WAUER, R. H. 1980: *Naturalist's Big Bend*. Texas A & M Univ. Press, College Station, Texas.
WEYGOLDT, P. 1970: Courtship behaviour and sperm transfer in the giant whip scorpion, *Mastigoproctus giganteus* (Lucas) (Uropygi, Thelyphonidae). *Behaviour* **36**: 1–8.
WEYGOLDT, P. 1971: Notes on the life history and reproductive biology of the giant whip scorpion, *Mastigoproctus giganteus* (Uropygi, Thelyphonidae) from Florida. *J. Zool., Lond.* **164**: 137–147.

Bull. Br. arachnol. Soc. (2001) **12** (1), 41–45

Relative tolerance and communication in agonistic behaviour between females of *Loxosceles gaucho* (Araneae, Sicariidae)

André Augusto Stropa and
Isabela Maria Piovesan Rinaldi
Instituto de Biociências da Universidade Estadual Paulista, Departamento de Zoologia, UNESP/Botucatu, 18618-000 Rubião Junior, Botucatu, SP, Brazil

Summary

We describe the agonistic behaviour of adult female pairs of the brown spider, *Loxosceles gaucho*, in a flow diagram based on the observation of 12 experimental contests. Three chronological phases were identified: perception, information exchange, and aggression. We provide evidence of a relative tolerance in the trials once the female pairs have shown intra-specific recognition, inhibition of aggression, and communication. The communicative behaviours included foreleg vibration on the silk, palpal drumming, and "contestants hugging".

Introduction

Spiders of the genus *Loxosceles* Heineken & Lowe are of considerable medical and veterinary importance, and the study of their behaviour contributes to the understanding of factors that may influence the population growth of species of that group. However, the main studies concerning their natural history date back to the 1960s and 1970s and rarely report their behaviours. Some data on intra-specific interactions can be found in Hite *et al*. (1966) and Horner & Stewart (1967) for *Loxosceles reclusa* Gertsch & Mulaik; Ennik (1971) for *L. unicolor* Keyserling; and Levi & Spielman (1964), Galiano (1967), Galiano & Hall (1973), and Waldron *et al*. (1975) for *L. laeta* (Nicolet). Regarding *L. gaucho* Gertsch, only Rinaldi *et al*. (1997) and Rinaldi & Stropa (1998) dealt with their life cycle and sexual behaviour.

Although the agonistic behaviour of female spiders is less elaborate than that of males (Foelix, 1982), some studies have described communication and aggression between them, e.g. Riechert (1984) and Hodge & Uetz (1995).

In this study, the agonistic behavioural acts of pairs of *L. gaucho* adult females were recorded and quantified, and are described in a flow diagram and discussed in relation to intra-specific tolerance and communication.

Methods

Experimental animals

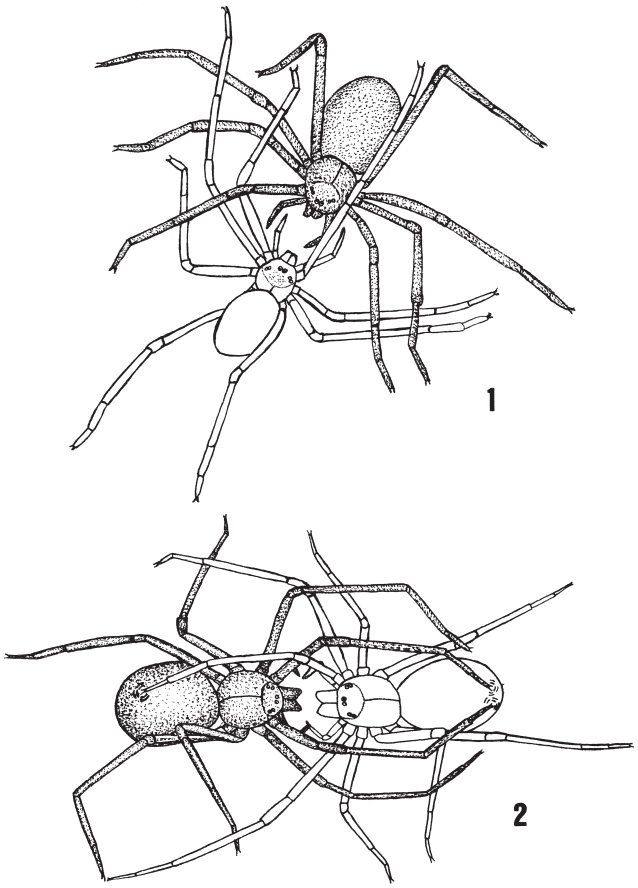
We used 24 adult females of *L. gaucho*, which had made at least one egg sac in the laboratory. These spiders were maintained individually in diet tubes (8.5 cm long × 2.5 cm internal diameter) from capture from nature or breeding from egg sacs produced in the laboratory. They were fed weekly with a varied diet of several types of insects obtained in the field by sweeping. The tests were performed in the Laboratory of Spiders of the Department of Zoology in the Institute of Bioscience of UNESP/Botucatu, SP, Brazil, under temperature and relative air humidity of 23°C and 70%.

