(9) 60.5±34.0	25.9-235.7(16) 123.6±69.8
Capture duration				
All prey	0.2-0.6(7) 0.4±0.2	0.1-8.4(24) 1.6±2.5	0.2-9.6(11) 1.7±2.8	0.1-2.0(29) 0.4±0.4
Beetle adults	0.4(1)	0.2-8.4(7) 3.8±1.4	0.2-9.6(4) 2.7±4.6	0.1-0.3(3) 0.3±0.1
Beetle larvae		0.1-2.8(11) 0.7±0.8	0.2-3.4(7) 1.2±1.1	0.1-2.0(11) 0.5±0.6
Crickets	0.3-0.4(3) 0.4±0.1	0.2(1)		0.1-0.5(9) 0.3±0.1
Ants	0.2-0.6(3) 0.3±0.3	0.1-2.3(5) 0.6±0.9		0.1-0.3(6) 0.2±0.1
Number strikes (per capture)	1(4)	1-4(21) 1.5±0.98	1-3(11) 1.5±0.82	1-3(26) 1.2±0.51

Table 2: Prey capture behaviour values for four *Ischnothele* morphs. Range, sample size (in parentheses), mean, and standard deviation given. Duration times in seconds. Speeds in mm per second. Approach duration and capture duration defined in Methods section. *Pause duration is the sum of the duration of all pauses in a complete approach sequence. [a]Pause/approach is pause duration divided by approach duration. [b]Approach speed is approach distance divided by approach duration. [c]Advance speed is approach distance divided by total advance duration (approach duration minus pause duration).

upon a highly variable environmental factor such as prey activity; (2) Pause durations were especially long when prey did not move for long periods of time, and these long pauses often ended immediately after the prey resumed visible movement; (3) Long pause durations seemed to be most common when prey were dropped into the outer reaches of complex three-dimensional webs (as opposed to simpler webs). To test our hypothesis further, we examined those taped capture sequences where both spider and prey could be observed during the entire approach phase, recorded the total approach phase time during which no prey movement could be visually detected, and examined the correlation between total pause duration and duration of prey inactivity. The resulting correlation (Fig. 8) supports the information gathering hypothesis for approach pause function. A plot of total pause duration against an index of prey inactivity, with prey type designated for each data point (Fig. 9), also is largely consistent with this hypothesis: (1) Beetle larvae, which were relatively inactive, tended to be associated with long approach pauses; (2) Crickets and ants, which were moderately to extremely active, were associated with short approach pauses; (3) Adult beetles, which were extremely active, were associated with brief pauses for most spiders, but not for all.

The longer approach pauses exhibited by a few spiders approaching adult beetles may be the result of hesitancy or caution associated with the greater cost and/or risk of handling active, large, and heavily armoured prey. Another observation supports the hypothesis that these spiders gather information during the approach (probably vibration information gathered during pauses) to predict the cost of a prey capture: occasionally a spider returned to its retreat before

completing its approach; these aborted approaches never involved beetle larvae or cricket nymphs, but only adult beetles ($n=3$), large millipedes ($n=2$) and ants ($n=2$), prey that appear to be more difficult to capture and/or carry (see below).

Orientation errors, such as incorrect turns or running past the prey or mouth of the retreat, never occurred during the approach phase and were rare during the carry phase. We observed no evidence that spiders were using web tension information to locate prey; for example, we never observed a spider flexing its legs or tugging at the web during a pause. Since the five spiders which were observed capturing prey at night in dim red light appeared to return to their retreats as quickly and accurately as spiders which captured prey in daylight, visual cues are apparently not necessary for effective orientation back to the retreat. This suggests that *Ischnothele* may, like *Cupiennius* (Seyfarth & Barth, 1972) and *Pardosa* (Görner & Zeppenfeld, 1980), be orienting back to the retreat on the basis of kinesthetic information learned during the approach to the prey. It is also possible that tactile topographic landmarks in the web (such as the access tunnels) are used.

