

Geographical variation in male courtship behaviour of the giant whipscorpion *Mastigoproctus giganteus* (Lucas) (Arachnida, Uropygi)

Fred Punzo* and Carla Reeves

Box 5F—Department of Biology,
University of Tampa,
Tampa, Florida, 33606, USA

Summary

We analysed geographical variation in male courtship behaviour in the giant whipscorpion *Mastigoproctus giganteus* (Lucas) under laboratory conditions. The various behavioural components (ethogram) for male courtship were observed and video recorded for individuals from a xeric habitat in southwestern Texas (TX population) and from southern Florida (FL population), which is characterised by a humid, subtropical climate. Males from the FL population spent significantly more time in their initial approach and contact with the female, and required a longer period of time to form their spermatophore and to push the sperm carriers into the gonopore of the female. In addition, FL males stroked the antenniform legs of the female more forcefully, causing her legs to bend. Eighty percent of the FL males stepped on the prosoma of the female immediately following their second approach, whereas only 7% of the TX males exhibited this behaviour. Upon the completion of courtship, males derived from the TX population moved further away from the female (separation distance) than did FL males. The implications of geographical variation in communicative behaviour for divergence, possible reproductive isolation, and subsequent speciation, are discussed.

Introduction

The formation of new species occurs when populations first become reproductively isolated from each other and then continue to diverge and evolve independently (Foster & Cameron, 1996; Martins *et al.*, 1998). Prezygotic isolation often results from evolutionary changes in behavioural displays associated with courtship (Tinbergen, 1951; Butlin, 1996; Punzo, 1998, 2000a). Previous studies have reported both subtle and significant geographical variation in the behavioural components of communicative displays between populations in many species, including mammals (Thompson, 1999), birds (Byers, 1996), reptiles (Martins *et al.*, 1998), amphibians (Ryan *et al.*, 1996), fish (Luyten & Liley, 1985; Huntingford & Wright, 1992), insects (Duijm, 1990) and spiders (Miller *et al.*, 1998; Riechert, 1999).

Little information is available on the courtship behaviour of various species of whipscorpions. Although Weygoldt (1970) described the ethogram for male courtship in the giant whipscorpion, *Mastigoproctus giganteus* (Lucas, 1895), his description was based on several individuals collected from one locality in Coral Gables, Florida. He divided male courtship behaviour into four phases, each consisting of well-defined behavioural components (Table 1).

Mastigoproctus giganteus has a relatively wide geographical distribution and is most commonly found in arid regions of southwestern USA and northern Mexico

(Kraepelin, 1899; Rowland, 1973; Levi 1982), as well as in southern Florida (Weygoldt, 1971; Levi 1982). In view of this geographical distribution, and the high degree of isolation between the Florida populations and those in the deserts of southwestern USA, we undertook an analysis of male courtship behaviour in whipscorpions from the western (Brewster County, Texas, TX) and eastern (Dade County, Florida, FL) parts of their range in order to determine if there was any geographical variation between the FL and TX populations.

Methods

All of the whipscorpions used to observe courtship patterns were adult males and females reared in captivity from brood produced by adults originally collected from the western part of their range (Study Butte, Brewster County, Texas; Chihuahuan Desert), and from Dade County, Florida in the southeastern region of the USA. Adult whipscorpions ranged in size from 45–57 mm (measured from the anterior end of the prosoma to the base of the flagellum). The animals were reared individually in plastic cages, maintained at $23 \pm 1^\circ\text{C}$ and 60–70% RH, under a natural photoperiod regime, and fed on a mixed diet of mealworms, crickets, cockroaches, and grasshoppers.

The data in this study were based on the courtship behaviour of 15 successfully mating pairs from each population. All mating bouts occurred in glass terraria (75 cm long, 45 cm wide) whose floors contained a layer of sand and several flat stones, and a small dish containing a plug of water-soaked cotton. Pairs of males and females were introduced into these terraria and observed daily for courtship activities between 2100–0200 h EST. This time interval was chosen because this species is strongly nocturnal in its diel periodicity (Weygoldt, 1971; Punzo, 2000b, 2001). Pairs which engaged in mating activities did so within 2 days to 3 weeks after being placed together. All observations were conducted under red light through a one-way mirror to minimise disturbance to the animals. Individual behavioural components of courtship were observed and recorded with a Panasonic video camera, and the amount of time required for specific behavioural acts was determined using a Daigger digital timer (Carolina Biological Supply, Burlington, North Carolina).

