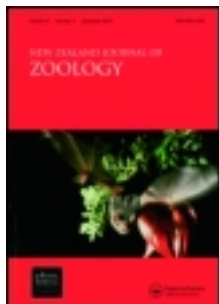


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Complex display behaviour of *Evarcha culicivora*, an East African mosquito-eating jumping spider

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Abstract *Evarcha culicivora*, an East African jumping spider (Salticidae), is an unusual predator because it feeds indirectly on vertebrate blood by choosing blood-carrying mosquitoes as preferred prey. It also associates with particular plant species, *Lantana camara* and *Ricinus communis*. Here we document this species' exceptionally complex display repertoire. In common with many other salticids, *E. culicivora* exhibits pronounced courtship versatility, with males using different tactics depending on the female's location and state of maturity. However, in contrast to most other salticids that have been studied, the males and the females of *E. culicivora* are both active at initiating and sustaining courtship, and both sexes are cannibalistic. Contrary to the emphasis in the literature on female spiders eating males, females of *E. culicivora* run a higher risk of being killed by males than vice versa

during courtship. *E. culicivora* males also differ from other salticids that have been studied by adopting pronounced copulatory courtship. Male-female interactions of *E. culicivora* are especially complex when encounters are in the foliage of *L. camara* and *R. communis*.

Keywords copulatory courtship; courtship; Salticidae; sexual cannibalism; spiders

INTRODUCTION

Most spiders have eyes that lack the structural complexity required for acute vision (Homann 1971; Land 1985), but salticids have a pair of distinctively large forward-facing anterior-medial eyes that support exceptional spatial acuity (Land 1969a,b; Williams & McIntyre 1980; Blest et al. 1990; Harland & Jackson 2004). Not surprisingly, the most elaborate vision-based display behaviour known for spiders (Foelix 1996), and among the most elaborate ever described for any animal group, is found in this family (Crane 1949; Jackson 1982a; Jackson & Pollard 1997; Maddison & Hedin 2003).

Here we provide the first detailed account of how conspecific individuals of *Evarcha culicivora* Wesolowska & Jackson interact during courtship (male-female interactions) and during same-sex interactions. This East African jumping spider (Araneae, Salticidae) is an unusual predator because it feeds indirectly on vertebrate blood by choosing blood-carrying mosquitoes as preferred prey (Jackson et al. 2005; Nelson et al. 2005; Nelson & Jackson 2006) and it is also an unusual spider because it associates with, and feeds on the nectar of, *Lantana camara* L. and *Ricinus communis* L., plant species that grow wild in the same habitat. *Ricinus communis* (family Euphorbiaceae), is native to tropical Africa (Cronk & Fuller 1995), but *Lantana camara* (family Verbenaceae) is native to tropical and subtropical America and has been introduced to many parts of the world as an ornamental plant (Ghisalberti 2000), including East Africa.

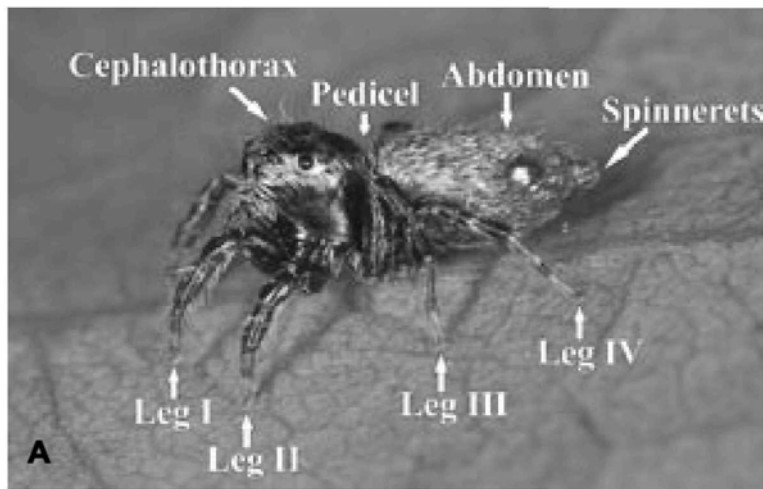
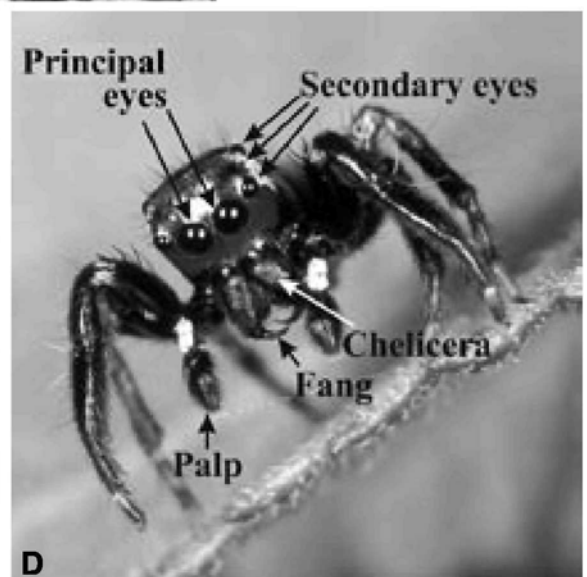
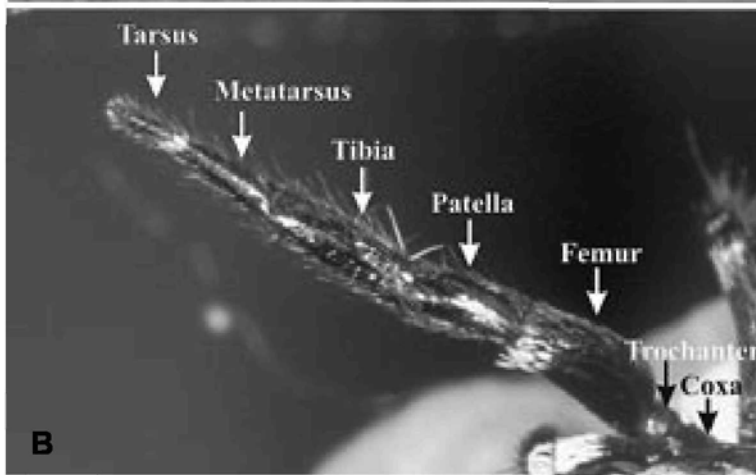


Fig. 1 Male and female of *Evarcha culicivora*, showing anatomical detail important for describing behaviour. **A**, Adult female (facing left) in normal posture showing location of body parts and appendages. **B**, Leg, showing segments. **C**, Palp, showing segments. Note: leg and palp segmentation similar, except for palps having no metatarsi. **D**, Adult male (facing forward) showing eyes, palps, chelicerae and fangs (partially extended). Clypeus ("face") blood red. White patches on carapace immediately behind principal eyes and palp tibia.



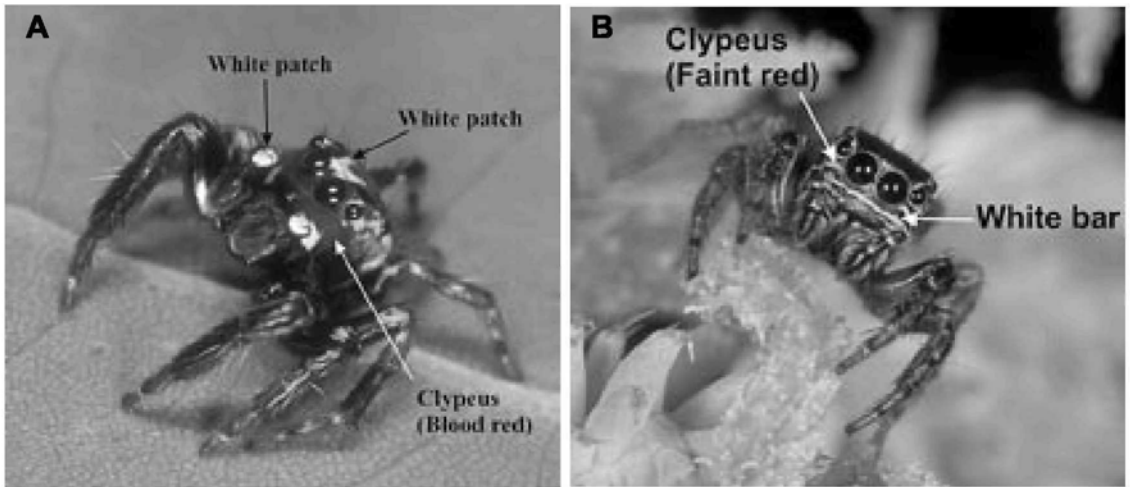


Fig. 2 *Evarcha culicivora* with palps in frontal posture. **A**, Male (facing 45° to left). Face blood-red. White patches above principal eyes, at side of clypeus and on palp tibia. Note: apparent white patch on the leg is an artefact in this photograph from reflected light. **B**, Female on *Ricinus communis* (facing forward). Face with faint red tinge. White bar at bottom of clypeus.

Our objective is primarily qualitative baseline information as a foundation for ongoing work on how *E. culicivora*'s unusual diet and its unusual affinity for particular plant species interrelate with mate-choice behaviour, display function, tactical design and selective attention. We also consider how *E. culicivora*'s intraspecific interactions relate to our understanding of salticid display behaviour in general.

MATERIALS AND METHODS

Our field site was at the Thomas Odhiambo Campus (TOC) of the International Centre of Insect Physiology and Ecology (ICIPE) (Mbita Point, western Kenya). Mbita Point is 1200 m above sea level (0°25'S–0°30'S by 34°10'E–35°15'E) and has a mean annual temperature of 27°C. Laboratory work was carried out at the TOC and at the University of Canterbury (UoC) using cultures established from individuals collected at Mbita Point (for standard salticid-laboratory procedures, see Jackson & Hallas 1986) (for anatomical details that are important for describing behaviour, see Fig. 1 and 2). *E. culicivora*'s laboratory-rearing environment was enriched (see Carducci & Jakob 2000), as we used spacious cages (90 × 90 × 125 mm) with a mesh work of twigs (not from *Lantana* or *Ricinus*) within each cage. A water-logged cotton roll was always

present in each spider's cage, and all spiders were fed to satiation on "lake flies" (non-biting midges from the families Chaoboridae and Chironomidae) and on blood-fed female mosquitoes (*Anopheles gambiae* ss) three times a week (Jackson et al. 2005).

Adult males (Fig. 1D and 2A), adult females (Fig. 1A and 2B), and all juvenile stages of *Evarcha culicivora* have grey-brown bodies (Wesolowska & Jackson 2003), but adult males are distinctive because of their blood-red faces and white-hair patches on and around their faces (Fig. 1D and 2A). These white patches are usually, but not always (see Fig. 3) absent from adult females and juveniles. Juveniles have grey-brown faces. The faces of adult females are also grey-brown, but with a faint red tinge. Body lengths of adults are variable (males, 3–6 mm; females, 4–7 mm; see Cross et al. 2007).

Except where stated otherwise, our summaries are for interactions between individuals that were similar in size (i.e., body lengths matched to the nearest mm). Hereafter, unless otherwise specified, the shorter expressions "male" and "female" will be used for "adult male" and "adult female". Earlier convention (Jackson & Hallas 1986) is adopted for indicating frequencies of occurrence: "usually", "often", "typically" and "typical" indicate c. 80% or more; "sometimes" and "occasionally" indicate 20–80%; "infrequently", "rarely" and "on rare occasions" indicate 20% or less.



Fig. 3 *Evarcha culicivora* female (facing forward and slightly up and to left) with palps in normal posture. Small white patch above principal eyes.

A “bout” is a period of continuous performance of a particular behaviour pattern (e.g., a bout of palp waving is a period of continuous up-and-down motion of a palp, which may include numerous complete cycles from the most dorsal to the most ventral position and back). “Amplitude” is the distance between the extreme positions in a movement sequence (e.g., for palp waving, the distance between the most dorsal and the most ventral position). The first major segment distal to the joint being articulated is referred to when specifying the site of an appendage’s movement (e.g., femoral movement: coxa-trochanter joint).

The following example illustrates how the terms “matching phase”, “alternating phase” and “irregular phase” are used. When two palps are waving dorso-ventrally at the same time, they are referred to as being in “matching phase” if both are in their most dorsal positions simultaneously. If one palp is in the most dorsal position when the other is in the most ventral position (phase difference 180°), they are “alternating”. Irregular phasing is anything between matching and alternating.

Encounters between spiders were staged by putting one spider in the presence of another. We staged male-female encounters, as well as encounters of males with subadult females (subadult: juvenile one moult away from maturity). Male-female encounters were staged with and without a nest present (with the male or with the female the resident of the nest). We also staged female-female and

male-male interactions, each with and each without a nest present. However, as males were reluctant to stay inside nests, it was particularly hard to observe interactions in which males were the nest residents.

By definition, an encounter began when one spider fixated the gaze of its principal-eye corneas on the other spider, or on the other spider’s nest, and then either maintained fixation for at least 30 s or else began displaying. One spider walking on to the nest of another spider was another criterion for the beginning of an encounter. When an encounter failed to ensue within 30 min, the test was terminated. By definition, interactions began when the spiders began to adopt display behaviour (see below), whereas interactions ended when one spider fled and the other spider failed to watch or follow it for the next 60 s.

Besides staging encounters inside bare cages (“no-plant tests”), as in earlier salticid studies (Jackson & Pollard 1997), we also staged male-male, female-female and male-female interactions (all in the absence of nests) on *L. camara* and *R. communis* (“plant tests”). Plant tests were staged in two ways: (1) leaves and flowers of *L. camara* were placed inside a cage; (2) the spiders were put together on potted *L. camara* or *R. communis* plants sitting on a laboratory bench in the open. All sex-age classes readily walked on to the cuttings and on to the potted plants, and *E. culicivora* was especially inclined to settle on the flowers of *L. camara*, seeming reluctant to leave even when prodded aggressively with a small paint brush.

For staging an interaction inside a cage, with or without a plant present, one spider (the “intruder”) was introduced through a hole (diameter 10 mm; plugged with rubber stopper) into a cage already occupied by another spider (the “resident”). For staging an interaction on a plant in the open, first the resident was put on the plant and then, 60 min later, the intruder was put on the plant 15–20 mm away from the resident.

Individuals were chosen at random from the laboratory stock, but no individual was used more than once in any one type of interaction (Table 1). Whether an individual spider was the intruder or the resident was decided at random.

Two broad groupings of behaviour are considered: (1) behaviour that was prevalent during encounters between individuals of *E. culicivora* but also prevalent in other circumstances (“general behaviour”); (2) behaviour that was seen largely, if not exclusively, during encounters between individuals

Table 1 Number of each type of interaction observed for *Evarcha culicivora* during same-size tests (i.e., to nearest millimetre, two individuals matched in body length) and different-size tests (i.e., one individual, in body length, at least 2 mm larger than other individual).

