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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 (41º 02'S, 173º 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 ß (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 ß 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
$$I_{mates} = (\frac{[V_{harem}]}{([H]^2)(1 - p_o)}) + (\frac{p_o}{(1 - p_o)}) \qquad [1]$$

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_0 is the proportion of unsuccessful males and

188    $1 - p_0$ 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 ± 1 standard error.

201

202   **Results**

203   *Effect of sex on mobility*

204   Males travelled significantly further per night (mean ± 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

266

267

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377

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379

379

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.

384

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 ($\sqrt{1 - r^2}$). $* P < 0.05$, $**P < 0.01$, $*** P <$
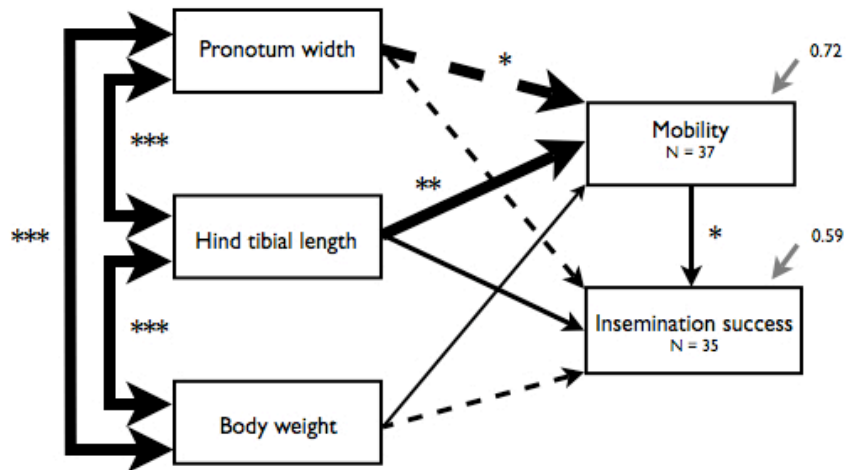
0.001

393

394

395

395   Fig 1

396

397

398

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FIG. 2

a) Males

b) Females