

# Male and Female Mate-Choice Decisions by *Evarcha culicivora*, An East African Jumping Spider

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## Abstract

There has been a considerable recent interest in the criteria by which animals choose mates and in the extent to which mating systems tend to be based on mutual mate choice. In this study, we consider *Evarcha culicivora*, a salticid spider from East Africa. This species has some unusual characteristics, including active display by females as well as males, males that kill females more frequently than females kill males and wide intrasexual variation in body size. For females, larger males are especially dangerous. Here, we demonstrate, using two experimental designs (live-mate choice and mount choice), that virgin males, virgin females and previously mated males prefer larger opposite-sex individuals as potential mates, but mated females prefer smaller, safer males as potential mates.

## Introduction

Qualitative differences in sex roles, usually with males being more active in courtship and females being more choosy (Andersson 1994), have been the traditional emphasis in the mate-choice literature, but there is a growing interest in the importance of mutual mate choice in the mating systems of a variety of animals (Altmann 1997; Kokko & Johnstone 2002; Drickamer et al. 2003; Gowaty et al. 2003; Cratsley & Lewis 2005), including wolf spiders (Rypstra et al. 2003). Numerous mate-choice studies also suggest that preference for larger potential mates is common in animals (Bonduriansky & Brooks 1998; Shine & Mason 2001; Dosen & Montgomerie 2004; Herdman et al. 2004; Byrne & Rice 2006). Here, we extend these earlier studies by investigating vision-based mate-size discrimination by *Evarcha culicivora*, a jumping spider (Family Salticidae) from East Africa.

*Evarcha culicivora* is a unique predator because its prey-choice decisions enable it to feed indirectly on vertebrate blood (Jackson et al. 2005). Moreover, males and females of this East African species are

both active at displaying during courtship (Cross & Jackson, unpubl.), suggesting that mutual mate choice might be pronounced. Questions about mate-size choice may be especially relevant for this species because the adult body length of males and females is unusually variable. Body size has been shown to influence the outcome of salticid male–male contests with larger individuals having an advantage (Wells 1988; Jackson & Cooper 1991; Faber & Baylis 1993; Taylor et al. 2001), but this is the first experimental study of salticid mate-size choice.

There is yet another unusual characteristic of *E. culicivora*. The popular portrayal of sexual cannibalism in spiders (Elgar 1992; Andrade 1996; Schneider et al. 2006) is of males being in mortal danger of females responding to them as prey. Contrary to this portrayal, *E. culicivora* males appear to be more dangerous to females than vice versa, with larger males seeming to be especially dangerous (Cross & Jackson, unpubl.).

We consider three hypotheses: (1) *Evarcha culicivora* is a species in which mutual mate-choice is pronounced (i.e. the male and the female both exercise

pronounced mate-choice behaviour); (2) females adopt a conditional mate-choice strategy that is sensitive to the danger posed by the male; and (3) for *E. culicivora*, cues from static appearance suffice for making mate-choice decisions.

Using a salticid for our experiments has particular advantages because, although the eyes of other spiders generally lack the structural complexity required for acute vision (Homann 1971; Land 1985), salticids have unique complex eyes, vision-based spatial acuity that is unrivalled by other animals in their size range (Harland & Jackson 2000, 2001, 2004; Land & Nilsson 2002) and some of the most elaborate vision-based courtship displays known for any animal group (Jackson & Pollard 1997). By using motionless mounts instead of living spiders as potential mates in choice experiments, we test for decisions based strictly on static appearance. However, by testing with living spiders, we also demonstrate that these decisions can be realistically interpreted as being decisions related to mating.

## Materials and Methods

### General

Our field site and laboratory were in western Kenya (Mbita Point) at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology. Standard spider-laboratory procedures were adopted (Jackson & Hallas 1986), and all testing was carried out between 08:00 h and 13:00 h (laboratory photoperiod 12 light:12 dark, lights on at 07:00 h).