All statistical procedures used for data analysis followed those described in the SAS user's guide (1989).

Results

The behavioural components (ethogram) of courtship in males from the FL and TX populations followed the outline shown in Table 1, although there were some differences between the two groups. The interval between the initial approach by the male (component 1, Table 1) to contact with the female (component 3) ranged between 24–93 min (mean 40.6 ± 9.3 SD) for FL whipscorpions compared with 9–27 min (mean 26.7 ± 7.4) for TX whipscorpions ($t=4.33$, $df=14$, $p<0.002$). FL males stroked the antenniform legs of the female (component 8) in a more forceful manner (often

*To whom all correspondence should be addressed.

causing her legs to bend) than their TX counterparts. In addition, twelve of the 15 FL males (80%) stepped on the prosoma of the female (component 12) immediately following their second approach, whereas only one (6.7%) of the TX males exhibited this behaviour ($\chi^2=33.64$, $p<0.01$).

At the beginning of phase 3, all of the FL males moved their bodies in a rigid backward and forward motion while rubbing their gonopores against the ground (component 20). In contrast, 73% of the TX males moved their bodies laterally as well as backward and forward. When courtship was completed, the males and females slowly backed away from one another (component 35), with their pedipalps extended, and then came to a stop. However, males from TX did not stop until they were separated from the anterior margin of the female's pedipalps by a distance ranging from 9–15 cm (mean 13.1 ± 2.3 SD); this separation distance was significantly less for FL males (3.5–10.5 cm; mean 8.3 ± 1.8 ; $t=4.92$, $p<0.01$). In no instance did either

sex engage in any type of aggressive interaction after separation.

There were also significant differences between the two populations with respect to the time allotted to complete certain behavioural components of courtship. For example, males from the FL population took considerably more time from their initial approach and contact with the female (components 1–3) to moving backward and pulling the female with them (component 15), as compared with the TX males (Fig. 1) ($t=6.61$, $df=14$, $p<0.001$). Males from the FL population also required more time for the formation of the spermatophore (Fig. 2A, component 24) ($t=5.78$, $p<0.001$), and took more time to search for the sperm carriers and push them into the gonopore of the female (Fig. 2B, components 30–31) ($t=3.70$, $p<0.002$). In contrast, there was no significant difference ($p<0.20$) between populations in the amount of time required to manipulate the flat ends of the sperm carriers by alternately pulling them apart and pushing them together (Fig. 2C, component 34).

Phase 1

1. Male approaches female (initial approach).
2. Rushes forward towards the female.
3. Makes contact with female using his pedipalps.
4. Grasps her antenniform (first pair) legs with his palpal chelae.
5. Female retreats backwards and male follows.
6. Grasps tips of her antenniform legs with his chelicerae.
7. Pulls her while walking backwards.

Phase 2

8. Strokes her antenniform legs with his pedipalps.
9. Strokes her pedipalps with his pedipalps.
10. Female retreats backwards and opens her pedipalps.
11. Male approaches female (second approach).
12. Steps on her prosoma.
13. His antenniform legs tremble, rapidly touching the ground (and occasionally one side or venter of female).
14. Female continues to step backwards.
15. Male moves backwards, pulling female with him.
16. Releases her antenniform legs from his pedipalps but continues to hold them with his chelicerae.
17. Male turns until both sexes are facing in same direction.
18. Female touches opisthosoma of male with her pedipalps.
19. Male begins to search for suitable place to deposit his spermatophore.

Phase 3

20. Slowly steps forwards, rubbing his gonopore against the ground.
21. Secretes the stalk of his spermatophore.
22. His legs tremble every few seconds while secreting spermatophore.
23. Slight swinging movement of male's body around a turning point marked by his gonopore.
24. Male lifts his body and the spermatophore is formed.

