Natural History Note

Sexual Selection for Male Mobility in a Giant Insect with Female-Biased Size Dimorphism

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ABSTRACT: Female-biased size dimorphism, in which females are larger than males, is prevalent in many animals. Several hypotheses have been developed to explain this pattern of dimorphism. One of these hypotheses, the mobility hypothesis, suggests that female-biased size dimorphism arises because smaller males are favored in scramble competition for mates. Using radiotelemetry, we assessed the mobility hypothesis in the Cook Strait giant weta (*Deinacrida rugosa*), a species with strong female-biased size dimorphism, and tested the prediction that male traits promoting mobility (i.e., longer legs, smaller bodies) are useful in scramble competition for mates and thus promote reproductive success. Our predictions were supported: males with longer legs and smaller bodies exhibited greater mobility (daily linear displacement when not mating), and more mobile males had greater insemination success. No phenotypic traits predicted female mobility or insemination success. In species with female-biased size dimorphism, sexual selection on males is often considered to be weak compared to species in which males are large or possess weaponry. We found that male giant weta experience sexual selection intensities on par with males of a closely related harem-defending polygynous

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species, likely because of strong scramble competition with other males.

Although sexual dimorphism was the inspiration for Darwin's (1871) theory of sexual selection, the fundamental cause of differences between the sexes is still a topic of interest to evolutionary biologists (Shuster and Wade 2003). For example, the causes of sexual size dimorphism, perhaps the most widespread sexual difference among animals, remain a subject of considerable interest (Fairbairn 1997; Badyaev 2002; Shuster and Wade 2003; Blanckenhorn 2005).

A widespread pattern of sexual size dimorphism among birds and mammals is male-biased dimorphism (Darwin 1871; Andersson 1994; Fairbairn 1997). This pattern is thought to evolve principally by intense sexual selection on males whereby larger males accrue greater reproductive success (Andersson 1994). Because greater reproductive success for some males inevitably results in poor success for others, species with a greater degree of male-biased dimorphism are expected to experience more intense sexual selection (Andersson 1994; Shuster and Wade 2003).

Female-biased dimorphism (also called reversed size dimorphism) can evolve via three patterns of sexual difference in selection intensities (Blanckenhorn 2005). In the first scenario, weak sexual selection on male body size is coupled with strong directional fecundity selection on females for larger body size (Prenter et al. 1999; Hormiga et al. 2000), for example, if larger females produce better (Ralls 1976) or more (Honek 1993; Shine 1988) offspring. Alternatively, females could be under weak selection while males experience strong sexual selection, for example, if males with smaller body size are more mobile and superior in scramble competition (Andersson 1994; Blanckenhorn 2005) or aerial courtship displays (the mobility hypothesis; Andersson and Norberg 1981; Figuerola 1999; Székely et al. 2000; Raihani et al. 2006). We note that female-biased

dimorphism could arise even if scramble competition favored larger males, provided that there was sufficient selection for large female size as well. Vollrath and Parker (1992) argue that in some spiders, greater adult male mortality results in female-biased adult sex ratios, which in turn relaxes the strength of sexual selection for large male body size and consequently selects for smaller males. Finally, directional selection could act on each sex but in opposite directions, with females experiencing fecundity selection while smaller males have a mating advantage (Hormiga et al. 2000; Blanckenhorn 2005).

Regardless of the direction of sexual selection on male size, species exhibiting female-biased dimorphism are often thought to be under weaker sexual selection than species with male-biased dimorphism (Promislow et al. 1992; Moore and Wilson 2002; see also Vollrath and Parker 1992). However, this need not be true if the mobility hypothesis accounts for dimorphism, because in that case small males arise as a result of strong negative selection on size. Recent studies of mammals and birds support this argument by showing that sexual selection intensities on males in reversed size-dimorphic species can be equal in magnitude to those observed in species with male-biased dimorphism (Székely et al. 2004; Rossiter et al. 2006).