Prey capture variation

The absence of strict control of variables in this study helped to generate the high variances in the quantitative prey capture data (Table 2). Nevertheless a few interesting intermorph differences appear (none are statistically significant) which are deserving of further testing under controlled conditions. The approach speed of morph D tends to be higher than that of morphs B and C (Table 2). This difference results from the tendency of the former to run faster (higher advance speed) and spend proportionally less of its approach time pausing than the latter two species. These differences may be largely the result of morph D's proportionally longer appendages (Fig. 10), which, in addition to providing the machinery for greater speed, could permit a bolder approach. Another difference between morph D and morphs B and C is the lower average capture duration of the former (Table 2), especially during the capture of adult beetles. Once again it is tempting to postulate that the proportionally longer appendages (only leg I was measured, but the pedipalps and chelicerae also look proportionally longer) of morph D spiders enables them to subdue prey, especially large, active adult beetles, more easily than can the other morphs. For morphs B and C, the average capture phase duration was markedly greater when capturing adult beetles than when capturing beetle larvae, crickets, or ants (Table 2). This longer capture time correlates with the larger size and hard exoskeleton of the adult beetles, with the difficulty spiders frequently encountered when carrying these beetles into their retreats, and with Riechert & Luczak's (1982) and Nentwig's (1987) categorisation of beetles as difficult-to-handle prey. In this study, the only failed attempt to capture an adult beetle involved a morph B spider.
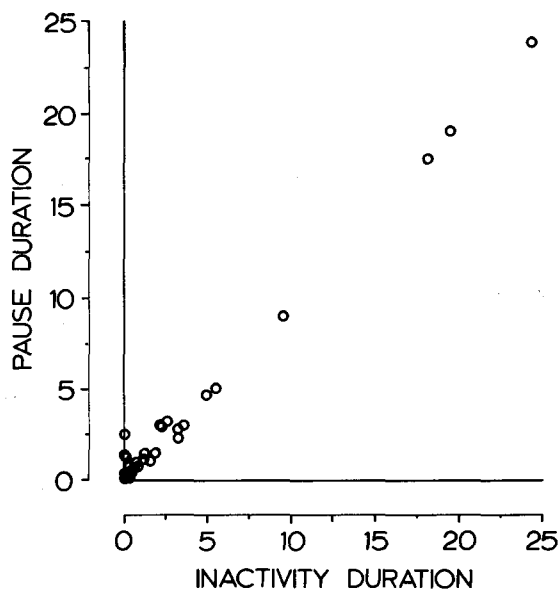

Fig. 8:   Relationship of *Ischnothele* spider's total pause duration (in seconds) to prey's inactivity duration (time in seconds during which no prey movement was visible) for each of 45 video-taped approaches in which both spider and prey were continuously visible. Data for morphs A, B, C and D, and all prey types. Correlation = 0.994.

Immobilisation occurred only slowly with all prey types. Captured prey were held by the chelicerae and embedded fangs, but continued to struggle for at least several minutes, indicating that *Ischnothele* venom cannot quickly paralyse prey. We did not observe any immobilisation wrapping, although two kinds of spinning activity were sometimes associated with prey capture. One type involved applying silk to the retreat wall immediately after returning to the retreat, while the spider still held the prey in its chelicerae. The other kind occurred in or near the retreat entrance when spiders experienced difficulty carrying adult beetles into the retreat; after releasing (or losing its grip on) such a beetle, the spider would sometimes apply silk to the web close to the struggling beetle, but not on the beetle itself, a behaviour somewhat similar to the
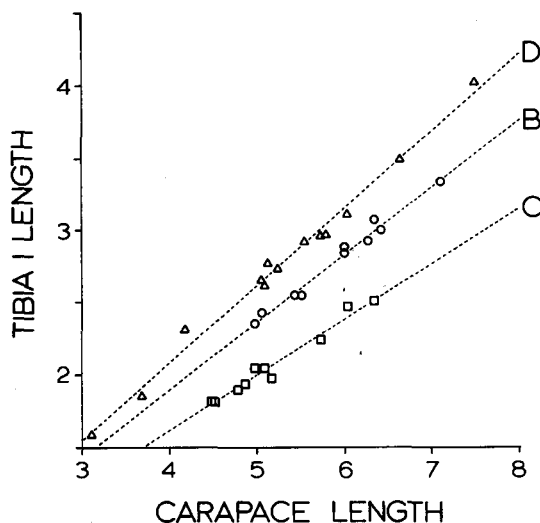
Fig. 10:   Scatterplot of tibia I length vs. carapace length for samples of *Ischnothele* morph B (circles), morph C (squares), and morph D (triangles) females. Regression lines drawn for each morph. Lengths in mm.

occasional post-capture spinning behaviour of thera-phosids (Eberhard, 1967). All four morphs exhibited these kinds of spinning activity, but they were rare in all but morph B. We also observed two morph B spiders pause and apply silk to the capture web while carrying ants back to the retreat.

This absence of immobilisation wrapping is note-worthy, since Nentwig & Wissel (1987) and A. E. Decae (pers. comm.) observed immobilisation wrapping of large and active prey by *Ischnothele guyanensis* from Panama. Decae observed this wrapping behaviour most commonly during ant capture, following an unsuccessful capture attempt that left the ant partly entangled in the web. In this situation "the spider rapidly encircled the prey, throwing silk over it in a way similar to attack wrapping in the Hersiliidae." Nentwig & Wissel (1987) claim that this immobilisation wrapping enables *I. guyanensis* to capture proportionally larger prey than species which do not perform immobilisation wrapping. Perhaps, in our study, we did not offer prey which were sufficiently large and/or active to trigger such behaviour.

