

**COURTSHIP AND MATING BEHAVIOR OF  
*THELECHORIS KARSCHI* (ARANEAE, DIPLURIDAE),  
AN AFRICAN FUNNELWEB SPIDER**

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**ABSTRACT**

The courtship of *Thelechoris karschi*, an African funnelweb mygalomorph spider, consists of an early non-contact phase of vibratory signaling and then a contact phase involving leg-fencing and, sometimes, lunging. Eventually the male clasps the female's pedipalps with his first tibial apophyses, tilts her upwards and backwards, and attempts to insert his palpal organs alternately. There was much variation among successful courtships in the amount of aggression (lunging and chasing). Mating was characterized by numerous bouts of unsuccessful palpal insertation attempts, relatively few successful insertations, and a tendency for repeated courtships and copulations. It is pointed out that ample opportunity for sexual selection by female choice exists during these courtships and copulation attempts, and that the lengthy and repeated copulations may be, in part, a consequence of genital anatomy.

**INTRODUCTION**

*Thelechoris karschi* Bösenberg and Lenz is a moderately large diplurid spider (adult body length 11-20 cm) with extremely long lateral spinnerets which are used to build conspicuous, perennial capture webs. The webs consist of a large (up to 1500 cm<sup>2</sup> viewed from above), three-dimensional, exposed capture area of interconnected sheets and passageways funneling into a protected tubular silk retreat, and are located in a wide variety of microhabitats, from rock piles and road banks to tree trunks and shrubs. This species is quite common in some localities and occurs in a wide variety of arid to mesic habitats (except for extreme habitats like desert and wet forest) over a large part of eastern and south-central Africa, from Kenya southwest to Namibia.

Of the 18 currently recognized genera of Dipluridae (Raven 1985; Coyle 1986a), observations of courtship and/or mating have been published for only four: *Microhexura* (Coyle 1985), *Euagrus* (Coyle 1986b), *Australothele* (Raven 1988), and *Phyxioschema* (Raven and Schwendinger 1989). The observations presented herein on the courtship and mating of *Thelechoris karschi* are the first for this genus and its subfamily (Ischnothelinae). A similar study of reproductive behavior in the other two ischnotheline genera (*Ischnothele* and *Lathrothele*) is currently being conducted by the first author.

Our primary objective in this study was to carefully describe the courtship and mating behavior of *T. karschi* to obtain behavioral characters for eventual use in

testing phylogenies. Secondary objectives were 1) to begin testing the hypothesis that the *T. karschi* populations we have been studying are not behaviorally isolated from one another and 2) to propose hypotheses about the functional significance and origins of some of the behaviors observed. We hope this paper will be a stimulus and a useful foundation for future studies.

## MATERIALS AND METHODS

Although the spiders used in this study were collected from the following eight localities in three different areas of East Africa, a preliminary analysis of morphological variation suggests that they all belong to one species, *T. karschi*. The four populations (A-D) from the coast of eastern Kenya are about 130 miles east of population E in Tsavo West National Park in the interior of Kenya. Both of these sets of populations are about 900 miles north of the three populations (F-H) in southern Malawi.

Coastal Kenya: population A - Kilifi and 9 km N Kilifi, 10-50 m elev., old field with scattered trees, shrubs, and hedgerow, 27-29 March 1989; population B - Jimba, 3 km SE Gedi, 100 m elev., second growth forest, 28 March 1989; population C - Shimba Hills Natural Reserve, S Kwale, 330 m elev., camping area in forest patch, 31 March 1989; population D - Shelly Beach Road, few km S Mombasa, 30 m elev., old field with scattered trees, 1 April 1989. Interior Kenya: population E - Tsavo West National Park, Kitani Lodge, 41 km S Mitito Andei, 750 m elev., rock garden, 15 April 1989. Malawi: population F - along Likhubula River at base of Mulanje Mountain, 750-850 m elev., 18 April 1989; population G - 24-26 km N Zomba on route M1, 750 m elev., road bank, 21-22 April 1989; population H - Blantyre, 1000 m elev., yard and garden, 22 April 1989.

In the laboratory each adult male was kept in a clear plastic drinking cup covered with a petri dish lid and nested in an identical cup. A pad of moist cotton between the bottoms of the two cups provided moisture through a hole punched in the bottom of the inner cup. The 17 females used in the study were large (therefore presumably mature) and were active silk-spinners. Each of these constructed a web in an observation arena. One type of arena was a clear plastic shoe box (29 × 15 × 8.5 cm high) with construction paper covering its floor. Either a clear vial was taped to the floor at one end to serve as a retreat or the female was allowed to construct her retreat and capture web in any part of the arena. These webs were misted with water every other day. The other type of arena, resembling an "ant farm" container, allowed for especially close observation of courtship and mating without unduly restricting the participants. It consisted of two panes of glass (15 × 24 cm) separated by a 1.5-3.0 cm thick U-shaped wooden frame mounted upright on a wooden base. The female constructed her web between the panes of glass, a piece of styrofoam plugged the opening at the top of the frame, and water was periodically added to a wet cotton ball in the bottom of the arena. The spiders were maintained at 24°C and a 12-hour photoperiod. They were fed a mealworm (*Tenebrio*) larva approximately once every ten days, and rarely a cricket nymph or a few house flies.

