

Relationship between male head size and mating opportunity in the harem-defence, polygynous tree weta *Hemideina maori* (Orthoptera: Anostostomatidae)

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Abstract: The most distinguishing feature of the tree weta genus *Hemideina* (Orthoptera: Anostostomatidae) is their cephalic weaponry, which is thought to be the result of sexual selection on males to aggressively defend groups of reproductive females. Mountain stone weta *H. maori* is a tree weta that shelters in cavities under flat rocks on rocky outcrops in the alpine region of the South Island. The main objectives of this study were to determine whether males with larger heads have access to greater numbers of females, and whether head size has an effect on male survival and longevity. Males with larger heads associated with larger groups of females than males with smaller heads. Male head size only accounted for 11% of the variation in mating opportunity when all rocks with females were considered, but explained 36% of the variation when only a few specific rocks that had large numbers of females were taken into account. The lower recapture rates of males in general and of small-headed males in particular, further suggested that small males intermittently retreat to small cracks or cavities within tor columns, where there are unlikely to be large female groups. Thus, larger males had access to more females than smaller males. Moreover, larger males had no detectable disadvantage in terms of daily survival and longevity. This study provides strong evidence that larger male tree weta do associate with larger harems in the wild, however, questions relating to male weaponry size and mating success will become clearer only through paternity testing of weta under natural conditions.

Keywords: mate competition; New Zealand; sexual dimorphism; Stenopelmatidae; weta.

Introduction

Tree weta of the genus *Hemideina* (Orthoptera: Anostostomatidae) are a group of flightless, nocturnal insects, endemic to New Zealand. The most distinguishing feature of tree weta is the sexual dimorphism of cephalic weaponry exhibited in all but one of the seven species (Gibbs, 1998; Field, 2001a). The head and jaws of adult males are conspicuously enlarged, about twice the size of those of females (Meads, 1990; Field and Deans, 2001). It is thought that this dimorphism is the result of sexual selection on males to aggressively defend groups of reproductive females (called 'harems') from rival males in refuge sites in cavities in trees or under rocks (Hudson, 1920; Field and Sandlant, 1983, 2001; Moller, 1985; Gwynne and Jamieson, 1998; Field 2001b). Males that win access to and defend female groups are likely to have higher reproductive success because matings occur most often inside the cavity (Field and Sandlant, 1983, 2001; A. Stuart (Univ. of Otago, Dunedin, N.Z.) and

I. Jamieson, *unpubl.*). This harem-defence behaviour is a life-history trait more typical of vertebrates (Gwynne and Jamieson, 1998). Cavities attract adult females of lowland forest species (e.g. *H. femorata* and *H. crassidens*) because of the safety they provide from predators (Gibbs, 1998; Field and Sandlant, 2001). The most attractive cavities contain a disproportionately large number of females, and surveys of *H. crassidens* have revealed one adult male with up to 7–9 females (Field and Sandlant, 1983; Moller, 1985).

Despite the conspicuous sexual dimorphism in cephalic weaponry, the relationship between resident male head size and harem size has been studied extensively only in the mountain stone weta *H. maori* in the Rock and Pillar Range in north Otago. *Hemideina maori* is unusual for a tree weta in that it lives above the tree line and takes shelter under flat rock slabs that have broken off rock outcrops or tors (King *et al.*, 1996; Jamieson *et al.*, 2000; Leisnham and Jamieson, 2002). Weta living in cavities under rocks are easier to sample than those living in cavities in trees because the

refuge does not have to be enlarged or destroyed to extract the weta (Fig. 1). *Hemideina maori*, therefore, appears an ideal species to answer questions about the mating system of tree weta. Gwynne and Jamieson (1998) showed a significant relationship between male head size and harem size, but only for two of the three tors they surveyed. Furthermore, each tor was sampled only once and the weta were unmarked, thus information on mating success of individual males over time was lacking. Jamieson (2002) improved on this earlier study by marking all adult weta found on three large tors and by sampling these tors every two weeks over one breeding season. The results showed a significant but weak relationship between male head size and harem size. Therefore the main objective of the present study was to extend the work of Jamieson (2002) by conducting a three-year mark-recapture study of adult *H. maori* on 18 tors within a c. 10 ha area in the Rock and Pillar Range to determine whether males with larger heads have access to greater numbers of females. We also examined whether there were any survival costs associated with varying head and body sizes in males.

