Identifying a causal agent of sexual selection on weaponry in an insect

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In many animal species, males do not seek females directly but instead locate and defend sites that contain spatially or temporally limited resources essential to female survival and reproduction. Resident males that successfully repel conspecific rivals can mate with females attracted to these resources. In theory, increasing resource value increases harem size and thus increases the opportunity (I_{mates}) for and strength of sexual selection on traits crucial to male resource-holding potential and mating success. I experimentally tested this hypothesis in the field using the Wellington tree weta, *Hemideina crassidens* (Orthoptera: Tettigonioidea: Anostostomatidae), a sexually dimorphic insect in which males use their enlarged mandibles as weapons in male–male contests over access to females sheltering in tree cavities (galleries). By manipulating gallery size, I showed that, compared with smaller galleries, larger galleries housed larger harems. Variation in gallery size was an important determinant of I_{mates}, but contrary to expectation, greater opportunity existed in small galleries compared with large galleries. As predicted, male weapon size was under stronger directional selection in large galleries because the fitness benefits were greater under these conditions compared with small galleries. My results help explain the positive association between average weapon size and average gallery size observed within and among tree weta populations in New Zealand. *Key words:* conservation, *Hemideina*, longitudinal study, resource defense, selection gradient, sexual dimorphism. *[Behav Ecol 19:184–192 (2008)]*

The opportunity for selection identifies the upper limit to the rate of evolutionary change in the mean phenotype in a population by selection (Crow 1958; Wade 1979; Shuster and Wade 2003). This upper bound is directly related to variance in relative fitness; greater variance in fitness in a population translates into greater opportunity for phenotypic change (Shuster and Wade 2003). When there are large differences between the sexes in the opportunity for selection, sexual dimorphism can arise (Wade 1979; Andersson 1994; Shuster and Wade 2003). For instance, in species with conventional sex roles, males typically possess more elaborate phenotypic traits than females because males have greater variance in fitness (Darwin 1871; Emlen and Oring 1977; Wade 1979; Andersson 1994; Shuster and Wade 2003; Hauber and Lacey 2005).

A high opportunity for sexual selection means that some males are more successful at acquiring mates than others (Shuster and Wade 2003), but high opportunities can arise by chance (Sutherland 1985). Successful males possess trait values of particular phenotypic characters that are either preferred by females or permit males to outcompete rivals such as in the successful defense of resources required by females for breeding (Darwin 1871; Andersson 1994; but see Sutherland 1985). Hence, although fitness variance is necessary for evolutionary change to occur, there must also be a relationship between fitness and phenotypic characters (Conner 1988). Selection gradients are used to measure the link between fitness and a particular trait, independent of other measured correlated traits (Lande and Arnold 1983; Arnold and Wade 1984b; Brodie et al. 1995). The magnitude of the link between fitness and phenotype is referred to as the strength of selection and has been quantified for a variety of traits in a number of taxa (reviewed in Kingsolver et al. 2001; see also Brooks and Endler 2001; Kwiatkowski and Sullivan 2002; LeBas et al. 2003; Mills et al. 2007).

Identifying the causal agents of selection and their interaction with the phenotype is just as important as determining how selection operates on the phenotype (Endler 1986; Wade and Kalisz 1990). However, selection gradients do not provide any information regarding why an association between fitness and trait value exists (i.e., covariation is not causation) (Mitchell-Olds and Shaw 1987; Mitchell-Olds and Shaw 1990; Wade and Kalisz 1990). To identify the agents of selection, experimental manipulations of the environment are required, which, in turn, require knowledge of a study organism's ecology (Wade and Kalisz 1990).

Examples of some of the most intense selection in nature include sexual selection that generates sexual dimorphism (Shuster and Wade 2003). One group of animals that exhibit extreme sexual dimorphism is New Zealand tree weta (Orthoptera: Tettigonioidea: Anostostomatidae)—large (ca. 65-mm body length), flightless, and nocturnal insects (Gibbs 2001). Of the 7 species of *Hemideina* tree weta (Gibbs 2001), the Wellington tree weta (*Hemideina crassidens*) appears to be the most sexually dimorphic (Field and Deans 2001) with males possessing highly exaggerated mandibles that are positively allometric (Kelly 2005). Males use their mandibles, as in other *Hemideina* species (Field and Sandlant 1983; Field 2001), as weapons in fights for control of females residing in tree cavities (hereafter galleries) (Kelly 2006a). Male weaponry varies considerably in length among individuals (Kelly 2005) apparently due to precocial male maturation: males can mature at either the 8th, 9th, or 10th instar, whereas females mature at the 10th instar only (Spencer 1995). Both sexes are polygamous, but there is greater variance in male mating success (Kelly CD, unpublished data).

Hemideina crassidens is a harem-defending polygynous insect in which males guard females rather than galleries per se; field evidence shows that male residency in a gallery is positively

correlated with harem size (Kelly 2006c, 2006d). Galleries are used year-round as diurnal refugia and are not used as oviposition or feeding sites. A single adult male typically resides in a gallery with 1 to several females (Moller 1985; Field and Sandlant 2001; Kelly 2005), and phenotypic correlations in the wild have shown a strong positive relationship between male head length (weapon size) and how many females reside with him (harem size) (Kelly 2005). Moreover, a laboratory study showed that larger galleries (higher quality resources) house larger harems, and males with bigger weaponry control these galleries more often than those with smaller weapons (Kelly 2006d). Despite larger galleries housing larger harems, I note that galleries in nature, except for the very smallest ones (i.e., single and double occupant), typically do not reach maximum occupancy (Kelly 2005). I also note that although females prefer to settle in unoccupied galleries, evidence suggests that female settlement in galleries does not exhibit an ideal free distribution because many galleries in a patch can be empty whereas others house several individuals (Kelly 2006b, 2006c). Mating typically occurs either in the gallery or near its entrance (Field and Jarman 2001) and male–female pairs will copulate both at night and during the day, with the latter copulations always occurring within the gallery, space permitting (Field and Jarman 2001).

