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**Sexual selection for male agility in a giant insect with female-biased size
dimorphism?**

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24 ABSTRACT: Female-biased size dimorphism in which females are larger than males is
25 prevalent in many animals, but the factors causing this pattern of dimorphism are still
26 poorly understood. The agility hypothesis suggests that female-biased size dimorphism
27 arises because smaller males are favoured in scramble competition for mates. Using radio
28 telemetry, we assessed the agility hypothesis in the Cook Strait giant weta (*Deinacrida*
29 *rugosa*), a species with strong female-biased size dimorphism, and tested the prediction
30 that male traits promoting mobility (i.e. longer legs, smaller bodies) are useful in
31 scramble competition for mates and thus promote reproductive success. Our predictions
32 were supported: males with longer legs and smaller bodies exhibited greater mobility
33 (daily linear displacement when not mating) and more mobile males had greater
34 insemination success. No phenotypic traits predicted female mobility or insemination
35 success. In species with female-biased size dimorphism, sexual selection on males is
36 often considered to be weak compared to species in which males are large and/or possess
37 weaponry. We found that male giant weta experience sexual selection intensities on par
38 with males of a closely related harem-defending polygynous species, likely because of
39 strong scramble competition with other males.

40 Although sexual dimorphism was the inspiration for Darwin's (1871) theory of sexual
41 selection, the fundamental cause of differences between the sexes is still poorly
42 understood (Shuster and Wade 2003). For example, the causes of sexual size dimorphism,
43 perhaps the most widespread sexual difference among animals, remains a subject of
44 considerable controversy (Badyaev 2002; Blanckenhorn 2005; Fairbairn 1997; Shuster
45 and Wade 2003).

46

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

54

55 Female-biased dimorphism (also called reversed size dimorphism) can evolve via three
56 patterns of sexual difference in selection intensities (Blanckenhorn 2005). In the first
57 scenario, weak sexual selection on male body size is coupled with strong directional
58 fecundity selection on females for larger body size (Hormiga et al. 2000; Prenter et al.
59 1999), if for example larger females produce better (Ralls 1976) or more offspring
60 (Honek 1993; Shine 1988). Alternatively, females could be under weak selection while
61 males experience strong sexual selection, for example if males with smaller body size are
62 superior in scramble competition (Andersson 1994; Blanckenhorn 2005) or aerial

63 courtship displays ('the agility hypothesis'; Andersson and Norberg 1981; Figuerola 1999;
64 Raihani et al. 2006; Székely et al. 2000). Vollrath and Parker (1992) argue that in some
65 spiders, greater adult male mortality results in female-biased adult sex ratios, which in
66 turn relax the strength of sexual selection for large male body size and consequently
67 selects for smaller males. Finally, directional selection could act on each sex but in
68 opposite directions with females experiencing fecundity selection while smaller males
69 have a mating advantage (Blanckenhorn 2005; Hormiga et al. 2000).

70

71 Regardless of the direction of sexual selection on male size, species exhibiting female-
72 biased dimorphism are often thought to be under weaker sexual selection than species
73 with male-biased dimorphism (Moore and Wilson 2002; Promislow et al. 1992; see also,
74 Vollrath and Parker 1992). However, this need not be true if the agility hypothesis
75 accounts for dimorphism, because in that case small males arise due to strong negative
76 selection on size. Recent studies of mammals and birds support this argument by showing
77 that sexual selection intensities on males in reversed size dimorphic species can be equal
78 in magnitude to those observed in species with male-biased dimorphism (Rossiter et al.
79 2006; Székely et al. 2004).

80

81 The Cook Strait giant weta, *Deinacrida rugosa* (Orthoptera: Anostostomatidae), a
82 nocturnal insect endemic to New Zealand and of high conservation importance (Gibbs
83 2001; McIntyre 2001), is an ideal candidate with which to test hypotheses of reversed
84 size dimorphism evolution. Adult males (ca. 10 g) are roughly half the weight of females
85 (ca. 20 g) (Kelly et al. in prep). *D. rugosa* inhabits old pastures, forests and coastal scrub