Experimental model and specific procedures

We set up experimental arenas, each consisting of a transparent plastic cage (11.0 cm diameter × 7.0 cm high) connected to a transparent plastic tube (4.0 cm internal diameter × 6.0 cm long), called the escape valve. Each spider described as the owner was transferred from its diet tube to one of these arenas, where it was kept for at least one week before the experiments. That period was sufficient for the owners to spin a web. The spiders described as intruders were kept in their diet tubes until the time of the experiments.

The escape valve was sealed at one end with damp cotton. Before the experiments, the sealed end was connected to the cage, so that the owner could not enter the escape valve. For each trial, we disconnected the escape valve from the cage and placed the intruder inside the escape valve. We then reconnected it, so that the intruder could enter the cage.

We standardised the feeding of the owners and intruders, to prevent this variable interfering in their aggressiveness. Each spider was offered 10 *Musca domestica*. After two days, we randomly selected an owner and an intruder for each experimental contest. All the spiders were weighed on a Mettler H20T balance (Pmax. 160 g; d≅0.01 mg), and food scraps were removed from the arenas and diet tubes to avoid the spiders consuming them after weighing. This procedure was carried out in such a way that the owners' silk was not damaged. We marked one female of each pair, sometimes the owner, and sometimes the intruder, to facilitate the recognition of the animals during the experiments. The



Figs. 1–2: Agonistic behaviour in adult female pairs of *L. gaucho*. **1** Beginning of the "hug"; contestants overlap their forelegs; **2** "Hug" immediately before aggression; contestants caress the opponent's abdomen with their forelegs.

mark was made with nail varnish on the dorsal side of the abdomen. After a further two or three days, the experiments were performed.

We filmed in VHS system (Panasonic M9000), from above, until the end of each trial, which did not usually last more than 30 minutes. By analysing the tapes, with the aid of a chronometer and a manual counter, we recorded the qualitative and quantitative frequencies of the behavioural acts exhibited by the spiders.

Analysis of the results

All data were extracted from videotape recordings. We recorded the qualitative frequency of each visible agonistic behaviour in the 12 trials. The percentage occurrence of these behaviours was used to construct a flow diagram (Fig. 3).

We also analysed the quantitative frequency of bouts of two types of behaviour (foreleg vibration and palpal drumming). These bouts were separated by either inactivity or by another type of behaviour. Thus, for each spider we calculated the number of bouts per movement time (bouts/sec.); we did not consider the period when the spiders were motionless. To compare the behaviours of female owners and intruders, we used the *t*-test for dependent samples on the square root of data.

Results

In eight out of the twelve trials we identified three chronological phases: perception, information exchange, and aggression. In one other case the trial finished before the aggression phase. In a further three trials we did not detect any of these phases, i.e. the intruding spiders displayed only the initial acts of the first phase (touching the owner's silk — Fig. 3).

Perception

The intruders left the escape valves slowly, keeping their forelegs stretched out. When they touched a thread of the owner's silk for the first time, they ceased all movements immediately and remained motionless for several seconds, sometimes for some minutes. They resumed moving slowly, testing the owner's silk with their tarsi. On very dense silk, the intruders frequently cut some threads with their chelicerae. The owners remained motionless after the intruder's first touch on the silk. In most cases, only after the intruders had tested the silk did the owners turn around and face them ($n=7$). In one case, the owner moved first and the perception happened as described only after it had touched the intruder with its tarsi. The movements described here and in the following sections are shown diagrammatically in Fig. 3.