	Same-size tests			Different-size tests	
	No. of encounters	No. of interactions		No. of encounters	No. of interactions
Male-female in bare cage; no nest present; resident is female	778	764 (98%)	Male-female in bare cage; no nest present; resident is female; resident is larger	280	277 (99%)
			Male-female in bare cage; no nest present; resident is female; resident is smaller	259	245 (95%)
Male-female in bare cage; no nest present; resident is male	517	485 (94%)			
Male-female in bare cage; nest present; resident is female	781	739 (95%)	Male-female in bare cage; nest present; resident is female; resident is larger	180	160 (89%)
			Male-female in bare cage; nest present; resident is female; resident is smaller	149	136 (91%)
Male-female in bare cage; nest present; resident is male	367	342 (93%)			
Male-female in cage with <i>Lantana camara</i> ; resident is female	263	248 (94%)	Male-female in cage with <i>L. camara</i> ; resident is female; resident is larger	138	131 (95%)
			Male-female in cage with <i>L. camara</i> ; resident is female; resident is smaller	160	154 (96%)
Male-female in cage with <i>L. camara</i> ; resident is male	283	256 (90%)			
Male-female on potted <i>L. camara</i> ; resident is female	263	251 (95%)	Male-female on potted <i>L. camara</i> ; resident is female; resident is larger	161	147 (91%)
Male-female on potted <i>R. communis</i> ; resident is female	230	206 (89.6%)	Male-female on potted <i>Ricinus communis</i> ; resident is female; resident is smaller	170	156 (92%)
Male-female on potted <i>L. camara</i> ; resident is male	270	250 (93%)			
Male-male in bare cage; no nest present	728	713 (98%)	Male-male in bare cage; no nest present; resident is larger	280	272 (97%)
			Male-male in bare cage; no nest present; resident is smaller	265	251 (95%)
Male-male in bare cage; nest present	235	222 (94%)			
Male-male in cage with <i>L. camara</i>	327	315 (96%)			
Male-male on potted <i>L. camara</i>	263	250 (95%)			
Male-male on potted <i>R. communis</i>	220	191 (86.8%)			
Female-female in bare cage; no nest present	354	335 (95%)	Female-female in bare cage; no nest present; resident is larger	189	170 (90%)
			Female-female in bare cage; no nest present; resident is smaller	165	158 (96%)
Female-female in bare cage; nest present	291	255 (88%)			
Female-female in cage with <i>L. camara</i>	236	215 (91%)			
Female-female on potted <i>L. camara</i>	250	234 (94%)			
Female-female on potted <i>R. communis</i>	199	171 (85.9%)			

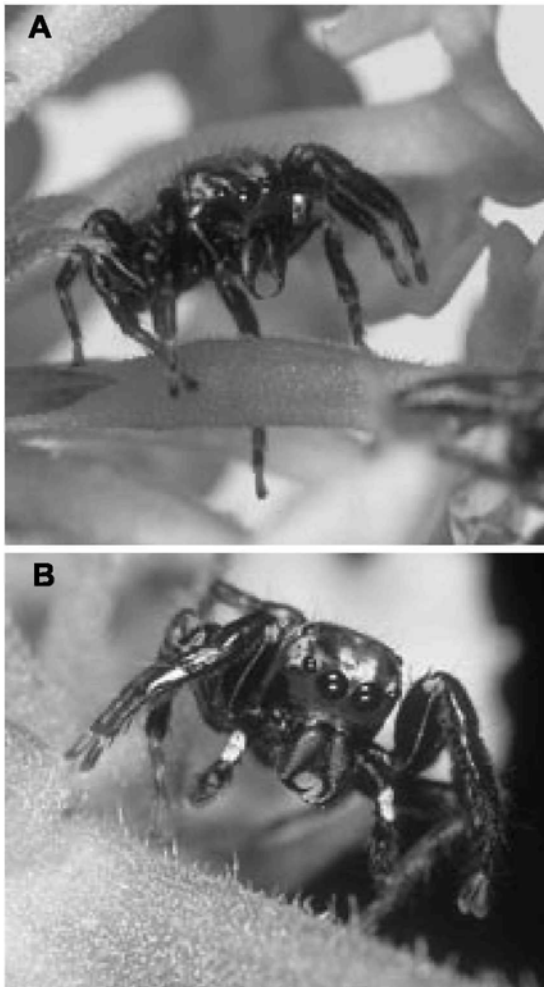


Fig. 4 *Evarcha culicivora* male on *Lantana camara* (facing slightly to right). Posturing with legs arched and chelicerae opened. **A**, Fangs fully extended (i.e., pointing perpendicular down to substrate). Palps in high retracted posture. **B**, Fangs partially extended (held about parallel with substrate). Palps lowered.

of *E. culicivora*. Besides mating behaviour, the second grouping includes behaviour with an apparent communication function (“displays”).

Data were analysed using chi-square tests for goodness of fit (null hypothesis: probability of making one of the two choices same as probability of making the other choice), chi-square tests of independence and Mann-Whitney U-tests (see Howell 2002).



Fig. 5 *Evarcha culicivora* male (facing right) mounted (standing over female) and leaning across right side of the female's flexed-up and rotated abdomen. Female facing left with her cephalothorax lowered (almost touching substrate). Male stroking with his right leg I.

GENERAL BEHAVIOUR

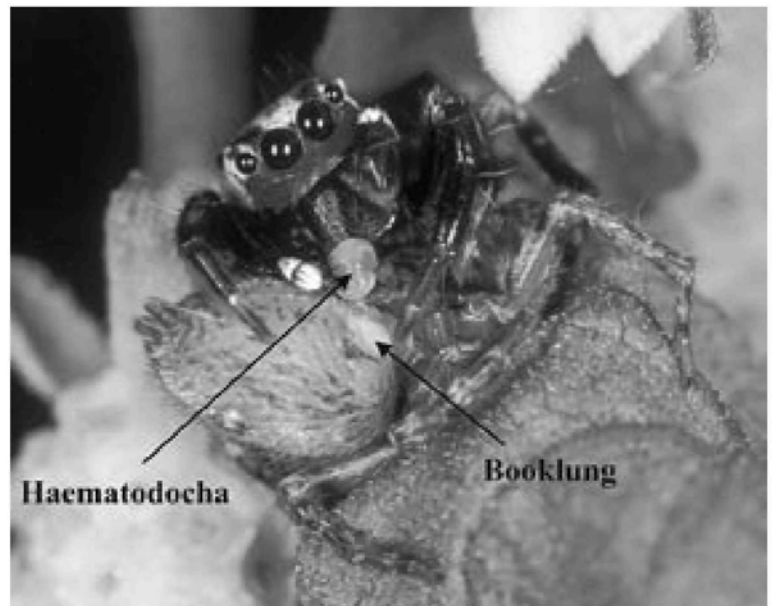
Quiescent individuals of *E. culicivora* typically rested on or close to the ground, usually hidden by tall grass or other vegetation and usually near tree trunks or the walls of buildings. They were also found in concealed places around the inside walls of houses (e.g., behind furniture or in spaces around window panes). Active individuals frequented open spaces on tree trunks as well as on the inside and outside walls of buildings.

In the normal body posture, the spider's body was parallel to, and only 0.5–1 mm above, the substrate. Legs were loosely flexed at various joints, and the abdomen was usually aligned with the cephalothorax (Fig. 1A).

In the normal palp posture (Fig. 3), the palps hung loosely down in front of the spider's chelicerae, with femur-patella joints flexed so that the tarsi were about parallel to each other and perpendicular to the substrate.

During normal locomotion, *E. culicivora* walked in a rapid stop-and-go fashion (e.g., stepping for 0.5 s, pausing for 0.5 s, etc), as is typical of most salticids. If severely provoked (e.g., by a researcher attempting to catch it), *E. culicivora* usually moved away rapidly, sometimes making repeated leaps combined with running. However, compared with most salticids, *E. culicivora*'s normal disposition seemed unusually calm (e.g., compared with many other salticids, *E. culicivora* was less easily provoked

Fig. 6 Male-female pair of *Evarcha culicivora* copulating. Male facing forward, leaning over female's carapace, with tarsi of legs I on ventral surface of female's rotated abdomen. Female's abdomen flexed up and rotated, with cephalothorax lowered (touching substrate). Male's palp applied to female's epigynum (plate on female's anterior ventral abdomen with three pores, one for oviposition and two for receiving sperm from male's two palpal organs), with haematodocha (membranous portion of palpal organ that inflates during sperm transfer) fully inflated and obscuring view of epigynum in this photograph.



into fleeing when being moved about in the course of laboratory observations).

A distinctive predatory posture (legs pulled in close to the body and body being lowered close to, if not touching, the substrate) normally preceded leaping on prey, and often preceded leaping on a conspecific individual.

A spider postured with opened chelicerae (Fig. 4) by holding the basal segments of the chelicerae spread apart (two chelicerae making angle of 45–90° to each other), typically with fangs extended. The degree of fang extension was highly variable. Fully extended: fangs pointing almost straight down (Fig. 4A). Partially extended: any extension of fangs short of fully extended (Fig. 1D and 4B).

POSITIONING OF CEPHALOTHORAX, ABDOMEN AND BODY

When a spider's cephalothorax was raised (Fig. 4B), it was held higher than normal above the substrate, with its anterior end sometimes tilting up 10–45°. When the spider's cephalothorax was lowered, its ventral surface was positioned no more than 1 mm above (Fig. 5), if not touching (Fig. 6), the substrate.

When the spider's abdomen was flexed down (Fig. 7), the spinnerets nearly or actually contacted the substrate, with the angle between the abdomen and substrate being 45–90° (i.e., the abdomen was



Fig. 7 *Evarcha culicivora* male swaying. Legs I and II 90° to body, with tarsi off substrate, palps lowered and abdomen flexed down. Leaning to his right. Viewed from above and side (spider facing left).

flexed ventrally from the cephalothorax; cephalothorax always raised). When flexed up (Fig. 5), the spider's abdomen angled up 10–80° from the cephalothorax, the cephalothorax usually being lowered.

Raised body (Fig. 8 and 9B) and lowered body (Fig. 9) refer to instances in which the spider's abdomen was aligned with its cephalothorax (i.e., the abdomen was neither flexed down nor flexed up)

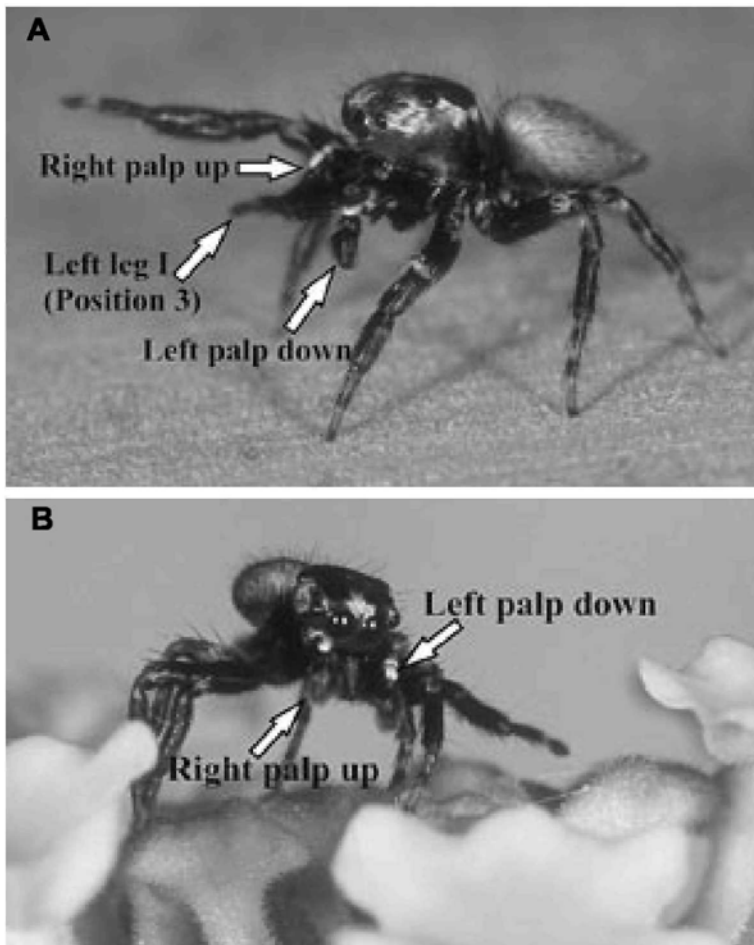


Fig. 8 *Evarcha culicivora* male with raised body. Legs in erect position 3 and palp stepping. **A**, Side view (facing left). **B**, Front view. Male on *Lantana camara* flowers.

and the abdomen and the cephalothorax both were raised or both lowered, respectively.

When flexed to the side, a spider's abdomen was angled 20–45° to either side of the cephalothorax, typically with its body lowered or with its cephalothorax raised and abdomen flexed down.

When a spider had its body tilted up, its cephalothorax and abdomen were aligned (cephalothorax higher and abdomen lower; body-to-substrate angle c. 45°) and the tip of the abdomen was close to, or touching, the substrate.

When a spider had its body rotated to the side (Fig. 10), its legs on one side of the body extended so that its body on that side was elevated. The legs on the other side of the body were pulled in so that this side of the body was held lower than the other side.

When head-standing, a spider angled its cephalothorax down in front by c. 45°, with its abdomen

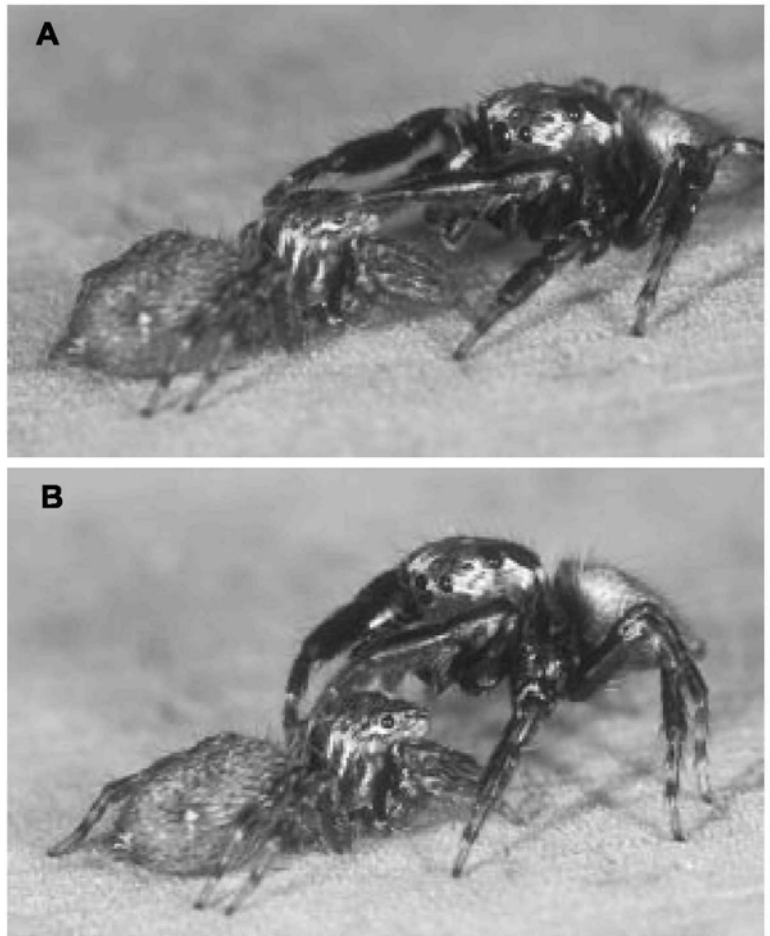
often flexed up c. 45° from the cephalothorax (i.e., the abdomen angled up c. 90° to the substrate). Legs II–IV (sometimes legs I–IV) were held out to the side and flexed down c. 90° at the femur-patella joints, with tarsi on the substrate, legs I and II often being especially close together. Legs I were sometimes in erect position 3 (see below). Head-standing bouts lasted 1–30 s.

Twitch abdomen: a spider moved its abdomen rapidly up and down from the pedicel (amplitude 0.5–1 mm; rate 10–20/s; bouts highly variable in duration, lasting from less than a second to many minutes).

POSTURES AND MOVEMENT OF LEGS

Raised legs (refers to legs I only) were either erect (all joints distal to the femur-patella, and some-

Fig. 9 *Evarcha culicivora* male (on right, facing left) tapping (using legs I) female (on left, facing right). Female's body lowered. **A**, Male erect taps (position 2) (palps semi-erect in position 1). **B**, Male flexed taps (legs no longer erect) while raising body and beginning to mount female.



times the femur-patella joints as well, were fully extended) or semi-erect (not quite fully extended). Sometimes there was superimposed bowing (Fig. 11, 19) of erect legs (i.e., there was slight angling down at the femur-patella joint and slight angling up at the tibia-metatarsus joint, and sometimes at the metatarsus-tarsus joint as well). Six modal positions were discernible.

In position 1 (Fig. 11), the two legs were held parallel to each other and, at least from the patellae to the tips of the tarsi, parallel to the substrate (i.e., tarsi pointed straight forward, but sometimes the femora were angled up with comparable downward flexion of the femur-patella joint so that, from the patella forward, the leg was parallel to the substrate). There were two modal versions of position 1. In extended position 1, the spider's femur varied from straight forward (Fig. 11) to up by as much as 45°. In flexed position 1, the spider's femur was angled straight



Fig. 10 *Evarcha culicivora* male rocking to side (in this frame, body rotated down on his left). Legs erect in position 3. Palps lowered.



Fig. 11 *Evarcha culicivora* male (on right) with legs I erect in extended position 1. Male's legs I bowed. Female (out of focus) immediately in front of and facing male.