The Cook Strait giant weta *Deinacrida rugosa* (Orthoptera: Anostostomatidae), a nocturnal insect endemic to New Zealand and of high conservation importance (Gibbs 2001; McIntyre 2001), is an ideal candidate with which to test hypotheses of reversed size dimorphism evolution. Adult males (about 10 g) are roughly half the weight of females (about 20 g; C. D. Kelly, L. F. Bussière, and D. T. Gwynne, unpublished manuscript). *Deinacrida rugosa* inhabits old pastures, forests, and coastal scrub and seeks refuge from predators in the daytime by hiding under vegetation or other objects on the ground (McIntyre 2001). Males do not appear to defend resources required by sexually receptive females, nor do they guard harems of females, as do other deinacridines (i.e., *Hemideina* tree weta; McIntyre 2001). Instead, males seek receptive females as mates at night while females are foraging away from refuges (McIntyre 2001). Once a male locates a receptive female, he remains in physical contact with her using either his antennae or his legs and follows her until she finds a diurnal refuge (Richards 1973; McIntyre 2001). The pair will remain together at least until the following night—longer if the weather is cool and wet—copulating repeatedly throughout the day while in the refuge (Richards 1973; McIntyre 2001). Using radiotelemetry, we studied the movements of adult *D. rugosa* to test two related hypotheses: (i) males with smaller body sizes and longer legs are more mobile and are favored in scramble competition for mates and (ii), if this is the case, then sexual selection on males is not expected to be weaker than in species with

male-biased dimorphism because there is high variance in mating success among males in both cases (Székely et al. 2004; Rossiter et al. 2006).

Methods

Field Site

We conducted our study during April 2004 and April–May 2006 on Te Hoiere/Maud Island, New Zealand (41°02′S, 173°54′E), a 309-ha scientific reserve free of alien predators (e.g., rodents [*Mus* and *Rattus* spp.] and stoats [*Mustela erminea*]). Of the known predators of adult giant weta, only the endemic morepork owl *Ninox novaeseelandiae* is present on Maud Island (C. D. Kelly, personal observation).

Marking, Measuring, and Radiotelemetry of Study Animals

We opportunistically collected adult giant weta by scanning the open ground and pastures at night. For each individual captured, we noted its sex and developmental stage (juvenile or adult) and whether it was in close contact with a member of the opposite sex (males in close contact with a female throughout the night typically mate with her the subsequent day; Richards 1973; McIntyre 2001). Every censused adult was measured with digital callipers (Mitutoyo Digimatic) to the nearest 0.05 mm for each of the left and right hind tibia and pronotum width, weighed to the nearest 0.10 g using an electronic field balance, and marked with a uniquely numbered and colored bee tag (H. Thorne). Following Lorch and Gwynne (2000), in 2006 we then glued (cyanoacrylate) 0.40-g radio transmitters (PIP3, Biotrack, Dorset) to the pronotum, with the antenna pointed backward (fig. 1). Each animal was released at its point of capture.

Assessing Mobility

We recaptured radio-tagged individuals (transmitters could be detected in brush or grass from about 500 m) the day after being tagged and twice subsequently at 24-h intervals, noting whether the individual was paired with a member of the opposite sex in the diurnal refuge. We estimated the linear displacement of animals using either a 50-m measuring tape or, in rare cases when animals traveled farther than 50 m or over difficult terrain (e.g., a cliff), a handheld GPS unit (GPS 60, Garmin International, Olathe, KS). We assume that the average nightly distance traveled by a solitary male reflects his mobility and hence his capacity to locate mates (see Biedermann 2002).

Figure 1: An adult male Cook Strait giant weta *Deinacrida rugosa* following an adult female. A radiotransmitter is attached to the male's pronotum, with the antenna pointing backward (photograph by L. F. Bussière).

Measuring Insemination Success

Mating bouts, in which males mate repeatedly with the female, can last several hours to days in giant weta. The number of inseminations varies during a single mating bout, with each insemination lasting about 1 h, during which a single spermatophore is produced and deposited beneath the female's subgenital plate (Richards 1973). After deposition, the male releases the subgenital plate, and during the next few minutes, the spermatophore is gradually forced out of the female by the pushing movements of the male's paraprocts during attempted recopulations (Richards 1973). The male then reattaches to the female's genitalia and deposits another spermatophore. The ejected spermatophores are not eaten (in contrast to most ensiferan orthopterans; Brown and Gwynne 1997) and can be collected from the area around the female or sometimes from the surface of her body or ovipositor and counted. We defined insemination success as the number of spermatophores that a male transferred to a female because additional sperm is expected to be transferred with each additional spermatophore (as in mogoplistid crickets; Laird et al. 2004).