Information exchange

Information exchange may occur in two ways: vibratory, by the vibration of mechanical waves emitted on the owner's silk or through the air, and tactile, by physical contact between the opponents. The vibratory manner always preceded the tactile one.

Vibratory exchange: In nine out of twelve trials, both opponents drummed their palps soon after the perception phase. And in four out of those nine cases, they also vibrated their forelegs on the silk. We observed that these acts were identical to those of males of this species when courting females (see Rinaldi & Stropa, 1998).

The intruders drummed their palps 2.4 times more frequently than the owners ($t=-3.258$, $p<0.012$, $n=9$, df=8), but the average frequencies of the vibration of the forelegs for owners and intruders were not significantly different ($t=0.726$, $p<0.521$, n.s., $n=4$, df=3). The frequency of palpal drumming and foreleg vibration in the owners was, on average: 0.0033 ± 0.0045 bouts/s and 0.0176 ± 0.0208 bouts/s, respectively. For the intruders the frequencies were 0.0079 ± 0.0057 bouts/s and 0.0063 ± 0.0091 bouts/s, respectively. The contestants approached each other progressively while displaying these agonistic behaviours (Fig. 3).

Tactile exchange: In six out of the nine trials where palpal drumming occurred there was the "hug" — which when present always preceded the aggression phase — but it also happened in a non-aggressive trial (Table 1 and Fig. 3). Both females, facing each other, touched with their forelegs and closed progressively, overlapping their forelegs so that, sometimes, their

palps touched (Fig. 1). With their first pair of legs, each female caressed the extremity of the other's abdomen (Fig. 2). The aggressor female was always the one that first touched the substrate over the opponent's abdomen.

Aggression

Aggressive behaviour was characterised by frontal, direct and fast attack between the opponents. One of the females jumped abruptly against the other and generally reached it with its chelicerae. This was recorded in eight out of twelve trials (Table 1 and Fig. 3).

In these eight aggressive trials, six owners were the aggressors, and the heavier spiders won five contests (62%) (Table 1). In spite of the owner usually having been the aggressor, it was also the one which fled most often, but not different from random (62%). In contest number 12, the owner bit the intruder with its fangs for more than two minutes. Soon after, the owner released it, allowing the intruder to stand up and walk away. The intruder was not attacked further or pursued by the owner. After being bitten, this injured intruder did not feed again, but it remained alive for ten more days.

Although we did not measure the owner's silk density, it seemed to influence the outcomes of the contests. In trials where the owners had denser silk (like a sheet web), the owners were clearly more aggressive and the communication phase was more intense.