Fig. 12 *Evarcha culicivora* female (on right) with legs I erect in flexed position 1. Male flexed taps female's carapace with his right leg I. Female's abdomen rotated (dorsal surface in view in photograph) and slightly raised.

up, or almost straight up, with the femur-patella joint flexed 90° (Fig. 12).

Position 2 (Fig. 13) was similar to position 1 (extended or flexed) except that, instead of being parallel, the two legs were angled toward each other so that the two tarsi almost or actually touched, or else crossed over by as much as 2 mm.

In position 3 (Fig. 8; spider below in Fig. 15A), the femur extended $20\text{--}45^\circ$ out to the side and up by $45\text{--}90^\circ$, with the femur-patella joint flexed down so that the tarsus pointed anywhere from down by 45° to up by 45° .

In position 4 (Fig. 14), each leg was held straight or almost straight (i.e., there was little or no flexion at the femur-patella joints) and the tarsi were angled out to the side by $20\text{--}45^\circ$ and up by $20\text{--}45^\circ$.

In position 5 (spider above in Fig. 15), the leg was pulled back 90° to the sagittal plane of the spider's body. The femur extended up by $45\text{--}90^\circ$ and the femur-patella joint flexed down so that the tarsus

was pointing anywhere from down by 45° to up by 45° .

Position 6 (spider below in Fig. 15B) was similar to position 5 except that the femur-patella joint was not flexed down, or else it was flexed down only slightly, so that the tarsus pointed $75\text{--}90^\circ$ up.

Before flicking, legs I were arched (see below) or, more often, in erect position 3. A spider flicked by suddenly and rapidly moving one leg I (Fig. 16) or both legs I up c. 1 mm (upward motion taking 0.1 s or less) and then, after a momentary pause, moving the leg or legs less rapidly back down (downward motion taking c. 0.25 s). When both legs flicked, they moved in matching phase.

When striking, one spider brought its erect legs I (positions 3 or 4) rapidly and forcefully down and forward. At the end of the strike, legs I extended forward in position 1 or 2, but now semi-erect instead of erect, and tarsi contacted the other spider or the substrate just in front of the other spider.



Fig. 13 *Evarcha culicivora* male (facing down in photograph) on *Ricinus communis* leaf with legs I erect in position 2, extended over female's carapace. Female facing up in photograph, with body lowered.

Fig. 14 *Evarcha culicivora* male (on right) on *Lantana camara* flowers with legs I erect in extended position 4. Female departing by walking away (cephalothorax between two flowers; only abdomen visible in photograph).



Arched legs (Fig. 4): legs I, or legs I and II, held about 45–90° to the side of the body (femur angled up 45–90°; femur-patella joint flexed so that patella and tibia angled down 20–45°; slight flexion (10–20° usual) at the tibia-metatarsus joint; tarsi on or close to the substrate).

When hunched (Fig. 17), legs I–III were held to the side of the cephalothorax (i.e., pulled back so that they were largely behind the chelicerae) and were highly flexed, especially at the femur-patella joints. Leg tarsi, especially tarsi I, were often held above, but close to, the substrate. When loose hunching (Fig. 17A), tarsi angled about perpendicular to the substrate, whereas they angled inward by as much as 45° when tight hunching (Fig. 17B). While hunching, the spider sometimes held its cephalothorax raised, its abdomen flexed down and its palps in the low-retracted posture (see below).

From the hunched posture, especially when with cephalothorax raised, a spider wagged by rapidly raising legs I (taking c. 0.2 s) and then more slowly returning the legs to the tight hunched posture (taking c. 0.5 s). Leg raising was primarily by extension of the femur-patella joints. When maximally raised during a wagging cycle, legs were usually erect or semi-erect (position 5 or 6). Usually both legs moved at the same time, and usually phasing was matching, although there were rare instances of phasing being irregular and of only one leg I wagging.

Males froze by remaining immobile, all the while holding legs hunched or erect.

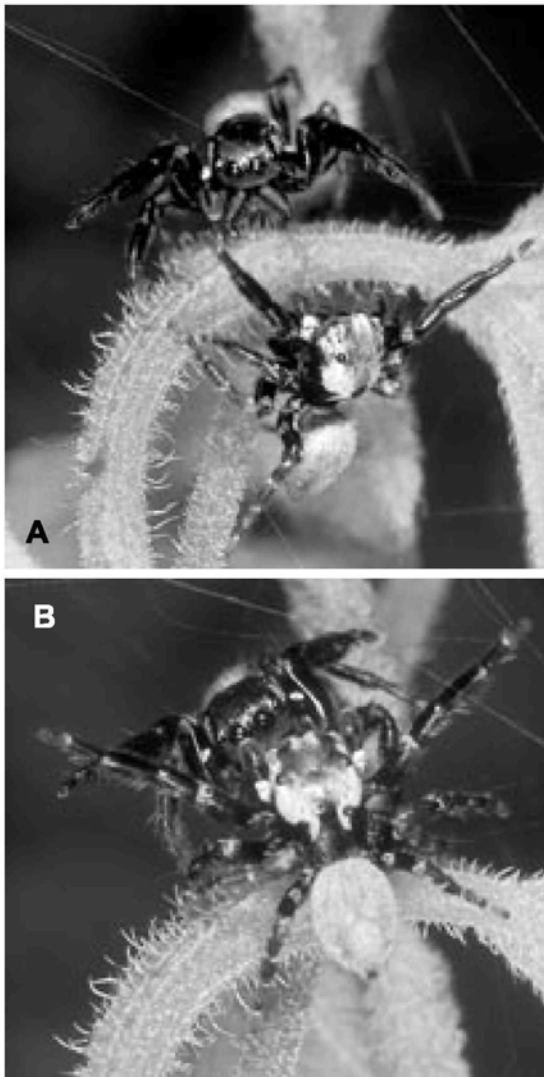


Fig. 15 Two *Evarcha culicivora* males on *Ricinus communis*. **A**, Male at top of photograph (front-on view) with legs erect in position 5 (tarsi angled down 45°) and palps in high retracted posture. Chelicerae opened, with fangs fully extended. Male below (dorsal view), with left leg I erect in position 3 and right leg I on leaf, moving toward male at top. **B**, Initiation of an embrace. Male at top has legs erect in position 5 with femora 90° up and rest of leg parallel to horizontal plane. Male below has legs I erect in position 6.

Before embracing, two spiders approached each other (Fig. 15A), both with legs hunched, both with legs erect (position 3 or 4) or one with legs hunched and the other with legs erect. Once within c. 5 mm of each other, the spiders moved their legs into erect position 5, continued to advance and sometimes



Fig. 16 *Evarcha culicivora* female on *Ricinus communis* (facing forward) flicking her left leg I (position 3). Palps in high retracted posture.

moved legs to erect position 6, and then brought their faces, legs I and chelicerae into contact (Fig. 15B). Chelicerae were usually open, with fangs extended. While continuing to stand face-to-face, with cephalothoraxes raised and legs I held out to the side and touching, the embracing spiders often moved their legs up and down by as much as 45°, sometimes with tarsi moving down to where they touched the substrate.

POSTURES AND MOVEMENT OF PALPS

Frontal palps (Fig. 2) were held in front of the face; femora extending almost vertically upward, with the rest of each palp angling straight down and almost pressed against the palp femur. The tips of palp tarsi were about even with the bottom of the chelicerae. The distance between the two palps in front of the spider's face varied from almost touching to 2 mm apart.

Retracted palps were similar to frontal palps except that, when retracted, the two palps were pulled back to the side of the spider's face instead of being held in front of the face. In the low retracted position, the palps' tarsi tips were even with the bottom of the chelicerae (Fig. 18). In the high retracted position (Fig. 4A, 16), palps were raised higher (tarsus tips above the bottom of the chelicerae). Held in the high-retracted position, the palps were only faintly visible when the spider was viewed front on.

Lowered palps (Fig. 4B, 7, 10) were held to the side of the chelicerae, with sharp flexion at femur-patella joints so that from the patella each palp angled

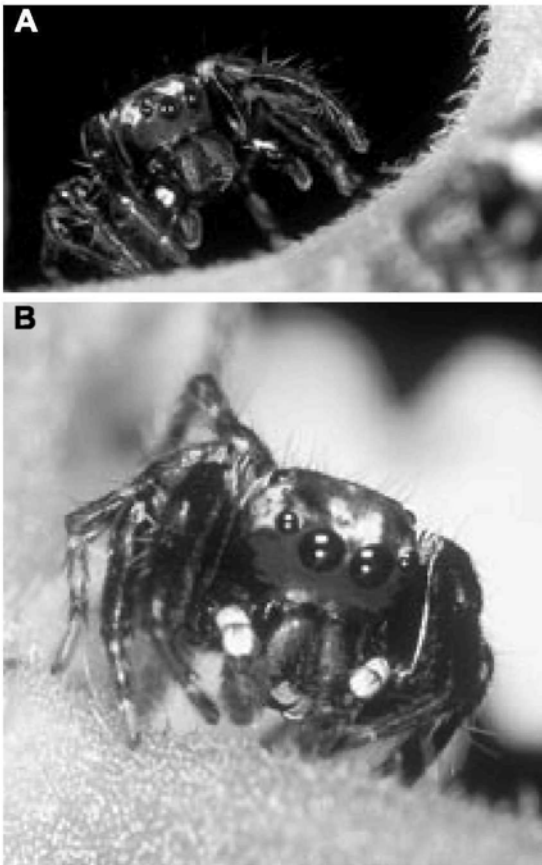


Fig. 17 *Evarcha culicivora* male on *Ricinus communis* with legs in hunched posture. **A**, Loose hunching. **B**, Tight hunching.

down (sometimes slightly rearward, forward or inward). Femora were about parallel to the substrate and tarsi were considerably below the chelicerae.

Raised palps were either erect or semi-erect. Forward position 1: two palps extended forward about parallel to each other and to the substrate, with all joints fully or almost fully extended (i.e., like legs in erect and semi-erect position 1). Forward position 2: palps held extended forward, about parallel with each other or diverging by as much as 20° or converging by as much as 20° ; femora angled up c. 20° and rest of each palp angled down c. 20° because of c. 20° flexion at femur-patella joint. Forward position 3: (i.e., similar to forward position 2 except that each femora angled up c. 45° and the rest of each palp angled down c. $45\text{--}90^\circ$).

Kinked palps (Fig. 19) were held with each femur angled up $45\text{--}90^\circ$. Each palp's patella and tibia were held about parallel with the substrate, or angled



Fig. 18 *Evarcha culicivora* male (facing forward) with palps in low retracted posture.



Fig. 19 *Evarcha culicivora* male (head-on view) with legs erect in position 3 and bowed. Palps kinked.

down by as much as 20° , and also angled in by $20\text{--}45^\circ$ so that they were converging toward each other. Tarsi angled down and back by $20\text{--}45^\circ$ and outward by as much as 20° so that they diverged slightly from each other.



Fig. 20 *Evarcha culicivora* male with legs arched, chelicerae partially opened and palps arched in position 1.

Femora of arched palps extended ventro-laterally alongside, or angled slightly forward from, the chelicerae. The rest of the palp angled ventro-medially so that the tips of the palps converged toward each other. When palps were in position 1 (Fig. 20), tarsi were not under the chelicerae, but tarsi were held under the chelicerae in position 2.

From the normal palp posture, there were two common and distinctive ways in which *E. culicivora* moved its palps. Palp waving was adopted by males, females and juveniles of both sexes, but only adult males adopted palp stepping.

Waving palps moved up and down in matching phase (amplitude 1–2 mm; 1–4/s; bout duration 1 s to 10 min or longer, with c. 10 s being typical; movement femoral and tibial: femora moved forward and up, and at the same time the femora-patellae joints were continuously adjusted so that, distal to the femora, the palps stayed oriented straight down). While the palps were being waved, the tips of their tarsi usually moved from below to above the fangs, but there were also occasions when the tips of the spider's palps stayed below or above the fangs.

When palp stepping (Fig. 8), femora moved up and forward, with the rest of each palp remaining straight (i.e., flexion of the femur-patella joint changed, but there was little or no change in the flexion of the other palp joints). The two palps moved up and down in alternating phase (amplitude 0.5–3 mm, 1–5/s), the result being that the two palps moved as though walking in the air. The tips of the tarsi usually went from below to above the fangs in each cycle, but there were also periods when they remained above or below the fangs. Simultaneous with the

palps moving up and down, a slight side-to-side wobble of the palps was often noticeable.

With palps lowered, a spider performed side-to-side palp waving by repeatedly moving its two palps inward and then outward (c. 1/s, 2–3 mm). There were two variations. In-and-out: both palps moved in together and out together. Left-right: the spider moved both of the palps together to the left (or right) and then both palps together to the right (or left).

PROPULSIVE DISPLAYS

A collective term, propulsive displays, is used for charging, long leaping, lunging, ramming, spurting, striking and truncated leaping (i.e., displays that entail sudden and rapid movement toward another spider).

A spider charged at another spider by suddenly running forward 10–40 mm and, when about one body length in front of the other spider, suddenly stopping.

A spider made a long leap by jumping 50–70 mm towards, and sometimes making contact with, another spider. When contact was made, the leaping spider did not hold on.

A spider lunged by moving its body forcefully forward 1–2 mm, achieving this by suddenly and rapidly extending legs III and IV rearward without the tarsi of these legs leaving the substrate.

Ramming was the same as charging except that, instead of stopping, the advancing spider kept going and contacted the other spider, usually head-on.

A spider spurted by stepping toward another spider in a rapid stop-and-go manner. The duration of each burst of moving forward and of each pause was about 0.25 s.

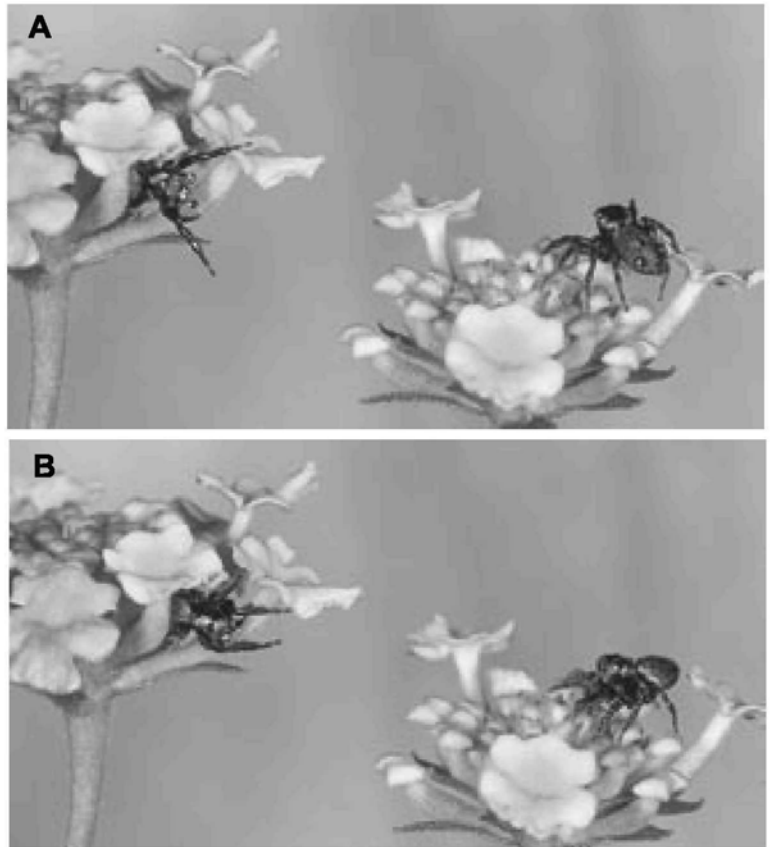
A spider made a truncated leap by suddenly jumping 5–10 mm toward, but not making contact with, another spider.

JERKING BACK, ROCKING, SWAYING AND STEPPING

A spider jerked back (Fig. 21B) by suddenly moving its body forcefully backwards 1–2 mm, achieving this by suddenly and rapidly extending legs II and IV (and sometimes also legs I) forward without the tarsi of these legs leaving the substrate.