Methods

Study site

The study was conducted in the Rock and Pillar Range (summit 1450 m a.s.l.), in the province of Otago, New Zealand. The study site is located in the southern part of the range, about 1 km east of McPhee's Rock (1250 m a.s.l.) (45°28'S 170°02'E). Four large tors with 30–40 rocks and 14 small tors with 1–12 rocks were surveyed approximately every two weeks from November to May for three field seasons (1997/98, 1998/99 and 1999/2000), as part of a concurrent mark-recapture study (see Leisnham *et al.*, 2003). Five of the small tors did not contain any adult males and were excluded from further analysis. Further descriptions of the habitat and study area can be found in Leisnham *et al.* (2003) and Leisnham and Jamieson (2002).

All loose rocks large enough for adult weta to take refuge under were lifted and subsequently numbered during initial surveys of each study tor. During each survey, weta were removed from under rocks and placed in plastic containers and the rock carefully placed back in the same position. Sex, age class (juvenile or adult) and location were recorded, and head width and right femur length were measured using vernier dial callipers. Head width is the most important morphological feature for adult males in fighting because it indicates how wide individuals can open their mandibles (Gwynne and Jamieson, 1998), while the right femur length has been shown to be a reliable correlate of body size (Koning and Jamieson,



Figure 1. Photo showing a large harem of adult females with a single adult male (on underside of rock) in the Rock and Pillar Range. (Photo by P. Leisnham.)

2001). Adult weta were marked as part of a concurrent study on survivorship (Leisnham *et al.*, 2003) and dispersal (Leisnham and Jamieson, 2002) using a waterproof numbered tag glued to the pronotum. Weta were released under the rock from which they came.

We were unable to obtain a direct measure of male mating success, but the number of females guarded by one male (harem size) is assumed to be at least an indication of mating opportunity, since resident males regularly mate with and guard females under their rocks (A. Stuart and I. Jamieson, *unpubl.*). On rare occasions when two males are present under the same rock with a group of females, laboratory observations indicate that a dominant male will guard the females while the other male remains on the edge of this group (A. Stuart, *pers. comm.*). In all ten of the multi-male harems that were monitored closely in the field during the 1999/2000 season, the male with the largest head width was closer to the majority of females, often positioned just behind the female's posterior (Leisnham, 2001). Therefore, when determining harem size in multi-male harems, we conservatively assumed that the largest male would most likely secure the matings from at least two females and then divided up the remaining potential mates between all the males equally.

Daily mating opportunity was estimated by taking the number of females guarded by a male multiplied by the number of days the male was resident with those females summed across the number of sightings of the male and then divided by the total number of days that male was known to be alive. The number of days that a male was resident under a rock with one or more females was estimated as the period between the midpoints of the intervals either side of a sighting and was calculated during the summer period (December to February) only (see below).

We tested for a significant relationship between male head width and mating opportunity using

linear regression. All body characteristics were normally distributed but mating opportunity was transformed using natural logs [$(Y' = \ln(Y+1))$] to reduce heteroscedasticity and normalise the data (Zar, 1996).

The effects of head width (HW) and body size (BS) on the daily survival rates (ϕ , the probability that an individual remains in the population) and recapture rates (p , the probability any one individual that is alive is recaptured) of adult males on the four largest tors were modelled using Cormack-Jolly-Seber (CJS) analysis in MARK 1.9 (White and Burham, 1999). Because there is low adult dispersal between local populations (< 4% of re-sighted weta; Leisnham and Jamieson, 2002) any differences in ϕ are likely due to differences in survival rather than emigration. The models listed in Table 1 were compared to the base model $\phi.p$ (constant survival and recapture across individuals with varying head widths and body sizes), and prioritised using the Akaike's Information Criteria, adjusted for sample size (AICc). Models with lower AICc values show better fit relative to models with higher AICc values (White and Burham, 1999). Components of the AICc models from each analysis of individual tors were pooled to form a composite test to select the model that had best fit with the overall data set from all four of the largest tors. For further details on survival and longevity analysis using MARK, see Leisnham *et al.* (2003).