Male-female encounters were initiated by gently dropping the male onto the female web far from her retreat. All encounters occurred between 6 May and 30 June (39 encounters) and 19 and 27 September (six encounters) 1989 during the

daylight period (primarily afternoon hours). Most encounters were recorded with a Panasonic WV-D5000 video recorder equipped with a Micro-Nikkor 55 mm close-up lens. The arenas were lighted from above by fluorescent ceiling lights and a fluorescent desk lamp and sometimes also from the front by a 75 watt incandescent bulb. Actions that were not being recorded through the lens were often recorded verbally on the audio channel of the recorder. Behaviors were analyzed with slow-motion and single frame advance modes (which allowed one second of action to be subdivided into 30 individual stop-action frames).

The spermathecae of 15 *T. karschi* females from several localities in East Africa were removed, cleared in 85% lactic acid, and examined and measured with a compound light microscope at 40X and 100X. The location of sperm and semen (recognized by their granular translucence) was recorded. Some spermathecae were drawn with the aid of a drawing tube. The palpal emboli of twelve males from the same localities were measured at 100X with a stereomicroscope.

## RESULTS

Adult males were moderately common in populations A and C when sampled in late March, just before the onset of the rainy season (late March through May), and were very common (although still seemingly much less abundant than adult females) in population E in mid April, during the rainy season. No adult males were found in populations F, G, and H when they were sampled in late April, after the end of the rainy season (November to April) in southern Malawi. While some adult males were apparently in their own webs, others were in webs with females.

Table 1 summarizes outcomes of the 45 male-female encounters. Ninety percent of all courtships were initiated by the male. Eight of the 16 unsuccessful courtships (those that failed to progress to a copulation attempt) involved non-receptive females which did not perform any courtship signals, one involved an apparently unreceptive male that was briefly courted by the female, and the other seven involved reciprocal courting. In eight of the 14 encounters that led to copulation attempts (A, A, or X in Table 1) (a copulation attempt was defined as all the palpal insertion attempts occurring between the onset of clasping and the subsequent uncoupling event) there were multiple attempts, giving a total of 28 copulation attempts (and thus 28 "successful" courtships) during this study. Only two of the 13 encounters among spiders from coastal Kenyan populations led to mutual courtship, and neither of these led to a copulation attempt. Five of the 14 encounters initiated among population E spiders resulted in successful copulations (X in Table 1) (a copulation was judged successful if at any time the embolus was observed to be fully inserted and palpal flexions moved the female's abdomen; no additional effort was made to determine whether insemination actually occurred). Six successful copulations occurred between individuals from distant populations. Females E11 and E28 and males E3 and E6 each copulated successfully with more than one individual.

Since we have little or no information about the reproductive history of the 21 females used in this study, and since at least some of them had mated before they were collected (four that did not attempt copulation deposited fertile eggs), correlations between observed reproductive success and observed mating behavior are meaningless.

Table 1.—Outcomes of laboratory encounters of male and female *Thelechoris karschi*. Specimen code letters identify populations as described in Methods section. Outcomes indicated by following symbols: O = no courtship behavior; M = male courts briefly; F = female courts briefly; MF = both individuals court, but do not attempt copulation; A = copulation attempted (palpal insertions attempted), but no palpal insertions (A) or uncertain whether insertions occurred (A); X = copulation with palpal insertions. Multiple A's and/or X's indicate multiple copulation attempts in a single encounter. Repeat encounters of same individuals are separated by commas. Asterisks designate encounters that were ended by female attacks.

	MALES												
	Coastal Kenya						Interior Kenya						
	A1	A2	A3	A4	C1	C2	D1	E1	E2	E3	E4	E5	E6
FEMALES													
Coastal Kenya													
A20		M	M*										
A21	M,O	M,M							X,O				
B10	O												
B12	O	O,O	MF										
C12		MF											
D11										O			X
D12					O								
Interior Kenya													
E11											X	X,AAA	X,A,AAA
E17											O*		X,AAA*
E25									MF*	O			
E27							X						
E28						XX							
E29	XA												O*
E30								M*					
E31									F				O
Malawi													
F10		A											
F11				M*									
F14											O		MF
G11											X		MF
H10											A,A*,M*		
H11				MF		O						AA	

Ten (22%) of the encounters were ended by clearly life-threatening attacks by the female (Table 1). Five of these were interrupted early (we removed the male before he was injured) and five (that were not interrupted as quickly) resulted in serious injury to the male, i.e., severed legs (three attacks), a broken leg (one attack), and a severed spinneret (one attack). Six of the attacks occurred early in the encounter, either before any courtship behavior (two attacks) or while the male was courting non-courting females (four attacks). Although three of the other four attacks occurred either after a failed attempt at clasping (one attack) or after copulation attempts (two attacks), none occurred immediately after uncoupling; the fourth attack occurred several minutes after uncoupling as the male moved about the web in the confines of the observation arena.

**Behavioral units.**—The following section describes each of the behavioral units which collectively comprise *T. karschi* courtship and mating behavior.

*Advance*: forward movement which brings one spider closer to the other. Often an advance is an ambulatory advance involving the displacement of all tarsi, but some advances consist only of a shifting forward of the anterior legs or body. Advances may be accompanied by other behavioral units (quivering, twitching, jerking, and tapping). Lunges and chases are special aggressive advances.

*Lunge*: sudden vigorous forward and/or downward thrust of the body toward the other spider with the chelicerae spread apart and the fangs extended. The lunges are stereotyped; they appear to be ritualized attacks which stop short of their target or are sometimes directed slightly to one side of the target. Only one lunging about (E3 × E11) escalated into what approximated a real fight, but neither spider was injured and the courtship eventually culminated in a successful copulation.

*Chase*: very rapid pursuit of the other spider.

*Retreat*: movement which increases the distance between the spiders. It may involve backing away or turning away (which may then continue as forward movement).

*Pause*: interval between two actions when the spider is not moving. Pause postures are variable.

