Sex- and season-dependent behaviour in a flightless insect, the Auckland tree weta (*Hemideina thoracica*)

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Abstract: In a polygynous mating system, males frequently compete by locating and defending sites with resources essential to female survival and reproduction. We investigated seasonal changes in site occupancy in a sexually dimorphic, harem-forming insect, the Auckland tree weta (*Hemideina thoracica*). First we established artificial cavities as diurnal refuge cavities and potential harem guarding sites. We then examined cavity occupancy changes, and, based on our knowledge of prior occupants, determined sex-specific patterns of arrival, departure, and aggregation at a population level throughout the year. Both season and the sex of prior occupants influenced weta occupancy patterns. Most observations were of single females. However, both males and females moved into cavities previously occupied by a weta of the opposite sex more often than expected by chance alone. Females avoided cavities where other females were present, except during summer when most harems formed. In early summer, male and female tree weta previously living apart began co-habiting. Generally there was little relationship between the number and sex of the weta inside cavities and female departure rates from cavities. Males who were sharing with other males departed cavities more frequently than single males, as might be expected in a polygynous species with male–male combat. Males were less likely to depart if they were sharing a cavity with a harem of more than two females during the summer–autumn period. Analysis of departure rates from artificial cavities indicates males are more mobile than females only in winter and spring. Based on our arrival and departure data, and high occupancy of artificial cavities, we suggest that female weta at this site are mobile and may search for mates during the summer. The data are consistent with a polygynandrous mating system as inferred for other tree weta species (*Hemideina* spp.).

Keywords: aggregation; harem; mating system; Orthoptera; polygyny

Introduction

Searching for mates can be costly (Gwynne 1987; Acharya 1995), but nonetheless is a requirement for most sexually reproducing organisms (Kokko & Wong 2007). Search effort in one sex is dependent on search effort in the other (Hammerstein & Parker 1987), but because males may benefit more from multiple mating than females (Bateman 1948) males are generally predicted to mate-search more than females when multiple mating is common and sperm competition occurs (Kokko & Wong 2007). However, males may attempt to monopolise resources, including females, if doing so increases reproductive success.

In a polygynous mating system, males compete directly for access to females through male–male combat (cf. Darwin 1874) or indirectly by locating and defending sites with resources essential to female survival and reproduction (Emlen & Oring 1977; Shuster & Wade 2003; Kelly 2006a). If male guarding of a limited resource (such as females, or refuge cavities) increases reproductive success, then males might be sedentary, and if females gain by enhancing their encounter rate with potential mates, they might be more mobile than otherwise expected. The ability of individuals to monopolise matings will in turn influence the intensity of sexual selection (Trivers 1972), particularly in polygynous species where mating effort, and the opportunity for sexual selection for males, is high (Bateman 1948; Trivers 1985).

Resource variation can lead to plasticity in mating systems so that, for example, mating system can vary within a species if resource availability varies spatially or temporally (Emlen & Oring 1977; Gwynne 1991). Seasonal effects can result if resources vary throughout the year. Thus, for example, if density is high, polygynous mating systems that have large numbers of sneakers (or satellites), as well as residents, can favour mobile males (Reichard et al. 2004). Differences in aggregation and occupancy patterns between the sexes can thus occur both spatially and temporally as a consequence of both sex-specific searching patterns and mating system (Lehmann & Perrin 2003). Nonetheless, data that report seasonal changes in sex-specific searching and aggregation behaviour are predominantly from well-studied, large diurnal species. Data are still lacking for many taxa, and particularly for many insects.

In many Orthopterans, males call, using stridulatory ridges on their limbs or wings, and females search for mates, with females benefiting from male nuptial gifts such as spermatophores. However, sexually dimorphic New Zealand tree weta (*Hemideina* spp., Anostostomatidae) have small spermatophores compared with other Orthoptera (Gwynne 1995; Stringer 2001), and both males and females have stridulatory ridges. In six of the seven tree weta species, males have enlarged mandibles used in male–male combat (McIntyre 2001), and females form aggregations, or harems, in cavities used as day-time refugia (Field & Sandlant 2001).

These characteristics suggest that tree weta movement patterns associated with mating may not be typical of Orthopterans as a whole. If male guarding of a limited resource (e.g. females) increases reproductive success, then males might be sedentary, and if females gain by enhancing their encounter rate with potential mates, they might be more mobile than otherwise expected. However, there are few data on the formation or duration of aggregations, and of female harems that males appear to defend (Field & Jarman 2001; Kelly 2006b).