*Evarcha culicivora*'s laboratory-rearing environment was enriched, as we used spacious cages (90 × 90 × 125 mm) with a mesh work of twigs within each cage (Carducci & Jakob 2000). 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). All testing was with adult spiders (virgin: matured 10 d before tested and had no encounters with conspecifics before testing) (mated spiders: matured 10 d before tested, mated with similar-sized virgin spider 5 d before tested; no other encounters with conspecifics before testing began).

Based on a sample taken in the field, we determined that 99% of the males were 3–6 mm in body length and 99% of the females were 4–7 mm (Fig. 1). We defined three spider sizes: small (male

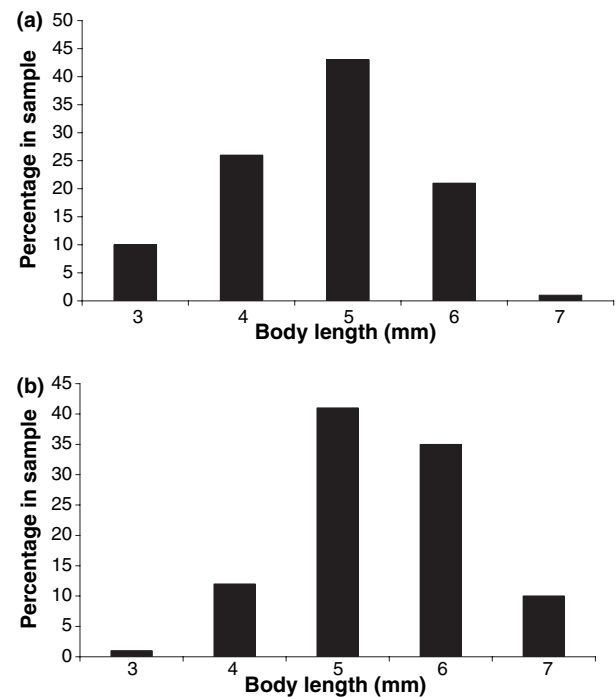


Fig. 1. Size distribution of *Evarcha culicivora* males (a) ( $\bar{x} \pm \text{SD} = 4.78 \pm 0.92$ ,  $n = 178$ ) and females (b) ( $\bar{x} \pm \text{SD} = 5.42 \pm 0.86$ ,  $n = 147$ ).

body length, 3 mm; female, 4 mm), medium (males and females, 5 mm) and large (male, 6 mm; females, 7 mm). Test spiders (size always medium) were presented with two different-size opposite-sex individuals (stimulus spiders).

Two experimental designs were adopted, expts 1 (testing with mounts) and 2 (testing with living spiders). Each experiment compensated for a limitation of the other. Experiment 1 was designed for ascertaining whether or not *E. culicivora* females and males make vision-based size choices in the absence of movement cues, without the decisions of another individual confounding interpretation of test outcome. However, calling outcomes from expt 1 'mate choice' is ambiguous because the test design did not allow for actual mating. This limitation was addressed in expt 2, the design of which allowed for mating and provided justification for saying that the outcome of expt 1 was meaningful in the context of mate choice.

No individual spider was used more than once as test spider, stimulus spider or mount in either of the two experiments, and no individual spider was used in both experiments.

Data were analysed by 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) and tests of independence (Howell 2002).

### Expt 1: Mount Choice

To make mounts, spiders were first immobilised with CO<sub>2</sub> and then placed in 80% ethanol. The next day, each spider was mounted in a life-like posture on the centre of a disc-shaped piece of cork (diameter 1.25 × the body length of the spider; thickness 2 mm). For preservation, the mount and the cork were then sprayed with a transparent plastic adhesive.

