Sexual selection for male agility 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, but the factors causing this pattern of dimorphism are still poorly understood. The agility hypothesis suggests that female-biased size dimorphism arises because smaller males are favoured in scramble competition for mates. Using radio telemetry, we assessed the agility 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 and/or possess weaponry. We found that male giant weta experience sexual selection intensities on par with males of a closely related harem-defending polygynous 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 poorly understood (Shuster and Wade 2003). For example, the causes of sexual size dimorphism, perhaps the most widespread sexual difference among animals, remains a subject of considerable controversy (Badyaev 2002; Blanckenhorn 2005; Fairbairn 1997; Shuster and Wade 2003).

A widespread pattern of sexual size dimorphism among birds and mammals is male-biased dimorphism (Andersson 1994; Darwin 1871; 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 (Hormiga et al. 2000; Prenter et al. 1999), if for example larger females produce better (Ralls 1976) or more offspring (Honek 1993; Shine 1988). Alternatively, females could be under weak selection while males experience strong sexual selection, for example if males with smaller body size are superior in scramble competition (Andersson 1994; Blanckenhorn 2005) or aerial courtship displays ('the agility hypothesis'; Andersson and Norberg 1981; Figuerola 1999; Raihani et al. 2006; Székely et al. 2000). Vollrath and Parker (1992) argue that in some spiders, greater adult male mortality results in female-biased adult sex ratios, which in turn relax 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 (Blanckenhorn 2005; Hormiga et al. 2000).

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 (Moore and Wilson 2002; Promislow et al. 1992; see also, Vollrath and Parker 1992). However, this need not be true if the agility hypothesis accounts for dimorphism, because in that case small males arise due to 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 (Rossiter et al. 2006; Székely et al. 2004).

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 (ca. 10 g) are roughly half the weight of females (ca. 20 g) (Kelly et al. in prep). *D. 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 in 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 legs, and follows her until she finds a diurnal refuge (McIntyre 2001; Richards 1973). 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 (McIntyre 2001; Richards 1973).

Using radio telemetry 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 favoured 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 (Rossiter et al. 2006; Székely et al. 2004).

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 (personal observation).

Marking, measuring and radio telemetry 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, 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; McIntyre 2001; Richards 1973). 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 coloured bee tag (H. Thorne Limited). Following Lorch and Gwynne (2000), in 2006 we then glued (cyanoacrylate) 0.40 g radio transmitters (PIP3, Biotrack Ltd., Dorset, UK) to the pronotum with the antenna pointed backwards (supplemental 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 ca. 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 travelled further than 50 m, or over difficult terrain (e.g., a cliff), a handheld GPS unit (GPS 60 model, Garmin International, Inc., Olathe, Kansas). We assume that the average nightly distance travelled by a solitary male reflects his mobility and hence his capacity to locate mates (see Biedermann 2002).

Measuring insemination success

The number of copulations vary during a mating bout in giant weta, but each one lasts about one hour, during which a single spermatophore is produced and deposited beneath the female's subgenital plate (Richards 1973). The male then 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 re-copulations (Richards 1973). 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 more 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 of 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 versus those mated in plastic containers under controlled laboratory conditions (Kelly et al. in prep).

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 ß (standardized partial regression coefficients; Arnold and Wade 1984; Lande and Arnold 1983), 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 quantifies ß for traits, it also reveals the behavioural mechanisms and their relative contribution to the underlying pattern of sexual selection. We analysed variables that are likely to affect sexual selection on male and female *D. 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, 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 three hours after sunset, we counted the number of adult males and females we observed while scan sampling the ground. 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

$$I_{mates} = \left(\frac{[V_{harem}]}{([H]^2)(1-p_o)}\right) + \left(\frac{p_o}{(1-p_o)}\right) \qquad [1]$$

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 only associate with one female at a time, variance among harems is always zero and harem size can only reach a maximum of 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 & 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).

For all analyses, we used probability plots to graphically inspect normality and residual plots to determine if variances were homogeneous. Data violating these assumptions were

$\log_{10}$ transformed. All statistical tests were two-tailed at the 0.05 α-level. Means are presented ± 1 standard error.