Tree weta are large-bodied (adults generally 3–6 g), flightless and nocturnal Orthopterans that seek refuge in tree cavities diurnally (Gibbs 1998). Eggs hatch in spring, and a minimum of eight instars is required to reach adulthood in these hemimetabolous insects. Adults are long lived (adult lifespan 9 months to 3 years; Leisnham et al. 2003). Because tree weta are nocturnal and their behaviour is difficult to observe directly, artificial cavities have proven useful to study tree weta ecology and behaviour (e.g. Trewick & Morgan-Richards 1995). Hypotheses about the genus have developed in large part from work on *Hemideina crassidens* Blanchard 1851 (e.g. Moller 1985; Kelly 2006a, b) and *Hemideina maori* Pictet & Saussure 1891 (e.g. Jamieson et al. 2000; Leisnham & Jamieson 2002; Leisnham et al. 2003). In contrast, little is known of Auckland tree weta (*Hemideina thoracica* White 1846) ecology despite its extensive distribution throughout much of the North Island, New Zealand. Field studies of *Hemideina crassidens* indicate that females apparently prefer unoccupied cavities, males defend females not cavities, and males are more transient than females (Kelly 2006c). Nonetheless, most of these field studies were undertaken in weta populations where more refuge cavities were empty than were occupied, in young forest (less than 30 years old), and with observations undertaken during the late summer and autumn only.

We investigated occupancy patterns of Auckland tree weta *Hemideina thoracica* in artificial cavities in an urban forest patch throughout the year to determine how aggregations change seasonally. We examined occupancy patterns of males and females in relation to conspecifics for a 16-month period by analysing occupancy changes in cavities at daily and then monthly intervals. We quantified male and female patterns of arrival to, and departure from, these cavities. Differential responses to other occupants of the artificial cavities allowed us to characterise sex-specific behaviour and consider the search for mates by both sexes. We predicted that *Hemideina thoracica* males would choose to occupy cavities housing adult females during the mating season, thought to be in summer and early autumn. We also predicted that aggregation patterns would change seasonally. If female *Hemideina thoracica* search for suitable cavities and potential mates, this would be evident in an increased number of occupancy changes in artificial cavities by females compared with males.

Methods

Field site

We selected an urban forest patch (1.5 ha) at Hillcrest Park in Hamilton City, New Zealand, in which to carry out our study. This patch of remnant lowland forest is dominated by mature *Dacrydium dacrydioides* (kahikatea) >100 years old and 20–25 m tall, with a sparse undergrowth of *Coprosma robusta* (karamū), *Melicytus ramiflorus* (māhoe), *Aristotelia serrata (*wineberry), *Kunzea ericoides* (kānuka), and other
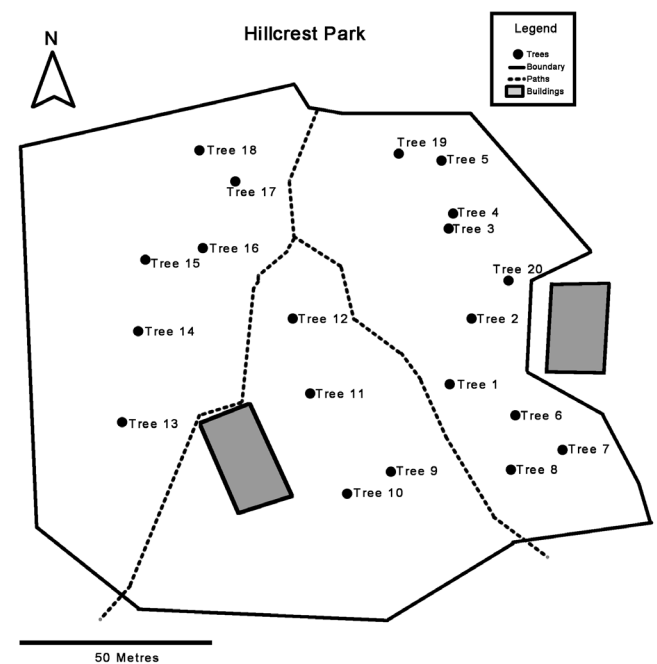
tree saplings less than 2 m high. Predation pressure from introduced mammals and native owls was low (Morgan et al. 2009; PMW unpubl. data). Human disturbance was generally low at night, when tree weta are active. Daytime disturbance, however, was greater, with paths through the forest fragment well used by members of the public.