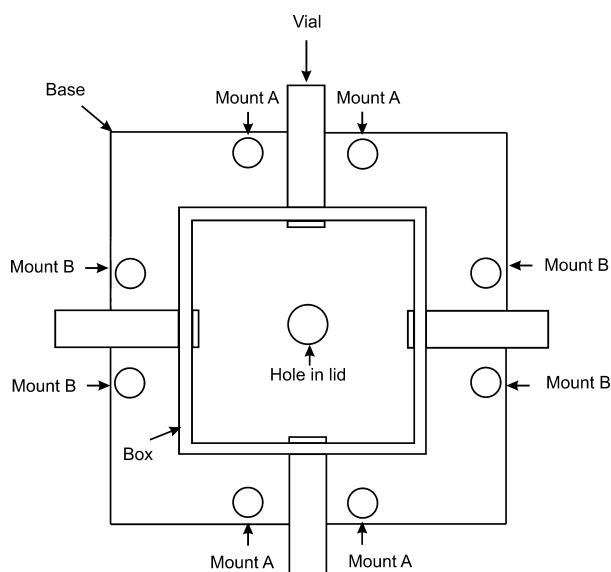
The testing apparatus (Fig. 2) was a square transparent glass box (100 × 100 mm, walls 35 mm high) with removable lid (100 × 100 mm) and on a plastic base (160 × 160 mm). Holes (diameter 16 mm) were centred on each of the four sides of the box (i.e. centre of hole 6 mm from top and 6 mm from bottom of box are 50 mm from left and right sides). There was a glass vial (length 50 mm) that fit snugly in each of the four holes (each vial open at end on inside of box, but closed on end on outside of box). In each test, two mount sizes were present (large and small, small and medium or large and medium). Each mount was secured to base with double-sided tape on the bottom of each cork and was positioned 10 mm to the side of each vial and 15 mm out from the side of the box. There were two mounts of the

same size next to each vial (positioned on either side of the vial, making a total of eight mounts positioned around the four sides of the box). The test spider could get closer to a mount by entering a vial. Each test began when the test spider entered through the hole (diameter 16 mm) centred in the lid of the box. Once the spider was inside, the hole was plugged with a rubber bung. The entire apparatus was lit with a 200-W incandescent lamp, positioned ≈ 400 mm overhead. Fluorescent lamps provided ambient lighting. Between tests, the apparatus was washed with 80% ethanol followed by distilled water and then dried.

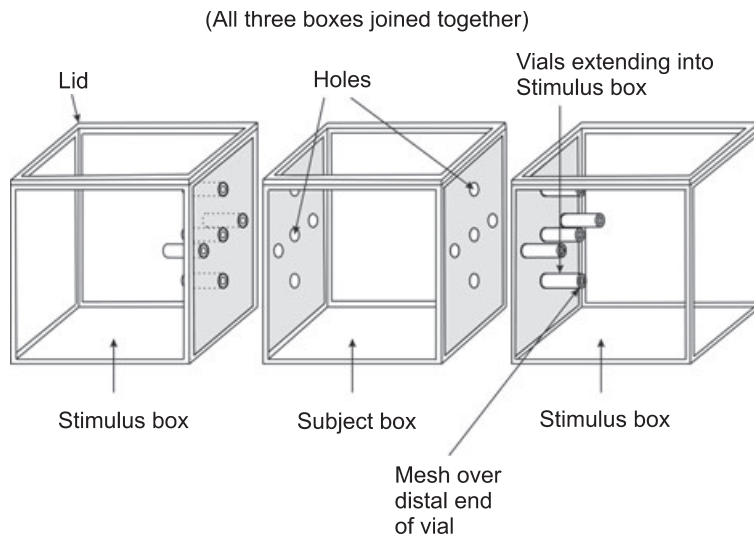
Displaying at mounts was uncommon and, when observed, typically lasted for only a few seconds. However, when the spider entered, and then stayed inside, any one of the four vials for 30 s, this was recorded as its choice. This criterion for 'choice' was met in most tests. The rationale for the 30-s criterion was that, in preliminary trials, although *E. culicivora* sometimes entered a vial for a few seconds and then left, any individual that stayed in a vial for 30 s continued to stay in this vial for at least 5 min and any that subsequently left this vial never entered and remained in another vial for as long as 30 s.