Gallery size limits harem size and should thus be an important ecological factor influencing the strength of sexual selection operating on male weaponry (Field and Sandlant 1983; Field and Sandlant 2001; Kelly 2006d). Field observations at several sites in New Zealand suggest that males inhabiting forests (e.g., broad-leaved forest) with larger galleries (>3 adult weta), on average, tend to have access to larger harems and exhibit larger weaponry compared with males living in forests (e.g., manuka, *Leptospermum scoparium*) offering smaller galleries (<3 adult tree weta), on average (Sandlant 1981; Field and Sandlant 1983; Field and Sandlant 2001; see also Discussion). The differences in gallery size between the 2 forest types is a consequence of the maximum diameter of the tree species comprising each forest (Field and Sandlant 2001; Kelly CD, personal observation): manuka is a small-diameter (<10-cm diameter at breast height; Dawson and Lucas 2000) tree species and thus accommodates small galleries, whereas broad-leaved species (e.g., kohekohe, *Dysoxylum spectabile*) have much larger diameters (>100-cm d.b.h; Dawson and Lucas 2000) and can thus accommodate larger galleries.

Here, I experimentally manipulated a putatively important ecological factor—gallery size—influencing the opportunity for and strength of sexual selection on male weaponry in the Wellington tree weta. More specifically, I use longitudinal field data to test the hypothesis that increasing gallery size increases the potential variation in harem size and thus increases sexual selection on traits crucial in male–male competition for female harems.

In this paper, I test the following predictions.
1. Larger galleries exhibit greater opportunities for sexual selection (I_{mates}) because these resources can host larger aggregations of females (m^*).
2. Males are under directional selection with individuals possessing larger weaponry having greater resource-holding potential and thus mating success.
3. Because larger galleries are expected to house larger harems and provide greater reproductive opportunities, male traits (e.g., mandibular weaponry and body size) used in taking control of galleries will be under stronger selection in larger galleries. This prediction assumes that each gallery within a treatment will not be occupied to maximum with females (i.e., assumes variance in harem size among equal-sized galleries) as observed in Kelly (2005).

4. If predictions (1) and (3) are met, then there should be a positive correlation between the opportunity for sexual selection (I_{mates}) and the strength of selection on male weaponry (partial regression gradients) (McLain 1992; Bjork and Pitnick 2006).

METHODS

Study sites

This study was conducted during April–May 2003 and 2006–2007 and March–April 2004 on Te Hoiere/Maud Island, New Zealand (41°02′S, 173°53′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 tree weta, only the native morepork owl, *Ninox novaeseelandiae*, is present on Maud Island (see Field and Glasgow 2001 for a list).

In 2002, I installed artificial galleries (Figure 1) approximately 1.5 m above the ground on mature trees at 2 sites approximately 200 m apart within a regenerating forest (ca. 40 years old) dominated by mahoe (*Melicytus ramiflorus*; up to 30- to 40-cm diameter) and makomako (*Aristotelia serrata*; up to 30-cm diameter). The natural galleries at both experimental sites were intermediate in average volume to those common in early successional (smaller galleries) or mature (larger galleries) forests. Both sites were similar in area, topography,
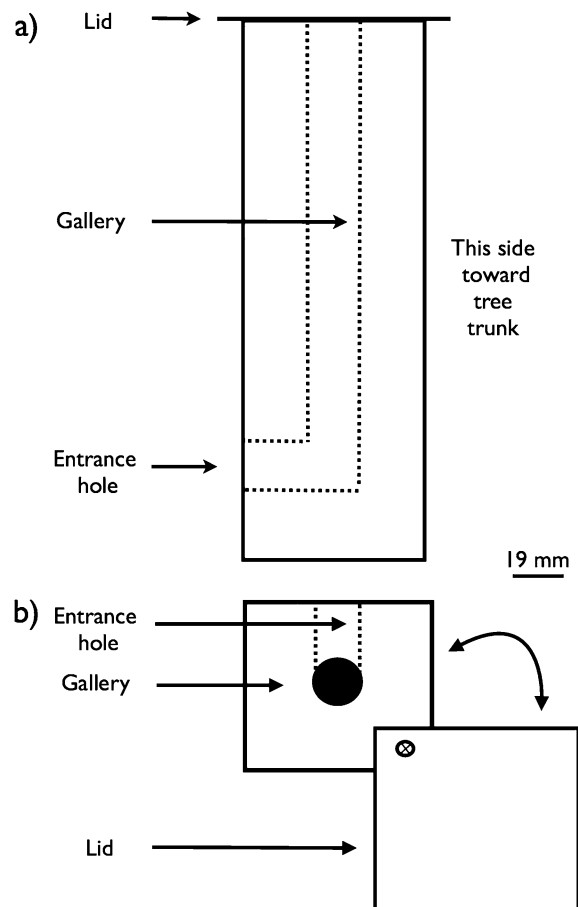