Phase 4

25. Male slowly steps forwards and pulls female towards spermatophore.
26. Female opens her gonopore, and her genital operculum grasps the hooks of the sperm carriers and pulls them out of the spermatophore (while elevating her opisthosoma).
27. Female releases opisthosoma of male.
28. Male releases her antenniform legs from his chelicerae.
29. He turns around, steps over anterior end of female, and grasps her opisthosoma from above with his pedipalps.
30. He slowly searches for the sperm carriers with the movable fingers of his palpal chelae.
31. He slowly pushes them into gonopore of female.
32. Pulls sperm carriers to sides of her genital slit.
33. Pushes them towards each other and then towards midline of her body (thereby compressing opisthosoma of female).
34. Manipulates flat ends of sperm carriers with tips of his movable palpal fingers, alternately pulling them apart and pushing them together.
35. Both sexes move away from one another.

Table 1: The four phases of male courtship behaviour (with the various behavioural components of each phase) in individuals of *Mastigoproctus giganteus* from southern Florida (Coral Gables). Behavioural components based on the descriptions of Weygoldt (1970).

Discussion

A closer inspection of the courtship behaviour of *M. giganteus* revealed several differences between males and females from allopatric populations. The TX and FL populations are separated by a distance of over 2900 km, with no opportunity for gene exchange. That these differences in behaviour exist at all suggests that courtship in this species may be under intense and relatively rapid selection pressure. It has been suggested that many FL populations of terrestrial invertebrates became separated from areas further west by a dramatic reduction in total land area and topographic relief during the late Pleistocene (Webb, 1990). In some cases, distinctive differences in the communicative displays between allopatric populations in certain species of vertebrates have been used in the description of subspecies (Martins *et al.*, 1998).

There were many behavioural components of courtship that did not differ in any significant way between these populations of *M. giganteus*. This may be due to biomechanical constraints associated with the movements and appendages involved in the elicitation of certain behaviours, thereby negating any opportunity for phenotypic plasticity.

It is interesting to note that males from the TX population spent significantly less time in their initial approach and contact with the female, in the formation of the spermatophore, and in pushing the sperm carriers into the gonopore of the female. This may in some part be due to the xeric conditions associated with the Chihuahuan Desert region of west Texas where the females were originally collected. Although *M. giganteus* is a common inhabitant of desert regions of southwestern USA and northern Mexico, nonetheless its cuticle is not a particularly effective barrier to evaporative water loss (EWL) and it will dehydrate more rapidly when exposed to dry air at the surface of the ground, in contrast to more xeric-adapted desert arthropods (Ahearn, 1970; Crawford & Cloudsley-Thompson, 1971; Punzo, 2000a). Spending less time in courtship would decrease the amount of time exposed to dry air and

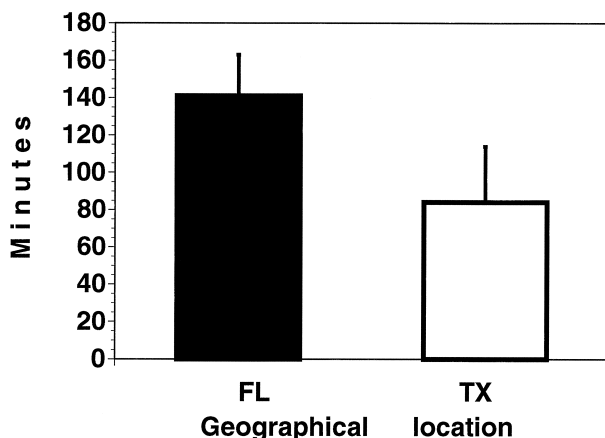


Fig. 1: The amount of time (min) required for males of *Mastigoproctus giganteus* from the Florida (FL) and Texas (TX) populations to complete behavioural components 1–15 of the courtship sequence. Data expressed as means; vertical lines represent \pm SD. See text for details.