Observations of movement patterns

Recent research has highlighted potential negative effects of tagging of study animals (e.g. Davis & Ovaska 2001; Boiteau et al. 2009; Barron et al. 2010; Saraux et al. 2011).Two trials to determine whether tagging might be a useful tool for this study raised questions about the effects of tagging on tree weta movement. A majority of tree weta (93.4%; total $n = 30$) did not return to cavities after pronotum tagging with either bee tags or paper tags, and were not seen again either in these cavities or elsewhere, despite data suggesting that *Hemideina thoracica* and *H. crassidens* individuals most likely have high site fidelity (Spurr & Berben 2004; PMW unpubl. data). Given this result, and the results from a previous tagging study (Ordish 1992), we minimised disruption by recording data from unmarked individuals; individual tracking is not essential to understand occupancy and movement patterns at the population level.

Refuge design and monitoring

Forty artificial refuges, consisting of two cavities each, were constructed from aged *Podocarpus totara* (tōtara) timbers and attached to 20 randomly selected, mature *Dacrycarpus dacrydioides* trees (Fig. 1). Refuges were attached vertically at 2.5 m and their direction randomised on each tree. Refuge design was generally similar to that suggested in Trewick & Morgan-Richards (2000) and Spurr & Berben (2004), but on a

Figure 1. Placement of artificial refuges for Auckland tree weta (*Hemideina thoracica*) on kahikatea trees (*Dacrycarpus dacrydioides*) in Hillcrest Park, Hamilton City, New Zealand. Circles represent approximate locations (from GPS readings) of trees with artificial refuges attached to the trunks.

smaller scale with one cavity and entrance on each side. Each artificial refuge thus had two unlinked, same-sized cavities, one with an entrance on the top left, and the other with an entrance on the bottom right. Cavity entrances were approximately 2×2 cm. Each cavity measured approximately $25 \times 150 \times 5$ cm internally, providing space to accommodate approximately eight adult tree weta.

Refuges were established in April 2008 and monitored until August 2009. In the first 28 days after attachment to trees, we recorded the number and sex of weta in each cavity daily, doing so without disturbing them while they were resting during the day. We analysed these data to detect initial colonisation patterns. We utilised monthly count data to investigate long-term colonisation, occupancy patterns and their implications for mating system. Most (>90%) weta in cavities during the study period were adults (see Results below), and our analysis therefore pertains to adult weta. The presence of immature weta in artificial weta cavities was however noted throughout the sampling period. During the main research period, four refuges were stolen, one in September 2008, two in October 2008, and one in June 2009. These refuges were not replaced. All remaining refuges with one exception were vandalised and destroyed in late August 2009, thereby ending data collection.

Data analysis

All statistical exploration and analyses were implemented in R (version 2.12.2; R Development Core Team 2010). We grouped the data to have enough observations for each of the four initial population states in our models (see below), thus giving separate analyses for four different seasonal time periods. We chose these time periods based on our knowledge of likely seasonal changes in behaviour. Period A comprised 28 daily visits by investigators after establishing the artificial cavities in autumn (21 April to 18 May 2008); Period B (winter–spring) comprised 10 fortnightly and then monthly visits by investigators from 18 May to 27 November 2008; Period C (summer) comprised five monthly observations from 27 November 2008 to 28 March 2009; and Period D (autumn–winter) comprised five monthly observations from 28 March to 19 July 2009. Until large numbers of weta became established in the cavities, most occupied cavities contained only a single weta.

To investigate tree weta occupancy and overall movement patterns we analysed occupancy changes in the cavities between each pair of consecutive monitoring visits over the 16-month period. We used a generalised linear mixed model (GLMM) with a binomial response distribution and a logistic link function to predict female population growth in a cavity between two visits from the population state (vacant, female only, male only, mixed male and female) at the first visit. The binary response variable indicates an increase, or otherwise, in the female population of a cavity between two consecutive site visits, with each of the 80 cavities having a corresponding value. The value of the response variable was 1 if an increase in the number of females occurred, 0 otherwise. We then repeated this GLMM for males. We ran two further models, where the response variables recorded cavity population decreases for females, and for males, respectively. All four models were fitted using the *lme4* package in R (Bates & Maechler 2010).