Figure 1
Side (a) and top (b) views of artificial gallery. The diameter of the cavity in the "large gallery" treatment was approximately 27 mm; however, the entrance hole was of the same diameter (ca. 20 mm) in both treatments. The lid swiveled open (denoted by double-headed arrow) on a pivot (30-mm stainless steel nail).

and flora, and each was inhabited previous to this study by males representing the full range of weapon sizes known for this population (Kelly 2005, 2006c). Tree weta readily occupy artificial galleries (Trewick and Morgan-Richards 2000; Kelly 2005, 2006c; Bowie et al. 2006). Artificial galleries were installed over natural galleries that were destructively excavated and emptied of all tree weta. This field experiment comprised a treatment with 2 levels: small and large galleries. At Site A (ca. 24 × 4 m), 19 small galleries (cavity volume in cubic millimeters) were installed, whereas at Site B (ca. 22 × 3 m), 13 large galleries (cavity volume in cubic millimeters), with twice the volume of the small galleries, were installed (Figure 1). This gave approximately 1 gallery/5 m^2 at each site. In 2003 and 2004, small galleries were in place at Site A and large galleries at Site B. In 2006, the galleries were switched between the sites to control for any differences between the sites.

Gallery census and trait measurement

I opened each gallery and censused all occupants every third morning in 2003 and 2007 and daily in 2004 and 2006. Census periods were considered independent because gallery composition can change considerably between days (Kelly 2006b). Handling tree weta does not affect their tenure at a gallery (Kelly 2006c). I counted the number of adult males and adult females in each gallery and noted their identity. If the occupant was unmarked, I measured its head length and width and right and left hind tibia and femur lengths using digital calipers (Mitutoyo Digimatic, Mitutoyo Canada Inc., Toronto, Ontario, Canada). Head length is an excellent predictor of weapon size (i.e., mandible length; $r = 0.99$, Kelly 2005). To permit individual identification, I glued a uniquely numbered and colored bee tag (H. Thorne Ltd, Market Rason, UK) to each individual's pronotum. After being identified and/or measured and marked, all individuals were then immediately replaced into their gallery. No tree weta was observed at both sites in either year, and no males were observed in 2 consecutive sample years (*H. crassidens* has a 2-year life cycle from egg to adult, but adults do not survive more than 1 breeding season).

Opportunity for sexual selection

Of the many methods available to measure the potential for sexual selection (Fairbairn and Wilby 2001; Shuster and Wade 2003; Mills et al. 2007), I chose to use I_{mates} approach of Shuster and Wade (2003) for 3 reasons. First, unlike the breeding sex ratio (Arnold and Duvall 1994) or Q (Ahnesjo et al. 2001), I_{mates} takes into account that much of the variance in male reproductive success lies between mating and nonmating males. Second, although calculating Bateman gradients (relationship between fitness or fertility and number of mates) is often regarded as a superior method for determining the strength of sexual selection (Arnold 1994; Gwynne and Kelly 2004; Lorch 2005; Mills et al. 2007; but see Wade and Shuster 2005), it requires reliable paternity assignment; I was unable to hatch a sufficient number of eggs to make this approach worthwhile. Third, the I_{mates} approach directly links the spatial distribution of females with the opportunity for sexual selection (see Emlen and Oring 1977).

I calculated female mean crowding, m^*, and the opportunity for sexual selection, I_{mates}, using the statistical framework of Shuster and Wade (2003). With this approach, only potential breeding aggregations, defined as only galleries that comprise 1 or more females with a single adult male, are considered for the analysis. The degree of female clumping is based on Lloyd's (1967) ecological measure of density-dependent competition (see Shuster and Wade 2003). Calcu-

lating mean crowding first requires determining the average density of females per breeding aggregation, m, using

$$m = \sum \frac{m_i}{M}, \tag{1}$$

where m_i is the number of females in ith breeding aggregation and M is the number of breeding aggregations containing at least 1 female. This value was then used to calculate the mean crowding of females at breeding aggregations using

$$m^* = m + [(V_m/m) - 1], \tag{2}$$

where V_m is the variance in female number among galleries. Mean crowding identifies the number of other females, the average female experiences in a gallery; larger aggregations of females cause the average experience of females, m^*, to exceed that expected from the average density per cluster, m (Shuster and Wade 2003).

The opportunity for sexual selection was calculated using

$$I_{mates} = \left(\frac{[V_{harem}]}{([H]^2)(1 - p_0)} \right) + \left(\frac{p_0}{(1 - p_0)} \right), \tag{3}$$

where V_{harem} is the variance in harem size 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 (Shuster and Wade 2003). With this approach, I_{mates} and m^* are calculated for each census day (n) in each treatment, and these values are then used to calculate a mean to test for treatment differences. I note that each n sample is 1 census day and is based on that day's occupation of either 19 (small gallery treatment) or 13 (large gallery treatment) galleries. For example, in 2004, there were 25 days in which censuses provided appropriate data (i.e., there were both successful and unsuccessful males present in galleries).

I determined whether response variables differed between years (random factor) and treatments (fixed factor) by using a general linear model (GLM).