In addition to survival and recapture rates, we also examined the relationship between the minimum estimated lifespan of adult males (see Leisnham *et al.*, 2003) and head width using correlation analysis. Since Rock and Pillar weta have relatively high recapture rates on the isolated 'island' tors (~60–70%), we are confident that minimum estimated lifespan is a good measure of true weta longevity (Leisnham *et al.*, 2003).

All frequency data were analysed as a contingency table using Chi-squared test with Yates' Correction for Continuity. Means \pm standard errors are presented throughout unless otherwise stated. All tests were two-tailed and significance was assigned at the 5% level.

Results

Composition of weta groups

The maximum number of adult females associating with a single male was eight (see Fig. 1). The proportion of times a group of females was guarded by a solitary male peaked in summer (December to February) and then declined for all three field seasons (data not shown). This seasonal effect was significant when we compared the frequency of single male versus multi-male harems across monthly periods in a contingency table analysis (pooling data across years and tors for higher expected values: $\chi^2 = 15.93$, d.f. = 6, $P < 0.025$). This result confirms the pattern found in an earlier study by Gwynne and Jamieson (1998), suggesting that weta aggregations from March till November may be mostly over-wintering groups when males are more tolerant of each other and less likely to defend rock cavities where groups of adult females live. Therefore, for all further analyses, we only included those data that were compiled during the summer breeding period (December to February), when mate competition was likely to be highest.

Male head size and mating opportunity

Adult male head width varied significantly among tors in the study site (One-way ANOVA, $F_{12, 221} = 5.33$, $P < 0.001$). Therefore, head width across all tors was standardised by calculating the difference in size between each individual and the tor average, before pooling all the data. There was a highly significant but relatively weak relationship between standardised head width and relative mating opportunity ($R^2 = 10.6$, $F_{1, 209} = 24.8$, $P < 0.001$; Fig. 2).

During any one survey, the vast majority of rocks that were monitored did not have any adult females (averaging between 80–92% of rocks across large tors). However, under two rocks on Tor L2 and one rock on Tor L1, there were consistently 4–6 females with 1–3 males. Although these rocks only constituted 3–5% of the monitored rocks on their tors, they normally contained over a third (37%, range 17–51%) of adult females captured on the two tors during any one

Table 1. Cormack-Jolly-Seber models used to test for the effects of head width and body size on the survival (ϕ) and recapture (p) rates of adult males on the four largest tors.

Effect tested	Parameter	General model	Notation
head width	ϕ	Survival varies with head width and recapture probability is constant	$\phi_{\text{head width}P}$.
	p	Survival is constant and recapture probability varies with head width	$\phi.P_{\text{head width}}$
body size	ϕ	Survival varies with body size and recapture probability is constant	$\phi_{\text{body size}P}$.
	p	Survival is constant and recapture probability varies with body size	$\phi.P_{\text{body size}}$

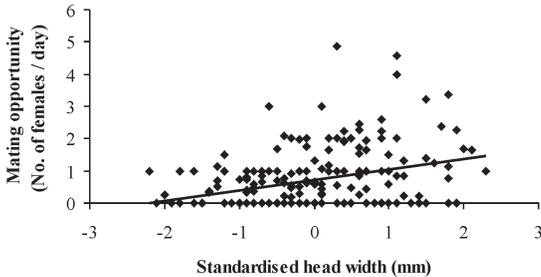


Figure 2. Standardised male head width plotted against male mating opportunity for the pooled data collected from the study site in the Rock and Pillar Range over three field seasons from November 1997 to April 2000. Standardised head width is the difference in size between an individual's head width and the tor average. $R^2 = 10.6$, $F_{1,209} = 24.8$, $P < 0.001$, $n = 211$.