  We were able to leave pairs with at least one radio-tagged member to mate in their natural refuges. We inspected the refuge of such pairs for spermatophores near dusk. There was an increased opportunity to miscount spermatophores for radio-tracked pairs simply because spermatophores were more difficult to find in the conditions of the natural refuge. However, we found no evidence that the numbers of spermatophores transferred by males of a given body size differed between animals left in their refuges and those mated in plastic containers under controlled laboratory conditions (C. D. Kelly, L. F. Bussière, and D. T. Gwynne, unpublished data).

Path Analysis

We used path analysis to study the mechanisms underlying sexual selection in both sexes (Arnold and Duvall 1994; Conner 1996; Sih et al. 2002). By calculating standardized partial regression coefficients (β; Lande and Arnold 1983; Arnold and Wade 1984), path analysis measures the relative statistical importance of different aspects of an a priori hypothesis embodied in a path diagram (fig. 2). This approach not only estimates β for traits but also reveals the behavioral mechanisms and their relative contribution to the underlying pattern of sexual selection. We analyzed variables that are likely to affect sexual selection on male and female *Deinacrida rugosa* (i.e., mobility, pairing success, and number of spermatophores transferred) and their relationship to several morphological measures (e.g., pronotum width, mean hind tibia length, and body weight).

Individual insemination success was calculated as the product of pairing success (proportion of observations in which an individual was in contact with a member of the opposite sex) and the average number of spermatophores transferred or received. We performed path analyses for males and females separately, with sample sizes (given in fig. 2) differing between the sexes and in particular analyses.

Opportunity for Sexual Selection

On each of 12 (2004) and 21 (2006) consecutive nights, approximately 3 h after sunset, we counted the number of adult males and females we observed while scanning the ground for weta. For all individuals, we noted their location, pronotum width, mass, and paired status. We calculated the opportunity for sexual selection, I_{mates}, using the statistical framework of Shuster and Wade (2003). With this approach, only potential breeding aggregations are considered in the analysis (i.e., only paired and single males). We considered each night as a sample unit because it represented a discrete opportunity to acquire a mate for the following day.

The opportunity for sexual selection was calculated using

$$I_{mates} = \frac{V_{harem}}{H^2(1 - p_0)} + \frac{p_0}{1 - p_0}, \tag{1}$$

where V_{harem} is the variance in harem size (i.e., number of females) of successful males, H is the mean harem size of successful males, p_0 is the proportion of unsuccessful males, and $1 - p_0$ is the proportion of successful males observed each night (Shuster and Wade 2003). Because each male giant weta can associate with only one female at a time, variance among harems is always 0, and harem size can reach a maximum of only $n = 1$ female. Therefore, I_{mates} is entirely attributed to the proportion of unmated to mated males, the strongest influence on the strength of sexual selection (Shuster and Wade 2003). We assess the opportunity for sexual selection in *D. rugosa* by comparing its I_{mates} value to that of *Hemideina crassidens*, a related harem-defending deinacridine weta in which males are known to be under strong sexual selection (Kelly 2005, 2008).

For all analyses, we used probability plots to graphically inspect normality and residual plots to determine whether variances were homogeneous. Data violating these assumptions were $\log_{10}$ transformed. Means are presented as untransformed values ± 1 SE. All statistical tests were two tailed at the 0.05 α level.

Results

Effect of Sex on Mobility

Males traveled significantly farther per night ($1{,}887.38 \pm 235.16$ cm night^{-1}) than did females (697.21 ± 159.04 cm night^{-1}; $F = 30.456$, df $= 1, 64$, $P < .0001$). The maximum distance traveled during a single night by an individual male (8,800 cm) was nearly twice that for females (4,600 cm). Males tended to move greater distances when solitary ($1{,}998.22 \pm 291.39$ cm night^{-1}) than when paired ($1{,}468.92 \pm 329.78$ cm night^{-1}), but this difference was not significant (paired *t*-test, $t = 1.115$, df $= 17$, $P = .28$). Conversely, females tended to move farther per night when paired (857.15 ± 216.69 cm night^{-1}) than when solo (604.90 ± 177.64 cm night^{-1}), but again this difference was not statistically significant ($t = -0.934$, df $= 11$, $P = .37$).