A spider rocked forward and backward by repeatedly moving its body first forward and then backward (amplitude 2–4 mm, 2–3 cycles/s, bout duration

Fig. 21 *Evarcha culicivora* male and female, each on a different *Lantana camara* flower. Male (upside down, on left). A, Female (on flower on right) walking (abdomen in view). Male, partially hidden under flowers, emerges and postures with legs in erect position 3. B, Female (on right) jerks back while facing male (on left).



usually 1–2 s). This was achieved by extending and then flexing its legs III and IV without stepping (i.e., the spider's tarsi remained on the substratum). Typically the spider had legs erect in position 1, 2 or 3 when it rocked forward and backwards. Except for being faster and at considerably smaller amplitude (5–10/s, <1 mm, 5–10 cycles per bout), shaking resembled rocking forward and backward.

When rocking side to side (Fig. 10), a spider rotated its body to the left (or right) and then, usually without pausing, to the right (or left) (amplitude 10–45°, 1–2 cycles/s, one cycle per bout). Legs I were usually in erect position 3 when the spider began to rock, but the leg I on the side of the body being lowered typically went down to the substrate and then was elevated to erect when this side of the body moved upward, with the opposite leg now going down to the substrate.

A spider swayed (Fig. 7) (i.e., moved its cephalothorax from side to side) by flexing the legs on

one side and simultaneously extending the legs on the other side. There was no stepping (i.e., the spider's legs remained on the substrate). When the spider combined hunching with swaying, legs I, II and III were more strongly flexed on the side toward which the cephalothorax was moving. The sagittal plane of the cephalothorax remained perpendicular to the direction of movement, but the posterior tip of the spider's abdomen usually stayed in place (i.e., the abdomen-cepbalothorax angle usually changed during swaying so that the abdomen was alternately flexed to the right and flexed to the left). Each swaying cycle (left, right, and back, or right, left, and back) took 0.5–1 s (body moved 2–4 mm) and the spider swayed as many as four times in a row before pausing. Simultaneous with swaying, the spider sometimes tilted its body 45° down on the side toward which it moved.

When stepping to the side, a spider walked sideways 5–10 mm in one direction, paused for c. 0.5

s, and then walked sideways 5–10 mm in the other direction. One or both legs I were usually held erect in position 3, and sometimes a spider flicked one or both legs I while stepping. When only one leg was flicked, it was usually the leg on the side toward which the spider stepped. When both legs were flicked, the leg on the side toward which the spider stepped moved up sometimes before the leg on the other side moved up. Sometimes, the spider also changed speed of stepping to faster or slower before changing direction.

Two modes of stepping to the side were discerned: smooth and jerky. Smooth: neither the beginning nor the ending of stepping was abrupt. Jerky: stepping abruptly began and abruptly ended, individual steps were shorter, and the spider's stepping gait had a distinctive up-and-down component.

Only males danced, and they danced only in male-female interactions. When linear dancing, a male stepped forward and then, either immediately or after a brief pause, stepped backward, usually repeating the sequence 5–10 times before taking a longer pause or stopping. While facing a female, a male zigzag danced by stepping to one side, pausing briefly, and then stepping to the other side, usually repeating the sequence 5–10 times before taking a longer pause or stopping.

By stepping slowly forward 1–3 mm, then pausing, then stepping forward 1–3 mm again, and so forth, a spider eased forward (i.e., one spider moved gradually towards the other spider). While easing forward, the spider's body was held lowered, and usually legs I were in erect position 1. Spiders were usually no more than about five body lengths apart when they began easing forward.

When a spider departed (Fig. 14 and 21A), it left the vicinity of another spider by stepping away at more or less normal walking speed.

A spider fled by running, and sometimes by leaping, quickly away.

When one spider fled, the other spider chased it by running, and sometimes by zigzag dancing or leaping, all the while following closely behind the fleeing spider.

Quiescent: male and female stationary, female usually in the normal posture and male usually frozen in erect posture or, in rare instances, frozen in the arched or hunched posture.

Quiet: male and female not very active, more or less stationary, but with the male repositioning his legs intermittently.

NESTS

Evarcha culicivora's nest (Fig. 22) was a silk tube (length and width 4–6 times the body length and width, respectively, of the resident spider) with one or more elastic openings ("doors"). In the field, nests were typically built in the enclosed spaces formed by dead, rolled-up leaves ("detritus"). The detritus used as nest sites was typically mixed in with grass growing near the ground beside tree trunks, the walls of buildings and boulders. It was also common to find nests in the detritus found in spider webs (undetermined species of *Argyrodes* (Theridiidae), *Cyrtophora* (Araneidae), *Nephilengys* (Nephilinae) and *Tetragnatha* (Tetragnathidae); undetermined genera of Agelenidae, Araneidae, Pholcidae and Theridiidae).

Whether a nest had one or two doors (or, rarely, three doors) appeared to depend on the space available. For example, nests were sometimes wedged in at the narrow end of the cone-like space made by a dead leaf that was tightly rolled-up at one end. In these instances, there was only one door (opening at the wider end). In the laboratory, we sometimes cut pits in the corks used to plug holes in the tops of the cages, with the pit on the side of the cork facing into the cage. *E. culicivora* readily adopted these holes as sites for one-door nests that opened into the cage.

BEHAVIOUR PATTERNS THAT OCCURRED EXCLUSIVELY IN THE PRESENCE OF NESTS

With fangs in the nest silk, a spider chewed by opening and closing the basal segments of its chelicerae (rate, amplitude and bout length highly variable).

Holding down silk was performed by a spider inside a nest. First it moved legs I up and contacted the silk with its tarsi. By lowering its legs, it then pulled the upper silk layer down against the lower layer. How long the spider held the silk down in this fashion varied from a few seconds to several minutes.

When palpating on a nest, a spider's palps moved up and down in a way that resembled how its palps moved when waving, except that tarsi were usually extended more forward. Repeated contact was made with the silk on down strokes.

A spider probed (Fig. 23) by moving legs I forward and backward (1–2 mm, c. 2/s, alternating phase) so that the tarsi jerkily pushed and pulled on the silk.

Fig. 22 Nest on dead leaf inside web of *Nephilengys* sp. *Evarcha culicivora* female facing out of nest door. Palps in normal posture.

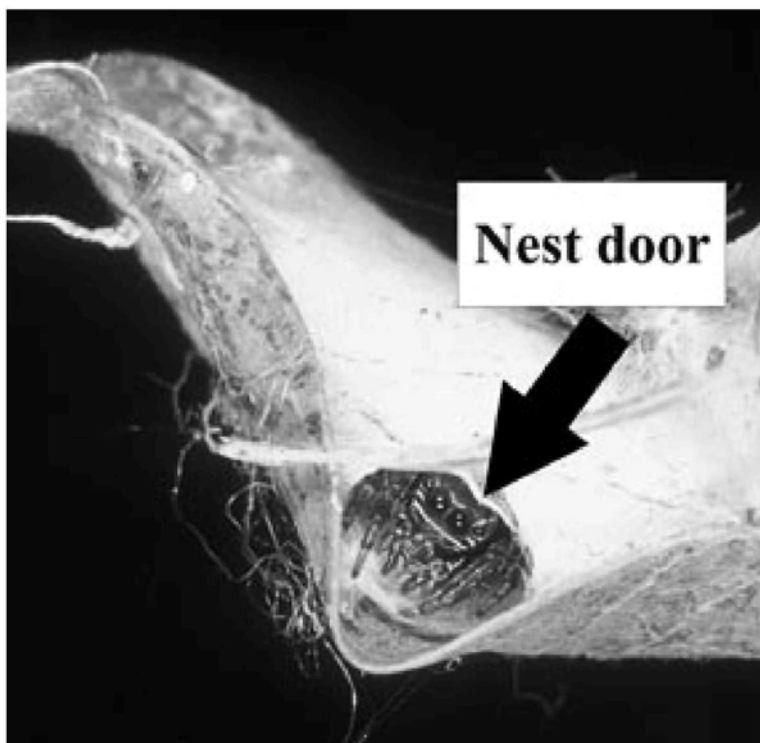


Fig. 23 Nest on dead leaf inside web of *Nephilengys* sp. *Evarcha culicivora* male (facing left) probes at nest door. Female in nest (only her legs I visible in photograph).

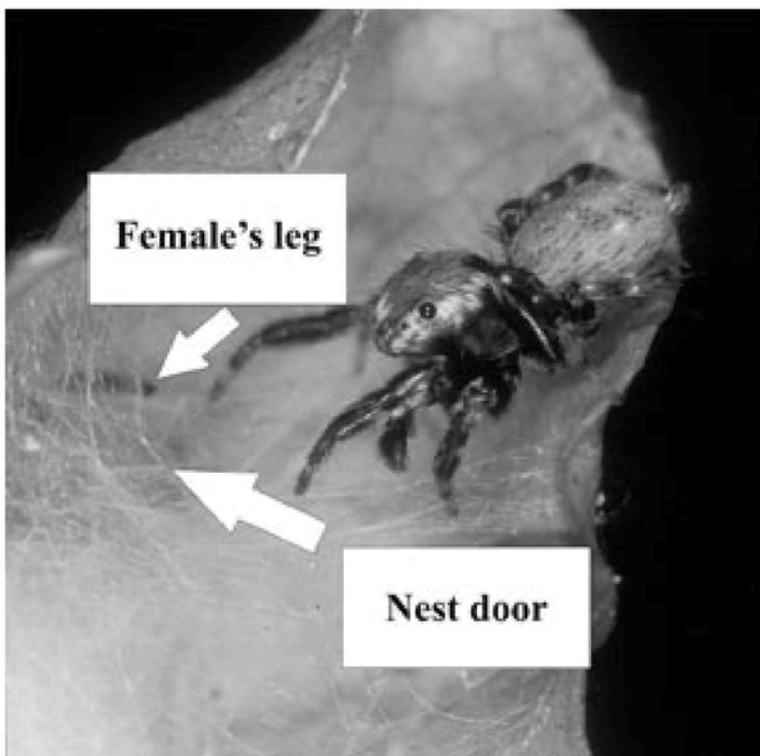




Fig. 24 *Evarcha culicivora* male (facing right) erect tapping female (facing left). Male's legs I in erect position 2. Female with legs I erect in position 3.

POST-CONTACT BEHAVIOUR

With his legs in erect position 1 or 2 and held over a female, a male erect tapped with legs (Fig. 24) by moving legs I up and down (movement femoral; c. 2/s; 1–2 mm; alternating, irregular or, most often, matching phase), so that tarsi I repeatedly contacted the female. Erect tapping was concentrated on the female's legs I, carapace and anterior abdomen. Later, as he stepped forward and began to mount, the male switched to flexed tapping, usually with tarsi first hitting the female's carapace, then her anterior abdomen (Fig. 25A) and then more posterior parts of her abdomen as he moved further over the female (Fig. 25B). When flexed tapping, legs moved similarly to how they moved when erect tapping, but there was considerably more flexion at the femur-patella and tibia-metatarsus joints. On rare occasions, males erect tapped briefly with a single leg I, but flexed tapping with a single leg was not seen.

A male quivered by moving erect legs I (position 1 or 2) up and down very rapidly (c. 10/s) and at low amplitude (0.5 mm). Bouts usually lasted 0.5–1 s.

A male palpated on a female in much the same way as he palpated on silk. There were two variations. Standing immediately in front of a female and facing her, a male forward palpated by repeatedly touching a female's face with his palps raised in forward position 1. This was normally a preliminary to mounting. A male flexed palpated (Fig. 26) while standing over a female, his palps flexed considerably and tarsi repeatedly contacting the female's carapace or dorsal abdomen. Once a female rotated

her abdomen, males sometimes also flexed palpated on the side or bottom of the female's abdomen.

Males mounted by walking over females, and there were three primary ways in which they did this: (1) the male first walked toward a facing female with legs I erect (position 1 or 2), quivered these legs over the female for variable, sometimes long, periods and then moved continuously over her until mounted; (2) as the male zigzag danced in the female's direction, he continued advancing and moved over her without pausing or after only a momentary pause; (3) the male stepped towards the female with his legs I erect (usually in position 1 or 2) and, when he got his legs I over the female, he moved in short spurts of 0.5–1 mm at a time until he gradually moved completely over her.

Before the male engaged a palp to begin copulation, the female always adopted a posture with her cephalothorax lowered and her abdomen raised and rotated (Fig. 5 and 6). Rotated abdomen: female's abdomen rolled c. 90° to the left or to the right, so that its ventral surface moved closer to the male. Before, after or simultaneous with rotating, females flexed their abdomens up. Females sometimes rotated their abdomens while the male was erect or flexed tapping but before he began to mount (Fig. 12).

Once mounted, the male leaned to his left or his right. However, before or while leaning to his left or right, and before or after the female rotated her abdomen, the male sometimes rubbed (Fig. 26) by moving the tips of his tarsi I across the female's abdomen (movement femoral; <1 mm; bout length c. 1 s; tarsi stayed in contact with the female) by repeatedly flexing and extending the tibia-metatarsus joint. The male rubbed with one or both legs, and phasing was highly variable. Depending on how far the female's abdomen had rotated, tarsi were in contact with the dorsal, lateral or ventral surface of the female's abdomen.

As the male leaned further to his left (or right), he brought his right (or left) leg I over and stroked by moving the side of this leg's tarsus (and sometimes also metatarsus) repeatedly across a female's ventral abdomen (1–2/s, 1–2 mm, bout length c. 1 s, tarsus stayed in contact with the female).

There were two categories of scraping, with legs and with a palp, both being performed only by males and only when females had their abdomens rotated but before palp engagement (i.e., not while mating). When scraping with legs (Fig. 27), both legs I moved up and down on the female's ventral abdomen (2–3 mm; c. 2/s; matching phase; tarsi remaining in contact with the female's abdomen for all or most of



Fig. 25 *Evarcha culicivora* male (facing left) flexed tapping female (facing right) as he mounts. Female with body lowered. **A.** Male's tarsi I contacting anterior dorsal abdomen of female just behind pedicel. **B.** Male's tarsi contacting posterior dorsal abdomen of female.



Fig. 26 *Evarcha culicivora* male (facing right) standing over female (below, facing left). Female's abdomen raised and beginning to rotate. Male flexed palps and also rubs right side of female's abdomen with his left leg I.



Fig. 27 *Evarcha culicivora* male (head on in photograph) scraping posterior ventral abdomen of female with both legs I and with his left palp. Female's abdomen raised and rotated (female's spinnerets forward in photograph).

the time; contact usually posterior to, but close to, the female's epigynum). When scraping with a palp, the male moved the palp that was closer to the female back and forth (2–4/s, c. 0.5 mm) across the ventral surface of her abdomen (Fig. 27), usually on or close to her epigynum (tarsi remained in contact with the female's abdomen for all or most of the time). Bout length for palp scraping was usually c. 2 s, although longer bouts (up to 2 min) were also seen.

Kicking (Fig. 28) was a distinctive manner in which males moved legs IV during mating. Simultaneous kicking with both legs IV was usual, but males kicked on rare occasions with only one leg IV, holding the other leg IV quiescent on the substrate

or in the air. Kicking legs moved up and down in matching phase. Before kicking, the male held legs IV elevated (Fig. 28A) so that tarsi were in the air and there was conspicuous flexion at the femur-patella (c. 90°) and tibia-metatarsus (c. 45°) joints. Just before kicking began, legs IV often were slowly elevated higher. Then the spider kicked by suddenly and forcefully moving the whole of each leg down

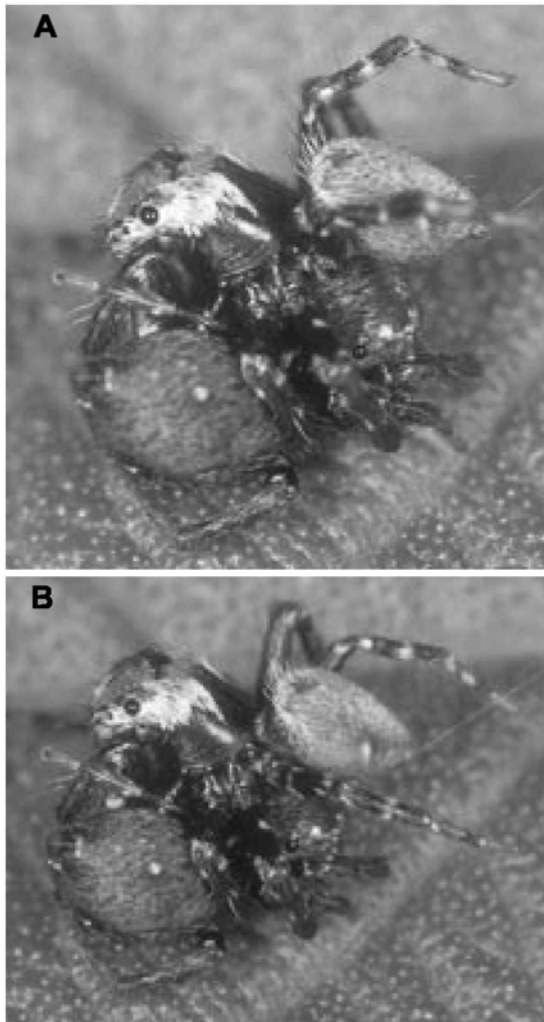


Fig. 28 *Evarcha culicivora* male kicking with legs IV while mating. Male above, facing to left. Female below, facing to right. Male leaning to his right. Female's abdomen raised and rotated. **A**, Male's legs IV elevated preceding kick. **B**, Male's legs IV moving down during kick.