86 and seeks refuge from predators in the daytime by hiding under vegetation or other
87 objects on the ground (McIntyre 2001). Males do not appear to defend resources required
88 by sexually receptive females nor do they guard harems of females as in other
89 deinacridines (i.e. *Hemideina* tree weta, McIntyre 2001). Instead, males seek receptive
90 females as mates at night while females are foraging away from refuges (McIntyre 2001).
91 Once a male locates a receptive female, he remains in physical contact with her using
92 either his antennae or legs, and follows her until she finds a diurnal refuge (McIntyre
93 2001; Richards 1973). The pair will remain together at least until the following night –
94 longer if the weather is cool and wet – copulating repeatedly throughout the day while in
95 the refuge (McIntyre 2001; Richards 1973).

96
97 Using radio telemetry we studied the movements of adult *D. rugosa* to test two related
98 hypotheses: (i) males with smaller body sizes and longer legs are more mobile and are
99 favoured in scramble competition for mates; and (ii), if this is the case, then sexual
100 selection on males is not expected to be weaker than in species with male-biased
101 dimorphism because there is high variance in mating success among males in both cases
102 (Rossiter et al. 2006; Székely et al. 2004).

103

104

Methods

105

Field site

106 We conducted our study during April 2004 and April – May 2006 on Te Hoiere/Maud
107 Island, New Zealand (41° 02'S, 173° 54'E), a 309 Ha scientific reserve free of alien
108 predators [e.g. rodents (*Mus* and *Rattus* spp.) and stoats (*Mustela erminea*)]. Of the

109 known predators of adult giant weta only the endemic morepork owl, *Ninox*
110 *novaeseelandiae*, is present on Maud Island (personal observation).

111

112 *Marking, measuring and radio telemetry of study animals*

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

124

125 *Assessing mobility*

126 We recaptured radio-tagged individuals (transmitters could be detected in brush or grass
127 from ca. 500 m) the day after being tagged and twice subsequently at 24 h intervals,
128 noting whether the individual was paired with a member of the opposite sex in the diurnal
129 refuge. We estimated the linear displacement of animals using either a 50 m measuring
130 tape or, in rare cases when animals travelled further than 50 m, or over difficult terrain
131 (e.g., a cliff), a handheld GPS unit (GPS 60 model, Garmin International, Inc., Olathe,

132 Kansas). We assume that the average nightly distance travelled by a solitary male
133 reflects his mobility and hence his capacity to locate mates (see Biedermann 2002).

134

135 *Measuring insemination success*

136 The number of copulations vary during a mating bout in giant weta, but each one lasts
137 about one hour, during which a single spermatophore is produced and deposited beneath
138 the female's subgenital plate (Richards 1973). The male then releases the subgenital
139 plate, and during the next few minutes the spermatophore is gradually forced out of the
140 female by the pushing movements of the male's paraprocts during attempted re-
141 copulations (Richards 1973). The ejected spermatophores are not eaten (in contrast to
142 most ensiferan orthopterans; Brown and Gwynne 1997) and can be collected from the
143 area around the female, or sometimes from the surface of her body or ovipositor, and
144 counted. We defined insemination success as the number of spermatophores that a male
145 transferred to a female because more sperm is expected to be transferred with each
146 additional spermatophore (as in mogoplistid crickets, Laird et al. 2004).

147

148 We were able to leave pairs with at least one radio-tagged member to mate in their
149 natural refuges. We inspected the refuge of such pairs for spermatophores near dusk.
150 There was an increased opportunity to miscount spermatophores for radio-tracked pairs
151 simply because of spermatophores were more difficult to find in the conditions of the
152 natural refuge. However, we found no evidence that the numbers of spermatophores
153 transferred by males of a given body size differed between animals left in their refuges

154 versus those mated in plastic containers under controlled laboratory conditions (Kelly et
155 al. in prep).