We introduced random effect terms into the models to account for the fact that observations were clustered in time (several inter-visit time intervals within each period were analysed) and in space; artificial cavities in the same refuge, and on the same tree, may not have been independent. The GLMM for the increase probability P_{cirt} for weta at a refuge r with initial population state c at the start of time interval i on tree t is thus expressed as:

$$\text{logit}\,(P_{cirt}) = \mu_c + a_i + b_r + c_{ir} + d_t,$$

where μ_c is a fixed constant giving means for the four initial configurations (vacant, male only, female only, mixed) and a, b, c and d are random variables that are independently and normally distributed with mean zero and variances σ_a^2, σ_b^2, σ_c^2 and σ_d^2 respectively. Because logistic regression models were fitted, effect sizes are expressed as odds ratios, the ratio of the odds of colonising a cavity in the female, male, and mixed initial state to the odds of colonising a vacant cavity. Odds of colonising a cavity thus means $p/(1 - p)$, where p is the probability of an event (colonising a cavity) to the probability of its non-occurrence. An odds ratio greater than one indicates that a particular cavity type is more likely to be colonised than a vacant cavity, whereas an odds ratio of less than one indicates that this type of cavity is less likely to be colonised than a vacant cavity.

We analysed cavity departures in a similar way to arrivals (except that the departing weta always originated in one of the cavities rather than from elsewhere in the study area). Because only cavities containing at least one weta of the appropriate sex could be included in the analysis, statistical power was reduced compared with the colonisation analyses. We therefore combined departure data from Periods A and B to determine overall patterns. To estimate the per-male and per-female departure rates, we used a binomial GLMM with a complementary log-log link function. Because more than one male (or female) might be present in a cavity, we incorporated an offset term, $\log(k)$, where k is the number of females or males in the cavity (see Vittinghoff et al. (2005) for discussion of link functions and a similar treatment of per-contact disease probability). As in the colonisation analyses, we also incorporated random effects terms for refuge and the period during which departures were observed. The odds ratios presented in the results compare the odds of departure with those cavities occupied by a single male (or female). Mathematically the model equation for decrease probability P_{cir} for male weta at a refuge r with initial configuration c at the start of time interval i is:

$$\log(-\log(1 - P_{cirt})) = \mu_c + \log(m_{ir}) + a_i + b_r + d_t,$$

where μ_c is the number of male weta present in refuge r at the start of time interval i on tree t, and similarly for female weta. As above, the μ_c are fixed constants giving means for the initial configurations and a, b and d are random variables that are independently normally distributed with mean zero and variances σ_a^2, σ_b^2 and σ_d^2 and respectively. The initial configurations have been grouped differently for the different combinations of season and gender according to the range of habitation types observed. We consider an effect significant at $p \leq 0.05$.

Results

The first artificial cavity was occupied one night after establishment of the refuges. After 14 days, 40% of the 80 cavities were occupied by at least one tree weta. Total numbers of weta using the cavities increased over the first 11 months

(maximum: $n = 142$ in March 2009), and the amount of cavities occupied reached 81% and 82% in March and June 2009. The mean number of weta per occupied cavity peaked in late summer ($\bar{x} = 4.5$ weta per cavity, excluding empty cavities).

Weta aggregations

Most observations of single tree weta ($n = 1249$) were of females ($n = 849$). Single weta observations were double those of tree weta sharing a cavity ($n = 660$). After single weta, male–female pairs, one male with two females, and one male with three females were the next most common groupings. Throughout the year, the number of cavities that were previously vacant, occupied by one female, a pair, or a harem changed significantly by visit (Friedman rank sum test p-value < 0.001; but p-value = 0.328 for cavities occupied by one male). Aggregation patterns changed dramatically after Day 221, at the end of spring (Fig. 2). Over the summer (days 250–310) increasing numbers of male and female weta were observed together in cavities, in contrast to previous observations of single weta. Fewer single females were observed, with an increase in both pairs and harems (Fig. 2). The maximum number of females with a single male in one cavity was five, which we recorded on three occasions (in December, February and July respectively). To further explore the positive correlation of male and female numbers during the summer, we analysed male and female arrivals and departures in the cavities.