(Fig. 28B). Sometimes, as the two legs moved down, they simultaneously moved slightly toward each other. Sometimes the femur-patella joints also flexed while the legs moved down. Often there was also a superimposed quivering movement of legs IV (up and down, $>10/s$, <1 mm) during the down stroke. At the end of the down stroke, legs IV stopped while still suspended in the air or else they hit one or more of the female's legs, the substrate or, on rare occasions, the female's cephalothorax.

Intermittent kicking was usual (kicked once and then paused, or kicked 2–6 times in a bout and then paused), but there were rare instances of males kicking continuously for several seconds to many minutes at a time. Amplitude was usually 2–3 mm. Kicking often began fast, and then it slowed down. For example, kicking rate sometimes began at c. 1/s, but soon slowed down to one kick every 2–3 s. As the male kicked, his legs IV went down fast, but then moved up more slowly, with a pause of 0.25–0.5 s between the leg reaching the lower position at the end of the down-stroke and going back up again. Initially the intervals between kicking bouts tended to be 2–3 s, but then they became less predictable and often longer. Males sometimes held legs IV elevated during these intervals.

BEHAVIOUR SEQUENCES

Most behaviour categories were performed by males and by females, in intra- and in inter-sexual interactions (Table 2). However, the manner in which behaviour categories were combined was exceedingly variable, especially in male-female interactions away from nests. The convention we follow here is to use the expression “sequence” for a combination of behaviour patterns, and below we will provide a largely qualitative summary of how sequences varied across the different kinds of interactions we investigated.

How male-female interactions began

The prevalent pattern in salticids is for the male to initiate male-female interactions by displaying first (Jackson & Pollard 1997), and this trend held for *E. culicivora* during male-female interactions when the female was inside, but not when she was outside, her nest. When encounters began outside nests, males sometimes displayed and approached first, with mutual displaying beginning only after the male came to within a few body lengths of the female. However, sometimes females displayed and approached first, with mutual displaying beginning only after the female came to within a few body lengths of the male (i.e., for *E. culicivora*, it was common for either the male or the female to initiate display).

Regardless of whether the male or the female displayed first, initial displays tended to be posturing, with males more often beginning with erect posturing and females more often beginning with hunched posturing. Females sometimes, but males only rarely, initiated interactions by performing propulsive displays (especially charging), and

there were infrequent instances of males initiating male-female interactions by immediately starting to dance.

How waving and stepping with palps were integrated into sequences

In same-sex and male-female interactions, as well as when stalking prey, when walking about and generally when looking at objects of interest, it was

routine for females to wave their palps and for males not only to wave their palps but also to step with their palps. Males frequently switched between palp stepping and palp waving, and sometimes there were dozens of switchovers in a row in bouts that lasted several minutes or longer. During these bouts, males sometimes paused briefly before switching, but they more often went from waving to stepping, or vice versa, without pausing.

Table 2 Categories, and dominant variations in categories, of behaviour seen during intraspecific interactions of *Evarcha culicivora* and the types of interactions in which they are used. A, Away from nests; N, on silk at nests; P, postmount; X, not seen.

	Male-female	Female-male	Male-male	Female-female
Arched-legs posturing	A	A	A	A
Chase	A	A	A	A
Chew	N	X	N	N
Dance and spurt forward	A	X	X	X
Ease forward	N	A	X	X
Embrace	A	A	A	A
Erect-legs posturing*	A	A	A	A
Flick legs	A	A	A	A
Freeze	A	X	X	X
Head stand	X	A	X	A
Hold down silk	X	N	X	N
Hunched-legs posturing	A	A	A	A
Kick	P	X	X	X
Mount	P	X	X	X
Open chelicerae	A	A	A	A
Palpate on female	A, N	X	X	X
Palpate on nest	N	X	N	N
Palp waving	A, N	A, N	A, N	A, N
Palp stepping	A, N	X	A, N	X
Probe	N	N	N	N
Propulsive displays†	A	A	A	A
Pull and hold	X	N	X	N
Quiver	A	X	X	X
Rock	A	A	A	X
Rub	P	X	X	X
Scrape	P	X	X	X
Shake	A	A	A	A
Side-to-side palp waving	A	A	A	A
Step to side	A	A	A	A
Strike	A	A	A	A
Stroke	P	X	X	X
Sway	A	A	A	A
Tap	A, N, P	X	X	X
Twitch abdomen	A	A	A	A
Wag	A	A	A	A

*Erect-legs posturing was seen in all types of interaction, except that positions 1 and 2 were only employed in male-female and female-male interactions.

†Propulsive displays were seen in all types of interaction, except females did not ram when interacting with other females.

How dancing and spurting forward were integrated into sequences

Dancing and spurting were behaviour patterns performed only by males and only in male-female interactions. They tended to occur together in complex, variable sequences. Zigzag dancing was especially elaborate and highly variable, the most common pattern being for a male to lower (or raise) his body and step to the side, pause and raise (or lower) his body, and then step to the side again.

When zigzag dancing, movement to the side was typically on an arc, with successive arcs bringing the male closer to the female. While stepping to the side, either the male kept his legs I erect and stepped with legs II–IV or else he lowered his legs I and used them for stepping as well. There were rare occasions when dancing males held their bodies raised while stepping, but dancing males usually held their bodies lowered. Males often tilted their bodies to the side toward which they were moving. Although males sometimes arced back-and-forth 30 or more times before pausing, 3–5 arcs per bout was more typical. When a dancing male paused between steps, he usually had his body raised and his legs I in erect position 1, 2 or 3, and usually he stepped rapidly with his palps (c. 4/s being typical). Males often alternated between erect posturing (in positions 1, 2, 3 and 4) and zigzag dancing, and posturing periods between dancing bouts varied greatly in duration, sometimes lasting for 20 min or longer.

Between bouts and within single bouts, the speed of the zigzag dance was highly variable, with the male on rare occasions slowing down and speeding up even while stepping in one direction on a single arc. There was a tendency for males to step faster when closer to the female and slower when further away. Arc amplitude (i.e., how far the male moved to the left or the right before changing direction or stopping) was typically 20–50 mm, but there were rare occasions when it was as much as 80 mm or more. Dancing tended to be faster when arcs were wider, but there was no clearly discernible relationship between the amplitude of arcs and a male's distance from a female.

Females only sometimes turned their bodies so as to remain oriented toward the zigzag-dancing male. When a male danced in narrow arcs, the female sometimes stepped toward him and then either fled suddenly or remained inactive. When a female remained inactive, a male that got close either brought his legs I over her and began to mount, or else he backed away from the quiescent female.

While only about 40 mm away from the female, it was common for males to switch suddenly from hunched posturing and swaying to zigzag dancing. Linear dancing and spurting were typically interjected briefly and intermittently during a sequence of zigzag dancing, erect posturing and hunched posturing. When linear dancing, a male stepped forward and backward several times with or without first pausing and with amplitude (distance moved forward or backward) rarely exceeding 50 mm (about 20 mm was typical). When spurting forward, the male usually lowered his erect legs I, placed his tarsi on the ground while stepping forward, and then moved legs I back to the erect posture (position 3), when he stopped.

How propulsive displays, fleeing and chasing were integrated into sequences

Propulsive displays, being interjected suddenly and seemingly unpredictably, were routine in male-female, male-male and female-female interactions, and they were combined in highly variable ways with other behaviour patterns. Immediately after one spider performed a propulsive display in a same-sex interaction, the other spider or both spiders usually turned and fled. For example, when one spider made a long leap and contacted another spider, the contacted spider sometimes landed on its back and then, after 1–30 s, regained its footing and fled while the other spider watched. However, except for charging (see below), fleeing did not so routinely follow propulsive displays during male-female interactions.

Sometimes a male approached a quiescent female by zigzag dancing and then suddenly made a truncated leap towards her, after which the male usually resumed zigzag dancing, or less often he hunch postured and swayed while the female watched, but leaping was more often performed by females. It was common for a female to make a single long leap or to make several truncated leaps in rapid succession toward a male. Males that were posturing when the female leapt tended to hold their ground and continue posturing, and males that were not already posturing often began posturing when leapt at. If a female stopped immediately in front of a male after leaping, it was common for the male to extend his legs over her in erect position 1 or 2, sometimes with mounting and mating following soon afterwards.

Sometimes females repeatedly charged toward males, with the interval between successive charges being only a fraction of a second (each charge in bout moving her forward only about 10 mm). If the male was dancing when the female charged, he often

fled, with the female chasing after him. Then, when the female stopped chasing, the male usually turned around and displayed by posturing with legs erect or hunched.

When a female fled, the male often chased after her, and sometimes he zigzag-danced or maintained erect posturing (especially position 3) at the same time while chasing her. Males sometimes made successive long leaps at a fleeing female, and occasionally the leaping male contacted the female briefly one or more times from the rear.

How arched, erect and hunched posturing was integrated into sequences

Hunched posturing was adopted by males and by females, in same-sex and in male-female interactions, but there were differences in how hunched posturing was used by the two sexes. For example, when females hunch postured, they usually kept their palps in the normal posture, and their palps were not especially active. Males, however, often waved and stepped with their palps while hunched posturing. When inactive, the male's palps were usually retracted or arched.

Males sometimes, but females only rarely, adopted a routine of repeatedly taking a few steps with legs held in the normal posture and then standing for several seconds with legs hunched or erect (especially in position 3), with there being no obvious rule pertaining to whether hunched or erect posturing was adopted when the spider stopped.

Hunched posturing was common in male-male interactions, but the two males often postured in different ways (e.g., one male posturing for a long time with one leg I hunched and with other leg I erect in position 3, while the other male was posturing with both legs I hunched).

Arched and erect posturing were frequently adopted during same-sex and male-female interactions. During male-female interactions, males especially often erect postured in position 3. While facing an arched- or erect-posturing male, it was common for a female to flick intermittently while posturing with arched or erect legs, or to wag while posturing with hunched legs. However, it was common for both sexes in all types of interaction to switch frequently between arched, hunched and raised posturing.

In longer interactions, posturing males sometimes froze when females became quiescent or quiet. On rare occasions, males sustained the frozen posture for many minutes at a time, or even for an hour or more, but 10–60 s was more typical. Although males froze with legs arched or hunched, it was

more common for them to freeze with legs raised (especially erect position 3). On rare occasions, a male switched from a frozen posture to being active while the female was still more or less quiescent, but freezing more often ended when the female began walking away. When a male broke out of freezing, even if the female was still quiescent, he often immediately began dancing towards her.

In the course of an interaction, a male sometimes ended up at the top of a cage with the female below. In these instances, the male sometimes attached a silk line to the top of the cage and then, holding on to this line, dropped down toward the female, sometimes erect posturing while suspended on the silk line.

How swaying and wagging were integrated into sequences

Repeated alternation between hunched posturing and swaying (hunch-sway alternation) was characteristic of females and of males in male-female and in same-sex interactions. However, it tended to be only one individual that adopted hunch-sway alternation in any one sequence, the other individual more often hunched posturing without swaying.

When males alternated between hunched posturing and swaying while interacting with females, there was usually a corresponding alternation in male palp activity: stepping with palps while hunched posturing and holding palps stationary in the low retracted posture while swaying. Males often leapt at females immediately after a bout of hunch-sway alternation. When the male leapt toward her, the female sometimes leapt away and fled immediately, with the male often running and leaping after her. There were rare occasions, however, when a female stood her ground after a male leapt at her, even when the leaping male contacted her.

There were two primary situations in which males swayed during male-male interactions: (1) The two males faced each other and swayed at the same time, with it being usual for each male to sway at the same time to his own right side and then for each male to sway at the same time to his own left side; (2) One male held legs hunched while stepping to the side and then swayed as soon as he stopped stepping, with these step-stop-sway sequences sometimes being performed by both males at the same time.

Males often, but females only rarely, wagged intermittently while posturing with their legs hunched, with the timing of wagging appearing to be unpredictable. In male-male interactions, it was common for hunched posturing and wagging to

follow rapidly after a bout of erect posturing. For example, sometimes one male suddenly switched from erect to hunched posturing, followed by the other male wagging and backing away with legs hunched.

How abdomen twitching was integrated into sequences

Abdomen twitching was a routine part of the male's pre- and post-contact behaviour during male-female interactions at and away from nests. For example, males twitched their abdomens almost continuously when mounting females and when they had their palps engaged, with higher-amplitude and especially forceful abdomen twitching being common during palp switchover. Males often twitched their abdomens when erect or hunched posturing, with each individual bout of abdomen twitching lasting for several seconds at a time and with numerous bouts typically following one after the other.

Males routinely twitched their abdomens while probing or chewing on nests. Males that were on or near a female's nest twitched their abdomens sometimes while just walking or standing. At or near a nest, abdomen twitching was usually performed intermittently for a few seconds at a time, but there were rare occasions when males twitched their abdomens continually for sustained periods lasting as long as many minutes at a time.

Females twitched their abdomens during male-female interactions, but not so noticeably or frequently as males. Individual bouts of abdomen twitching by females usually lasted c. 0.5 s, although there were rare occasions when females twitched their abdomens for several seconds, or even minutes, at a time.

Females only rarely twitched their abdomens during interactions with other females, but abdomen twitching was routine in male-male interactions.

Male-male interactions away from nests

When two males were approaching each other, it was usual for one or both to posture with legs hunched or arched, and frequently one or both wagged. Intermittently and seemingly unpredictably, one or the other male wagged, flicked, swayed, rocked, waved palps side to side or performed propulsive displays. Males sometimes embraced during longer interactions. While embracing, fangs were extended, and it was also common for males to hold their fangs extended even when not in contact, with the magnitude of fang extension being highly variable. Retracted was the most common palp posture.

Female-female interactions away from nests

One or both females typically postured, especially in erect position 3, with cephalothoraxes raised and with palps either arched in or held in the normal palp posture. One or both females usually switched repeatedly between posturing with legs erect and adopting the prey-stalking posture while slowly approaching the other female. Whenever a female came to within about 10 mm of the other female, one or both usually fled. When only one female fled, the other only rarely followed.

Female-female and male-male interactions at nests

When the resident was quiescent inside a nest, the intruder usually began by probing and then, after pushing its face energetically into the silk, chewed and tugged. The resident spider often responded by pulling on the silk.

Sometimes during male-male interactions, there were brief bouts of the intruder palpating or probing, or both, on the nest silk, with accompanying intermittent abdomen twitching. At nest doors, two males (sometimes) or two females (rarely) embraced, lunged or both.

Male-female interactions away from nests

Regardless of whether the male-female pair mated, male-female interactions away from nests were complex, highly variable and hard to characterise. Males in particular appeared to run through much of their large repertoire of display behaviour in endlessly varying arrangements. Female behaviour may have been less variable, but no particular female behaviour pattern provided a clear-cut prediction of whether or not the female would subsequently mate.

Although there were rare instances of females head-standing in female-female interactions, this uniquely female behaviour was performed primarily in male-female interactions. Females usually performed a head-stand for a few seconds and then immediately fled, but there were rare instances of females performing head-stands for several minutes at a time before fleeing.

Females often performed head-stands, propulsive displays, erect posturing or hunch posturing and then mated, with mating sometimes coming almost immediately after the performance of one of these seemingly aggressive behaviour patterns. At the other extreme, females sometimes appeared passive for most of the interaction and even allowed males to mount, and then fled and failed to mate.

It was common for a female to make lunges or truncated leaps when a male was only a few millimetres in front of her, including when a male was quivering with his legs over her, after which she might or might not mate. Sometimes females leapt over erect-posturing or dancing males, or else leapt almost straight up, and then fled, after which they might or might not mate later in the interaction.