*Quivering, twitching, and body jerking*: vibration-generating appendage (and often body) movements which comprise a continuum. They are sometimes difficult to distinguish from one another and may occur together in the same bout. Twitching is one or a few distinctly separate sudden flexions or extensions of one or more legs and/or pedipalps. Quivering is high frequency, usually low amplitude, continuous twitching. Sometimes quivering involves only one or a few appendages, but usually all legs and appendages are moving simultaneously. Sometimes the entire body, especially the abdomen, quivers. Body jerking is a particularly high amplitude twitching of all legs and pedipalps so that the entire body jerks one or more times in succession. Female body jerking may visibly vibrate the web and the male, even if he is several body lengths from the female.

Bouts which combine quivering, twitching, and even body jerking are common. A courting male often begins low amplitude twitching which gradually increases in frequency and amplitude to become a high amplitude quivering (or rapid twitching). Sometimes a female's legs quiver as she slowly flexes them and then twitch as they are suddenly relaxed and reextended. At other times all her legs and pedipalps twitch simultaneously and then quiver for a while. Sometimes a female whose pedipalps and anterior legs are twitching or quivering will suddenly

shift to body jerking. Often the pedipalps and first legs appear to quiver or twitch with greater amplitude than other appendages. Although quivering, twitching, and body jerking are usually performed when the spider is not advancing, sometimes a female will jerk-walk, jerking and quivering her appendages and body while she walks through the web. Although most quivering, twitching, or body jerking lasts for less than 1 or 2 s, occasionally a bout lasts longer; one especially long bout (48 s) of virtually continuous quivering and body jerking was performed by a female (H10) just before the final leg-fencing bout leading to clasping.

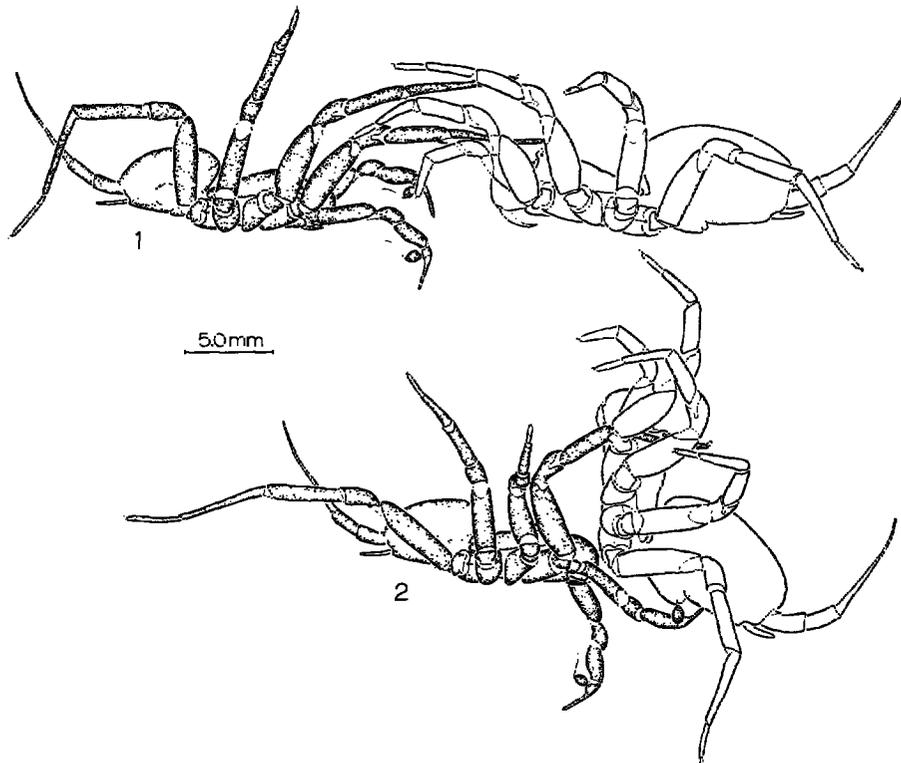
*Tapping*: repeated, rather rapid, non-synchronous lifting and lowering of the pedipalps and first legs so that they contact the web forcefully. Tapping often occurs just prior to or during advances and silk-walking. Sometimes tapping is combined with quivering, or alternates with quivering or twitching bouts, or occurs alone in the same behavioral context.

*Silk-walking*: jerky stop-and-go walk performed by the female during which she periodically applies silk to the web. Silk-walking is often performed directly in front of the male, and may continue all the way back to, and inside, her retreat. Males were observed to briefly spin silk while courting only two times during this study.

*Leg-fencing*: semi-stereotyped sparring of the male with the female. The spiders face one another and lower and raise and flex and extend their first and second legs and pedipalps so that each spider's appendages overlap, move past, and brush against those of the other spider (Fig. 1). During leg-fencing the body is often raised and lowered and the fangs are sometimes extended. The female usually flexes her fencing appendages further, moves them more rapidly, and is more likely to extend her fangs than is the male. The male's legs tend to be more extended and stiffer than those of the female; in general his movements appear less aggressive and more protective than hers. Lunges sometimes occur during leg-fencing. As a fencing bout proceeds, the male's first legs may extend more fully and decrease their movement as they prepare to slide into the clasping position. During fencing the male usually raises and forcibly lowers his pedipalps (more or less alternately) so that the cymbial apophyses punch down into the web. The duration of leg-fencing bouts is quite variable (Table 2), but they usually last less than 6 s.