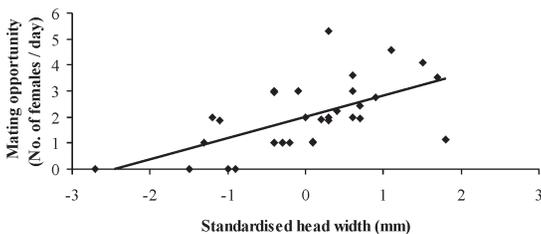


Figure 3. Standardised male head width plotted against male mating opportunity for data collected from three rocks that had consistently large female harems over three seasons. See Figure 2 caption for definition of standardised head width. $R^2 = 36.3$, $F_{1,29} = 16.5$, $P < 0.001$, $n = 31$.

survey. Therefore, one might expect that the most intense competition among adult males for mates would occur under these rocks. When pooling samples from these three rocks, a significant and much stronger relationship between head width and relative mating opportunity was observed ($R^2 = 36.3$, $F_{1,29} = 16.5$, $P < 0.001$; Fig. 3). In addition, the vast majority (72%, $n = 18$) of male 'takeovers' under these rocks were also by a larger male. We assumed a takeover had occurred when a male that had been previously recorded under the rock was not found on a subsequent survey, and a new male had taken his place.

Survival rates and adult lifespan

During any one survey, the majority (71%, range 23–81%) of adult weta across all four large tors were recaptured under the same rock. Since adult male tree weta often have to fight for access to rock cavities, we might expect them to move more often between different rocks than adult females. On the four large tors,

however, there was no difference in the mean percentage of times an individual was recaptured under the same rock between adult males ($63\% \pm 4.67$) and females ($67\% \pm 5.23$) (Nested ANOVA, $F_{1,291} = 0.38$, $P = 0.57$). However, there was a weak but significant positive relationship among adult males between head width and the proportion of recaptures under the same rock (pooled data from large tors: $R^2 = 5.4$, $F_{1,137} = 7.75$, $P < 0.05$; Fig. 4), which was not seen among adult females ($R^2 = 0.40$, $F_{1,151} = 3.71$, $P = 0.98$).

Previous mark-recapture analysis (Leisnham *et al.*, 2003) indicated that males had a lower recapture probability on a tor, but the sexes did not vary in terms of survival or longevity estimates. Further analysis of the effects of head and body size on male survival using CJS modelling (see Table 1) revealed that the constant survival model (ϕ , AICc = 1433.89) showed a better fit to the total data set than when either head width ($\phi_{\text{head width}}$, AICc = 1439.68) or body size ($\phi_{\text{body size}}$, AICc = 1440.05) was modelled as having an effect on survival. This was also the case when each of the tors was analysed separately (data not shown). However, in terms of explaining the variation in the probability of recapture among adult male weta, head width ($p_{\text{head width}}$, AICc = 1425.09) showed a better fit than either body size ($p_{\text{body size}}$, AICc = 1433.89) or constant recapture rate (p , AICc = 1436.40) for the composite dataset and for three of the four tors when analysed separately (data not shown).

Finally, there was no significant negative correlation between male head width and estimated adult lifespan ($r = -0.11$, $P = 0.56$, $n = 33$), indicating there were no survival costs associated with increasing head size. A plot of the data suggested there might be a trend for males with intermediate head sizes to have longer lifespan, but a quadratic equation fitted to the data was also non-significant ($F_{2,28} = 1.12$, $P = 0.34$; Fig. 5).

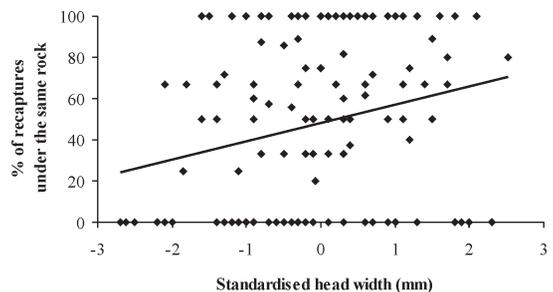


Figure 4. Standardised male head width plotted against the percentage of recaptures under the same rock as the previous recapture. See Figure 2 caption for definition of standardised head width. $R^2 = 5.4$, $F_{1,137} = 7.75$, $P < 0.05$, $n = 139$.