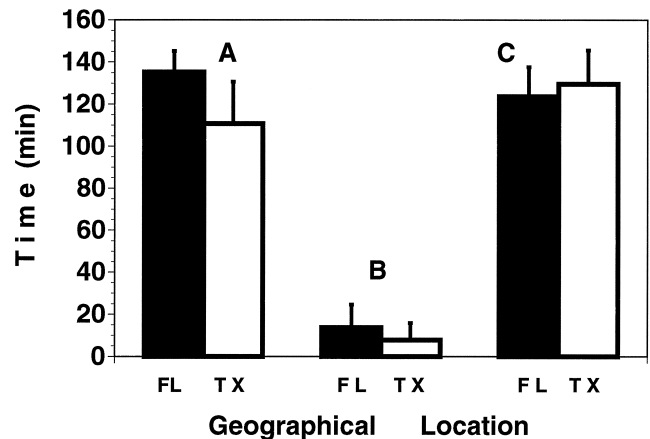


Fig. 2: The amount of time (min) required for males of *Mastigoproctus giganteus* from the Florida (FL) and Texas (TX) populations to complete various behavioural components of courtship. Data expressed as means; vertical lines represent \pm SD. (A) Behavioural component 24 (Table 1) (formation of spermatophore); (B) Components 30–31 (search for sperm carriers and their insertion into the gonopore of the female); (C) Component 34 (manipulation of sperm carriers). See text for details.

reduce the risk of death or debilitation caused by desiccation. On the other hand, males from southern FL are associated with a semitropical climate characterised by moist conditions where rates of EWL are greatly reduced. As a result, selective pressure on temporal aspects of courtship behaviour would be minimised.

The greater separation distance exhibited by the TX males as they moved away from the female following courtship may be related to differences in the levels of aggression among populations. Although sexual cannibalism is reported to be quite rare in whipscorpions (Kraepelin, 1899; Weygoldt, 1971; Levi, 1982), it has not been thoroughly investigated and merits closer inspection. Geographical variation in the levels of male-male and male-female aggression has been reported for other arachnids including scorpions (Polis & Sissom, 1990), solifugids (Punzo, 1998) and spiders (Riechert, 1999).

Geographical variation in communicative displays has been reported in other arachnids. In an analysis of several populations of the wolf spider, *Schizocosa crassipes* (Walckenaer) (Lycosidae), Miller *et al.* (1998) observed variation in both the frequency of occurrence and in the sequence of four major male courtship behaviours. Punzo & Henderson (1999) found that the male-male agonistic displays were more pronounced and incidences of sexual cannibalism higher in a population of the tarantula spider *Aphonopelma hentzi* (Girard) (Theraphosidae) from Trans-Pecos Texas as compared with observations reported for this spider from more mesic habitats. Levels of aggression between territorial males (contest behaviour) in populations of the funnel-web spider *Agelenopsis aperta* (Gertsch) (Agelenidae) inhabiting a xeric grassland habitat were more pronounced, resulting in higher rates of fighting and subsequent mortality, compared with that exhibited by spiders from riparian woodlands (Riechert, 1999). Various behavioural components of male courtship behaviour in scorpions including clubbing, cheliceral massage, sand-scraping, and juddering have also been shown to

vary between allopatric populations in several species (Polis & Sissom, 1990).

If such differences in courtship displays between populations become more pronounced, they could lead to reproductive isolation and subsequent speciation, as has been documented in salamanders (Verrell & Arnold, 1989), spiders (Stratton & Uetz, 1981), lacewings (Henry *et al.*, 1993), and a number of species of *Drosophila* (Wantanabe & Kawanishi, 1979; Krebs & Markow, 1989). The degree to which *M. giganteus* in TX may be diverging from FL populations needs further investigation, including an analysis of phenotypic plasticity in courtship patterns and other behaviours among allopatric populations in Texas, New Mexico, Arizona, California, and northern Mexico. Future studies using molecular techniques (mDNA, allozymes, etc.) could also provide important additional information on the genetic relationships between these various populations of *M. giganteus* in North America.

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