*Clasping*: The clasping process begins during leg-fencing as the male gradually raises, extends, and stiffens his first legs. He then advances a little to place each of them between the nearest chelicera and pedipalp of the female. The mating apophysis at the end of the male's first tibia (Fig. 1) engages the base of the female pedipalp prolaterally, presumably at either the trochanter or the coxal endite (we were not able to observe the exact point of engagement). After the claspers are engaged, the male continues advancing and tilts the female's cephalothorax up and back. During the clasping process, the male continues the pedipalp tapping/drumming that commenced during leg-fencing.

*Palpal insertion attempts*: Shortly after the clasping male has advanced so that his chelicerae are nearly touching the female's fourth leg coxae, he begins a series of palpal insertion attempts. One pedipalp is lifted into position, fully extended, and rotated (primarily at the coxa-trochanter joint) 100-120° (clockwise for the left and counterclockwise for the right pedipalp) to position the palpal organ above and ectal to the cymbium and close to the female's genital opening (Fig. 2).



Figures 1-2.—Courtship and mating behavior of *Thelechoris karschi*; side view, drawn from video tape and preserved specimens; male dark, female light. Only appendages on near side are illustrated, except for male's left pedipalp. 1, leg-fencing. 2, copulation.

The other pedipalp is held semi-extended below the male. Periodic flexions of the distal three joints of the active pedipalp lift the tibia and tarsus. These and synchronous lateral movements at the patella-tibia joint and 90° twisting movements of the palpal organ at its junction with the cymbium generate probing thrusts (typically about one per s) of the long embolus close to the female's genital opening. A palpal insertion attempt bout consists of a series of these thrusts which are sometimes interrupted by pauses. At the end of a bout the active pedipalp is lowered to the resting position below the male and the other pedipalp is lifted and a new bout of insertion attempts begins.

The following posture characteristics were consistently observed during these palpal insertion attempts (Fig. 2): 1) The male's chelicerae were touching or almost touching the female's fourth coxae. 2) The angle between the male and female cephalothoraxes was 80-100°. 3) The female's pedicel was flexed upwards so that the cephalothorax-abdomen angle was 40-80°. 4) The male's first legs were bent approximately 90° at the femur-patella joint and the distal (clasp) end of each tibia was against the prolatateral surface of each female pedipalp base. 5) The female appeared to be cataleptic (motionless with legs and pedipalps partly flexed) except for occasional quivering or other movements. During some copulation attempts it was possible to see that the female's genital area was distended and the anterior and posterior genital lips were protruding and parted so that the genital opening was more exposed than usual. The male's second legs

Table 2.--Data for the 21 *Thelechoris karschi* courtships and copulation attempts that were video recorded. In the "palp insert" column, N means no palp insertions, Y means at least one insertion bout, and a question mark indicates that we could not be certain whether an insertion occurred. In the "duration" column, "A" is the time from the first courtship behavior to the onset of leg-fencing, "B" is the time from onset of first leg-fencing to clasping, and "C" is the duration of the copulation attempt (from clasping to uncoupling). Range, mean, and standard deviation given for leg-fencing durations. The number of lunges by the male ("M") and the female ("F") are given in the "lunges" column. The "uncouple" column indicates which individual appeared to actively uncouple. Question mark in the leg-fencing or lunges columns indicates that segments of these courtships, and therefore some of these actions, may not have been recorded.

Spiders	Date	Palp insert	Duration (min)			C	Bouts	Leg-fencing		Lunges		Uncouple
			A	B	B			Duration (s)	M	F		
E3XH10	5/15	N?	5.00	6.30	4.95	4	3-18	(8.0 ± 6.8)	15	10	M	
		N?			11.38						F	
E6XE17	5/15	Y	27.10	3.45	6.67	7?	1-10	(6.4 ± 3.1)	7?	12?	MF	
		?	0.07	16.78	3.40	13?	1-18	(4.0 ± 4.6)	15?	22?	M	
		?			< 2.00						M	
		?			6.03							
A2XF10	5/17	?	30.92	0.10	~26.00	1	6		2	1		
E2XB10	5/17	Y			31.10						M	
E6XE11	5/19	Y	9.57	13.18	17.72	17	1-20	(6.9 ± 6.5)	12	36	F	
		N	0.05	1.68	0.47	3	5-6	(5.3 ± 0.6)	1	0	M	
E6XD11	5/23	Y	7.83	46.57	14.08	3	4-12	(6.7 ± 4.6)	0	0	M	
E3XE11	5/23	Y	0.30	0.97	90.73	10	1-47	(16.3 ± 14.1)	10	18	F	
E6XE11	5/30	N	0.08	0.32	1.08	3	1-25	(11.0 ± 12.5)	5	6	F	
		N	0.02	0.53	5.00	1	9		0	0	F	
		Y	0.02	0.53	14.32	2	5,19		0	0	F	
		N	3.50	1.32	5.03	2	1,12		0	0	M	
E3XG11	6/7	Y	19.83	0.17	39.67	1	10		0	0	M	
E5XE11	6/13	Y	0.47	7.00	108.85	2	9,45		0	0	F	
		?	0.02	3.52	4.47	5	7-28	(18.4 ± 7.9)	0	0	F	
		?	0.13	0.28	1.30	1	17		0	0	F	
		N?	0.55	0.15	1.55	1	9		0	0	F	

were either extending upward and outward against the web or upward and forward to lightly contact the female's first or second legs. Male legs III and IV were usually extended (pushing) backwards and outwards against the web. If the spiders were suspended in the web (probably the normal situation), the male's cephalothorax was horizontal or inclined slightly downward and his abdomen was on nearly the same plane. However, if the pair was on solid substrate, the male was typically under the front of the female with his cephalothorax inclined upward at an angle of 35-75° and his abdomen nearly horizontal. During one apparently unsuccessful copulation, the pair maintained this posture (relative to one another) while gradually rotating 110° onto their sides.

