

## SHORT COMMUNICATION

# Movement patterns and gallery use by the sexually dimorphic Wellington tree weta

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**Abstract:** The Wellington tree weta, *Hemideina crassidens*, is a harem-polygynous nocturnal insect whose males defend and mate groups of females residing in cavities in trees. In this study I examined sexual differences in gallery use (number of galleries occupied per unit time), distance travelled per night and activity patterns after sunset. In addition, I investigated how gallery size affected each of these variables. On average, males and females did not differ in the number of galleries visited per night, or in the distance they travelled per night; however, adult males were more likely to be seen earlier in the night than later. Although males and females did not differ in their gallery use or distance travelled, adult males occupied a significantly greater number of galleries and travelled greater distances per night at sites with small galleries than did males at sites with large galleries. These results suggest that habitat structure of a forest patch influences intrasexual tree weta behaviour.

**Keywords:** harem; weaponry; refuge; *Hemideina crassidens*; distance travelled; movement

## Introduction

The Wellington tree weta, *Hemideina crassidens* (Orthoptera: Tettigonioidae: Anostostomatidae), is a large, nocturnal, flightless insect endemic to New Zealand (Hudson, 1892; Gibbs, 2001). A remarkable feature of this species is the exaggerated mandibles of males, a trait used as a weapon in fights for control of harems in cavities in trees (hereafter termed galleries) (Field and Deans, 2001; Kelly, 2005; Kelly, in press). Galleries are used as diurnal shelters year round by tree weta and can contain one or more adult females (Hudson, 1920; Field and Sandlant, 1983; Kelly, 2005). Galleries serve as refugia from predators and may also provide more favourable environmental conditions during daylight. Galleries do not serve as feeding, oviposition or offspring-rearing sites (Field and Sandlant, 2001). Sexual selection on male *H. crassidens* is thought to be intense because galleries can house large groups of sexually receptive females and thus offer males the potential for high reproductive success (Moller, 1985; Kelly, 2005; Kelly, 2006b).

Although long thought to be a resource-defence polygynous species (Hudson, 1920; Field and Sandlant, 1983) in which males control particular galleries and their females for a considerable amount of time, a

recent experimental study in the wild revealed that male *H. crassidens* appear to defend females and not the galleries per se (Kelly, 2006a). Kelly (2006a) found that the duration of time a male resides in a gallery was related significantly to the number of adult females in the gallery, and because more females can reside in larger galleries, males spend more time at these sites. Therefore, the Wellington tree weta appears to exhibit a mating system more in line with harem defence rather than classical resource-defence.

Another remarkable feature of *H. crassidens* is the considerable variation among males, but not females, in the variation in weapon (mandible) size. This variation is likely due to head size covarying with the instar at which individuals become sexually mature. Because males maturing in the 8th instar have smaller mandibles than males maturing in the 10th instar, and 9th instar males have mandibles of intermediate size (Spencer, 1995; Stringer and Cary, 2001), mature males exhibit a trimorphic distribution in head size. Because all females mature in the 10th instar, the variation in mandible size exhibited by them is considerably smaller than that of males.

Surprisingly little is known about the behavioural ecology of *H. crassidens*, particularly in the wild. Here, I examine aspects of gallery use and movement

by adult males and females within a forest patch. Given Kelly's (2006a) finding that adult male tree weta appear to be more transient than adult females, I predict that females would reside in fewer galleries than males, particularly at sites where galleries were small. Further, I predict that males would reside in a greater number of galleries, on average, at sites where galleries were small than at sites where galleries were larger. I also expand on Moller's (1985) earlier work, which estimated the distance travelled per night and the activity time (relative to sunset) of adults and juveniles of both sexes. For each dependent variable examined in this study I determined whether male weapon size predicted male behaviour. Spencer (1995) predicted that males with smaller weaponry should adopt an alternative mating strategy in which males wander in search of opportunistic matings.

## Methods

Tree weta were studied on Te Hoiere/Maud Island, New Zealand (41° 02' S, 173° 54' E), a 309-ha scientific reserve free of alien predators [e.g. rodents (*Mus* and *Rattus* spp.) and stoats (*Mustela erminea*)]. The endemic morepork, *Ninox novaeseelandiae*, is the only known predator of adult tree weta on the island (personal observation).