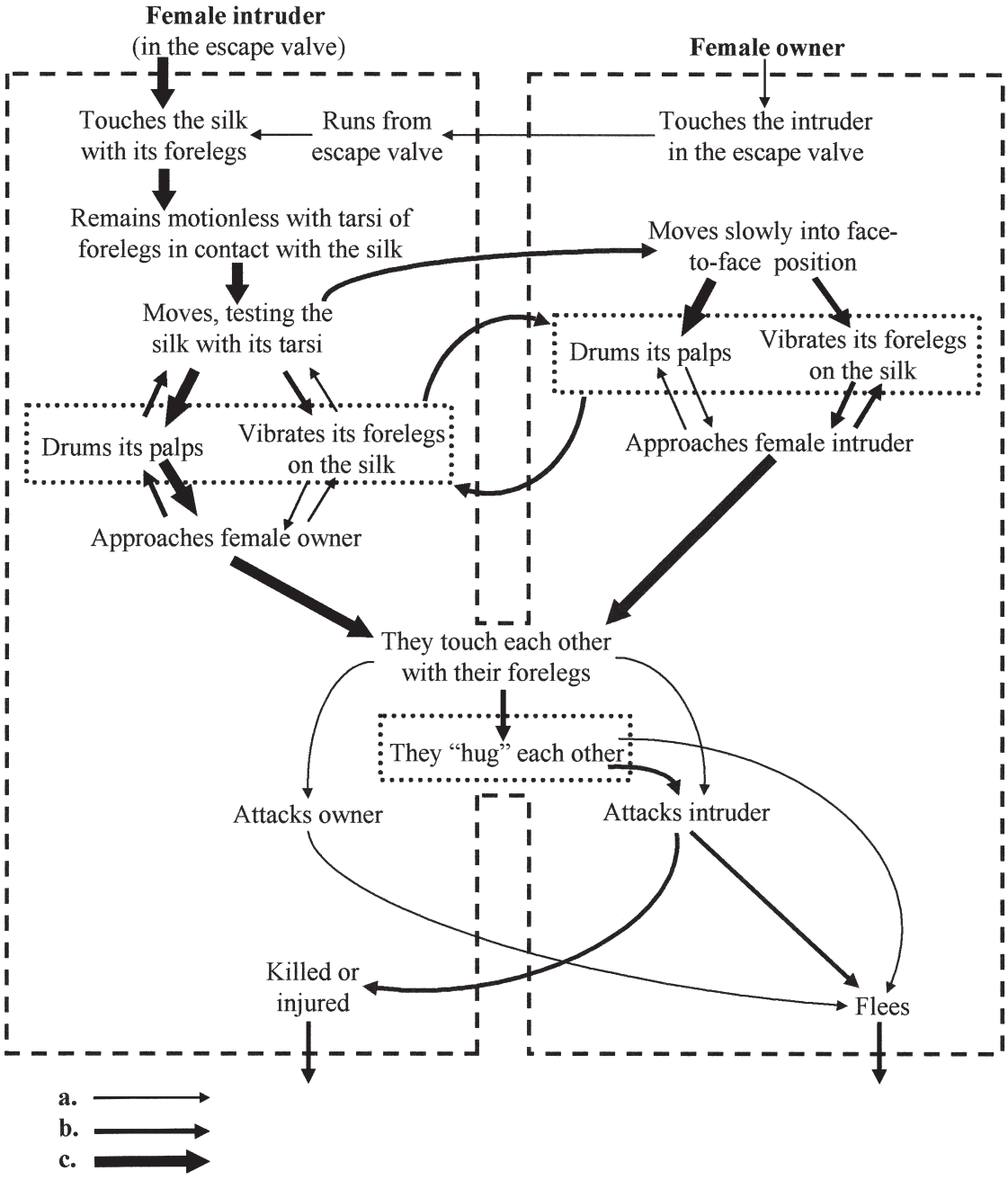


Fig. 3: Flow diagram of agonistic behaviour in adult female pairs of *L. gaucho* based on 12 trials. Arrows a, b and c indicate frequency between 8.3–25%, 33.3–58.3%, and 66.7–91.7%. Dashed lines delimit agonistic behaviour. Communicative behaviours are shown in the rectangles within dotted lines.

Discussion

Our results indicate that intra-specific communication exists between adult females of *L. gaucho* in an agonistic situation. Although simple, this system may be efficient in increasing females' tolerance of each other. By delaying aggression the contestant females can abort the contest without injuries.

In spiders, the occurrence of intra-specific communication implies that the individuals of a given species show a relative tolerance, which can be seen when there is intra-specific recognition (Krafft, 1982). Based on our data we suppose that in encounters between *L. gaucho* females, they first recognise each other by the inherent characteristics of the owner's silk and by the pattern of the intruder's movements in the owner's territory. They can then interact directly by stereotyped behaviours which inhibit aggression between the contestants — showing the existence of intra-specific tolerance. All these behavioural acts indicate the occurrence of communication, since a contestant's action alters the probability pattern of behaviour in its opponent (see Wilson, 1971, 1975).

The legs of a sedentary spider, especially the forelegs, are essential because of the sensory organs that, located in the tarsi, are the first structures to contact the environment (D'Andrea, 1987). In this way, an intruding spider would notice the inherent characteristics of the web such as tenacity, elasticity, density and chemical constitution. Assuming that those characteristics are intrinsic sources of intra-specific recognition, the female intruder of *L. gaucho* recognises the territory as being of its own species or perhaps of a related species at the first touch of its front tarsi on the owner's silk.