### Expt 2: Live Mate Choice

A test began with a test spider (male or female) in the subject box of the apparatus (Fig. 3) and with each of the two stimulus boxes housing a different-size stimulus spider: a large and a small spider, a small and a medium spider or a large and a medium spider. Which stimulus box housed the smaller of the two spiders was decided at random. Each box (100 × 100 × 100 mm, walls 5-mm thick) was made of clear Perspex and had a removable lid (100 × 100 mm). Five holes (diameter 10 mm) on each side of the subject box lined up with the five holes on the adjacent wall of the adjacent stimulus box (one hole in centre of wall, with other four holes positioned evenly around centre hole; distance between adjacent holes, 25 mm). Transparent glass tubes (8-mm diameter; 25-mm long) connected each stimulus box to the subject box. One opening of each tube was flush with the inside of the subject box, whereas the other end of the tube extended 20 mm into the stimulus box. The opening into the stimulus box was covered with a 'curtain' (mosquito netting held in place with rubber band). Each curtain extended 10 mm beyond the tip of the tube and had two holes (diameter 8 mm). One hole was on



**Fig. 2:** Mate-choice apparatus (not to scale) for expt 1 (mount tests). One mount on each side of each vial (size of mount A differed from size of mount B).



**Fig. 3:** Mate-choice apparatus (not to scale) for expt 2 (live-mate choice) made of clear Perspex. During testing, boxes pressed together (for clarity, walls that touch during testing shaded in drawing), forming a single 300-mm long box with three cubical compartments. Subject box (in centre) houses test spider. Each stimulus box houses a stimulus spider.

the left and one on the right side of the curtain. Test spiders readily entered the opening that was flush with the subject box, walked to the other end of the tube, left the tube by squeezing through one of the holes in the curtain and entered the stimulus box. The tube-and-mesh arrangement served as a one-way door because stimulus spiders only rarely moved on to the ends of the tubes and then entered by squeezing through the curtain (testing aborted whenever this happened).

Test spiders were given 60 min to observe the two stimulus spiders and get closer to one of them by entering a tube. Tests were aborted whenever a test spider entered one of the stimulus boxes before fixating the gaze of its principal eye corneal lenses on each of the two stimulus spiders at least once (happened in fewer than 5% of tests for any combination of test- and stimulus-spiders).

Once the test spider was inside a stimulus box, the test continued until the pair mated or 30 min elapsed, whichever came first. After each test, all boxes, tubes and curtains were washed with 80% ethanol followed by distilled water and then dried.

We recorded the test spider's 'choice' (i.e. size of stimulus spider in stimulus box entered) and whether or not the spiders mated.

## Results

### Expt 1: Mount Choice

The opposite-sex conspecific individuals chosen by virgin males and by virgin females were large more often than small, medium more often than small and large more often than medium (Table 1). Mated males, like virgin males, chose large females more often than small females, medium females more often than small females and large females more often than medium females. However, mated females chose small males more often than large males, small males more often than medium males and medium males more often than large males.

Choices made by virgin females were significantly different from choices made by mated females when presented with large and small males ( $\chi^2 = 20.82$ ,  $p < 0.001$ ), medium and small