I monitored tree weta behaviour on Maud Island during March–May 2002, April–May 2003 and March–April 2004. In 2002, I installed wooden artificial galleries on mature trees approximately 1.5 m above the ground at two sites less than 200 m apart. Each artificial gallery was placed near or over a natural gallery that was currently used by tree weta. All tree weta were removed from the natural gallery, which was destroyed or plugged to maintain the natural density of galleries. I measured the distance (to the nearest cm) from the entrance hole of each gallery to the entrance hole of every other gallery at each site. The sites were at approximately the same elevation in relatively young forest, which was sheep pasture until 30 years ago and, because they were south-facing, experienced very similar temperatures, precipitation and daylight. Moreover, the sites were similar in area (see below), topography and flora.

At Site A (ca. 24 m × 4 m), 19 small galleries (cavity volume = 53.84 cm<sup>3</sup>) were installed, whereas at Site B (ca. 22 m × 3 m), 13 large galleries (cavity volume = 107.68 cm<sup>3</sup>), each with twice the internal volume of those at Site A, were installed. This gave approximately one gallery per 5 m<sup>2</sup> at each site. The diameter of the entrance to each gallery was at least 20 mm. The galleries differed in volume to address predictions of how resource quality (gallery size) affects harem size and the duration of residency of

males and females (see Kelly, 2006a).

In 2002, I repeatedly seeded each artificial cavity at each site with adult males and females from the natural galleries that were plugged or destroyed, and occasionally from locations outside Sites A and B. Seeding was undertaken because previously occupied artificial galleries are more quickly accepted by tree weta than new ones erected and allowed to be occupied, naturally (Trewick and Morgan-Richards, 2000; personal observation). In addition to being seeded, galleries were occupied naturally during 2002. After 2002 seeding was discontinued because continual occupation of galleries by tree weta occurred naturally.

In 2002 at Site A, I scanned the ground and all tree trunks and foliage from a height of 5 m to ground-level each night from 27 March to 8 May. Because individuals can climb high into the canopy, this sampling procedure may be biased. However, by sampling daily for 48 days and by varying the observation times, I reduced this bias. I recorded the identity, lifestage (adult or juvenile) and sex of each tree weta found. New adult individuals were measured and marked before being replaced at the exact location where they were found. Individual adults were marked with uniquely numbered and coloured bee tags (H. Thorne Ltd., England) attached to their pronotum with acrylate glue. This procedure did not appear to affect tree weta behaviour. I used digital callipers to measure head length to the nearest 0.05 mm. Head length is an excellent predictor of mandible length (weapon size) (Pearson correlation coefficient,  $r_{353} = 0.99$ ; Kelly, 2005). Juveniles were sexed when possible and numbered uniquely with white correction fluid.

All observation periods were approximately 30 min in duration but were at different times (haphazardly selected) each night in order to obtain a representative picture of weta activity throughout the night. Occasionally, I conducted more than one set of observations per night. Observations were rarely conducted more than 6 hours after sunset because tree weta appeared to be most active on Maud Island in the first 6 hours after sunset.

In 2003, I censused galleries every third morning (22 days in total), whereas in 2004 I censused galleries daily (39 days in total). Censusing involved removing all individuals from their galleries, noting their identity, and immediately replacing them back into the gallery. If an individual was unmarked it was measured, marked and replaced, immediately.

## Data analysis

To obtain an accurate picture of tree weta movement within a patch and to estimate the number of galleries they occupy over a given time period, it is best to use data for individuals observed for two or more consecutive days. Thus I used data from 2004 only

when censuses were conducted daily. For ease of discussion, throughout this paper I describe the estimated distance travelled by a weta between sightings on two or more consecutive nights as the straight-line distance travelled per night. Data from 2003 and 2004 were used to determine the mean length of time individuals spent in the two treatment patches. For each adult tree weta, I calculated the number of days between the first and last observation.