Selection analysis of male weaponry

Fitness estimate for male H. crassidens
Male mating success was estimated as the number of adult females residing with an adult male in a gallery (harem size). I tested the assumption that male harem size predicts mating success by allowing wild-caught males ($n = 33$) access to harems varying in number of adult females. In the late afternoon on the day of a trial, I placed in a cage (plastic 5-L pail with perforated lid) a single adult male and an artificial gallery (identical to the small galleries installed on trees in experimental sites, see above) housing 1, 2, or 3 adult females, the range typically encountered by males in nature (Kelly 2005, 2006c). Harem size for each male was chosen at random. Each trial lasted for 48 h, the average duration of time a male resides in a gallery (Kelly 2006c), and each female's mating status was checked daily at approximately 18:00, 21:00, 24:00, 05:00, and 12:00 h on each day. Mating status was assessed by lifting the female's subgenital plate and looking for a spermatophore; spermatophores are fully absorbed by females after approximately 5 h (Kelly CD, personal observation), and so my 3-h observation window provided reasonable opportunity to observe a mating. If a female was mated at night, I removed her from the cage because males typically evict mated females from the gallery; however, they do not evict females if mated inside the gallery during the day, and so in this case females were put back into the gallery (Kelly CD, unpublished data). All cages were supplied daily with fresh apple ad libitum.

Table 1
Descriptive statistics (mean ± standard deviation) for each morphological trait and harem size for both treatments in the 4 study years

GLM terms	Year	Gallery size	No. of males	Head length (mm)	Head width (mm)	Femur length (mm)	Tibia length (mm)
	2003	Small	61	20.88 ± 4.55	10.54 ± 1.56	18.41 ± 1.70	19.57 ± 1.81
	2003	Large	38	20.69 ± 4.07	10.67 ± 1.82	18.31 ± 1.54	19.27 ± 1.75
	2004	Small	49	19.59 ± 4.36	10.04 ± 1.72	18.05 ± 1.64	18.89 ± 1.77
	2004	Large	36	20.76 ± 4.25	10.68 ± 1.65	18.37 ± 1.42	19.23 ± 1.63
	2006	Small	30	19.64 ± 3.97	10.27 ± 1.66	17.97 ± 1.63	18.92 ± 1.92
	2006	Large	40	20.12 ± 3.57	10.38 ± 1.42	18.01 ± 1.39	19.10 ± 1.43
	2007	Small	41	18.91 ± 3.36	10.00 ± 1.34	17.84 ± 1.40	18.55 ± 1.64
	2007	Large	31	19.23 ± 3.58	10.04 ± 1.38	18.00 ± 1.33	18.95 ± 1.64
Year	$F_{3,318}$			2.49	1.83	1.41	2.08
Gallery size	$F_{1,318}$			0.92	0.84	0.36	0.64
Gallery size × year	$F_{3,318}$			0.42	0.90	0.29	0.76

The effect of the main factors (year and gallery size) and their interaction were tested using a univariate GLM. None of the *F* values are statistically significant at the 0.05 α level.

Calculation of gradients

No trait differed significantly in mean size between years within any treatment (Table 1), and all morphological traits (head length, head width, tibia length, and femur length) within each year in each treatment were highly correlated (Kelly 2005). Some multiple regressions using the 4 morphological traits showed multicollinearity (tolerance < 0.001), thus violating assumptions of multiple regression (Sokal and Rohlf 1995). I estimated selection gradients for a reduced set of orthogonal variables extracted from a principal components analysis (PCA) in which the component scores are uncorrelated with one another even if composed of variables that are correlated. The first 2 components were extracted from the phenotypic covariance matrix for all males in the cohort using varimax rotation. Multiple regression of mating success on the rotated factor loadings estimated the partial gradients of these composite morphological variables. Because selection acts within a generation (Endler 1986), I generated principal components for each of the treatments by each sample year.

I included year as an independent variable along with head and body size in the regression analysis by treatment. There was no significant effect of year on harem size in either treatment (small: $F_{3,177} = 1.58$, $P = 0.196$, year term, $P = 0.273$; large: $F_{3,141} = 3.53$, $P = 0.017$, year term, $P = 0.054$); therefore, I pooled data within each treatment and performed the regressions with the year term removed.

I estimated linear ($\beta_{\tilde{n}}$) selection gradients as the partial regression coefficients from multiple regressions with mating success as the dependent variable and 2 PCA factors (head size and body size) as the predictors. To maintain statistical independence, I calculated mean harem success for males observed more than once. Because studentized residuals from regressions were nonnormal and variances were heterogeneous, parametric tests of significance were not appropriate (Mitchell-Olds and Shaw 1987). Therefore, I tested the significance of partial regression coefficients using 9999 permutation tests (Legendre 2002). I note that when independent variables are principal components, the selection differentials (*S*) calculated by using univariate regressions are identical to partial regression coefficients (β), and hence, I report only the latter (see also Schluter and Smith 1986). Selection gradients were visualized using nonparametric cubic splines (Schluter 1988).

All analyses of variance (ANOVAs) were conducted using the GLM and post hoc tests conducted using Ryan's *Q* stepwise multiple comparisons procedure. Statistical power and sample size calculations were performed after Hersch and Phillips (2004). Because the statistical power is low for most selection analyses (Kingsolver et al. 2001) and thus gradients tend to be statistically nonsignificant at the 0.05 α level, I followed Fairbairn and Preziosi (1996) and also denote (but do not discuss) selection gradients significant at the 0.10 α level. Unless otherwise noted, means are presented ± 1 standard error (SE). All analyses were conducted using SPSS 11.0 for Mac OS X.

RESULTS

Opportunity for sexual selection

Experimental manipulation of gallery size changed the potential mating success of resident males as the mean harem size of successful males was significantly greater in large galleries ($F_{1,118} = 45.23$, $P < 0.0001$; Figure 2A). Mean harem size did neither differ between years ($F_{3,118} = 1.27$, $P = 0.29$) nor was the interaction between treatment and year significant ($F_{3,118} = 0.13$, $P = 0.95$).