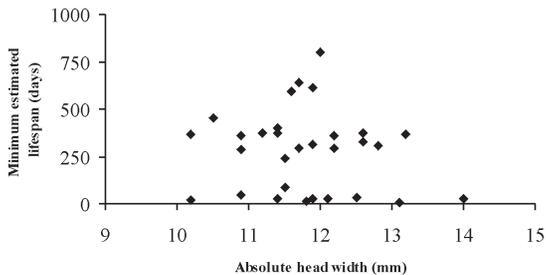


Figure 5. Absolute male head width correlated with minimum estimated adult lifespan (days) of the males marked after the first three survey periods in 1997/98 season. $r = -0.11$, $P = 0.56$, $n = 33$.

Discussion

The results of this mark-recapture study show that males with larger heads associate with larger groups of females than males with smaller heads. Head size only accounted for 10.6% of the total variation in mating opportunity when all rocks with females were considered, but explained much more of the variation (36.3%) when only a few rocks, which had the majority of females on a tor, were taken into account. These results support the findings from two previous studies of *H. maori* from the same study area, which investigated the relationship between variation in head size and potential mating success (Gywnne and Jamieson, 1998; Jamieson, 2002). They also support a number of field and laboratory studies that showed adult male tree weta in the genus *Hemideina* use their large cephalic weaponry to fight aggressively for access to refuge sites where reproductive females shelter (Hudson, 1920; Field and Sandlant, 1983, 2001; Moller, 1985).

The lower recapture rates of males in general, and of small-headed males in particular, suggest that small males intermittently retreat to inaccessible small cracks or cavities within tor columns where there is unlikely to be space for large groups of females (Leisnham 2001). As well as appearing to have a mating advantage over smaller rivals, larger males had no detectable disadvantage in terms of survival and longevity.

The relationship between male head size, body size and harem size in tree weta is likely to be a complex one. The results of recent mate competition trials, involving two males of varying head size, found that males with larger heads won significantly more of the aggressive encounters and attempted more matings, but did not achieve significantly higher mating (i.e. copulation) success (A. Stuart and I. Jamieson, *unpubl.*). Males that won aggressive encounters adopted a

guarding strategy while males that lost aggressive encounters subsequently adopted a sneaking strategy. However, there was no behavioural advantage to being physically small *per se*, as extremely small males that competed against much larger males had the worst mating success. Interestingly, unlike *H. maori*, head sizes in the Wellington tree weta *H. crassidens* on predator-free Maud Island show a bimodal distribution (A. Stuart and I. Jamieson, *unpubl.*). Small males of *H. crassidens* adopt a different type of sneaking strategy in which they avoid confrontations with large guarding males in tree cavities and are more likely to attempt mating while females are foraging outside (see also Spencer, 1995). Laboratory observations indicate that small males of *H. crassidens* achieve relatively high copulation success compared with small males in *H. maori* (A. Stuart and I. Jamieson, *unpubl.*).

Accurately assessing the true mating success of *H. maori*, and tree weta in general, remains difficult under more natural conditions. Even the relatively intensive sampling of refuge sites in this study (i.e. about every two weeks) may not have been often enough to account for all of the movements of adult weta between rocks, especially those of small males. These weta appear to move more frequently than their larger rivals. Furthermore, because weta are nocturnal and shelter in refuges by day, it is difficult to determine their mating dynamics through use of daytime monitoring, despite attempting to account for male residency with female harems. Although this study provides strong evidence that larger male tree weta do associate with larger harems in the wild, questions relating to male weaponry size and mating success will become much clearer through paternity testing of weta under natural conditions. However, even this may prove difficult. Female tree weta oviposit in the ground over a large area adjacent to their daytime shelters. The eggs are not likely to hatch until the following season (Gibbs 1998), and thus the chances of matching emerging nymphs with a large pool of potential parents where neither the mother nor father is known, would be challenging even with use of molecular techniques.

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