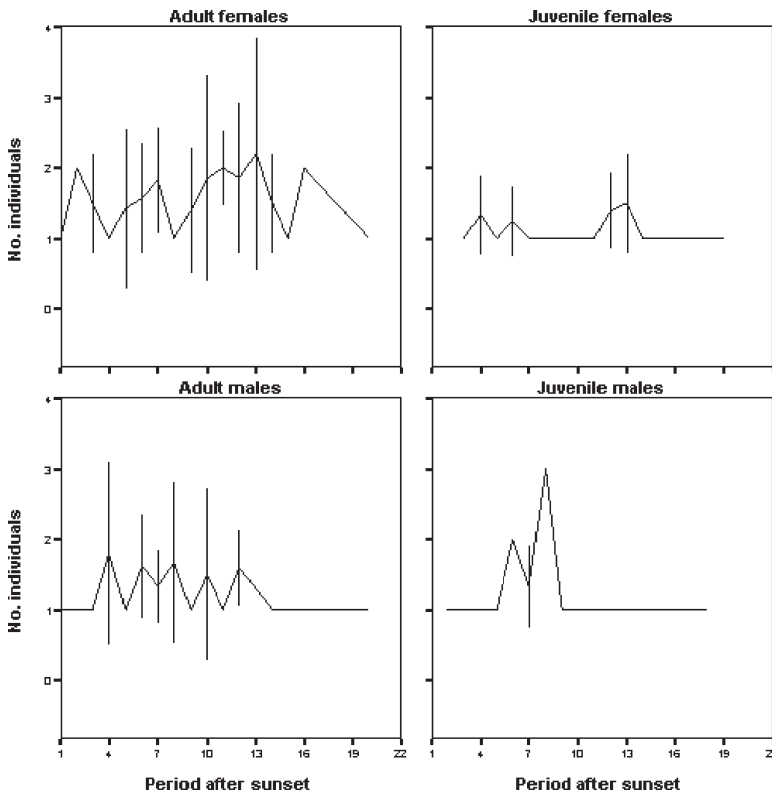
To maintain statistical independence for all variables, means were used for individuals that were observed more than once. All interaction terms from two-way ANOVAs were statistically non-significant and are not presented (but see analysis of time tree weta spent in each treatment plot). Data were  $\log_{10}$  transformed prior to ANOVA when residuals were non-normal and variances were heterogeneous. To determine which group means differed after a significant ANOVA  $F$  test I used Tukey's HSD *post hoc* multiple comparison test. The Kolmogorov-Smirnov goodness-of-fit test for a single variable was used to determine whether individuals were observed uniformly across sample periods. All correlation analyses were performed using Pearson product-moment correlation

because data were bivariate normal. Means are given  $\pm$  one standard error and all statistical tests are two-tailed ( $\alpha = 0.05$ ).

## Results

In 2002, I conducted 32 nocturnal observations within 6 h of sunset and five within 2 h of sunrise. The start times for the nocturnal observations were distributed uniformly across the 6 h window (start times binned in 15 min intervals; Kolmogorov-Smirnov goodness-of-fit test,  $Z = 1.21$ ,  $P = 0.105$ ). During the five pre-dawn surveys I observed only one tree weta, an adult female.

The mean number of adult females observed per survey was distributed uniformly across the 6 h observation window (Kolmogorov-Smirnov test,  $Z = 1.21$ ,  $P = 0.106$ ,  $n = 17$ ; Fig. 1). In contrast, the mean number of adult ( $Z = 2.67$ ,  $P < 0.001$ ,  $n = 17$ ) and juvenile ( $Z = 2.94$ ,  $P < 0.001$ ,  $n = 14$ ) males was significantly more likely to be observed closer to sunset than at other times of the night (Fig. 1). The time after sunset at which males were observed was not related to head length ( $r = -0.26$ ,  $P = 0.32$ ,  $n = 17$ ).



**Figure 1.** Mean ( $\pm$ SD) number of male (bottom panels) and female (top panels) *Hemideina crassidens* of each lifestage observed within 6 h after sunset. Each period represents a 15 min interval beginning 1 h after sunset [i.e., to calculate the upper bound in minutes for a time period:  $60 \text{ min} + (\text{period} \times 15 \text{ min})$ ; thus, period 4 represents 1:45 h – 2:00 h after sunset].

Juvenile females were significantly less likely to be observed 2.5–4 h after sunset than at other times of the night ( $Z = 3.00$ ,  $P < 0.001$ ,  $n = 16$ ; Fig. 1).