Interrelationships among Morphology, Mobility, and Insemination Success

Measures of body size (pronotum width), body weight, and leg length (hind tibia length) were significantly positively correlated in both males ($N = 66$) and females ($N = 51$; for correlation strength and statistical significance, refer to fig. 2; see also C. D. Kelly, L. F. Bussière, and D. T. Gwynne, unpublished manuscript). As predicted, males with longer legs and smaller bodies showed significantly greater mobility, and males that traveled farther per night had significantly greater insemination success (fig. 2*a*). No path coefficients were significant for females (fig. 2*b*).

Opportunity for Sexual Selection

As predicted, I_{mates} for *Deinacrida rugosa* (2.00 ± 0.30, $N = 33$) was significantly >0 ($t = 6.77$, df $= 32$, $P < .0001$) and did not differ from I_{mates} for *Hemideina crassidens*, a deinacridine weta with male weaponry (elongated mandibles) at the same study site (2.34 ± 0.18, $N = 99$; $F = 0.892$, df $= 1, 130$, $P = .347$; Kelly 2008).

Discussion

As predicted, the intensity of sexual selection on males in *Deinacrida rugosa*, a species with female-biased size dimorphism, was similar to that of another deinacridine, *Hemideina crassidens*, a classical harem-defending polygynous species in which males have mandibular weaponry (Kelly 2006*a*). Similarly, Rossiter et al. (2006) recently showed that male greater horseshoe bats (*Rhinolophus ferrumequinum*), a species with female-biased sexual size dimorphism, can experience intensities of sexual selection
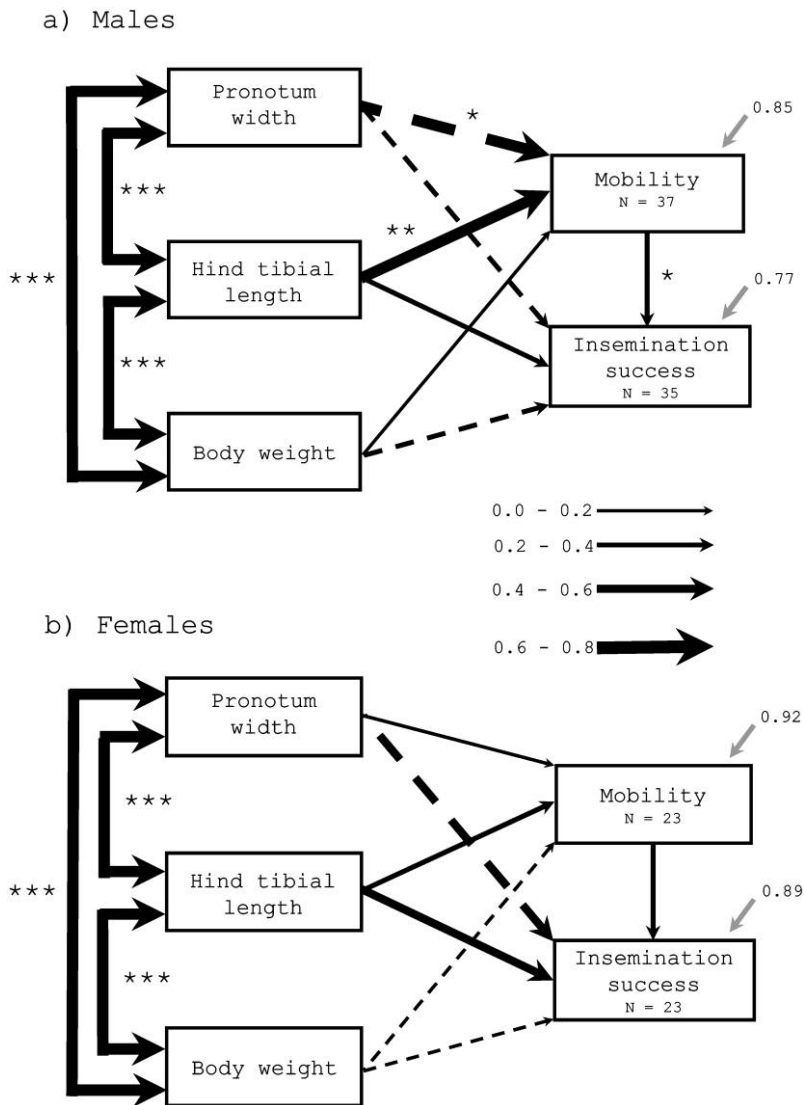
a) Males