**Table 1:** Choices made in mount-choice tests

Test spider	Large vs. small			Medium vs. small			Large vs. medium		
	Chose large	Chose small	Test for goodness of fit*	Chose medium	Chose small	Test for goodness of fit*	Chose large	Chose medium	Test for goodness of fit*
Virgin male	53	24	$\chi^2 = 10.92$ , $p = 0.001$	45	25	$\chi^2 = 5.71$ , $p = 0.017$	51	27	$\chi^2 = 7.38$ , $p = 0.007$
Virgin female	49	24	$\chi^2 = 8.56$ , $p = 0.003$	55	21	$\chi^2 = 15.21$ , $p < 0.001$	55	25	$\chi^2 = 11.25$ , $p = 0.001$
Mated male	41	21	$\chi^2 = 6.45$ , $p = 0.011$	43	19	$\chi^2 = 9.29$ , $p = 0.002$	44	21	$\chi^2 = 8.14$ , $p = 0.004$
Mated female	13	38	$\chi^2 = 12.25$ , $p = 0.001$	19	40	$\chi^2 = 7.47$ , $p = 0.006$	9	34	$\chi^2 = 14.53$ , $p < 0.001$

\*Null hypothesis: chose either size equally often.

males ( $\chi^2 = 21.63$ ,  $p < 0.001$ ) or large and medium males ( $\chi^2 = 25.62$ ,  $p < 0.001$ ). The choices made by mated females and by mated males were significantly different when presented with large and small ( $\chi^2 = 18.52$ ,  $p < 0.001$ ), medium and small ( $\chi^2 = 16.70$ ,  $p < 0.001$ ) or large and medium opposite-sex conspecific individuals ( $\chi^2 = 22.64$ ,  $p < 0.001$ ). The choices made by virgin males were not significantly different from the choices made by mated males when presented with large and small females ( $\chi^2 = 0.11$ ,  $p = 0.735$ ), medium and small females ( $\chi^2 = 0.38$ ,  $p = 0.538$ ) and large and medium females ( $\chi^2 = 0.08$ ,  $p = 0.771$ ).

**Expt 2: Live Mate Choice**

The opposite-sex conspecific individuals chosen by virgin males and by virgin females were large more often than small, medium more often than small and large more often than medium (Table 2). Virgin males and virgin females also mated with large more often than small spiders, with medium more often than small spiders and with large more often than medium spiders (Table 3).

Mated females chose small males more often than large males and medium males more often than large males, but how often they chose small males was not significantly different from how often they chose medium males (Table 2). Mated females also re-mated with small males more often than large males and with medium males more often than large males, but how often they re-mated with small males was not significantly different from how often they re-mated with medium males (Table 3).

Virgin and mated females made significantly different size choices when presented with a large and small male ( $\chi^2 = 42.30$ ,  $p < 0.001$ ), when presented with a medium and small male ( $\chi^2 = 7.67$ ,  $p = 0.006$ ) and when presented with a large and medium male ( $\chi^2 = 32.93$ ,  $p < 0.001$ ). Mating by virgin females was significantly more common than re-mating by previously mated females ( $\chi^2 = 113.58$ ,  $p < 0.001$ ). Of the 77 virgin females that made a choice, 87% mated. However, only 17% of the 180 mated females that made a choice re-mated. The size of male with which virgin and mated females mated with was also significantly different when presented with a large and small male ( $\chi^2 = 23.43$ ,  $p < 0.001$ ), when presented with a medium and small male ( $\chi^2 = 5.53$ ,  $p = 0.019$ ) and when presented with a large and medium male ( $\chi^2 = 16.36$ ,  $p < 0.001$ ).

**Table 2:** Choices made in live-choice tests

Test Spider	Large vs. small			Medium vs. small			Large vs. medium			Test for goodness of fit*
	Did not choose	Chose large	Chose small	Did not choose	Chose medium	Chose small	Did not choose	Chose large	Chose medium	
Virgin male	4	16	2	6	16	2	8	18	2	$\chi^2 = 10.89$ , $p = 0.001$
Virgin female	9	28	6	8	16	5	6	18	4	$\chi^2 = 14.24$ , $p < 0.001$
Mated female	52	3	37	53	37	50	60	7	46	$\chi^2 = 28.90$ , $p < 0.001$

NS, not significant.

\*Null hypothesis: chose either size of spider equally often (only spiders that made a choice relevant to analysis).