156

157 *Path analysis*

158 We used path analysis to study the mechanisms underlying sexual selection in both sexes
159 (Arnold and Duvall 1994; Conner 1996; Sih et al. 2002). By calculating β (standardized
160 partial regression coefficients; Arnold and Wade 1984; Lande and Arnold 1983), path
161 analysis measures the relative statistical importance of different aspects of an a priori
162 hypothesis embodied in a path diagram (Fig. 2). This approach not only quantifies β for
163 traits, it also reveals the behavioural mechanisms and their relative contribution to the
164 underlying pattern of sexual selection. We analysed variables that are likely to affect
165 sexual selection on male and female *D. rugosa* (i.e. mobility, pairing success and number
166 of spermatophores transferred) and their relationship to several morphological measures
167 (e.g. pronotum width, mean hind tibia length, body weight). Individual insemination
168 success was calculated as the product of pairing success (proportion of observations in
169 which an individual was in contact with a member of the opposite sex) and the average
170 number of spermatophores transferred or received. We performed path analyses for males
171 and females separately with sample sizes (given in Fig. 2) differing between the sexes
172 and in particular analyses.

173

174 *Opportunity for sexual selection*

175 On each of 12 (2004) and 21 (2006) consecutive nights, approximately three hours after
176 sunset, we counted the number of adult males and females we observed while scan

177 sampling the ground. For all individuals we noted their location, pronotum width, mass,
178 and paired status. We calculated the opportunity for sexual selection, I_{mates} , using the
179 statistical framework of Shuster and Wade (2003). With this approach only potential
180 breeding aggregations are considered in the analysis (i.e. only paired and single males).
181 We considered each night as a sample unit because it represented a discrete opportunity
182 to acquire a mate for the following day.

183

184 The opportunity for sexual selection was calculated using

$$185 \quad I_{\text{mates}} = \left(\frac{[V_{\text{harem}}]}{([H]^2)(1-p_o)} \right) + \left(\frac{p_o}{(1-p_o)} \right) \quad [1]$$

186 where V_{harem} is the variance in harem size (i.e. number of females) of successful males, H
187 is the mean harem size of successful males, p_o is the proportion of unsuccessful males and
188 $1-p_o$ is the proportion of successful males observed each night (Shuster and Wade, 2003).
189 Because each male giant weta can only associate with one female at a time, variance
190 among harems is always zero and harem size can only reach a maximum of $n = 1$ female.
191 Therefore I_{mates} is entirely attributed to the proportion of unmated to mated males, the
192 strongest influence on the strength of sexual selection (Shuster & Wade, 2003). We
193 assess the opportunity for sexual selection in *D. rugosa* by comparing its I_{mates} value to
194 that of *Hemideina crassidens*, a related harem-defending deinacridine weta in which
195 males are known to be under strong sexual selection (Kelly 2005).

196

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

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

201

202 **Results**

203 *Effect of sex on mobility*

204 Males travelled significantly further per night (mean \pm se back-transformed \log_{10} values,
205 1438.80 ± 11.5 cm night⁻¹) than females (419.8 ± 11.9 cm night⁻¹) ($F_{1,64} = 30.456$, $p <$
206 0.0001). The maximum distance travelled during a single night by an individual male
207 (8800 cm) was nearly twice that of the maximum for females (4600 cm). Males tended to
208 move greater distances when solitary (1162.8 ± 13.3 cm night⁻¹) than when paired (706.8
209 ± 13.7 cm night⁻¹) but this difference was not significant (paired t-test, 1.115. $df = 17$, $p =$
210 0.28). Conversely, females tended to move further per night when paired (472.50 ± 13.9
211 cm night⁻¹) than when solo (328.55 ± 14.1 cm night⁻¹) but again this difference was not
212 statistically significant ($t = -0.934$, $df = 11$, $p = 0.37$).

213

214 *Interrelationships among morphology, mobility and insemination success*

215 Measures of body size (pronotum width), body weight and leg length (hind tibia length)
216 were significantly positively correlated in both males ($N = 66$) and females ($N = 51$)
217 (refer to Fig. 2 for correlation strength and statistical significance; also Kelly et al. in
218 prep). As predicted, males with longer legs and smaller bodies showed significantly
219 greater mobility and males that travelled further per night had significantly greater
220 insemination success (Fig. 2a). No path coefficients were significant for females (Fig.
221 2b).

222

223

Opportunity for sexual selection

224 As predicted, I_{mates} for *D. rugosa* (2.00 ± 0.30 , $N = 33$) was significantly greater than zero
225 ($t = 6.77$, $df = 32$, $p < 0.0001$) and did not differ from I_{mates} for *Hemideina crassidens*, a
226 deinacridine weta with male weaponry (elongated mandibles) at the same study site (2.34
227 ± 0.18 , $N = 99$; Kelly, in press) ($F_{1,130} = 0.892$, $p = 0.347$).