Embracing may have been the closest thing to behaviour predicting female rejection of a male (i.e., pairs that embraced only rarely mated), but embracing was not a routine preliminary to females rejecting males (i.e., embracing was rare during all male-female interactions, regardless of whether mating did or did not follow).

Male-female interactions at nests

Unlike other salticids studied (Jackson & Pollard 1997), the distinction between at-nest and away-from-nest male-female interactions was typically blurred in *E. culicivora*. This was because females often left and then re-entered their nests during the interaction, because females often stood with their front legs and the front ends of their bodies extending out of a nest door and males often displayed from a distance at these exposed females. Even when resident females seemed not to be visible to the male and even when the female was absent from the nest, males that were oriented in the direction of a nest often adopted displays typical of male-female interactions away from nests (i.e., males often seemed to be directing posturing and dancing at the nest itself rather than at a female).

Once a male arrived at a nest's door, he usually began probing immediately. If the male arrived on the nest away from the door, sometimes he probed away from the door, but more often he moved to the door before beginning to probe. Females usually held the door down while the male probed.

Sometimes males and females went back and forth between doors (i.e., the male moved away from the door at which the female was pulling on silk, walked over the nest to the opposite door and began to probe there, with the female usually moving quickly through the inside of nest to this door and pulling on it). There were also rare instances of the female leaving the door at which the male was probing and going through the inside of the nest to the opposite door. When this happened, the male usually did not enter but instead walked across the nest to the door at which the female was now located and resumed probing.

Periods during which a male and female were highly active sometimes alternated with quiescent or quiet periods that sometimes lasted 5–10 min, but on rare occasions lasted several hours.

Males usually alternated at highly variable intervals between being at the nest and being away from the nest. Periods away from nests usually lasted only a few seconds or minutes, although there were rare instances of staying away for up to an hour. While away, the male sometimes stepped about actively in a localised area beside and near the nest, generally moving no more than 10 mm from the nest and facing the nest for most of the time while away. There were intermittent bouts of chewing by the male, but the location of chewing followed no discernible pattern. Between chewing bouts, the male sometimes stood for several seconds or minutes at a time with his face pressed against the silk.

It was usual for males eventually to begin probing with legs I extended through a door and to ease themselves through the nest door in successive 0.5 s bouts. Sometimes the probing male moved his legs to erect position 1 or 2, and sometimes he also held his palps erect or semi-erect. As the male entered the nest, he often tapped and probed with his palps and, once he had his body at least partly in the nest, he advanced toward the female, sometimes with intervening periods of the male and female being quiescent, with the male holding his legs extended over the female in erect position 1 or 2.

Cohabitation

There were about 50 observations of males cohabiting with subadult females in the field, either with each spider in a separate chamber of a dual nest (two silk tubes woven together, with the doors of one chamber aligned with the doors of the other chamber) or, more often, with the male standing on or near the female's nest but not in a silk chamber.

In the laboratory, when a male encountered a subadult female in a nest, the two spiders interacted in much the same way as in male-female interactions, but without the male mounting the female. Sometimes a female left her nest while a male was still outside or else the male entered a nest, with the female inside, followed soon afterwards by the male and the female both leaving the nest. When a female left her nest, the male usually remained near or in the nest. Sometimes she left the nest's vicinity and the interaction ended, but there were other times when the female remained nearby for several minutes or hours and then returned and entered the nest again.

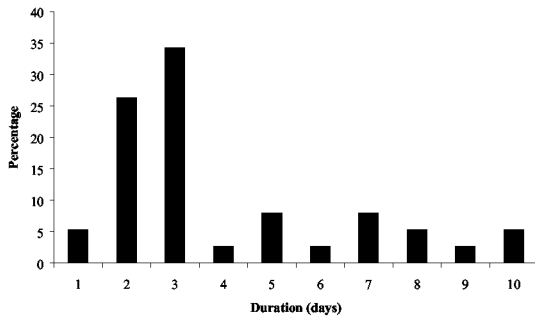


Fig. 29 Cohabitation duration. How long *Evarcha culicivora* male remained with subadult female before she matured and the pair mated (mean \pm SD = 4.00 \pm 2.51, $N = 38$).

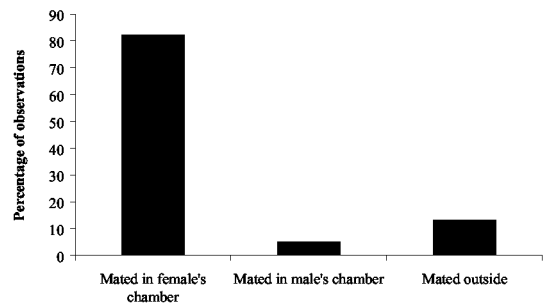


Fig. 30 Location of mating by *Evarcha culicivora* after cohabitation ($N = 38$).

If the male was in the nest when she returned, he usually left the nest several seconds or minutes later and then remained in the vicinity.

Successful cohabitation (i.e., instances that ended with the female moulting and the pair mating) lasted 1–10 days (Fig. 29). Most males gradually spent more and more time spinning silk on and near the subadult female's nest, usually completing an enclosing chamber within 1–2 days. After the female matured, the male most often mated with the female inside her chamber, although there were instances of the female first coming out of her chamber and the pair mating outside or in the male's chamber (Fig. 30).

Mounting and post-mount pre-copulatory behaviour

Regardless of whether the female was in her nest or out in the open, there were similar and predictable sequences immediately preceding copulation. Just before mounting, the male and female were usually facing and usually the male had his legs extended in erect position 1 or 2 over the female's carapace. Often the male's palps were in forward erect position 1, sometimes with tarsus tips touching the female's face.

Although the male typically tapped the female with his legs I and then quivered his legs I over her, there were also rare bouts that lasted c. 0.5 s during which males tapped and quivered at the same time, quivered only or tapped only. Sometimes a female repeatedly jerked back or else stepped a few millimetres away (backwards or to the side), stopped, and then let the male move forward and quiver again. Alternatively, the female turned and walked away,

only to turn and face the male again, sometimes posturing (typically in erect position 3) at a male and then allowing him to resume quivering.

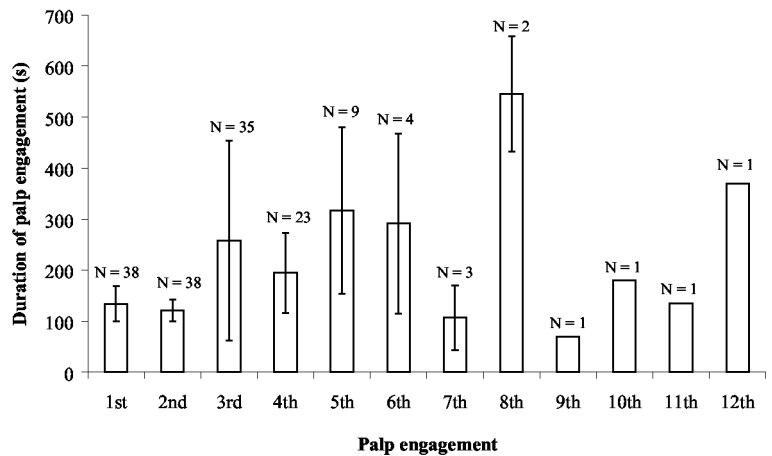
Sometimes a male succeeded in mounting by stepping over a female's hunched or raised legs, and raised cephalothorax. After lowering her legs and body, the female sometimes mated with the male. There were rare instances of a male zigzag dancing and, when close, moving his erect legs I (position 1 or 2) over a female that was facing 45–180° away. When this happened, the male sometimes mounted the female while she continued to face away from him. However, successful mounting usually began with the female facing the male, her body lowered (Fig. 9 and 25) or in the rest posture, and her legs raised (position 3) or hunched.

Copulation

During copulation, defined by palp engagement (palpal organ of one palp positioned against one side of female's epigynum), *E. culicivora* adopted the copulatory posture (Fig. 6) that is typical of most salticids (male dorsal to the female; male and female facing opposite directions: Posture 2 in the classification of Gerhardt & Kaestner 1938; see Jackson & Pollard 1997). The male's haematodocha (membranous part of the palpal organ) pulsed intermittently during palp engagement (Fig. 6).

There was no clear preference for the male to engage his left or right palp first: left palp first: $N = 22$; right palp first $N = 16$; test for goodness of fit, $\chi^2 = 0.947$, $P = 0.330$). About 2 min later, he switched to the other palp (Fig. 31). About 2 min later, the male switched palps again. If the female remained more or less quiescent, the male usually continued

Fig. 31 Duration (mean \pm SD) of each successive palp engagement.



to alternate palps (Fig. 32), but successive palp-engagement duration now became more variable. Sequencing also became more variable (i.e., there was occasional re-engagement of the same palp instead of strict alternation).

During the interval between palp engagements, the female's abdomen regained alignment with the cephalothorax and the male usually moved back to the centre of the female's abdomen. The male's haematodocha, which was often still inflated immediately after he disengaged his palps, was usually deflated by the time the male was centred over the female. Centred over the female, the male resumed rubbing and tapping. If the female remained more or less quiescent, the male soon resumed copulation, but eventually he walked away from the female and the interaction ended.

Between or during palp-engagement intervals, females sometimes raised legs I, began walking or both. Males were typically dislodged when females began walking, but the dislodged male often displayed, mounted and renewed copulation. There were rare instances of a female walking for a few seconds or even several minutes, with the male remaining mounted. He continued to rub and tap and eventually he sometimes resumed copulation.

Kicking

Males always kicked, either intermittently or continuously, when their palps were engaged, and sometimes they kicked after mounting but before the initial palp engagement or between successive palp engagements. On rare occasions, males kicked while moving over a female, but before fully mounted.

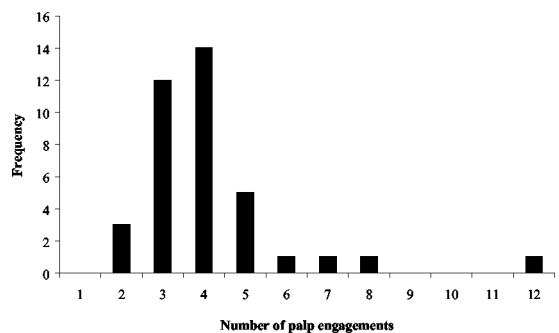


Fig. 32 Total number of palp engagements per copulation (mean \pm SD = 4.11 \pm 1.81, N = 38).

When an individual palp engagement lasted for 60 s or longer (i.e., during most palp engagements), it was common for a male to adopt a routine of twitching his abdomen and kicking at the same time, his abdomen moving down simultaneous with his legs moving down. After legs IV reached the lowest position in the kicking cycle, the male then continued twitching his abdomen for c. 1 s longer.

When a female became active while a male was kicking, the male usually began kicking faster and more forcefully. When a female became active while a male was not kicking, although he had his palp engaged, he almost always started kicking immediately.



Fig. 33 *Evarcha culicivora* male (above) preying on female (below) immediately after courtship. Male's chelicerae gripping female's posterior carapace (both spiders facing to left). Immediately beforehand, female turned and fled from displaying male, whereupon male chased, leapt and killed female.

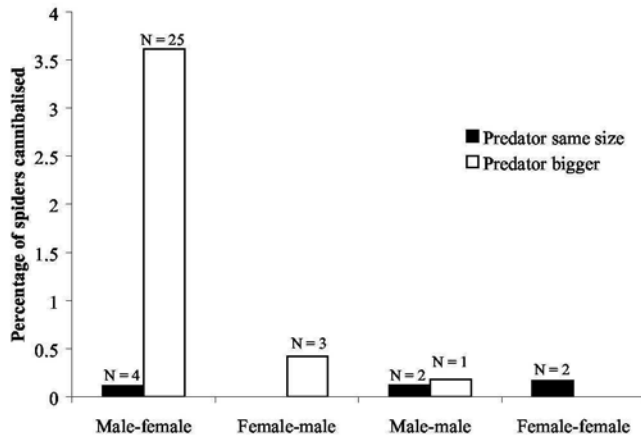


Fig. 34 Percentage of *Evarcha culicivora* interactions that ended with cannibalism: one spider ("predator") killed other ("prey"). Male-female: male was the predator. Female-male: female was the predator. There were no instances of smaller spider killing larger spider.

Cannibalism

Cannibalism (i.e., one individual killing and eating another during intraspecific encounters) was observed primarily when the two individuals differed in body length, with the larger of the two individuals usually being the predator. For instance, of a total of 3335 same-size male-female encounters, four males killed females, whereas 3331 males did not kill females. In 691 different-size male-female encounters (male larger), 25 males killed females, whereas 666 males did not kill females (test of independence, $\chi^2 = 97.94$, $P < 0.001$). Most instances of cannibalism were during male-female away-from-nest encounters during which there was no interaction (i.e., the predatory individual stalked and attacked

the other individual seemingly before the prey individual became aware of being stalked).

It was more common for males to kill and eat females than vice versa (Fig. 33 and 34). The typical preliminary to cannibalism during male-female interactions was for one spider to flee and the other spider to leap on and kill it. However, there were also instances of males displaying at a quiescent female, continuing to display while approaching and then killing her when he got close, typically switching suddenly from displaying to attacking. There were also instances of males mounting and initiating postmount courtship, and then killing the female on which he was mounted while she was quiescent, with or without her abdomen being rotated.



Fig. 35 Male-female pair of *Evarcha culicivora* interacting on *Ricinus communis*. Female partly obscured by vegetation (below).

While copulating with a quiescent female, there were instances of the male suddenly biting and killing the female, after which one of four possible actions followed: he ate the female immediately, walked away without eating her, attempted to continue copulating and then ate her or attempted to continue copulating and then walked away without eating her.

Interactions on *Lantana camara* and *Ricinus communis*

All the behaviour categories seen during interactions in bare cages were also seen during interactions on *L. camara* and *R. communis*, and vice versa. Sequences during interactions when on *L. camara* and *R. communis* were also in basic respects similar to interactions when the spiders were in bare cages. However, interactions on *L. camara* and *R. communis*, especially male-female interactions, were distinctive because of much greater variability in the performance of individual categories of behaviour and in sequencing.

With the two spiders moving about actively through the dense inflorescences (especially on *L. camara*), each spider's view of, and path to, the other spider was routinely occluded by the flowers and other vegetation (Fig. 35). It was common for one spider to leap about on the plant, with the other spider usually orienting toward the leaping spider and this spider's orienting response, in turn, attracting

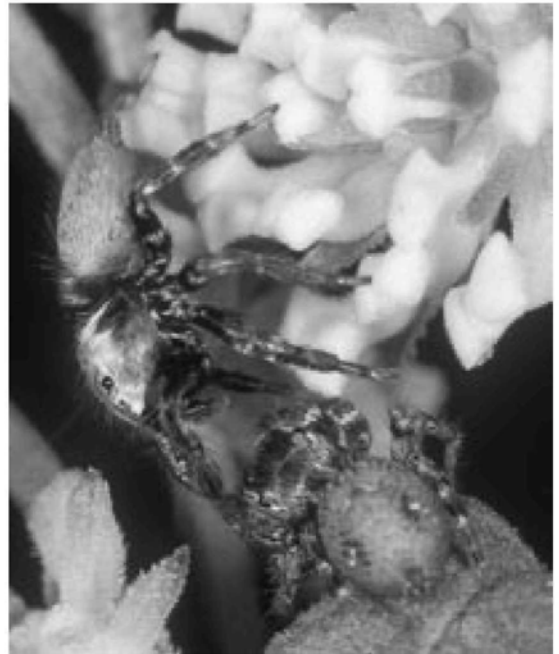


Fig. 36 *Evarcha culicivora* male (above) standing on *Lantana camara* flower and pre-mount tapping female that is standing below on leaf (facing away in photograph). Female's dorsal carapace faces male. Male viewed side on (his dorsal body turned to left in photograph). Male's legs I contacting left side of female's cephalothorax.

the attention of the spider that had been leaping. Another impression we got from observation was that sometimes, when a male saw a female before she saw him, he deliberately hid behind leaves and stems, or in the inflorescence, until the female passed by, and then he suddenly emerged and began posturing (Fig. 21A) or dancing.