In line with my first prediction, mean crowding of females (m^*) was, on average, significantly greater at large galleries compared with small galleries ($F_{1,118} = 37.58$, $P = 0.001$). There was no effect of sample year on mean crowding ($F_{3,118} = 5.21$, $P = 0.10$), and the interaction term was nonsignificant (gallery size × year, $F_{3,118} = 0.21$, $P = 0.89$).

Opposite to prediction, I_{mates} was significantly greater for small galleries than large galleries ($F_{1,118} = 43.71$, $P = 0.002$; Figure 2B). Their effect of year ($F_{3,118} = 9.05$, $P = 0.054$) and the interaction term (gallery size × year, $F_{2,118} = 0.51$, $P = 0.68$) were nonsignificant. Recall that I_{mates} (Equation 3) is comprised of 2 components—the opportunity for selection among successful males ($1 - p_0$) and the opportunity for selection between successful ($1 - p_0$) and unsuccessful males (p_0). The difference in values for I_{mates} observed here was mainly influenced by a change in the proportion of unsuccessful males rather than an increase in harem size among successful males. This component of selection (between mated and unmated males) was significantly stronger in small galleries compared with large ones ($F_{1,118} = 32.41$, $P = 0.006$). There was no effect of year ($F_{3,118} = 4.58$, $P = 0.12$), and the interaction was nonsignificant (gallery size × year, $F_{3,118} = 0.876$, $P = 0.46$).

The higher mean proportion of unsuccessful males in small galleries was not due to a lack of females in this treatment as the mean adult sex ratio (males:females) was significantly female biased in each year (1-sample *t*-test testing expectation that sex ratio differed from unity, 2003: $t_{18} = 5.02$; 2004: $t_{24} = 7.45$; 2006: $t_5 = 5.81$; 2007: $t_{11} = 4.52$, all $P < 0.002$).
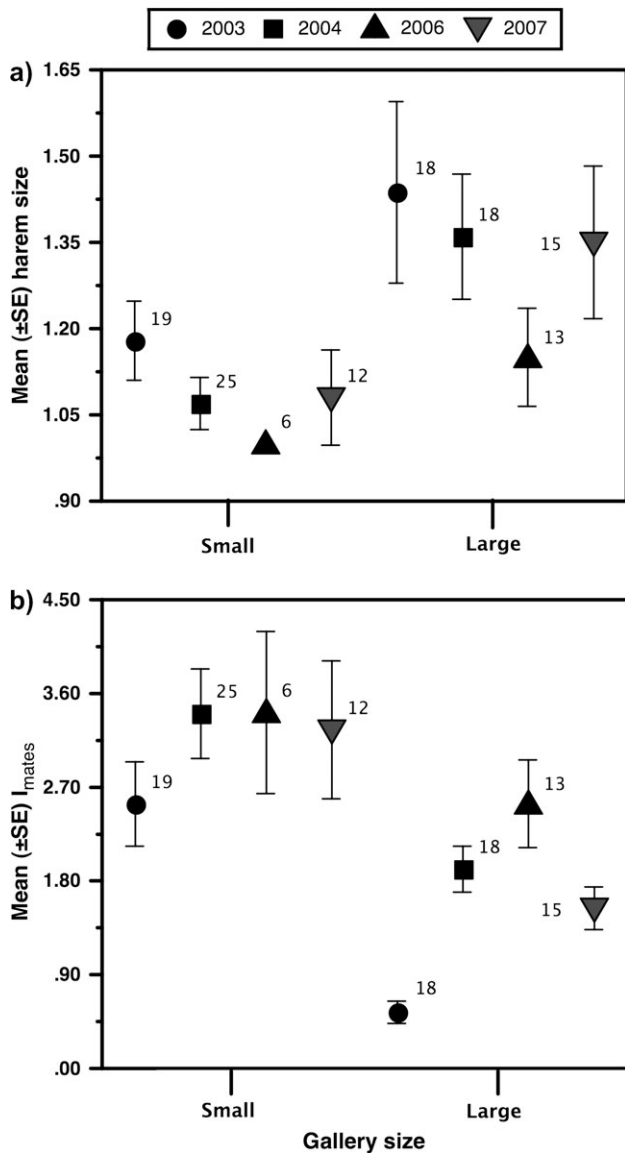
Figure 2

Mean ± SE values for (a) harem size and (b) I_{mates} in small and large galleries for each of 4 field seasons. Sample sizes (i.e., number of census periods) are given beside each symbol and apply to both panels.

Figure 3

The effect of harem size on mean (±SE) male mating success in *Hemideina crassidens*. Males with harems have significantly greater mating success than males with 1 female but there was no significant difference between males with either 2 or 3 females. Means with same letters above bars are not significantly different.

Harem size predicts male mating success

Male mating success increased significantly with harem size (1-way ANOVA, $F_{2,42} = 7.79$, $P = 0.001$). I did not detect a significant difference between males placed with either 2 or 3 females (Ryan's Q, $P = 0.07$), but males residing with a single female had significantly lower mating success than males with harems (Ryan's Q, $P < 0.05$) (Figure 3).