Repetitive prey capture

After witnessing how readily *Ischnothele* spiders will capture a second prey shortly after one prey capture, we endeavoured to determine whether these spiders exhibit the unlimited functional response, or overkill phenomenon — capturing prey in excess of apparent need — observed in some other spider taxa (Riechert & Luczak, 1982). Cricket nymphs (6-9 mm long) were dropped into the webs of two spiders (morphs B and D, 14 and 16 mm long including chelicerae, respectively) in the following pattern: shortly after (within 4 minutes) the spider had captured and returned to the retreat with one cricket, another was dropped into the capture web. Both spiders exhibited the unlimited functional response; spider D captured 12 crickets in a 29-minute period and spider B captured nine crickets in 25

beetle adults   o
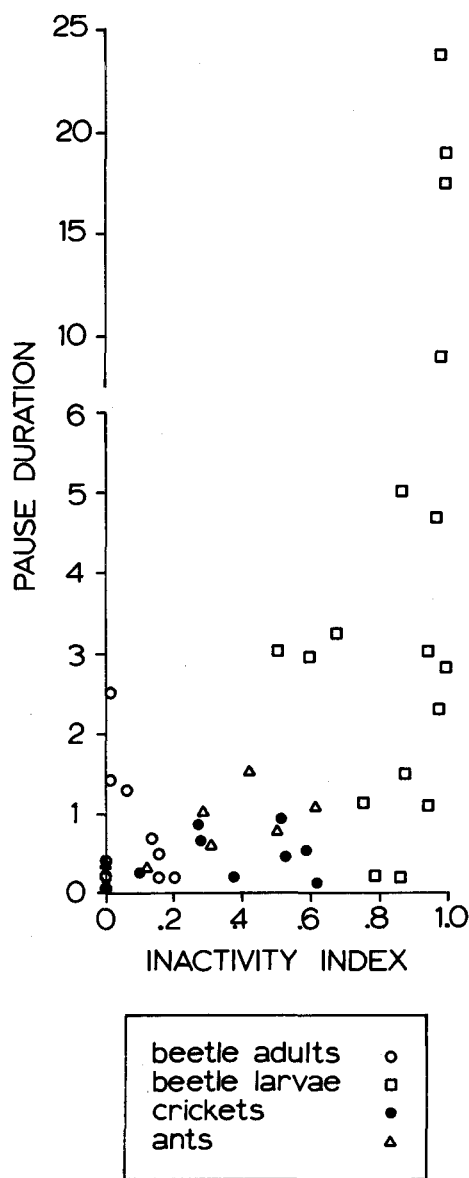beetle larvae   □
crickets   ●
ants   △

Fig. 9:   Relationship of *Ischnothele* spider's total pause duration (in seconds) to prey's inactivity index (duration of prey inactivity during spider's approach divided by total approach time) for each of 45 videotaped approaches, with prey identified for each data point. Upper part of pause duration scale is condensed. Data for morphs A, B, C and D, and all prey types. Correlation = 0.530.

minutes. Third and fourth instar spiderlings of morphs B and D often captured within one minute all of the two to four fruit flies (*Drosophila*) dropped simultaneously into their webs.

The paraxial strike pattern: A constraint on aerial prey-capture?

The prey manipulation and strike behaviour of *Ischnothele* is basically the same as that in mygalomorphs without capture webs [theraphosids (Eberhard, 1967), antrodiaetids (Coyle, 1971), and ctenizids (Buchli, 1969; Coyle, 1981)]; all these reach over the prey with the pedipalps and front legs and pull it under the chelicerae for the downward strike. Bristowe (1954) maintained that "the striking and piercing powers of mygalomorph fangs are greater when the victim is on hard ground than when spider and victim are suspended on elastic threads" and that this constraint explains why a diaxial cheliceral design was selected early in the evolution of araneomorph spiders. Bristowe's hypothesis loses much of its original appeal when one observes how quickly and effectively an *Ischnothele* spider can pluck a cricket nymph from a web surface well above any hard substrate by using its pedipalps and front legs to position and hold the cricket under its chelicerae during the strike. A comparative cost/benefit analysis of the prey capture manipulation and strike of *Ischnothele* and an araneomorph funnelweb analogue like *Coras, Wadotes,* or *Agelenopsis* would help test Bristowe's hypothesis.

Acknowledgements

References

BRISTOWE, W. S. 1954: The chelicerae of spiders. *Endeavour* **13**: 42-49.

BUCHLI, H. R. 1969: Hunting behavior in the Ctenizidae. *Am. Zool.* **9**: 175-193.

COYLE, F. A. 1971: Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae: Antrodiaetidae). *Bull.Mus.comp.Zool.Harv.* **141**(6): 269-402.