Results

Effect of sex on mobility

Males travelled significantly further per night (mean ± se back-transformed $\log_{10}$ values, 1438.80 ± 11.5 cm $night^{-1}$) than females (419.8 ± 11.9 cm $night^{-1}$) ($F_{1,64} = 30.456$, $p < 0.0001$). The maximum distance travelled during a single night by an individual male (8800 cm) was nearly twice that of the maximum for females (4600 cm). Males tended to move greater distances when solitary (1162.8 ± 13.3 cm $night^{-1}$) than when paired (706.8 ± 13.7 cm $night^{-1}$) but this difference was not significant (paired t-test, 1.115. df = 17, p = 0.28). Conversely, females tended to move further per night when paired (472.50 ± 13.9 cm $night^{-1}$) than when solo (328.55 ± 14.1 cm $night^{-1}$) but again this difference was not statistically significant (t = -0.934, df = 11, p = 0.37).

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) (refer to Fig. 2 for correlation strength and statistical significance; also Kelly et al. in prep). As predicted, males with longer legs and smaller bodies showed significantly greater mobility and males that travelled further per night had significantly greater insemination success (Fig. 2a). No path coefficients were significant for females (Fig. 2b).

Opportunity for sexual selection

As predicted, I_{mates} for *D. rugosa* (2.00 ± 0.30, N = 33) was significantly greater than zero ($t = 6.77$, $df = 32$, $p < 0.0001$) 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; Kelly, in press) ($F_{1,130} = 0.892$, $p = 0.347$).

Discussion

As predicted, the intensity of sexual selection on males in *D. rugosa*, a species with female-biased size dimorphism, was similar to that of another deinacridine, *H. crassidens*, a classical harem-defending polygynous species in which males have mandibular weaponry (Kelly 2005, 2006a, c). 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 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 male-male competition for mates leads to high variance in mating success, which in turn, is related to phenotypic traits that covary with agility. Adult male giant weta with longer legs and smaller bodies travelled 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 agility in driving size dimorphism in that species.

We found that the average distance travelled per night by giant weta was far greater than that recorded for the Wellington tree weta, (ca. 3 m night-1, Kelly 2006b) and the Raukumara tusked weta, *Motuweta riparia*, (ca. 10 m night-1, McCartney et al. 2006). This was expected because both tree weta (Kelly 2006b, c) and probably tusked weta (Gwynne, Kelly and Bussière, unpublished data) return to a gallery every morning. We also found that giant weta males travelled significantly further per night than 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, their optimum phenotype. That is, fecundity selection should favour larger females while greater agility should favour 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, post-copulatory sexual selection, and aspects of natural selection, such as longevity and predation risk.

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Figure captions

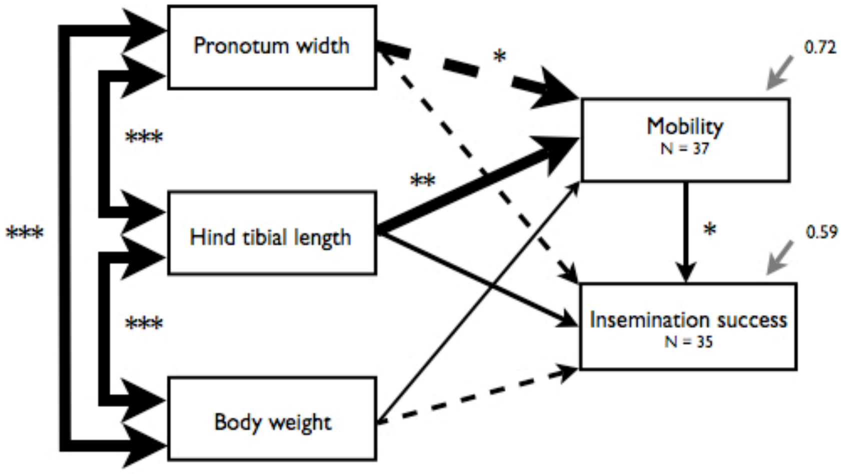
Figure 1: An adult male Cook Strait giant weta, *Deinacrida rugosa*, following an adult female (photo by L.F. Bussière). A radiotransmitter is attached to the male's pronotum with the antenna pointing backward.

Figure 2: Path diagram for a) male and b) female 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) on the right side. 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 grey arrows on the right are unexplained variance ($\sqrt{1 - r^2}$). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fig 1

FIG. 2

a) Males



b) Females