**Table 3:** Size of stimulus spider with which test spider mated in live choice tests

Test spider	Large vs. small		Medium vs. small		Large vs. medium		Test for goodness of fit*
	Mated with large	Mated with small	Mated with medium	Mated with small	Mated with large	Mated with medium	
Virgin male	14	1	15	2	17	2	$\chi^2 = 11.84, p = 0.001$
Virgin female	24	3	15	3	18	4	$\chi^2 = 9.94, p = 0.002$ $\chi^2 = 8.00, p = 0.005$
Mated female	1	11	4	6	0	8	$\chi^2 = 0.40, p = 0.527, NS$ $\chi^2 = 8.00, p = 0.005$

NS, not significant.

\*Null hypothesis: mated with either size equally often.

### Discussion

Theory from Trivers (1972), derived from Bateman (1948), may often be perceived as an argument that sex roles are qualitatively different, with only one sex doing the active courting and only one sex being especially choosy (Altmann 1997). However, a more accurate reading of the argument is that males and females exhibit differences in degree of choosiness, not qualitative (all-or-none) differences (Hubble & Johnson 1987; Gowaty et al. 2003).

Here, we have provided the first experimental evidence of pronounced mutual mate choice in a salticid and also the first experimental evidence of a salticid making size-choice discriminations in the context of mating. For *E. culicivora*, the adaptive significance of choosing larger mates remains unknown, but preference for larger mates is widespread in the animal kingdom (Andersson 1994). With *E. culicivora*, however, we have also found something especially unusual, a switching rule that applies to the female's, but not the male's, mate-size preferences.

*Evarcha culicivora* males more often kill and eat (cannibalise) females than vice versa and females may be especially vulnerable to being killed by a larger male (Cross & Jackson, unpubl.). We found that virgin females more often chose larger males and mated females more often chose smaller males. It is as though females start out prepared to take the risk in choosing larger males and then, once mated, become less inclined to take this risk again. However, the adaptive significance of this example of conditional mate-choice behaviour is currently unknown.

Although rarely acknowledged (Andersson 1994; Pryke & Andersson 2002), findings from prey-choice and mate-choice experiments are ambiguous when the experimental design does not actually permit eating or mating by the subject. Moreover, findings from choice experiments using two or more living animals are ambiguous because the outcome of a test may be the outcome of each animal influencing the other in largely unknown ways. We minimised these interpretation problems by using two experimental designs. The consistency of our findings from the different experiments provides unusually strong evidence of mate-size discrimination by *E. culicivora*. Experiment 1 demonstrated that *E. culicivora* can, by sight alone, even in the absence of movement, discriminate the size of opposite-sex individuals whereas expt 2 demonstrated that it is realistic to interpret test outcomes in the context of mate choice.

For salticids, it is normally unrealistic to envisage mate-choice as a simple yes-no decision. At the start of each test, for both of our experimental designs, the test spider was not in especially close proximity to any opposite-sex individual, and our criteria for 'choice' was behaviour by which the test spider moved into closer proximity to conspecifics of one or the other size. We confirmed that the criteria we used for 'choice' are related to mating (i.e. mating took place more often with the opposite-sex individual of the chosen size than with the other size individual), but we did not find, nor did we expect to find, a one-to-one match up between choosing and mating in live tests (i.e. mating was considerably less frequent than choosing).

There is another salticid, *Phidippus johnsoni*, for which we have extensive data on the re-mating decisions of females (Jackson 1981). In this species, already mated females mated again in about 7% of the tests, which is less than half as often as the frequency of re-mating we found for *E. culicivora* (17%). Whether *P. johnsoni* makes mate-size choices has not been investigated, but mated females of this species become stricter in their choice of males that perform zigzag dancing, a particularly active and seemingly demanding courtship routine.