Morphological traits and fitness components

There was no effect of treatment or sample year on the size of the 4 male morphological traits (Table 1). The males observed in this study exhibited a trimodal head length frequency distribution identical to that reported in other years in this study population (Kelly 2005).
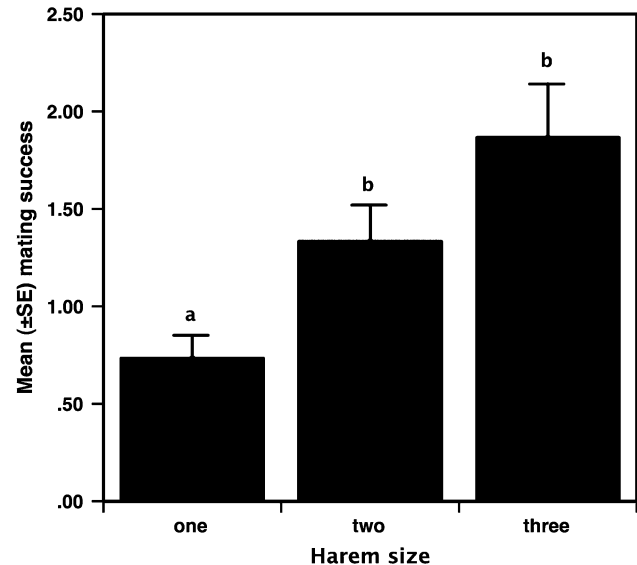
Univariate linear selection gradients

The first component (PC1) from a PCA quantified head size, and the second component (PC2) quantified body size in 6 of 8 cases (Table 2). The overall multiple regression was significant for the large gallery treatment ($r^2 = 0.045$, $F_{2,142} = 3.34$, $P = 0.038$) but not for the small gallery treatment ($r^2 = 0.019$, $F_{2,178} = 1.76$, $P = 0.175$). Neither univariate nor bivariate nonlinear selection gradients were significant and are not reported here.

Male traits important to male mating success

My prediction that male weapon size would be favored in both treatments was only partially supported: larger male weapon size was significantly selected in the large gallery treatment only (Table 3, Figure 4A,C). There was a trend for males with smaller body size to have greater mating success in small galleries (Table 3, Figure 4B,D).

The relationship between opportunity and strength of selection

I tested the relationship between opportunity and strength by correlating the value for I_{mates} with the harem size selection gradient calculated for each year. Contrary to prediction 4, the opportunity for sexual selection (I_{mates}) was not related to the strength of selection (magnitude of partial regression coefficient) on body size (Pearson correlation, $r = -0.59$, $P = 0.12$, $n = 8$) but showed a negative trend with regard to head size ($r = -0.70$, $P = 0.053$, $n = 8$).

DISCUSSION

My study supports the hypothesis that an ecological factor, gallery size, significantly affects sexual selection on male tree weta. Variation in gallery size was an important determinant of the opportunity of sexual selection in tree weta; however, contrary to expectation, greater opportunity existed in small

Table 2

PCA of 4 male phenotypic traits in *Hemideina crassidens* for each treatment (gallery size) in each year

Male trait	2003		2004		2006		2007	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Small gallery treatment								
Head length	0.825	0.564	0.828	0.561	0.517	0.856	0.883	0.455
Head width	0.802	0.581	0.800	0.587	0.721	0.672	0.842	0.526
Tibia length	0.549	0.830	0.559	0.811	0.750	0.625	0.674	0.701
Femur length	0.650	0.739	0.567	0.794	0.849	0.485	0.458	0.881
Eigenvalue	2.05	1.89	1.96	1.95	2.07	1.81	2.15	1.75
Proportion of variance	51.19	47.27	48.99	48.67	51.75	45.24	0.538	0.438
Cumulative proportion of variance	51.19	98.46	48.99	97.66	51.75	96.99	0.538	0.976
Large gallery treatment								
Head length	0.584	0.812	0.879	0.477	0.848	0.529	0.805	0.587
Head width	0.650	0.754	0.829	0.537	0.806	0.571	0.830	0.55
Tibia length	0.809	0.582	0.562	0.805	0.541	0.806	0.609	0.770
Femur length	0.756	0.639	0.458	0.863	0.525	0.814	0.537	0.830
Eigenvalue	1.99	1.96	1.98	1.91	1.94	1.92	2.00	1.93
Proportion of variance	0.467	0.493	0.496	0.477	0.484	0.479	0.499	0.482
Cumulative proportion of variance	0.497	0.991	0.496	0.973	0.484	0.964	0.499	0.982

Traits describing head size consistently loaded highly together as did those traits describing male body size. For each component, the traits with the highest factor loadings are underlined.

galleries and not in large galleries. Also in line with prediction, significantly larger weaponry was favored when gallery size permits larger harems to form.

The experimental results reported here mirror patterns observed in the field on Maud Island and at several sites across New Zealand. For example, on Maud Island, males inhabiting a manuka (*L. scoparium*) forest patch (ca. 50 ha), which has only small galleries (<3 adult tree weta), possess significantly smaller weaponry (mean ± SE: 17.93 ± 0.89 mm, $n = 16$) than males (25.41 ± 0.84 mm, $n = 16$ males randomly selected from Kelly [2005]; *t*-test, $t_{30} = 6.30$, $P < 0.0001$; Kelly CD, unpublished data) in a broad-leaved forest patch (ca. 15 ha) in which large galleries (>3 adult weta) are available. In addition, male *H. crassidens* captured in broad-leaved forests with large galleries on Mana and Stephens Islands (Moller 1985), as well as at Palmerston North/Manawatu Gorge (Kelly CD, personal observation), exhibit head lengths greater than 20 mm. However, in 3 other New Zealand populations of *H. crassidens* (Lake Kaniere: 42°48′S, 171°09′E; Somes Island: 41°02′S, 173°53′E; Baton Valley: 41°17′S, 172°45′E) that tend to lack large natural galleries, typical male head lengths are less than 21 mm (Kelly CD, personal observation). Interestingly, the tree weta on Somes/Matiu Island, a scientific reserve in the Wellington Harbor that is free of nonnative predators, is descended from Mana Island individuals (Gibbs G, personal