b) Females

Figure 2: Path diagram for male (*a*) and female (*b*) Cook Strait giant weta. Phenotypic traits on which selection is measured are on the left, with correlations among them, and hypothesized causal links to fitness components (mobility and insemination success) are on the right. Correlations are depicted as double-headed arrows and causal relationships as single-headed arrows. Dashed arrows denote negative coefficients, and arrow width is proportional to the standardized coefficients (see scale). The numbers next to the gray arrows on the right are unexplained variance ($(1 - r^2)^{1/2}$). *One asterisk, P* < .05; *two asterisks, P* < .01; *three asterisks, P* < .001.

on par with males in male-dimorphic polygynous species. However, they were unable to link the opportunity for selection to selection on particular male traits. We show that intense indirect competition for mates leads to high variance in mating success, which in turn is related to phenotypic traits that co-vary with mobility. Adult male giant weta with longer legs and smaller bodies traveled significantly farther per night and accrued significantly greater insemination success. Biedermann (2002) found that in the male-biased size dimorphic spittlebug *Cercopis*

sanguinolenta, larger males were more mobile; however, he was unable to link mobility with mate acquisition and thereby support the role of mobility in driving size dimorphism in that species.

We found that the average distance traveled per night by giant weta was far greater than those recorded for the Wellington tree weta (about 3 m night^{-1}; Kelly 2006*b*) and the Raukumara tusked weta *Motuweta riparia* (about 10 m night^{-1}; McCartney et al. 2006). This was expected because both tree weta (Kelly 2006*b*, 2006*c*) and probably

tusked weta (D. T. Gwynne, C. D. Kelly, and L. F. Bussière, unpublished data) return to a gallery every morning. We also found that giant weta males traveled significantly farther per night than did females, unlike in the Wellington tree weta, in which there is little apparent sex difference in nightly movement distance (Kelly 2006b).

The importance of sexual selection relative to fecundity selection in driving the evolution of sexual size dimorphism in *D. rugosa* is an exciting direction for future research. If fecundity selection plays a role in the evolution of giant weta size dimorphism, then an intriguing possibility is that intense ontogenetic conflict arises between the sexes whereby the expression of alleles during development may move one sex toward and the other away from its optimum phenotype. That is, fecundity selection should favor larger females, while greater mobility should favor smaller males. Such avenues of research will, however, require detailed estimates of fecundity selection on females and should attempt to incorporate longer-term studies of male mate acquisition, postcopulatory sexual selection, and aspects of natural selection, such as longevity and predation risk.

Acknowledgments

Literature Cited

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

Andersson, M., and R. A. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biological Journal of the Linnean Society 15:105–130.

Arnold, S. J., and D. Duvall. 1994. Animal mating systems: a synthesis based on selection theory. American Naturalist 143:317–348.

Arnold, S. J., and M. J. Wade. 1984. On the measurement of natural and sexual selection: theory. Evolution 38:709–719.

Badyaev, A. V. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. Trends in Ecology & Evolution 17:369–378.

Biedermann, R. 2002. Mating success in the spittlebug *Cercopis sanguinolenta* (Scopoli, 1763) (Homoptera, Cercopidae): the role of body size and mobility. Journal of Ethology 20:13–18.

Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. Ethology 111:977–1016.

Brown, W. D., and D. T. Gwynne. 1997. Evolution of mating in crickets, katydids and wetas (Ensifera). Pages 281–314 in S. K. Gangwere, M. C. Muralirangan, and M. Muralirangen, eds. The bionomics of grasshoppers, katydids and their kin. CAB International, Wallingford.

Conner, J. K. 1996. Understanding natural selection: an approach integrating selection gradients, multiplicative fitness components, and path analysis. Ethology Ecology and Evolution 8:387–397.

Darwin, C. 1871. The descent of man, and selection in relation to sex. J. Murray, London.

Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual Review of Ecology and Systematics 28:659–687.