With *P. johnsoni*, *E. culicivora* and probably most, if not all, salticids, it is unrealistic to envisage females as scrutinising males and then making, all at once, a definite decision to mate or not to mate. A more realistic portrayal of what happens with salticids, and probably with many animals, is that mating is the outcome of a drawn out negotiation between two individuals (i.e. expecting to find evidence of a definite early decision either to mate or not to mate tends to be unrealistic when studying salticid courtship and, instead, mating appears to be a consequence of multiple partial decisions made piecemeal).

*Evarcha culicivora* individuals often build nests inside rolled-up dead leaves on the ground, and this might account for how readily they entered narrow plastic tubes in the laboratory experiments. Sometimes, population density of *E. culicivora* appears to be such that a male or a female might encounter more than one opposite-sex individual at the same time, and this might have some relevance in explaining this species' willingness to make simultaneous-presentation choices. However, on the whole, we view our combination of apparatus and methods, based on using mounts and using living individuals, as jointly providing a practical bioassay by which we could assess *E. culicivora*'s mate-choice decisions.

Rather than attempting a close simulation of the conditions under which individuals would meet and possibly mate in nature, our goal was to arrive at an effective bioassay by which we could assess the mate-choice decisions.

In mount tests, mated females chose small males more often than medium males, but how often mated females chose small males was not significantly different from how often they chose medium males in live tests (i.e. live tests suggest that mated females have an aversion to large males while being indifferent to the size difference between medium and small males whereas mount tests suggest that mated females adopt an active preference for smaller males even when the alternative is a medium male). The explanation for this disparity in the outcome of mount and live tests is currently unknown.

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### Literature Cited

- Altmann, J. 1997: Mate choice and intrasexual reproductive competition: contributions that go beyond acquiring more mates. In: *Feminism and Evolutionary Biology* (Gowaty, P. A., ed). Chapman & Hall, New York, pp. 320–333.
- Andersson, M. 1994: *Sexual Selection*. Princeton Univ. Press, Princeton.
- Andrade, M. C. B. 1996: Sexual selection for male sacrifice in the Australian redback spider. *Science* **271**, 70–72.
- Bateman, A. J. 1948: Intra-sexual selection in *Drosophila*. *Heredity* **2**, 349–368.
- Bonduriansky, R. & Brooks, R. J. 1998: Male antler flies (*Protophila litigata*; Diptera: Piophilidae) are more selective than females in mate choice. *Can. J. Zool.* **76**, 1277–1285.
- Byrne, P. G. & Rice, W. R. 2006: Evidence for adaptive male mate choice in the fruit fly *Drosophila melanogaster*. *Proc. R. Soc. B.* **273**, 917–922.
- Carducci, J. P. & Jakob, E. M. 2000: Rearing environment affects behaviour of jumping spiders. *Anim. Behav.* **59**, 39–46.
- Cratsley, C. K. & Lewis, S. M. 2005: Seasonal variation in mate choice of *Photinus ignitus* fireflies. *Ethology* **111**, 89–100.