Table 3

Standardized linear (β ± SE) selection gradients for head and body size in male Wellington tree weta estimated in 2 experimental treatments

Male character	β_i (*P* value)
Small galleries ($n = 181$)	
Head size	0.019 ± 0.132 (0.890)
Body size	−0.247 ± 0.132 (0.063)
Large galleries ($n = 145$)	
Head size	0.250 ± 0.102 (0.015)
Body size	0.082 ± 0.102 (0.420)

Linear selection gradients are given with significance computed using permutation tests.

communication), a population in which males exhibit a range of head sizes similar to males on Maud Island (Moller 1985).

These observations, together with my experimental results, suggest that less intense male–male competition at sites with small galleries relaxes selection for increased weapon size. Maybe the reduced selection pressure on weaponry in small gallery sites played a role in the evolution and/or maintenance of precocial male maturation in this species. That is, perhaps selection favored males that responded to environmental cues (average gallery size in a patch) and matured early at the 8th instar, whereas males in larger gallery forests maximized their fitness by continuing their development until the 10th instar (sensu Shuster and Wade 2003).

The opportunity for sexual selection

The observed effect of resource quality on selection was opposite to that predicted despite larger galleries housing significantly larger harems and exhibiting greater clumping of females. Contrary to conventional theory (e.g., Emlen and Oring 1977), the upper limit to sexual selection was not dictated by the average harem size of successful males (i.e., operational sex ratio) or the degree to which females clump in space; instead sexual selection was most affected by the difference in the proportion of successful (males residing with one or more females) versus unsuccessful males. A larger proportion of unsuccessful males in Equation 3 produced larger values of I_{mates}. This observation supports the claim of Shuster and Wade (2003; see also Wade 1979; Wade and Arnold 1980) that the most important determinant of the strength of sexual selection is the magnitude of the difference between successful (males residing with one or more females) and unsuccessful (males residing alone) males.

Why would smaller galleries more often house unsuccessful males than larger galleries? I posit that this phenomenon is a consequence of female-searching behavior and gallery preferences. First, larger female aggregations form in larger galleries (Kelly 2006c, 2006d), and through acoustic and/or chemical cues (Field and Jarman 2001), groups of weta likely attract other gallery-searching females (see also Wade 1995) as well as mate-searching males. Second, although females prefer to reside alone in galleries, they will take up residence with
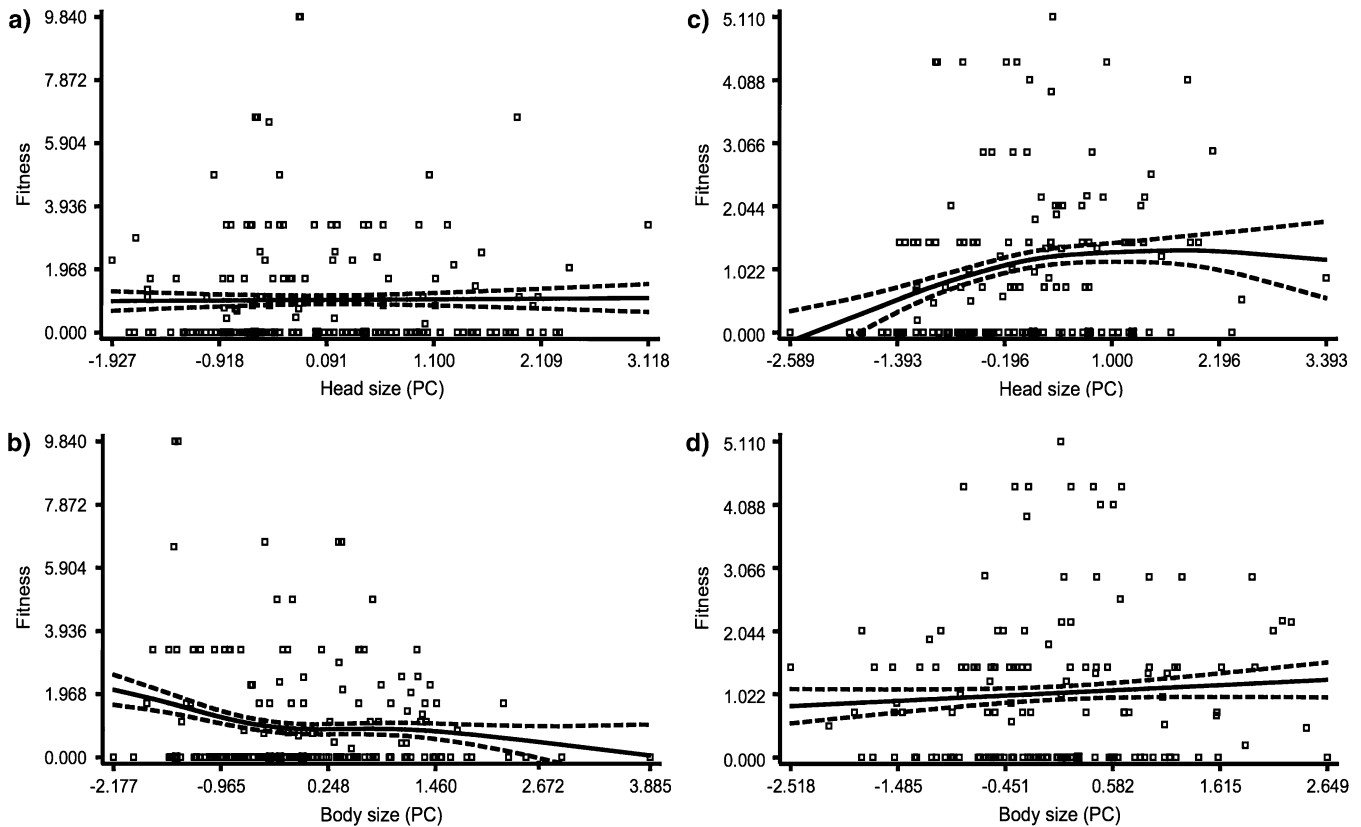
Figure 4
Nonparametric cubic splines of the fitness surfaces for male head and body size in (a and b) small and (c and d) large galleries. Dotted lines are the SE of the fitness surface from 999 bootstraps.