Contrary to prediction, there was no significant difference between males and females in the number of galleries visited per night (two-way ANOVA, sex:  $F_{1,70} = 3.43$ ,  $P = 0.068$ , 95% C.I. for difference between the means =  $-0.199 - 0.007$ ). However, there was a strong trend for males ( $0.52 \pm 0.03$  galleries night<sup>-1</sup>,  $n = 47$ ) to visit more galleries than females ( $0.38 \pm 0.04$  galleries night<sup>-1</sup>,  $n = 27$ ). Tree weta in the small-gallery treatment visited significantly more galleries per night ( $0.53 \pm 0.03$  galleries night<sup>-1</sup>,  $n = 52$ ) than individuals in the large-gallery treatment ( $0.33 \pm 0.04$  galleries night<sup>-1</sup>,  $n = 22$ ;  $F_{1,70} = 10.72$ ,  $P = 0.0016$ ). A post-hoc analysis showed that males in the small-gallery treatment visited significantly more galleries ( $0.59 \pm 0.04$  galleries night<sup>-1</sup>,  $n = 34$ ) than males in the large-gallery treatment ( $0.34 \pm 0.04$  galleries night<sup>-1</sup>,  $n = 13$ ; Tukey's HSD,  $P < 0.05$ ). Male head length was not correlated with the number of galleries occupied in either the large-gallery ( $r_{13} = -0.46$ ,  $P = 0.11$ ) or small-gallery ( $r_{34} = -0.05$ ,  $P = 0.78$ ) treatments.

Only one adult was observed in both years: a female found in the large-gallery treatment (and in the same gallery) in 2003 and 2004. The greatest estimated distance travelled by a male in a single night was 11.9 m (small-gallery treatment, 2004) and by a female it was 4.25 m (small-gallery treatment, 2004).

Females ( $1.22 \pm 0.74$  m night<sup>-1</sup>,  $n = 27$ ) did not travel greater distances per night than males ( $2.68 \pm 0.59$  m night<sup>-1</sup>,  $n = 47$ ;  $F_{1,70} = 0.68$ ,  $P = 0.41$ , 95% C.I. =  $-2.67 - 1.11$ ); in contrast, there was a trend for males to travel further between observation periods. Tree weta in the small-gallery treatment tended to travel greater distances per night ( $2.82 \pm 0.53$  m night<sup>-1</sup>,  $n = 52$ ) compared with individuals in the large-gallery treatment ( $0.55 \pm 0.79$  m night<sup>-1</sup>,  $n = 22$ ); however, the mean distance was not significantly different between gallery treatments ( $F_{1,70} = 3.83$ ,  $P = 0.054$ ). Males in the small-gallery treatment moved greater distances per night ( $3.61 \pm 0.71$  m night<sup>-1</sup>,  $n = 34$ ), on average, than males in the large-gallery treatment ( $0.26 \pm 0.50$  m night<sup>-1</sup>,  $n = 13$ ; Tukey's HSD,  $P < 0.05$ ). The above analyses included nights in which individuals did not move (i.e. total distance travelled/number of consecutive days observed), however, when only the nights in which tree weta moved were considered it was found that individuals in the small-gallery treatment moved significantly greater distances ( $11.10 \pm 1.07$  m night<sup>-1</sup>,  $n = 49$ ) than weta in the large-gallery treatment ( $2.81 \pm 1.89$  m night<sup>-1</sup>,  $n = 15$ ;  $F_{1,60} = 13.40$ ,  $P = 0.0005$ ). Males tended to move greater distances ( $10.02 \pm 1.46$  m night<sup>-1</sup>,  $n = 38$ ) than females ( $7.88 \pm 1.62$  m night<sup>-1</sup>,  $n = 26$ ), although this difference was

not significant ( $F_{1,60} = 0.13$ ,  $P = 0.72$ ). Males in the small-gallery treatment moved significantly greater distances per night ( $12.07 \pm 1.57$  m night<sup>-1</sup>,  $n = 30$ ) than males in the large-gallery treatment ( $2.37 \pm 0.71$  m night<sup>-1</sup>,  $n = 8$ ; Tukey's HSD,  $P < 0.05$ ). Male head length was not correlated with distance travelled per night in either the large-gallery ( $r_{13} = -0.08$ ,  $P = 0.79$ ), or small-gallery ( $r_{34} = 0.05$ ,  $P = 0.78$ ), treatments.