- Dosen, L. D. & Montgomerie, R. 2004: Female size influences mate preferences of male guppies. *Ethology* **110**, 245—255.
- Drickamer, L. C., Gowaty, P. A. & Wagner, D. M. 2003: Free mutual mate preferences in house mice affect reproductive success and offspring performance. *Anim. Behav.* **65**, 105—114.
- Elgar, M. A. 1992: Sexual cannibalism in spiders and other invertebrates. In: *Cannibalism* (Elgar, M. A. & Crespi, B. J., eds). Oxford Univ. Press, Oxford, pp. 128—155.
- Faber, D. B. & Baylis, J. R. 1993: Effects of body size on agonistic encounters between male jumping spiders (Araneae: Salticidae). *Anim. Behav.* **45**, 289—299.
- Gowaty, P. A., Drickamer, L. C. & Schmid-Holmes, S. 2003: Male house mice produce fewer offspring with lower viability and poorer performance when mated with females they do not prefer. *Anim. Behav.* **65**, 95—103.
- Harland, D. P. & Jackson, R. R. 2000: 'Eight-legged cats' and how they see – a review of recent research on jumping spiders (Araneae: Salticidae). *Cimbebasia* **16**, 231—240.
- Harland, D. P. & Jackson, R. R. 2001: Prey classification by *Portia fimbriata*, a salticid spider that specializes at preying on other salticids: species that elicit cryptic stalking. *J. Zool.* **255**, 445—460.
- Harland, D. P. & Jackson, R. R. 2004: *Portia* perceptions: the *Umwelt* of an araneophagic jumping spider. In: *Complex Worlds from Simpler Nervous Systems* (Prete, F. R., ed). MIT Press, Cambridge, Massachusetts, pp. 5—40.
- Herdman, E. J. E., Kelly, C. D. & Godin, J.-G. J. 2004: Male mate choice in the guppy (*Poecilia reticulata*): do males prefer larger females as mates? *Ethology* **110**, 97—111.
- Homann, H. 1971: Die Augen der Araneae: Anatomie, Ontogenie und Bedeutung für die Systematik (Chelicerata, Arachnida). *Z. Morphol. Oekol. Tiere* **69**, 201—272.
- Howell, D. C. 2002: *Statistical Methods for Psychology*. Wadsworth, Belmont, California.
- Hubble, S. P. & Johnson, L. K. 1987: Environmental variance in lifetime mating success, mate choice and sexual selection. *Am. Nat.* **130**, 91—112.
- Jackson, R. R. 1981: Relationship between reproductive security and intersexual selection in a jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). *Evolution* **35**, 601—604.
- 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.
- Jackson, R. R. & Hallas, S. E. A. 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. *N. Z. J. Zool.* **13**, 423—489.
- Jackson, R. R. & Pollard, S. D. 1997: Jumping spider mating strategies: sex among cannibals in and out of webs. In: *The Evolution of Mating Systems in Insects and Arachnids*. (Choe, J. C. & Crespi, B. J., eds). Cambridge Univ. Press, Cambridge, pp. 340—351.
- Jackson, R. R., Nelson, X. J. & Sune, G. O. 2005: A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. *Proc. Natl. Acad. Sci. USA.* **102**, 15155—15160.
- Kokko, H. & Johnstone, R. A. 2002: Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philos. Trans. R. Soc. Lond. B.* **357**, 319—330.
- Land, M. F. 1985: The morphology and optics of spider eyes. In: *Neurobiology of Arachnids* (Barth, F. G., ed). Springer-Verlag, Berlin, pp. 53—78.
- Land, M. F. & Nilsson, D.-E. 2002: *Animal Eyes*. Oxford Univ. Press, Oxford.
- Pryke, S. R. & Andersson, S. 2002: A generalized female bias for long tails in a short-tailed widowbird. *Proc. R. Soc. Lond. B.* **269**, 2141—2146.
- Rypstra, A. L., Wieg, C., Walker, S. E. & Persons, M. H. 2003: Mutual mate assessment in wolf spiders: differences in the cues used by males and females. *Ethology* **109**, 315—325.
- Schneider, J. M., Gilberg, S., Fromhage, L. & Uhl, G. 2006: Sexual conflict over copulation duration in a cannibalistic spider. *Anim. Behav.* **71**, 781—788.
- Shine, R. & Mason, R. T. 2001: Courting male garter snakes (*Thamnophis sirtalis parietalis*) use multiple cues to identify potential mates. *Behav. Ecol. Sociobiol.* **49**, 465—473.
- Taylor, P. W., Hasson, O. & Clark, D. L. 2001: Initiation and resolution of jumping spider contests: roles for size, proximity, and early detection of rivals. *Behav. Ecol. Sociobiol.* **50**, 403—413.
- Trivers, R. L. 1972: Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Campbell, B., ed). Aldine, Chicago, pp. 136—179.
- Wells, M. S. 1988: Effects of body size and resource value on fighting behaviour in a jumping spider. *Anim. Behav.* **36**, 321—326.