A successful insertion bout begins with the insertion attempt movements described above. Then, as the embolus tip enters the genital opening, these earlier movements stop and the three distal palpal joints flex to insert the entire length of the embolus into the opening (Fig. 2). Occasionally the palpus is held motionless in this inserted position for awhile, but more commonly the pedipalp performs repeated pulsing flexions (of the distal joints), each of which visibly pulls and twists the female's abdomen toward the male. During this series of alternate flexions and extensions, the embolus is never withdrawn from the genital opening, indeed its sliding movement within the female genitalia appears minimal. One such series of 20 flexions by an inserted palp lasted 38 s. Another much longer series (274 s) of slower and less regular palpal flexions involved one flexion every 2-5 s.

*Uncoupling*: pulling away of one spider from the other to end the copulation attempt.

Figure 3 summarizes our observations on the sequence of both male and female behaviors during courtship and mating in *T. karschi*. The courtship and mating process can be divided into two phases. Phase I includes non-contact behaviors and phase II includes behaviors which involve contact (or virtual contact) between male and female. Transition from phase I to phase II necessitates an advance into contact. Retreats and chases are transitional behaviors that shift the courtship from phase II back to phase I.

Male activity in phase I is primarily cyclic, i.e., a series of short advances, or quivers then advances, or quivers, with each action separated by a pause of highly variable duration. This cycle of male activity ends when contact with the female leads to leg-fencing and/or lunges (phase II behaviors). Re-entry to this cycle may occur after retreats from contact courtship (phase II). Often, female behaviors (quivers, silk-walking, advances) follow the retreats and appear to trigger a new cycle of male non-contact signaling.

Ninety percent of the time that the spiders advance into contact from phase I behavior, leg-fencing or lunges occur. Sooner or later these phase II behaviors usually lead to retreats back to phase I courtship; only 23% of the leg-fencing bouts we observed led directly to clasping. The number of leg-fencing bouts performed before a courtship proceeded to clasping varied from 1 to 17 (Table 2).

From courtship to courtship, there is much variation in the amount of lunging. Both male and female lunging were common in only 6 of the 17 courtships for which we have complete video records of contact courtship (Table 2). None of the spiders (E3, E6, E11) that mated with more than one mate were consistently aggressive or non-aggressive in all courtships. In two (E6 × E11) of the three encounters with a sequential series of multiple courtships and matings for which