COYLE, F. A. 1981: Notes on the behaviour of *Ummidia* trapdoor spiders (Araneae, Ctenizidae): burrow construction, prey capture, and the functional morphology of the peculiar third tibia. *Bull.Br.arachnol.Soc.* **5**(4): 159-165.

COYLE, F. A. 1986: The role of silk in prey capture by nonaraneomorph spiders. *In* W. A. Shear (ed.), *Spiders: webs, behavior, and evolution*: 269-305. Palo Alto, Stanford Univ.

COYLE, F. A. 1988: A revision of the American funnel-web mygalomorph spider genus *Euagrus* (Araneae, Dipluridae). *Bull. Am.Mus.nat.Hist.* **187**(3): 203-292.

DARCHEN, R. 1967: Biologie d'une mygale gabonnaise nouvelle, *Macrothele darcheni* Benoit (Araneida, Dipluridae). *Biologia gabon.* **4**: 253-257.

EBERHARD, W. G. 1967: Attack behavior of diguetid spiders and the origin of prey wrapping in spiders. *Psyche, Camb.* **74**: 173-181.

FOELIX, R. F. 1982: *Biology of spiders.* Cambridge, Harvard Univ.

GÖRNER, P. & ZEPPENFELD, C. 1980: The runs of *Pardosa amentata* (Araneae, Lycosidae) after removing its cocoon. *Proc.Int.Congr.Arachnol.* **8**: 243-248.

HICKMAN, V. V. 1964: On *Atrax infensus* sp. n. (Araneida: Dipluridae), its habits and a method of trapping the males. *Pap.Proc.R.Soc.Tasm.* **98**: 107-112.

KRAFFT, B. 1969: Various aspects of the biology of *Agelena consociata* Denis when bred in the laboratory. *Am.Zool.* **9**: 201-210.

LAING, D. J. 1973: Prey and prey capture in the tunnel web spider *Porrhothele antipodiana. Tuatara* **20**: 57-64.

LAING, D. J. 1975: The postures of the tunnel web spider *Porrhothele antipodiana:* A behavioural study. *Tuatara* **21**: 108-120.

LAING, D. J. 1978: Studies on populations of the tunnel web spider *Porrhothele antipodiana. Tuatara* **23**: 67-81.

LAING, D. J. 1979: Studies on populations of the tunnel web spider *Porrhothele antipodiana* (Mygalomorphae: Dipluridae). *Tuatara* **24**: 1-21.

LEVITT, V. 1961: The funnel-web spider in captivity. *Proc.R.zool. Soc.N.S.W.* **1958-1959**: 80-84.

MCKEOWN, K. C. 1952: *Australian spiders.* Sydney, Angus and Robertson.

NENTWIG, W. 1987: The prey of spiders. *In* W. Nentwig (ed.), *Ecophysiology of spiders*: 249-263. Berlin, Springer-Verlag.

NENTWIG, W. & WISSEL, C. 1986: A comparison of prey lengths among spiders. *Oecologia (Berl.)* **68**: 595-600.

PALMER, J. M. 1985: The silk and silk production system of the funnel-web mygalomorph spider *Euagrus* (Araneae, Dipluridae). *J.Morph.* **186**: 195-207.

PAZ, N. 1988: Ecologia y aspectos del comportamiento en *Linothele* sp. (Araneae, Dipluridae). *J.Arachnol.* **16**: 5-22.

PETRUNKEVITCH, A. 1911: Sense of sight, courtship, and mating in *Dugesiella hentzi*, a theraphosid spider from Texas. *Zool.Jb.* (Syst.) **31**: 355-371.

RAVEN, R. J. 1984: Systematics of the Australian curtain-web spiders (Ischnothelinae: Dipluridae: Chelicerata). *Aust.J. Zool.*(Suppl.Ser.) **93**: 1-102.

RIECHERT, S. E. & LUCZAK, J. 1982: Spider foraging: behavioral responses to prey. *In* P. N. Witt & J. S. Rovner (eds.), *Spider communication: mechanisms and ecological significance:* 353-385. Princeton, Princeton Univ.

SEYFARTH, E.-A. & BARTH, F. G. 1972: Compound slit sense organs on the spider leg: Mechanoreceptors involved in kinesthetic orientation. *J.comp.Physiol.* **78**: 176-191.

STERN, H. & KULLMANN, E. 1975: *Leben am seidenen Faden.* München, Bertelsmann.

STROHMENGER, T. & NENTWIG, W. 1987: Adhesive and trapping properties of silk from different spider species. *Zool.Anz.* **218**: 9-16.

VOLLRATH, F. 1979: A close relationship between two spiders (Arachnida, Araneidae): *Curimagua bayano* synecious on a *Diplura* species. *Psyche, Camb.* **85**(4): 347-353.