Male arrivals

Male occupation of cavities (Table 1) overall was non-random. During the initial colonisation period (Period A), no male-occupied cavities were occupied in the next observation period by two males ($n = 2160$ total observations, $n = 63$ male colonisation events; see Table 2). In the following winter–spring (Period B), only two male-occupied cavities were colonised by a second male and the male-avoids-male effect was strong ($n = 701$ total observations, $n = 61$ male colonisation events; see Table 2). This effect was insignificant (p > 0.05) in both summer and late autumn (Periods C and D). In contrast there is no evidence that male weta avoided cavities based on the previous presence of females at any time of the year. The strongest and most significant 'attraction' effect, where males colonised cavities occupied by females, was found in summer. Male weta generally did not colonise cavities previously occupied by both male and female weta. No such cavities were colonised by males in Periods A and B. However, we made single observations of two males with five females, and three males with three females in late summer (Period C).
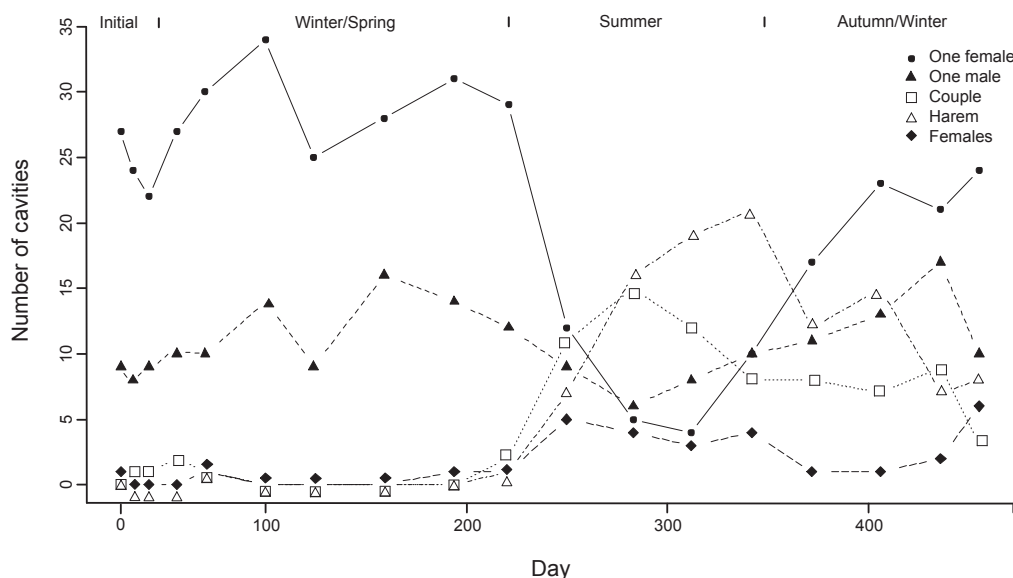
Female arrivals

Through all time periods, female weta colonised cavities that were inhabited by one or more males more often than they colonised vacant cavities (Table 1). The effect appeared strongest in summer, in agreement with male occupation patterns during this period. Only in summer (Period C) was there no difference in female colonisation patterns of female-inhabited cavities and previously vacant cavities (see odds ratios; Table 1). Females were not deterred from colonising mixed-inhabitant cavities at any time of the year (all p-values >0.05, Table 1).

Departures from cavities

During the initial autumn and winter–spring (periods A and B) most male and female departures were from cavities that contained no other weta ($n = 99$ for males and $n = 122$ for females). Relatively few departures were from cavities that contained other weta ($n = 9$ for males and $n = 12$ for females respectively; see Table 2 for total sample sizes). Male departure rates were not significantly influenced by the presence of a female, but female departure rates were higher (odds ratio = 2.83, p-value = 0.045) when a male was present.