Trial number	"Hug"	Aggression	Weight (mg)	Winner (Loser)
1	yes	—	O: 145.0 I: 112.0	intruder (owner fled)
2	no	—	O: 111.0 I: 78.0	?
3	no	—	O: 178.0 I: 141.0	?
4	yes	O: 1 I: 0	O: 183.0 I: 135.0	owner (intruder killed)
5	no	O: 1 I: 0	O: 135.0 I: 244.0	intruder (owner fled)
6	yes	O: 5 I: 0	O: 205.0 I: 216.0	owner (intruder killed)
7	no	—	O: 190.0 I: 173.0	?
8	no	O: 0 I: 1	O: 143.0 I: 181.0	intruder (owner fled)
9	yes	O: 1 I: 1	O: 176.0 I: 191.0	intruder (owner fled)
10	yes	O: 1 I: 0	O: 189.0 I: 163.0	intruder (owner fled)
11	no	O: 0 I: 2	O: 184.0 I: 157.0	intruder (owner fled)
12	yes	O: 2 I: 0	O: 204.0 I: 133.0	owner (intruder injured)

Table 1: Experimental contests between adult females of *L. gaucho*: occurrence of "contestants hugging", number of aggressive acts per contestant (O=owner, I=intruder); weight of opponents and the trial outcome.

In the same way, the simple pattern of the intruder's movements on the owner's silk also contributes to intra-specific recognition. Thus, the female owner of *L. gaucho* should be able to discriminate between an intruder of the same species and a prey animal without needing any elaborate behaviour to be performed by the intruder, but the stereotyped behaviour (palpal drumming and foreleg vibration) should enhance recognition. In *L. unicolor*, Ennik (1971) stated that the intruder's simple random movement also allows intra-specific recognition. Therefore, this kind of recognition may be widespread in several or in all the species of this genus.

In the sexual behaviour of *L. gaucho*, palpal drumming by intruding males may have the primary function of suppressing females' aggression (Rinaldi & Stropa, 1998). Probably, palpal drumming by intruding females in agonistic behaviour has that same function, since this behaviour was performed more frequently by the intruding spiders.

As in Rinaldi & Stropa (1998), this study shows that recognition between adult individuals of *L. gaucho* usually happens before physical contact. However, the behaviour of female owners was different in this situation. In a sexual context the behaviours displayed by the intruding male (palpal drumming, foreleg vibration and abdominal pulsation) often caused the adoption of the sexual receptivity posture by the female for mating (Rinaldi & Stropa, 1998). But in this study, the behaviour of the intruding female never caused the adoption of this posture in female owners. As intruding females never displayed abdominal pulsation, this behaviour is probably the main sign for sexual recognition. Thus, abdominal pulsation exhibited by the male should promote the female's receptivity for mating. Krafft (1982) stated that, perhaps, the male's abdominal movements have the function of causing movements in the air that are perceived by the females' trichobothria.

Although we expected aggression when the "hug" took place (Table 1 and Fig. 3), especially when the females caressed each other's abdomen (Fig. 2), we interpreted the "hug" as a communicative act which serves as the last barrier to avoid aggression. Thus, this behaviour can be useful for both contestants because, by the "hug", the aggression phase is delayed and each spider could estimate its opponent's size. If a spider notices that it is much smaller than the other, it can abort the contest without any injury, before reaching the stage where abdomen caressing occurs. This could help explain the natural coexistence of these cannibal animals.

In contests between males, the larger contestant is generally the winner (Suter & Keiley, 1984; Wells, 1988; Jackson & Cooper, 1991). However, repeated contests

by male winners of the theridiid spider *Argyrodes antipodiana* O. P.-Cambridge, qualified them to compete successfully with opponents of the same size (Whitehouse, 1997). In this study, we did not know the level of experience of the females in contests, and the heavier female was the winner randomly (Table 1). Perhaps with a larger sample we might be able to detect some effect of opponents' weight in contest outcomes. However, more research is needed to identify the main variables that influence the outcome of these contests (perhaps the owner's silk density, territorial status of owner or intruder, and length of the opponents' fasting period).