In bare cages, when one spider departed or fled from the other spider, this was primarily by walking or running, but spiders on plants often shuffled or dodged out of the way by quickly moving under vegetation, leaping from one part of the plant to another or dropping on a dragline to a lower part of the plant. There were also instances of one spider dropping on a dragline from higher up in the vegetation toward another spider lower down, with males approaching females this way more often than vice versa and sometimes posturing as they did so.

It was routine for one spider to display at another spider that was facing up, down, left, right or at almost any conceivable angle (Fig. 36), with the displaying spider often tilting so as to achieve closer

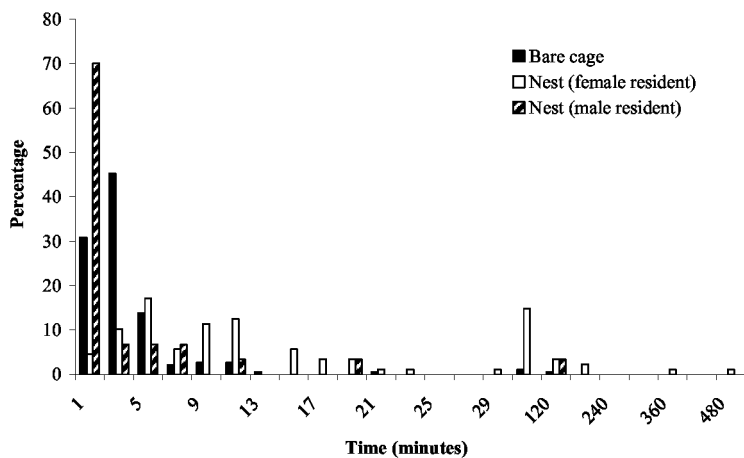


Fig. 37 Duration (min) of male-female interactions, with or without nests present (bare cage: mean \pm SD = 4.81 ± 14.35 , $N = 188$; nest (female resident): mean \pm SD = 33.50 ± 69.79 , $N = 88$; nest (male resident): mean \pm SD = 6.70 ± 21.75 , $N = 30$).

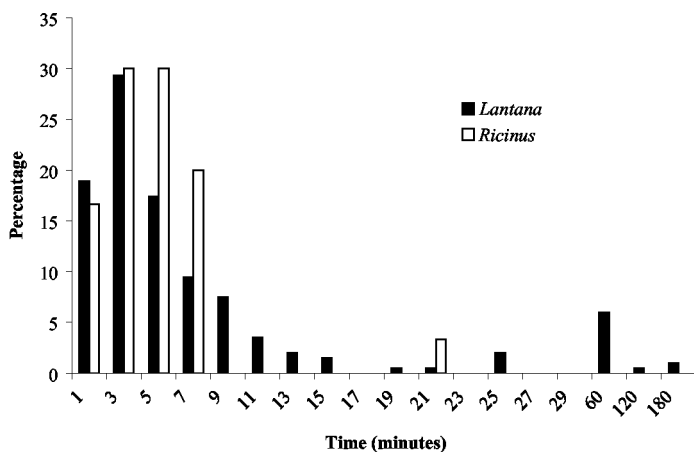


Fig. 38 Duration (min) of male-female interactions on *Lantana camara* and *Ricinus communis* (*Lantana*: mean \pm SD = 10.81 ± 23.24 , $N = 201$; *Ricinus*: mean \pm SD = 4.67 ± 3.68 , $N = 30$).

approximation to being head-on and oriented in the same plane with the other spider.

Dancing was especially complex on plants. While moving in an arc during a zigzag dance, for example, a male sometimes had to maintain his footing on a slender shred of vegetation, make repeated leaps from flower to flower, and so forth. The male's dancing path sometimes took him one or more times from the top side to the bottom side of a leaf and back, or vice versa. Although combining zigzag dancing with linear dancing was uncommon when in bare cages, males often combined zigzag dancing with linear dancing when on plants. For example, males sometimes linear danced by moving up and down the stalk of a plant after zigzag dancing on a flower or leaf.

When in the vegetation, mounting and mating often appeared to be especially challenging.

Sometimes the male began pre-mount tapping while reaching from a part of the vegetation where he was standing to another part where the female was standing (Fig. 36), with mounting being achieved not by simply walking forward over the female, as was routine in bare cages, but instead by moving over the female from some other angle. When the female was buried deep within an inflorescence, it often seemed impossible for males to mount, yet males tried and sometimes succeeded in reaching over to the female's rotated abdomen to engage a palp, sometimes with a leaf or a stem running between the male and female.

Interaction durations

The data we review here were durations recorded from a representative subset of each interaction type.

Fig. 39 Duration (min) of male-male interactions (bare cage: mean \pm SD = 1.55 \pm 1.49, N = 80; nest present: mean \pm SD = 1.40 \pm 1.22, N = 30; *Lantana*: mean \pm SD = 3.77 \pm 3.08, N = 60; *Ricinus*: mean \pm SD = 4.60 \pm 2.94, N = 30).

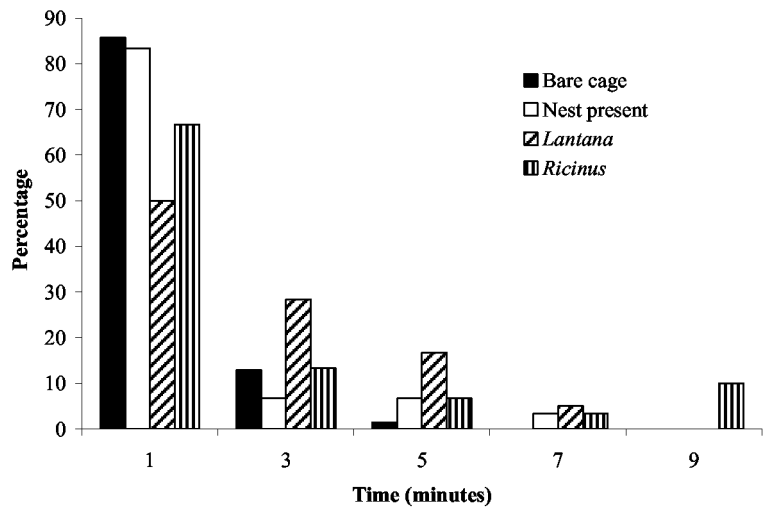
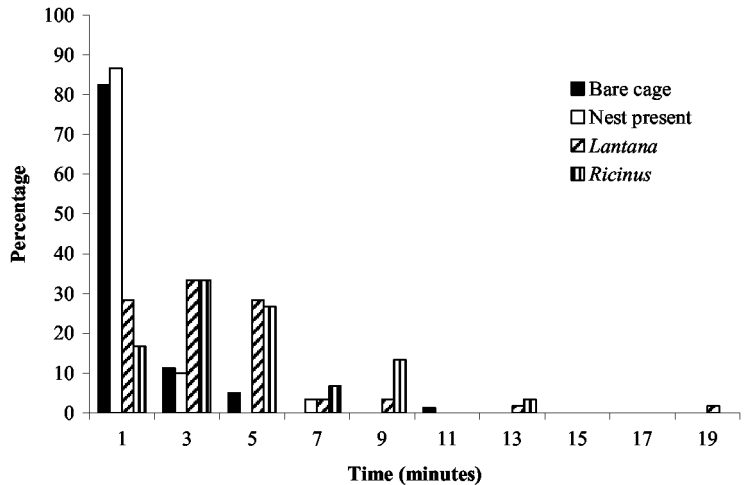


Fig. 40 Duration (min) of female-female interactions (bare cage: mean \pm SD = 1.31 \pm 0.81, N = 70; nest present: mean \pm SD = 1.60 \pm 1.50, N = 30; *Lantana*: mean \pm SD = 2.53 \pm 1.82, N = 60; *Ricinus*: mean \pm SD = 2.53 \pm 2.66, N = 30).



When in bare cages with no nests present, some male-female interactions lasted for hours, although 2–5 min was more typical (Fig. 37). Interactions when males encountered females in nests usually lasted 10–60 min, although they sometimes lasted for many hours and, in rare instances (not part of our recorded samples), several days. Male-female interactions at nests were significantly longer than male-female interactions in bare cages (male resident at nest: $Z = 2.51$, $P = 0.012$; female resident: $Z = 9.70$, $P < 0.001$; Mann-Whitney U-tests). Interactions at nests where the female was the resident were significantly longer than interactions at nests where the male was the resident ($Z = 5.96$, $P < 0.001$).

As durations of male-female interactions on *Lantana camara* were not significantly different from durations of male-female interactions on *Ricinus communis* ($Z = 0.74$, $P = 0.46$; Fig. 38), we pooled these data (“on plants”). Male-female interactions were significantly longer on plants than in bare cages ($Z = 8.73$, $P < 0.001$).

Males displayed actively when interacting with each other, but usually only briefly (1–5 min being typical) (Fig. 39). Female-female interactions were also short, usually lasting 1–5 min (Fig. 40). Male-male and female-female interactions at nests were not significantly longer than interactions in bare cages (males: $Z = 0.35$, $P = 0.73$; females: $Z = 0.29$,

$P = 0.78$). For male-male and for female-female interactions, durations on *Lantana camara* were not significantly different from durations on *Ricinus communis* (males: $Z = 1.48$, $P = 0.139$; females: $Z = 0.89$, $P = 0.38$), and we pooled these data ("on plants"). Using the pooled data, male-male and female-female interactions were significantly longer on plants than in bare cages (males: $Z = 6.86$, $P < 0.001$; females: $Z = 3.54$, $P < 0.001$).

In bare cages, male-female interactions were significantly longer than male-male interactions ($Z = 6.71$, $P < 0.001$) and female-female interactions ($Z = 7.09$, $P < 0.001$), but durations of male-male interactions were not significantly different from durations of female-female interactions in bare cages ($Z = 0.41$, $P = 0.68$). On plants, male-female interactions were significantly longer than male-male interactions ($Z = 2.51$, $P = 0.012$) and female-female interactions ($Z = 6.53$, $P < 0.001$), and male-male interactions were significantly longer than female-female interactions ($Z = 3.95$, $P < 0.001$).

DISCUSSION

Although the display behaviour of *E. culicivora*, on the whole, fits within the prevalent pattern known from recent research on other salticids, there are also some interesting differences.

Crane's (1949) conclusion that visual stimuli are both necessary and sufficient for releasing salticid courtship (defined as intersexual communicatory behaviour that forms the normal preliminaries to mating; see Jackson 1982a) may have been compatible with commonsense expectations about adaptive tradeoffs in small animals, yet there are now numerous studies illustrating that salticids make extensive use of acoustic, percussion (seismic), silk-borne, tactile and chemical signalling during intraspecific interactions (Edwards 1981; Gwynne & Dadour 1985; Jackson 1987; Pollard et al. 1987; Maddison & Stratton 1988; Noordam 2002; Elias et al. 2003, 2005).

Courtship versatility is an especially striking example of how salticids make extensive use of other sensory modalities despite their exceptional eyesight. First documented in detail in a study of a North American species, *Phidippus johnsoni* Peckham & Peckham (Jackson 1977), "courtship versatility" refers to a conditional strategy of male salticids where they use vision-based displays when they encounter mature females outside nests (type 1 courtship), use silk-borne signals when they encounter adult females

inside nests (type 2 courtship), and cohabit with subadult females (i.e., make a second chamber fastened to subadult females' nests where they wait until the subadult female matures; see Jackson 1986). Vision is necessary and sufficient for eliciting the type 1 courtship of many, but not all (see Elias et al. 2005), salticids. However, salticids readily communicate with type 2 courtship in total darkness (Jackson & Pollard 1997). We documented courtship versatility for *E. culicivora* and this conditional strategy may, in fact, be a universal characteristic of salticid spiders, as every detailed published study designed to look for evidence of this conditional strategy has succeeded in documenting it (for references, see Jackson 1992; Jackson & Pollard 1997). Post-contact tactile or chemotactic courtship, a phase common to type 1 and 2 courtship, was also documented for *E. culicivora* and may also be universal in salticid courtship.

Another characteristic of *E. culicivora* is the adoption of a repertoire of distinct display elements during type 1 and during type 2 courtship, with the way elements are combined and sequenced being highly variable. This also may be universal for salticids (Jackson & Pollard 1997). Although the influence of classical ethology (for references see Tinbergen 1963) was evident in how much of the early literature characterised salticid display behaviour as stereotypic and reflex-like (Heil 1936; Crane 1949; Drees 1952), later work has largely supplanted this portrayal with an emphasis on how salticid intraspecific interactions tend to be highly variable and complex (Jackson & Pollard 1997; Elias et al. 2003).

It is likely that the evolution of salticid display complexity has been driven by sexual selection (Jackson & Pollard 1997). Sexual selection has, in fact, been a dominant topic in the literature on salticid courtship from the 19th century to the present (Peckham & Peckham 1889; Bristowe 1941; Jackson 1981; Richman 1982; Masta & Maddison 2002; Hebets & Maddison 2005; Elias et al. 2006), and hypotheses concerning sexual selection in salticids have most often pertained specifically to intersexual selection (i.e., selection resulting from mate choice; see Harvey & Bradbury 1991). Consistent with the prevailing trend in the animal kingdom as a whole (Bradbury & Anderson 1987), in salticids males typically display more persistently than females during male-female interactions (Jackson & Pollard 1997), with females tending to alternate between watching the male and moving a short distance away. Salticid females are typically envisaged as determining

whether mating takes place (i.e., it is primarily the female that does the choosing) by either allowing or not allowing the male to approach, mount and copulate.

Female choosiness seems to account for male behaviour relatively easily (i.e., the male's mating success depends on doing what the female prefers), but precisely what advantage females might gain by favouring particular types of male courtship remains uncertain for *E. culicivora*, as it does for salticids in general (see Jackson & Pollard 1997; Hebets & Maddison 2005; Elias et al. 2006). Yet, with *E. culicivora*, and perhaps with numerous other salticids (see Hoefler 2007), the traditional way of phrasing this question about sexual selection needs to be revised. *Evarcha culicivora* appears unconventional because both the male and the female of this species display actively and both sexes are prone to initiating courtship. From other studies, we have evidence that both sexes of *E. culicivora* exercise pronounced mate-choice behaviour, choosing on the basis of the body size of potential mates (Cross et al. 2007) and also on the basis of the odour potential mates acquire by feeding on blood-carrying mosquitoes (Cross & Jackson unpubl. data).

Sexual cannibalism is another topic that has a long history in the literature on spider courtship, and *E. culicivora* seems to go against tradition here as well. Female spiders, according to conventional wisdom, are ravenous predators and males need to identify themselves or else risk being perceived as prey (Robinson 1982). Certainly there are spider species for which conventional sexual cannibalism (i.e., females eating males) is frequent during courtship and mating (Elgar 1992; Schneider & Lubin 1998; Andrade 2003) and, regardless of whether it is frequent or not, the potential of cannibalism seems to be generally applicable for courting spiders, as all spiders are predators of other arthropods, including arthropods that are similar in size to a potential mate. However, for salticids (Jackson 1982b; Richman & Jackson 1992; Jackson & Pollard 1997), and perhaps for spiders in general (Jackson & Pollard 1982, 1990), the idea that males reduce their risk of being eaten by identifying themselves to females as non-prey does not hold up well to close scrutiny.

Envisaging identification as being primarily the female's problem is a peculiar bias in the literature on the cannibalism-identification hypothesis, because it seems to overlook the fact that salticid males do not normally display indiscriminately. On the contrary, they tend to reserve courtship displays specifically for encounters with conspecific females.

By displaying first, a male demonstrates that he has identified a female without needing to see her display. Moreover, males are primed to escalate conflict more intensely during encounters with other conspecific males when they can see that a conspecific female rather than some other organism, such as a heterospecific female or a prey item, is present (Wells 1988; Cross et al. 2006; Jackson et al. 2006). Given that males can accurately identify females without females necessarily displaying at them, an explanation would be needed if females were shown to not have comparable perceptual ability. *E. culicivora* is one species for which it is clear that females certainly do have this ability, as females of this species frequently displayed first.

Another problem with the cannibalism-identification hypothesis is that, although cannibalism may be a significant risk during encounters between conspecifics, this risk runs both directions. In the Salticidae (Jackson 1982a, 1992) and other spiders (Jackson & Pollard 1990), we see males eating females as well as females eating males, along with males eating other males and females eating other females. For salticids, with their extraordinarily good eyesight, misidentification seems to have little to do with who eats whom. *E. culicivora*, in particular, seems to turn the traditional identification-cannibalism hypothesis on its head because, during courtship and mating, males of this species are apparently more dangerous to females than females are to males.