Departure rates were high during the initial period, but reduced in the following months (Fig. 3). Male departures did not occur significantly more often than expected from any particular grouping over the summer (Period C), but in the autumn–winter (Period D) males were significantly less likely to depart when with a harem of more than two females (odds ratio = 0.180, p-value = 0.049), and more likely to depart if occupying a cavity with other males (odds ratio = 3.63, p-value = 0.028). Estimates of these effects are in the same direction
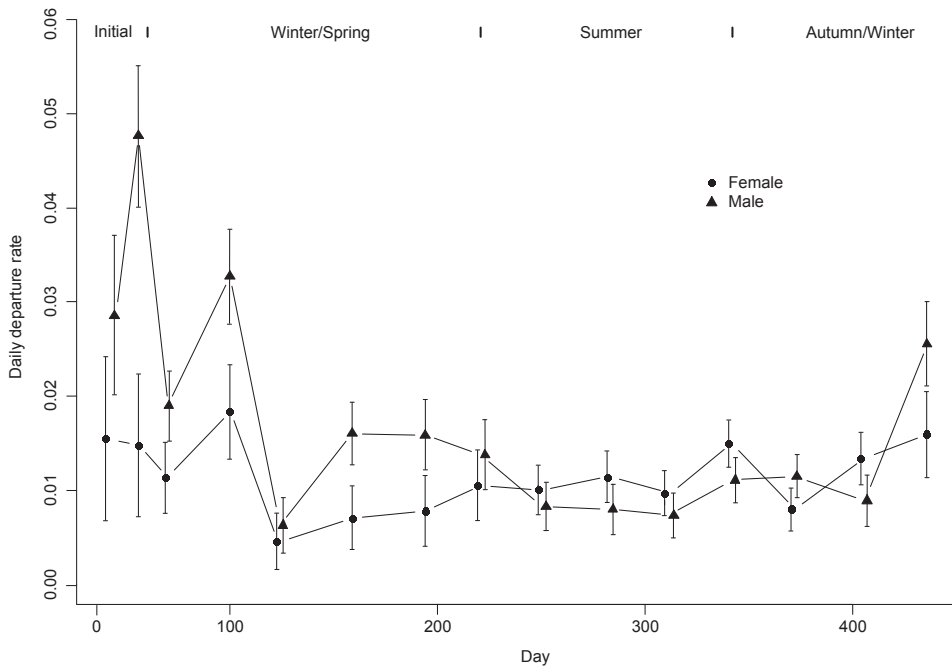

Figure 2. Occupancy of artificial cavities by single and multiple Auckland tree weta (*Hemideina thoracica*). A clear change occurs around Day 221 (28 November; end of spring in New Zealand). We have omitted groups with multiple males ($n = 3$) as these account for fewer than 2 of 80 cavities.