a male when other females are present likely because other conspecifics dilute the costs associated with residing with males (e.g., injury to limbs during forced copulations) (Kelly 2006c). On the other hand, because larger aggregations of females cannot occur in smaller galleries, females are less likely to enter a gallery housing an adult male as harassment costs will not be diluted. In addition, from the male perspective, a lack of large aggregations should also make it more difficult for males to find female-occupied galleries.

Linear selection on male weaponry and body size

The opportunity for sexual selection, I_{mates}, describes the upper limit of the strength of selection. As it does not provide information on the relationship between fitness and phenotypic characters, I_{mates} does not measure selection acting on the phenotype per se. I identified targets of phenotypic selection by using multivariate statistical techniques (Lande and Arnold 1983; Arnold and Wade 1984a, 1984b; Brodie et al. 1995). Selection gradients support my prediction that selection on weaponry should be strongest in the large gallery treatment because male–male competition should be more intense at these sites given that they likely offer greater reproductive rewards to successful males. These findings support a correlational field study conducted on the same population and using large artificial galleries of identical size (Kelly 2005). That male weaponry is a target of selection is not surprising because laboratory experiments show that male tree wetas use their weapons in fights for possession of galleries housing harems, and males with larger mandibles have a greater probability of winning a contest (Kelly 2006a). In

addition, smaller weaponry, or smaller body size in general, maybe favored in patches with small galleries if smaller males are better at searching for mates (see above) and/or fitting into spaces too small to accommodate large males (Kelly 2006d).

My findings on *H. crassidens* are similar to those on a congener, *Hemideina maori*, which inhabits cavities under rocks (Gwynne and Jamieson 1998; Jamieson 2002; Leisnham and Jamieson 2004). Gwynne and Jamieson (1998) found a strong positive correlation between head size and harem size in a cross-sectional study in the wild, and, in follow-up longitudinal studies, Jamieson (2002) and Jamieson and Leisnham (2004) found weak positive selection on male weaponry (head width). The latter 2 studies were not multivariate selection analyses and so did not provide partial regression coefficients; thus, direct comparisons with selection gradients for *H. crassidens* are not possible.

In general, that most gradients calculated in this study are statistically nonsignificant is not surprising given that the most powerful studies (i.e., sample size > 1000) of selection gradients on a diversity of traits indicate that selection is typically quite weak (Kingsolver et al. 2001). Detecting nonlinear selection requires even greater power than needed to detect linear selection (Conner 2001). A recent literature review showed that only 26% of reported β estimates were significantly different from zero at a α level of 0.05 (Hoekstra et al. 2001). Thus, one factor likely contributing to the nonsignifcant results in my study was small sample size; the need for very large sample sizes plague studies of selection in the wild (Endler 1986; Kingsolver et al. 2001). Obtaining large sample sizes is difficult with *H. crassidens* because weta do not occur in very high numbers in nature.

The relationship between opportunity and strength of sexual selection

Contrary to prediction, the relationship between the opportunity for sexual selection (I_{mates}) and the strength of selection (selection gradient) on weapon size was not positive. In fact, this relationship showed a marginally nonsignifcant negative trend. Bjork and Pitnick (2006) found a negative relationship between opportunity and strength of sexual selection among *Drosophila* species. They found that as sperm size increased among species the strength of selection on males decreased, whereas the opportunity for sexual selection increased. Similar to my prediction, they expected measures of opportunity and strength to complement each other. Why do the patterns differ? Even though both approaches measure sexual selection, they measure different aspects of the process. I_{mates} is a variance-based method estimating the potential of sexual selection, whereas selection gradients measure the degree to which selection operates on particular phenotypic traits. Contrary to these results, McLain (1992) found that selection opportunity indexed selection intensity, as measured using selection differentials, on traits in the seed bug *Neacoryphus bicrucis*. He found that when sexual selection was intense, body size accounted for a greater amount of variation in male mating success than otherwise.

Although longitudinal selection experiments on natural populations of animals provide powerful tests of sexual selection theory (Endler 1986; Wade and Kalisz 1990), this approach is rarely employed despite a call to attention more than 17 years ago (see Wade and Kalisz 1990). The present study is one of very few to experimentally manipulate, in a natural population, the environmental factors affecting the opportunity and strength of sexual selection in an animal. I have shown that refuge size directly affects harem size, which ultimately dictates the opportunity for sexual selection as well as the strength of selection on male weaponry and body size. Finally, my results have practical applications: by providing large artificial galleries in forests comprised of small galleries (e.g., early succession and/or immature regenerating forests), conservationists can maintain the full range of male tree weta phenotypes within populations.

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