Acknowledgements

We would like to thank Pedro R. Evangelista, Flávio da Silva and Amilton A. Rodrigues for field and laboratory assistance, and José M. Pisani for the illustrations. We also thank an anonymous reviewer and MSc Luciana C. Jordão for valuable suggestions. This study was supported by a fellowship to A A S from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP No. 96/09389-0).

References

D'ANDREA, M. 1987: Social behaviour in spiders (Arachnida, Araneae). *Monitore zool. ital.* (N.S.), Monogr. **3**: 1–156.

ENNIK, F. 1971: Laboratory observations on the biology of *Loxosceles unicolor* Keyserling (Araneae, Loxoscelidae). *Contr. Sci., Santa Barbara* **3**: 1–16.

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

GALIANO, M. E. 1967: Ciclo biológico y desarrollo de *Loxosceles laeta* (Nicolet, 1849) (Araneae, Scytodidae). *Acta zool. lilloana* **23**: 431–464.

GALIANO, M. E. & HALL, M. 1973: Datos adicionales sobre el ciclo vital de *Loxosceles laeta. Physis B. Aires* **32**: 277–288.

HITE, J. M., GLADNEY, W. J., LANCASTER Jr., J. L. & WHITCOMB, W. H. 1966: Biology of the brown recluse spider. *Bull. Ark. agric. Exp. Stn* **711**: 1–26.

HODGE, M. A. & UETZ, G. W. 1995: A comparison of agonistic behaviour of colonial web-building spiders from desert and tropical habitats. *Anim. Behav.* **50**: 963–972.

HORNER, N. V. & STEWART, K. W. 1967: Life history of the brown spider, *Loxosceles reclusa* Gertsch and Mulaik. *Tex. J. Sci.* **19**(4): 333–347.

JACKSON, R. R. & COOPER, K. J. 1991: The influence of body size and prior residency on the outcome of male-male interactions of *Marpissa marina*, a New Zealand jumping spider (Araneae, Salticidae). *Ethol. Ecol. Evol.* **3**: 79–82.

KRAFFT, B. 1982: The significance and complexity of communication in spiders. *In* P. N. Witt & J. S. Rovner (eds.), *Spider communication: mechanisms and ecological significance*: 15–66. Princeton, Princeton University Press.

LEVI, H. W. & SPIELMAN, A. 1964: The biology and control of the South American brown spider, *Loxosceles laeta* (Nicolet), in a North American focus. *Am. J. trop. Med. Hyg.* **13**: 132–136.

RIECHERT, S. E. 1984: Games spiders play. III: Cues underlying context-associated changes in agonistic behaviour. *Anim. Behav.* **32**: 1–15.

RINALDI, I. M. P., FORTI, L. C. & STROPA, A. A. 1997: On the development of the brown spider *Loxosceles gaucho* Gertsch (Araneae, Sicariidae): The nympho-imaginal period. *Revta bras. Zool.* **14**(3): 697–706.

RINALDI, I. M. P. & STROPA, A. A. 1998: Sexual behaviour in *Loxosceles gaucho* Gertsch (Araneae, Sicariidae). *Bull. Br. arachnol. Soc.* **11**(2): 57–61.

SUTER, R. B. & KEILEY, M. 1984: Agonistic interactions between male *Frontinella pyramitela* (Araneae, Linyphiidae). *Behav. Ecol. Sociobiol.* **15**: 1–7.

WALDRON, W. G., MADON, M. B. & SUDDARTH, T. 1975: Observations on the occurrence and ecology of *Loxosceles laeta* (Araneae: Scytodidae) in Los Angeles County, California. *Calif. Vector Views* **22**(4): 29–36.

WELLS, M. S. 1988: Effects of body size and resource value on fighting behaviour in a jumping spider. *Anim. Behav.* **36**(2): 321–326.

WHITEHOUSE, M. E. A. 1997: Experience influences male-male contests in the spider *Argyrodes antipodiana* (Theridiidae: Araneae). *Anim. Behav.* **53**: 913–923.

WILSON, E. O. 1971: *The insect societies*. Cambridge, Harvard University Press.

WILSON, E. O. 1975: *Sociobiology: the new synthesis*. Cambridge, Harvard University Press.