228

229

Discussion

230 As predicted, the intensity of sexual selection on males in *D. rugosa*, a species with
231 female-biased size dimorphism, was similar to that of another deinacridine, *H.*
232 *crassidens*, a classical harem-defending polygynous species in which males have
233 mandibular weaponry (Kelly 2005, 2006a, c). Similarly, Rossiter et al. (2006) recently
234 showed that male greater horseshoe bats (*Rhinolophus ferrumequinum*), a species with
235 female-biased sexual size dimorphism, can experience intensities of sexual selection on
236 par with males in male-dimorphic polygynous species. However, they were unable to link
237 the opportunity for selection to selection on particular male traits. We show that intense
238 male-male competition for mates leads to high variance in mating success, which in turn,
239 is related to phenotypic traits that covary with agility. Adult male giant weta with longer
240 legs and smaller bodies travelled significantly farther per night and accrued significantly
241 greater insemination success. Biedermann (2002) found that in the male-biased size
242 dimorphic spittlebug, *Cercopis sanguinolenta*, larger males were more mobile, however,
243 he was unable to link mobility with mate acquisition and thereby support the role of
244 agility in driving size dimorphism in that species.

245

246 We found that the average distance travelled per night by giant weta was far greater than
247 that recorded for the Wellington tree weta, (ca. 3 m night⁻¹, Kelly 2006b) and the
248 Raukumara tusked weta, *Motuweta riparia*, (ca. 10 m night⁻¹, McCartney et al. 2006).
249 This was expected because both tree weta (Kelly 2006b, c) and probably tusked weta
250 (Gwynne, Kelly and Bussière, unpublished data) return to a gallery every morning. We
251 also found that giant weta males travelled significantly further per night than females,
252 unlike in the Wellington tree weta in which there is little apparent sex difference in
253 nightly movement distance (Kelly 2006b).

254

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

265

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267

268

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379

380 **Figure captions**

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

384

385 **Figure 2:** Path diagram for a) male and b) female Cook Strait giant weta. Phenotypic
386 traits on which selection is measured are on the left, with correlations among them and
387 hypothesized causal links to fitness components (mobility and insemination success) on
388 the right side. Correlations are depicted as double-headed arrows and causal relationships
389 as single-headed arrows. Dashed arrows denote negative coefficients and arrow width is
390 proportional to the standardized coefficients (see scale). The numbers next to the grey
391 arrows on the right are unexplained variance ($\sqrt{1 - r^2}$). * $P < 0.05$, ** $P < 0.01$, *** $P <$
392 0.001

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395 Fig 1

396



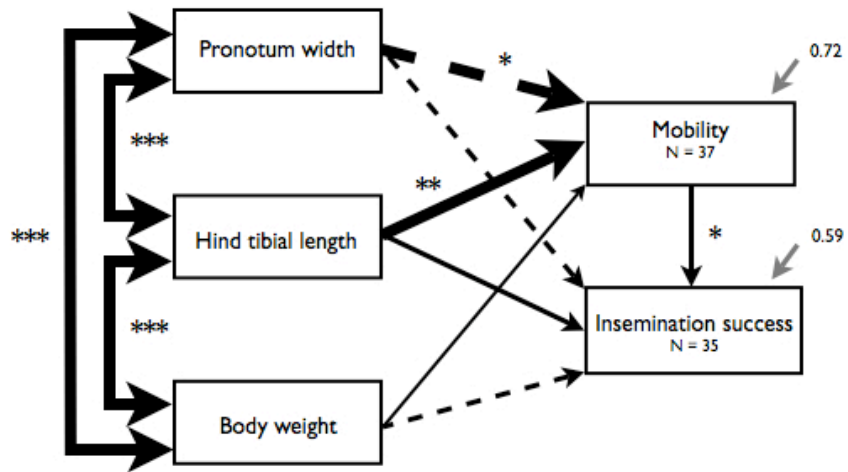
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FIG. 2

a) Males



b) Females