I found no year  $\times$  sex effect on the number of days ( $\log_{10}$  total number of days) that tree weta were observed in either the small-gallery (interaction term from two-way ANOVA,  $F_{1,118} = 0.133$ ,  $P = 0.72$ ) or large-gallery treatment ( $F_{1,117} = 1.649$ ,  $P = 0.20$ ). Therefore, data for both years for each treatment were pooled. Females spent significantly longer periods of time in the patch with small galleries ( $15.66 \pm 1.80$  days,  $n = 73$ ) than did males ( $7.95 \pm 0.94$  days,  $n = 110$ ;  $F_{1,120} = 12.35$ ,  $P = 0.001$ ). However, no significant difference between the sexes was found in the large-gallery treatment (males:  $3.11 \pm 0.67$  days,  $n = 74$ , females:  $5.81 \pm 1.10$  days,  $n = 98$ ;  $F_{1,119} = 0.859$ ,  $P = 0.36$ ).

## Discussion

My study showed that male and female *H. crassidens* did not differ in the number of galleries visited or distance travelled per night, and that females remained in particular forest patches for significantly longer periods of time than males. However, males in the patch with smaller galleries (accommodating up to three adult tree weta) visited significantly more galleries and tended to move greater distances than males in the patch with larger galleries. These results are consistent with those from a related study in which I found that males from a small-gallery treatment resided in galleries for significantly shorter durations than males in a large-gallery treatment (Kelly, 2006a). Presumably these results simply illustrate that longer residency in any particular gallery limits the number of galleries an individual can occupy and the distance they can travel. For example, if a male tree weta remains in a gallery for five consecutive nights it obviously will not occupy more galleries or walk further during those five nights than a male that occupies five different galleries. Results of the present study and the earlier one (Kelly 2006a) suggest that males consider galleries to be sites for mate location and that they abandon the galleries as soon as they have mated with all available females. In other words, males do not acquire a gallery and control it indefinitely; instead, they reside for a period that is positively related to the number of females in the gallery and not to gallery size per se (Kelly, 2006a). These observations are consistent with a harem-defence mating system, or more generally, male-dominance polygyny (sensu Shuster and Wade, 2003).

Like Moller (1985), I found that male and female weta did not differ in the estimated distance travelled per night and that the greatest net distance travelled by a tree weta in one night was nearly 12 m [11.6 m recorded by Moller (1985) and 11.9 m in this study]. The lack of a significant effect of sex on distance travelled per night could be due to the conservative nature of the measurements. Thus, in both studies, estimates of travel distance were linear, whereas tree weta are more likely to follow a non-linear path along branches and foliage. Nightly distances travelled have not been recorded for other *Hemideina* species. However, although they typically move no further than an adjacent rock (Jamieson *et al.*, 2000), individual mountain stone weta, *Hemideina maori*, have been observed to move 36 – 672 m between rock outcrops (tors) over the course of three years (Leishnam and Jamieson, 2002). Like *H. crassidens*, *H. maori* did not exhibit gender differences in distances moved (Leishnam and Jamieson, 2002). The Raukumara tusked weta (*Motuweta isolata*) have been observed to travel at least 80 m in one night (McCartney *et al.*, in press). Among other flightless orthopteran insects, mormon crickets (*Anabrus simplex*) have been shown to travel, on average, 0.66 m per day (non-band-forming population) to 331 m per day (band-forming population) (Lorch *et al.*, 2005).

Interestingly, adult male *H. crassidens*, as well as juveniles of both sexes, were less likely to be observed later in the night than adult females. This difference may be a consequence of a difference in habitat use (males may climb higher in the canopy over the course of a night and thus out of observation range), or it could reflect a tendency for adult males to leave their galleries early in the night, take over a new gallery and be out of sight much earlier than females. Alternatively, females may have greater nutritional requirements than males and therefore may stay out longer to feed, or perhaps to oviposit.

Finally, males with smaller weaponry were not seen more frequently earlier in the night, did not travel greater distances, and did not visit more galleries than males with larger weapons. Thus, they do not appear to adopt an alternative mating strategy in which they wander in search of opportunistic matings (Spencer 1995). Instead, smaller males may be better at mating with females in small, restricted spaces which are off-limits to larger males (Kelly, 2006b).

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