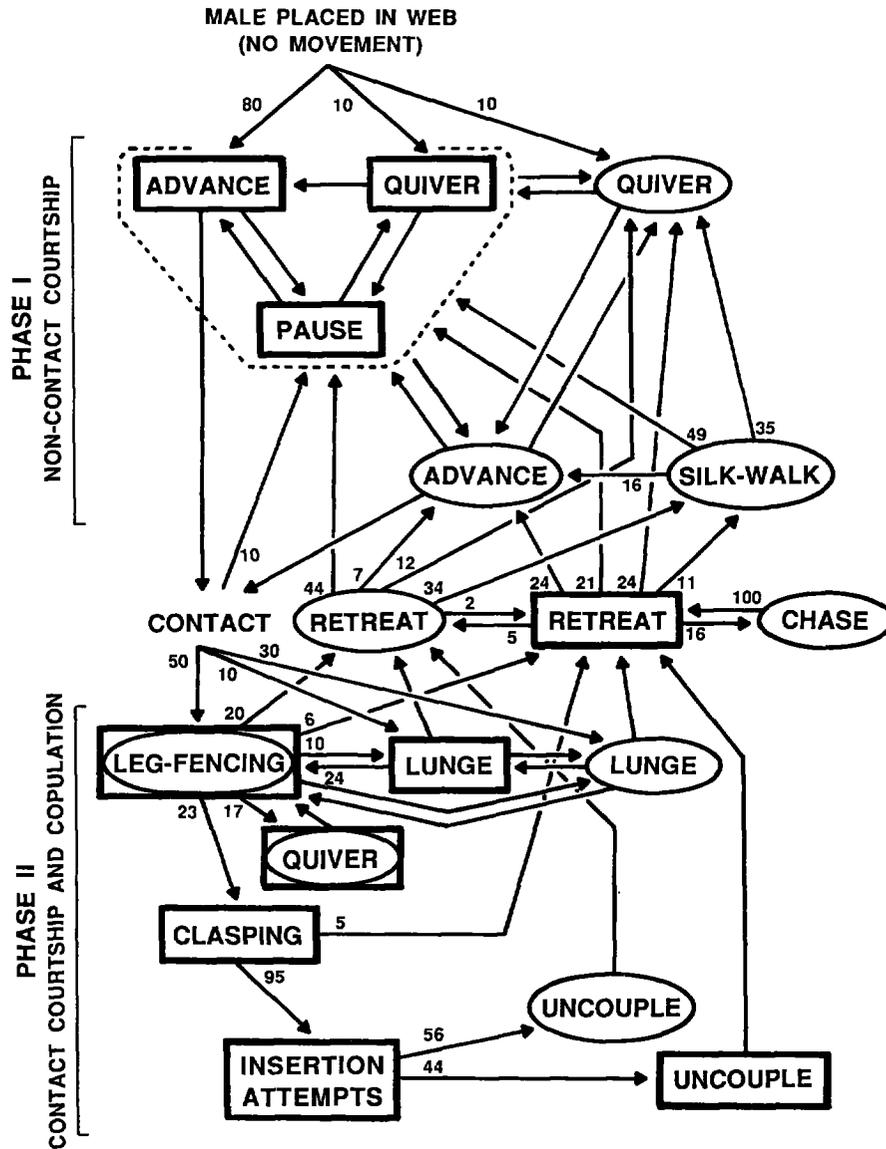


Figure 3.—Summary of the sequence of *Thelechoris karschi* courtship and mating behaviors, based on an analysis of the 21 courtships and copulation attempts recorded on video tape. Male behaviors in boxes; female behaviors in ellipses. Arrows indicate sequence and numbers indicate the percentage of times a particular behavioral unit is followed by another. Quiver boxes and ellipses represent not only quivering, but also related behavioral units commonly associated with quivering; i.e., twitching, body jerking, and some forms of tapping. Although both male and female frequently pause during courtship and mating, only the male pauses which occur repeatedly during the non-contact phase of courtship are included in this diagram.

we have complete video records, there was a drastic decrease in lunges after the first courtship of each series; the other such encounter (E5 × E11) involved no lunging. The courtship lunging of female E11, which mated successfully on four different days during a four-week period, decreased gradually and drastically during that period.

Overall, we observed 105 female and 67 male lunges. In four of the six courtships with many lunges, females lunged considerably more often than males. The amount of lunging tends to be correlated with the amount of leg-fencing, which is a consequence of the fact that lunges tend to precede, follow, and/or be nested within leg-fencing bouts. A higher proportion of female lunges (71%) than male lunges (37%) were nested in leg-fencing; females lunged 3.2 times more often than males during leg-fencing. The male lunge box and female lunge ellipse in Fig. 3 represent individual lunges or bouts of repeated lunges that were not nested within a leg-fencing bout. Although lunges are sometimes followed by full retreats from contact courtship, most lunges are followed by other lunges or leg-fencing; these lunges usually cause the other spider to momentarily reel backward, but we did not count this as a retreat since the spider rebounds instantly. Sometimes lunging was reciprocal; sometimes it was not, with two or more female lunges (common) or two or more male lunges (less common) in succession. Chasing, which occurred only in courtships with much lunging, was performed only by females.

The transition from leg-fencing to clasping to palpal insertion attempts occurs rather quickly. The clasper positioning process lasts from 2 to 15 s (mean = 5.4, SD = 2.9  $N = 17$ ) and the period between the completion of clasper attachment and the first palpal insertion attempt lasts from 1 to 30 s (mean = 6.8, SD = 6.7,  $N = 16$ ). Following the onset of clasping, female leg-fencing rapidly decelerates and shifts to quivering so that by the first palpal insertion attempts, she exhibits the typical cataleptic copulatory posture (Fig. 2). The only time this did not occur was when a male (E6) was clasping the female (E17) abnormally (with only his left first leg); she extended her fangs and pushed him away while he was reaching with his pedipalps to initiate insertion attempts.

The recorded courtships and copulation attempts varied widely in duration (Table 2). Successful copulations were significantly longer ( $N = 8$ , range = 6.67–108.85 min, mean = 40.39, SD = 38.4) than the clearly unsuccessful copulation attempts ( $N = 4$ , range = 0.47–5.03 min, mean = 2.90, SD = 2.5) and the copulation attempts of questionable success ( $N = 9$ , range = 1.30–26.00 min, mean = 6.79, SD = 7.8) ( $P < 0.01$ , Mann-Whitney  $U$ ).

Unsuccessful copulation attempts consisted of a series of unsuccessful palpal insertion attempt bouts and occasional pauses within bouts or between bouts when neither pedipalp was moving (usually both pedipalps were lowered). Even within one copulation attempt, these insertion attempt bouts varied considerably in duration. For example, in one apparently unsuccessful copulation attempt (E3 × H10) there were 22 bouts of unsuccessful insertion attempts and these bouts ranged from 2 to 34 s (mean = 10.5, SD = 7.4) in duration.

Successful copulations involved bouts of unsuccessful palpal insertion attempts and one or more bouts with successful insertions. These successful insertion bouts did not occur at the beginning of a copulation, and were more common during the second half than during the first half of a copulation attempt. Successful insertion bouts typically lasted longer (range = 58–277 s, mean = 111.8, SD =

68.0,  $N = 13$ ) than unsuccessful bouts (range = 2-87 s, mean = 18.0, SD = 19.5,  $N = 35$ ) ( $P < 0.01$ , Mann-Whitney  $U$ ). Marked left-right asymmetry in palpal insertion attempts was observed in two successful copulation attempts ( $E6 \times E11$ ,  $E3 \times E11$ ); in both cases the left palp became tangled in silk and only the right palp (with longer insertion attempt bouts than the left) achieved successful insertions. Since it was not possible to observe every insertion attempt bout carefully enough to determine whether it was successful, we could not determine the ratio of successful to unsuccessful insertion bouts for the seven successful video-recorded copulation attempts (Table 2).

During a few of the copulation attempts, the male occasionally shifted his legs and body and moved the female, usually pushing her further upwards and backwards. During nearly all the copulation attempts, the female was motionless except for occasional quivering of her legs and pedipalps. On only three or four occasions during the 21 copulation attempts we observed did the female perceptibly shift her legs and body position. Female quivering was most likely to occur at the very beginning of a copulation period, during pauses within or between palpal insertion attempt bouts, and was more common during unsuccessful copulations than during successful ones. The longest and most intense female quivering (three long periods of especially high amplitude whole-body quivering) occurred during one short (4.47 min) unsuccessful copulation attempt ( $E5 \times E11$ ).