When we consider *E. culicivora*, it might be tempting to flip the cannibalism-identification hypothesis around and argue that the unusually active way females display at males is an adaptation by which females identify themselves as non-prey to males, but this is a superficial explanation for display complexity in this or any salticid species. For understanding the ultimate causation of salticid display complexity, simplistic emphasis on identification can be counted on to be misleading. As has been suggested elsewhere (Jackson & Pollard 1997), a more realistic perspective might be derived from ideas related to sensory exploitation (e.g., Proctor 1992; Clark & Uetz 1992, 1993; Ryan et al. 2001) and receiver psychology (e.g., Guilford & Dawkins 1991; Rowe 1999), but with greater emphasis on complexity, flexibility and dynamic interaction between signaller and receiver. This may seem like a subtle distinction, but this is a significant departure from the idea that the male's problem (and, for *E. culicivora*, the female's problem as well) is simply to use an identification signal as a way to turn off the predatory inclinations of a potential mate. For the

male and for the female salticid, courtship just does not appear to be fundamentally about a displaying individual revealing that, rather than being just another potential meal, he or she is a potential mate.

It may often be more useful to envisage each displaying salticid as orchestrating a careful balance between stimuli that provoke and stimuli that inhibit predatory attacks from the other salticid, as though the male and the female were each playing mind games with a predator, something similar to a lion trainer and a lion, where each salticid is analogous to the trainer and to the lion at the same time (Jackson & Pollard 1997). Simple identification would be more compatible with highly stereotypical courtship, not the complex, highly variable sequences actually found in salticids. With *E. culicivora*, a species with especially variable, complex display behaviour, we may have found a species that is especially appropriate for future research that examines the mind-games hypothesis more carefully.

Lesser variability may be characteristic of the display behaviour of some other salticids. For example, the females of some salticid species (e.g., *Maevia inclemens*) are said to perform receptivity displays (Clark & Uetz 1993; Clark & Biesiadecki 2002) (i.e., displays after which mating is almost certain not to be resisted by the female). However, in the display repertoire of *E. culicivora*, and that of all salticid species investigated in the University of Canterbury Spider Laboratory (Jackson & Pollard 1997), no comparable receptivity signals have ever been evident.

Selective attention is an often neglected topic in the mate-choice literature (see Dukas 2002), but much of *E. culicivora*'s display behaviour may function in attracting the attention, and sustaining the attention, of potential mates. Interaction complexity, and especially the adoption of displays that are rich in movement, may function in part as anti-habituation mechanisms (Jackson 1982b). Resurrecting long-forgotten, yet still important, ideas from the literature on bird song, *E. culicivora*'s display behaviour might be explained in part as each individual striving to avoid the other individual's "monotony threshold" (see Hartshorne 1956, 1958).

The variability of *E. culicivora*'s display behaviour may be especially relevant when considered in the context of courting and mating in the dense inflorescences of plants, especially *L. camara* and *R. communis*, where the surfaces on which the interacting spiders move about is complex and visual obstructions intervene between the spiders as they

exchange signals. *E. culicivora*'s display behaviour often appeared more exaggerated when individuals met on plants, and perhaps being predisposed to meet on the foliage of plants functions as a means by which spiders challenge each other's ability to orchestrate complex display behaviour. Setting up challenges of this sort might function in the context of intersexual selection (see Andersson 1994).

The mating behaviour of *E. culicivora* also appears to be unusual in comparison to other salticids, forcing us to reconsider the definition of courtship as intersexual communicatory behaviour that forms the normal preliminaries to mating (Jackson 1982a). There has been considerable recent interest in potential examples of copulatory courtship in animals (i.e., communicatory behaviour during, instead of strictly before, mating; see Eberhard 1991, 1994; Edvardsson & Arnqvist 2000), and a long-standing interest in this topic in the Salticidae in particular (see Jackson 1980). The kicking behaviour of *E. culicivora* males is normally performed while mating and this behaviour pattern, which is unique for salticids studied to date, may be an especially rewarding example of copulatory courtship for future research. One of the hypotheses that should be considered is that females make decisions about whether to use a male's sperm on the basis of his kicking behaviour during copulation (see Hoikkala et al. 2000). Kicking may also be a way in which males avoid exceeding the female's monotony threshold, as suggested by the male's variable kicking rhythms and by how variability seemed to increase when previously quiescent females began moving.

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REFERENCES

- Andersson M 1994. Sexual selection. Princeton, Princeton University Press.

- Andrade MCB 2003. Risky mate search and male self-sacrifice in redback spiders. *Behavioral Ecology* 14: 531–538.
- Blest AD, O'Carroll DC, Carter M 1990. Comparative ultrastructure of layer I receptor mosaics in principal eyes of jumping spiders: the evolution of regular arrays of light guides. *Cell & Tissue Research* 262(3): 445–460.
- Bradbury JW, Anderson MB 1987. *Sexual selection: testing the alternatives*. Chichester, Wiley.
- Bristowe WS 1941. *The comity of spiders*. London, Printed for the Ray Society.
- Carducci JP, Jakob EM 2000. Rearing environment affects behaviour of jumping spiders. *Animal Behaviour* 59(1): 39–46.
- Clark DL, Biesiadecki B 2002. Mating success and alternative reproductive strategies of the dimorphic jumping spider, *Maevia inclemens*. *Journal of Arachnology* 30: 511–518.
- Clark DL, Uetz GW 1992. Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behaviour. *Animal Behaviour* 43(2): 247–254.
- Clark DL, Uetz GW 1993. Signal efficacy and the evolution of male dimorphism in the jumping spider, *Maevia inclemens*. *Proceedings of the National Academy of Sciences of the United States of America* 90(24): 11954–11957.
- Crane J 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. *Zoologica* 34: 159–215.
- Cronk QCB, Fuller JL 1995. *Plant invaders*. London, Chapman & Hall.
- Cross FR, Jackson RR, Pollard SD 2007. Male and female mate-choice decisions by *Evarcha culicivora*, an East African jumping spider. *Ethology* 113: 901–908.
- Cross FR, Jackson RR, Pollard SD, Walker MW 2006. Influence of optical cues from conspecific females on escalation decisions during male-male interactions of jumping spiders. *Behavioural Processes* 73: 136–141.
- Drees O 1952. Untersuchungen iiber die angeborenen Verhaltensweisen bei Springspinnen (Salticidae). *Zeitschrift fur Tierpsychologie* 9: 169–209.
- Dukas R 2002. Behavioural and ecological consequences of limited attention. *Philosophical Transactions of the Royal Society of London B* 357(1427): 1539–1547.
- Eberhard WG 1991. Copulatory courtship and cryptic female choice in insects. *Biological Reviews* 66(1): 1–31.
- Eberhard WG 1994. Copulatory courtship in 131 species of insects and spiders, and consequences for cryptic female choice. *Evolution* 48: 711–733.
- Edvardsson M, Arnqvist G 2000. Copulatory courtship and cryptic female choice in red flour beetles *Tribolium castaneum*. *Proceedings of the Royal Society of London Series B* 267: 559–563.
- Edwards GB 1981. Sound production by courting males of *Phidippus mystaceus* (Araneae: Salticidae). *Psyche* 88: 199–214.
- Elgar MA 1992. Sexual cannibalism in spiders and other invertebrates. In: Elgar MA, Crespi BJ ed. *Cannibalism: ecology and evolution among diverse taxa*. Oxford, Oxford University Press. Pp. 128–155.
- Elias DO, Hebets EA, Hoy RR 2006. Female preference for complex/novel signals in a spider. *Behavioral Ecology* 17: 765–771.
- Elias DO, Hebets EA, Hoy RR, Mason AC 2005. Seismic signals are crucial for male mating success in a visual specialist jumping spider (Araneae: Salticidae). *Animal Behaviour* 69: 931–938.
- Elias DO, Mason AC, Maddison WP, Hoy RR 2003. Seismic signals in a courting male jumping spider (Araneae: Salticidae). *Journal of Experimental Biology* 206: 4029–4039.
- Foelix RF 1996. *Biology of spiders*. 2nd ed. Oxford, Oxford University Press.
- Gerhardt U, Kaestner A 1938. Araneae. In: Kuenthal WG, Krumbach T ed. *Handbuch der Zoologie*. Berlin, De Gruyter. Pp. 394–656.
- Ghisalberti EL 2000. *Lantana camara* L. (Verbenaceae). *Fitoterapia* 71: 467–486.
- Guilford T, Dawkins MS 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour* 42: 1–14.
- Gwynne DT, Dadour IR 1985. A new mechanism of sound production by courting male jumping spiders (Araneae: Salticidae, *Saitis michaelsoni* Simon). *Journal of Zoology* 207: 35–42.
- Harland DP, Jackson RR 2004. *Portia* perceptions: the *Umwelt* of an araneophagic jumping spider. In: Prete FR ed. *Complex worlds from simpler nervous systems*. Cambridge, Massachusetts, MIT Press. Pp. 5–40.
- Hartshorne C 1956. The monotony-threshold in singing birds. *Auk* 73: 176–192.
- Hartshorne C 1958. Some biological principles applicable to song-behavior. *Wilson Bulletin* 70(1): 41–56.
- Harvey PH, Bradbury JW 1991. Sexual selection. In: Krebs JR, Davies NB ed. *Behavioral ecology: an evolutionary approach*. 3rd ed. London, Blackwell Scientific Publications. Pp. 203–233.

- Hebets EA, Maddison WP 2005. Xenophilic mating preferences among populations of the jumping spider *Habronattus pugillis* Griswold. *Behavioral Ecology* 16: 981–988.
- Heil KH 1936. Beiträge zur Physiologie und Psychologie der Springspinnen. *Zeitschrift für Vergleichende Physiologie* 23: 125–149.
- Hoefler CD 2007. Male mate choice and size-assortative pairing in a jumping spider, *Phidippus clarus*. *Animal Behaviour* 73: 943–954.
- Hoikkala A, Crossley S, Castillo-Melendez C 2000. Copulatory courtship in *Drosophila birchii* and *D. serrata*, species recognition and sexual selection. *Journal of Insect Behavior* 13(3): 361–373.
- Homann H 1971. Die Augen der Araneae: Anatomie, Ontogenie und Bedeutung für die Systematik (Chelicerata, Arachnida). *Zeitschrift fuer Morphologie und Oekologie der Tiere* 69: 201–272.
- Howell DC 2002. *Statistical methods for psychology*. 5th ed. Belmont, California, Wadsworth.
- Jackson RR 1977. Courtship versatility in the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). *Animal Behaviour* 25: 953–957.
- Jackson RR 1980. The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae): II. Sperm competition and the function of copulation. *Journal of Arachnology* 8: 217–240.
- Jackson RR 1981. Relationship between reproductive security and intersexual selection in a jumping spider *Phidippus johnsoni* (Araneae: Salticidae). *Evolution* 35(3): 601–604.
- Jackson RR 1982a. The behaviour of communicating in jumping spiders. In: Witt PN, Rovner JS ed. *Spider communication: mechanisms and ecological significance*. Princeton, NJ, Princeton University Press. Pp. 213–247.
- Jackson RR 1982b. Habituation as a mechanism of intersexual selection. *Journal of Theoretical Biology* 97: 333–335.
- Jackson RR 1986. Cohabitation of males and females: a prevalent mating tactic of spiders. *Journal of Natural History* 20: 1193–1210.
- Jackson RR 1987. Comparative study of releaser pheromones associated with the silk of jumping spiders (Araneae, Salticidae). *New Zealand Journal of Zoology* 14: 1–10.
- Jackson RR 1992. Conditional strategies and interpopulation variation in the behaviour of jumping spiders. *New Zealand Journal of Zoology* 19(3–4): 99–111.
- Jackson RR, Hallas SEA 1986. Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata* and *P. schultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. *New Zealand Journal of Zoology* 13(4): 423–489.
- Jackson RR, Pollard SD 1982. The biology of *Dysdera crocata* (Araneae, Dysderidae): intraspecific interactions. *Journal of Zoology (London)* 198: 197–214.
- Jackson RR, Pollard SD 1990. Intraspecific interactions and the function of courtship in mygalomorph spiders: a study of *Porrothoele antipodiana* (Araneae: Hexathelidae) and a literature review. *New Zealand Journal of Zoology* 17(4): 499–526.
- Jackson RR, Pollard SD 1997. Jumping spider mating strategies: sex among cannibals in and out of webs. In: Choe JC, Crespi BJ ed. *The evolution of mating systems in insects and arachnids*. Cambridge, Cambridge University Press. Pp. 340–351.
- Jackson RR, Nelson XJ, Sune GO 2005. A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. *Proceedings of the National Academy of Sciences (USA)* 102(42): 15155–15160.
- Jackson RR, Walker MW, Pollard SD, Cross FR 2006. Influence of seeing a female on the male-male interactions of a jumping spider, *Hypoblemum albobittatum*. *Journal of Ethology* 24(3): 231–238.
- Land MF 1969a. Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *Journal of Experimental Biology* 51: 443–470.
- Land MF 1969b. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *Journal of Experimental Biology* 51: 471–493.
- Land MF 1985. The morphology and optics of spider eyes. In: Barth FG ed. *Neurobiology of arachnids*. Berlin, Springer-Verlag. Pp. 53–78.
- Maddison WP, Hedin M 2003. Phylogeny of *Habronattus* jumping spiders (Araneae: Salticidae), with consideration of genital and courtship evolution. *Systematic Entomology* 28: 1–21.
- Maddison WP, Stratton GE 1988. Sound production and associated morphology in male jumping spiders of the *Habronattus agilis* species group (Araneae: Salticidae). *Journal of Arachnology* 16: 199–211.

- Masta SE, Maddison WP 2002. Sexual selection driving diversification in jumping spiders (Araneae: Salticidae). *Proceedings of the National Academy of Sciences (USA)* 99: 4442–4447.
- Nelson XJ, Jackson RR 2006. A predator from East Africa that chooses malaria vectors as preferred prey. *PLOS One* 1: e132.
- Nelson XJ, Jackson RR, Sune GO 2005. Use of *Anopheles*-specific prey-capture behavior by the small juveniles of *Evarcha culicivora*, a mosquito-eating jumping spider. *Journal of Arachnology* 33: 541–548.
- Noordam AP 2002. Abdominal percussion and ventral scutum in male *Euophrys frontalis* (Araneae: Salticidae). *Entomologische Berichten Amsterdam* 62: 17–19.
- Peckham GW, Peckham EG 1889. Observations on sexual selection in spiders of the family Attidae. *Occasional Papers of the Wisconsin Natural History Society* 1: 3–60.
- Pollard SD, Macnab AM, Jackson RR 1987. Communication with chemicals: pheromones and spiders. In: Nentwig W ed. *Ecophysiology of spiders*. Berlin, Springer-Verlag. Pp. 133–141.
- Proctor HC 1992. Sensory exploitation and the evolution of male mating behaviour: a cladistic test using water mites (Acari: Parasitengona). *Animal Behaviour* 44(4): 745–752.
- Richman DB 1982. Epigamic display on jumping spiders (Araneae: Salticidae) and its use in systematics. *Journal of Arachnology* 10: 47–67.
- Richman D, Jackson RR 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). *Bulletin of the British Arachnological Society* 9(2): 33–37.
- Robinson MH 1982. Courtship and mating behavior in spiders. *Annual Review of Entomology* 27: 1–20.
- Rowe C 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour* 58: 921–931.
- Ryan MJ, Phelps SM, Rand AS 2001. How evolutionary history shapes recognition mechanisms. *Trends in Cognitive Sciences* 5: 143–148.
- Schneider JM, Lubin Y 1998. Intersexual conflict in spiders. *Oikos* 83: 496–506.
- Tinbergen N 1963. On aims and methods in ethology. *Zeitschrift für Tierpsychologie* 20: 410–433.
- Wells MS 1988. Effects of body size and resource value on fighting behaviour in a jumping spider. *Animal Behaviour* 36(2): 321–326.
- Wesolowska W, Jackson RR 2003. *Evarcha culicivora* sp. nov., a mosquito-eating jumping spider from East Africa (Araneae: Salticidae). *Annales Zoologici* 53(2): 335–338.
- Williams DS, McIntyre P 1980. The principal eyes of a jumping spider have a telephoto component. *Nature* 228(5791): 578–580.