Figuerola, J. 1999. A comparative study on the evolution of reversed size dimorphism in monogamous waders. Biological Journal of the Linnean Society 67:1–18.

Gibbs, G. W. 2001. Habitats and biogeography of New Zealand's Deinacridine and tusked weta species. Pages 35–55 in L. H. Field, ed. The biology of wetas, king crickets and their allies. CAB International, Wallingford.

Honek, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66:483–492.

Hormiga, G., N. Scharff, and J. A. Coddington. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). Systematic Biology 49:435–462.

Kelly, C. D. 2005. Allometry and sexual selection of male weaponry in Wellington tree weta, *Hemideina crassidens*. Behavioral Ecology 16:145–152.

———. 2006a. Fighting for harems: assessment strategies during male-male contests in the sexually dimorphic Wellington tree weta. Animal Behaviour 72:727–736.

———. 2006b. Movement patterns and gallery use by the sexually dimorphic Wellington tree weta. New Zealand Journal of Ecology 30:273–278.

———. 2006c. Resource quality or harem size: what influences male tenure at refuge sites in tree weta (Orthoptera: Anostostomatidae)? Behavioral Ecology and Sociobiology 60:175–183.

———. 2008. Identifying a causal agent of sexual selection on weaponry in an insect. Behavioral Ecology 19:184–192.

Laird, G., D. T. Gwynne, and M. C. B. Andrade. 2004. Extreme repeated mating as a counter-adaptation to sexual conflict? Proceedings of the Royal Society B: Biological Sciences 271:S402–S404.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Lorch, P. D., and D. T. Gwynne. 2000. Radio-telemetric evidence of migration in the gregarious but not the solitary morph of the Mormon cricket (*Anabrus simplex*: Orthoptera: Tettigoniidae). Naturwissenschaften 87:370–372.

McCartney, J., D. A. Armstrong, D. T. Gwynne, C. D. Kelly, and R. Barker. 2006. Estimating abundance, age structure and sex ratio of a recently discovered New Zealand tusked weta *Motuweta riparia* (Orthoptera, Anostostomatidae), using mark-recapture analysis. New Zealand Journal of Ecology 30:229–235.

McIntyre, M. E. 2001. The ecology of some large weta species in New Zealand. Pages 225–242 *in* L. H. Field, ed. The biology of wetas, king crickets and their allies. CAB International, Wallingford.

Moore, S. L., and K. Wilson. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. Science 297: 2015–2018.

Prenter, J., R. W. Elwood, and W. I. Montgomery. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. Evolution 53:1987–1994.

Promislow, D. E. L., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. Proceedings of the Royal Society B: Biological Sciences 250:143–150.

Raihani, G., T. Szekely, M. A. Serrano-Meneses, C. Pitra, and P. Goriup. 2006. The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae). Animal Behaviour 71:833–838.

Ralls, K. 1976. Mammals in which females are larger than males. Quarterly Review of Biology 51:245–276.

Richards, A. M. 1973. A comparative study of the biology of the giant wetas *Deinacrida heteracantha* and *D. fallai* (Orthoptera: Henicidae) from New Zealand. Journal of Zoology (London) 169: 236.

Rossiter, S. J., R. D. Ransome, C. G. Faulkes, D. A. Dawson, and G. Jones. 2006. Long-term paternity skew and the opportunity for selection in a mammal with reversed sexual size dimorphism. Molecular Ecology 15:3035–3043.

Shine, R. 1988. The evolution of large body size in females: a critique of Darwin's fecundity advantage model. American Naturalist 131: 124–131.

Shuster, S. M., and M. J. Wade. 2003. Mating systems and strategies. Princeton University Press, Princeton, NJ.

Sih, A., M. Lauer, and J. J. Krupa. 2002. Path analysis and the relative importance of male-female conflict, female choice and male-male competition in water striders. Animal Behaviour 63:1079–1089.

Székely, T., J. D. Reynolds, and J. Figuerola. 2000. Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. Evolution 54:1404–1413.

Székely, T., R. P. Freckleton, and J. D. Reynolds. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. Proceedings of the National Academy of Sciences of the USA 101: 12224–12227.

Vollrath, F., and G. A. Parker. 1992. Sexual dimorphism and distorted sex-ratios in spiders. Nature 360:156–159.