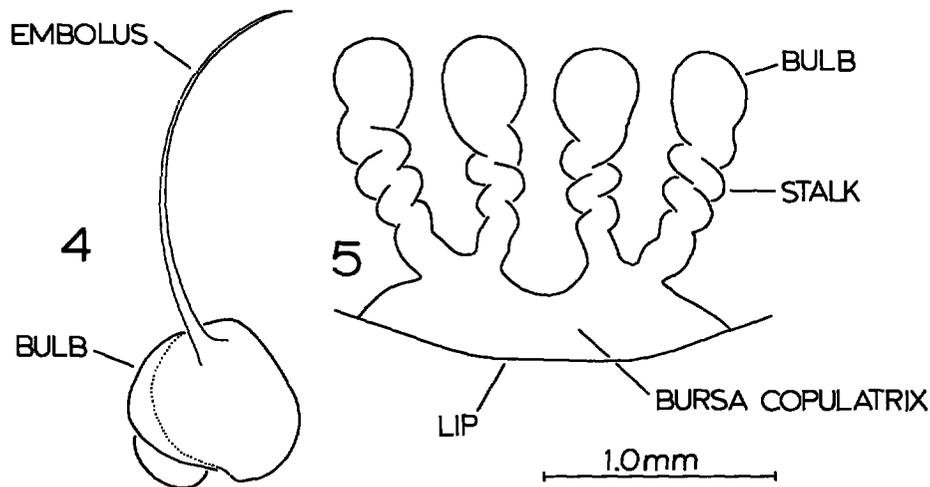
Approximately equal numbers of male uncouplings and female uncouplings followed both successful and unsuccessful copulations (Table 2). None of the uncouplings was followed immediately by a female attack. Following three of the male-initiated uncouplings, the female remained cataleptic for at least 2 s.

A survey of the structure of the palpal organ and spermathecae of *T. karshci* demonstrates that the embolus, when fully inserted into the genital opening during the successful insertion attempts described above (Fig. 2), should extend far into one of the four spermathecal stalks and possibly into the bulb (Figs. 4, 5). The curved, slender, and semi-flexible nature of the embolus may permit it to conform to the lumen of the spiraled spermathecal stalk as it is inserted and/or the stalk may be flexible enough to uncoil at least partly during this insertion. Of the eight females with sperm, five had all four spermathecal stalks and bulbs filled; the other three each had one stalk/bulb unit empty of sperm and the other three filled.

## DISCUSSION

Our field data hint that male maturation in *T. karschi* may be regulated so that mating occurs just before or during the rainy season, but the Humboldt Museum (Berlin) collection contains a large number of males collected in 1907 by Scheffler just 40 miles north of population E between July and October in the dry season. The apparent high ratio of adult females to adult males observed in population E during the breeding season is probably characteristic of mygalomorph spiders in general and may, because of the increased mating opportunities for males, have important effects on their courtship and mating strategies (Coyle 1986b).

Although we did not design this study to test rigorously for behavioral isolation among the populations observed, two results provide support for the hypothesis that these populations are conspecific: 1) the absence of obvious



Figures 4-5.—Male and female genital organs of *Thelechoris karschi* drawn to same scale. 4, left male palpal organ, ventral and slightly retrolateral view with the embolus in horizontal plane. 5, female genitalia showing outline of anterior genital lip, bursa copulatrix, and the four spermathecae with coiled stalks and bulbs in horizontal plane.

differences in courtship signals among the males (populations A, C, D, and E) and females (populations B, D, E, F, G, and H), and 2) the presence of palpal insertions between individuals from populations A and E, B and E, C and E, D and E, and E and G. The low frequency (31%) of encounters resulting in copulation attempts is perhaps not surprising in view of the unknown and surely varied reproductive histories of the subjects, the 2- to 23-week hiatus between collection and observation, and the lack of strictly natural conditions.

The possible functions and origins of the courtship behavior patterns of *T. karschi* deserve comment. The male quivers and advances are probably distinct enough from prey struggles to generate vibrations that inhibit the predatory response of receptive females, and the female quiver response appears to encourage the male to continue courting. Such vibratory courtship signals are common among spiders and may, as Robinson and Robinson (1980) suggest, be ritualized conflict behaviors shaped from locomotor hesitancy in situations where both attack and flee control centers are active. Lunging appears to be ritualized agonistic behavior and, as we suggest later, may play a role in assessment of male fitness. The same may be true of leg fencing, but its function and origin might be more closely linked to clasping behavior. The female silk-walk, which appears to foster renewed male courting after a retreat from contact courtship, might be ritualized web maintenance behavior. Clasping, a male mating behavior widespread among mygalomorph taxa, may serve to protect the male, to position and steady the mating pair for more effective sperm transfer, and/or to convince the female to permit palpal insertions (Eberhard 1985; Coyle 1986). The rejection of male E6's palpal insertion attempt by female E17, when only one of his two clasping legs was positioned properly, supports the third function. Clasping may be a ritualized form of the defensive rearing response common to virtually all mygalomorphs. Male palpal tapping during leg fencing and clasper positioning may help convince the female to permit clasping.

A number of the courtship and mating behavior units of *T. karschi* are similar in form, context, and presumably function (and are perhaps homologous) to behaviors observed in one or more of the four other diplurid taxa whose courtship and mating behaviors have been described (*Microhexura montivaga* (Coyle 1985), *Euagrus* (Coyle 1986b), *Australothele jamiesoni* (Raven 1988), and *Phyxioschema suthepia* (Raven and Schwendinger 1989)). Males of at least the first three of these taxa rely upon similar vibratory signals, especially jerking and quivering. The "jerking bouts" of *M. montivaga*, the "jerk-quivers" of *Euagrus*, and the body jerking and anterior leg-trembling behavior of *A. jamiesoni* involve more vigorous up and down motion of the whole body and are more stereotyped than the quivering and twitching patterns of *T. karschi*. Perhaps the tapping/drumming of pedipalps by *T. karschi* males is homologous to the pedipalpal drumming performed by *A. jamiesoni*. Leg fencing appears similar to the "leg-grappling" of *M. montivaga*, and resembles the onset of clasping in *Euagrus* and *A. jamiesoni*. The drumming and quivering of pedipalps and first legs by *Euagrus* females occurs in the same context (serves the same function?) as the tapping, quivering, twitching, and jerking behavior of *T. karschi* females. Behavior resembling the silk-walking of *T. karschi* females has been observed during unsuccessful *M. montivaga* courtships but not at all in *Euagrus* or *A. jamiesoni*. The mating posture of *T. karschi* is the front-to-front posture typical of non-araneomorph spiders; in its details it is much more similar to that of *M. montivaga* than to the postures observed in *Euagrus*, *A. jamiesoni*, and *P. suthepia*, all of which employ mating clasps found on the male's second leg. The female catalepsis and alternate palpal insertion attempts characteristic of *T. karschi* copulation attempts were observed in *M. montivaga* and *Euagrus* (catalepsis) and in *M. montivaga* and *A. jamiesoni* (alternate insertions).

It is important to realize that the risk to *T. karschi* males of female-inflicted attacks and injury is probably lower in nature than in the confines of a mating arena. Although the data suggest that males are at risk during all stages of courtship and mating, from the time they enter the female's web until they depart, they also indicate that *T. karschi* males are not in as much danger of attack immediately after uncoupling as are the males of *Euagrus* and *P. suthepia* (Coyle 1986b; Raven and Schwendinger 1989).

The occurrence of both aggression-rich and aggression-poor successful courtships in *T. karschi* is of particular interest. Although the aggressive behaviors (lunging and leg-fencing) appear to be ritualized and therefore not very risky, they may increase the cost (in time and energy) of aggression-rich courtships when compared to the aggression-poor courtships. The proclivity of *T. karschi* males to lunge at females and to continue or resume courting in spite of female lunges and chases is a phenomenon not yet observed in other diplurids (Coyle 1985, 1986b, in prep.; Raven 1988). Perhaps these hawk-like interactions are fostered by females (who tend to lunge more often than the males) and serve to test the males' fitness. The sudden drastic decrease of aggression twice observed in the second consecutive courtship of a pair (E6 × E11) might indicate that once a male has "convinced" a female that he is fit, she no longer tests him. Possibly leg fencing bouts constitute a more highly ritualized test of aggressive fitness than lunges, and supply the female with adequate fitness information in those courtship encounters devoid of lunges. Alternatively, it may be true that the observed variation in aggression is the result of variation in female receptivity

caused by habituation or other factors not necessarily related to sexual selection by female choice.

The observed willingness of female *T. karschi* to accept copulation attempts from more than one male is a prerequisite for sexual selection of male anatomical and behavioral traits associated with clasping and copulation (Eberhard 1985). Our observations that a female may reject a male which has not "properly" clasped her (E6 × E17) and that palpal insertion attempts often do not lead to successful insertion are consistent with Eberhard's hypothesis that sexual selection by female choice commonly occurs during copulation attempts. It is possible that the female, even though largely cataleptic, may be providing mechanical challenges to the male's copulatory ability, monitoring his performance, and adjusting her behavior and/or physiology to maximize her fitness. If this is not happening, it seems even harder to understand why such a large fraction of palpal insertion attempts are unsuccessful and why females sometime quiver during pauses in male activity within copulation attempts.

The ability of *T. karschi* males to attempt copulations repeatedly over a period of days with different females is consistent with the apparent high ratio of adult females to adult males, with observations of other diplurids (Coyle 1985, 1986b, in prep.), and with the general pattern of male promiscuity in animals. It is not so easy, however, to understand why males which have achieved successful insertions in one copulation bout will continue to court and attempt additional copulations with the same female unless sperm is not always transferred during a successful insertion or unless, as our observations suggest, a single successful insertion (and sperm transfer) bout is not sufficient to fill all four of his mate's spermathecae. If either or both of these constraints exist, a large number of copulation attempts might be required to fill her spermathecae sufficiently to 1) fertilize all of her eggs and/or 2) inhibit her motivation to mate with other males (and, therefore, to guarantee his paternity).

We suspect that the mechanics of sperm transfer in *T. karschi* make it difficult for a male to fill all four of a female's spermathecae in one copulation attempt. Given the long embolus, the dimensions of the bursa copulatrix and spermathecae (Figs. 4, 5), the observation that the entire embolus is inserted, and the observation that the embolus is not withdrawn during an insertion bout, each successful palpal insertion bout can probably deliver sperm to only one of the four bulbs. Add to this the additional possibilities that 1) the male may have difficulty directing the embolus tip into a particular unfilled stalk at will and 2) the right pedipalp is probably designed to insert into the pair of spermathecae on one side and the left pedipalp into the other pair, and it becomes even more apparent why it might normally take more than one copulation attempt for a male to fill all four spermathecae.

In general, our observations of *T. karschi* behavior suggest that the functions of courtship may continue to be performed after the onset of clasping and during the copulation attempt that follows. The large amount of copulatory effort required per successful insertion may be partly the result of this spider's genital morphology or of female testing of male copulatory performance or both. Clearly much more information is needed about the physiology and functional morphology of reproduction and about the behavioral ecology of natural populations of this species before our observations can be understood and the questions they have generated can be answered.

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