Table 1. Likelihood of occupancy in an artificial cavity by a new Auckland tree weta (*Hemideina thoracica*) arrival is dependent on the previously recorded occupier of that cavity. An odds ratio of >1.00 indicates that a particular cavity type is more likely to be colonised than a vacant cavity, whereas an odds ratio of <1.00 indicates that this type of cavity is less likely to be colonised than a vacant cavity. n/a indicates no test was carried out due to limited data. Total arrival observations = 2160 (Table 2).
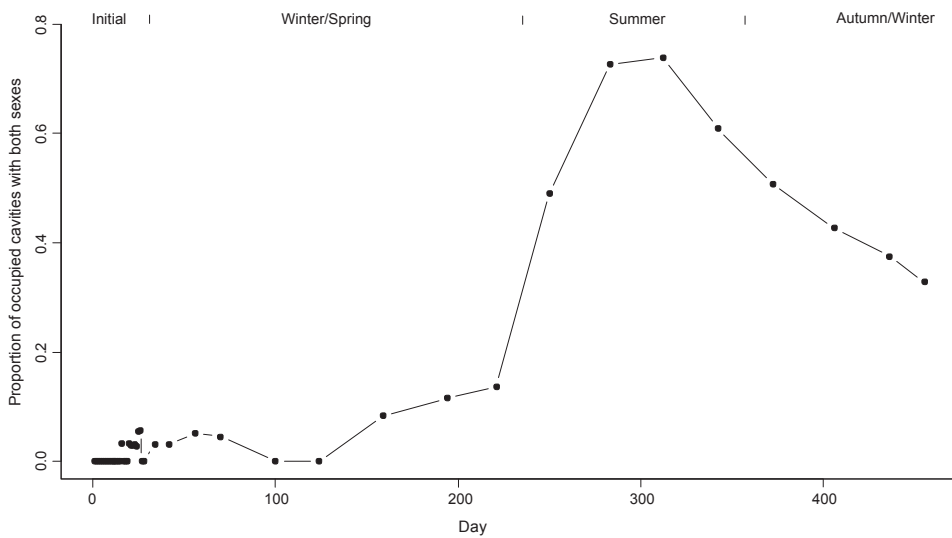
Arrival pattern	Period	Season	Number of events observed	Estimated odds ratio	95% confidence interval	p-value
Male arrivals in cavities with other males	A	Autumn	0	n/a		
	B	Winter–Spring	2	0.14	0.03, 0.63	0.010
	C	Summer	2	0.21	0.04, 1.04	0.056
	D	Autumn–Winter	5	0.46	0.12, 1.73	0.250
Male arrivals in cavities with female(s) present	A	Autumn	25	6.1	1.84, 20.2	0.003
	B	Winter–Spring	26	1.12	0.62, 2.0	0.713
	C	Summer	34	5.73	2.64, 12.43	< 0.001
	D	Autumn–Winter	17	1.81	0.65, 5.04	0.255
Male arrivals in cavities with both sexes	A	Autumn	0	n/a		
	B	Winter–Spring	0	n/a		
	C	Summer	4	0.15	0.04, 0.53	0.003
	D	Autumn–Winter	4	0.17	0.04, 0.69	0.014
Female arrivals in cavities with males	A	Autumn	30	4.28	2.50, 7.32	< 0.001
	B	Winter–Spring	29	2.68	1.52, 4.73	<0.001
	C	Summer	23	5.48	2.43, 12.32	<0.001
	D	Autumn–Winter	27	2.95	1.31, 6.65	0.010
Female arrivals in cavities with females	A	Autumn	2	0.08	0.02, 0.33	0.001
	B	Winter–Spring	1	0.021	0.003, 0.165	<0.001
	C	Summer	17	1.35	0.64, 2.82	0.427
	D	Autumn–Winter	2	0.081	0.02, 0.39	0.002
Female arrivals in cavities with both sexes	A	Autumn	1	1.34	0.15, 11.69	0.791
	B	Winter–Spring	2	3.39	0.56, 20.37	0.182
	C	Summer	26	1.50	0.77, 2.92	0.235
	D	Autumn–Winter	22	0.90	0.41, 1.96	0.783

Table 2. Sample sizes for movement patterns into (*Arrivals*) and from cavities (*Departures*) by Auckland tree weta (*Hemideina thoracica*) throughout the study period.
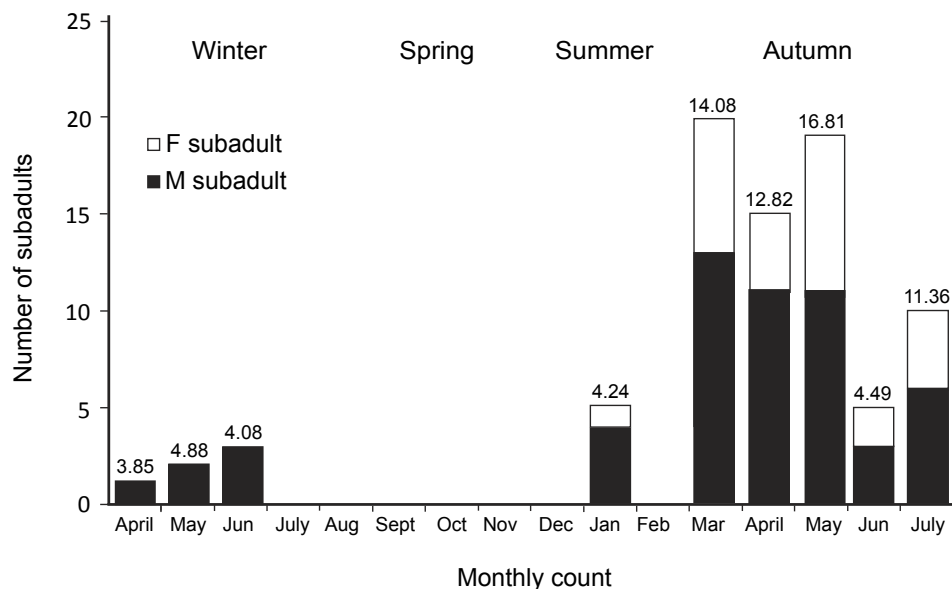
Arrivals	Period A	Period B	Period C	Period D
Total observations where male and female increase could occur	2160	701	284	292
Actual female increase	90	78	87	65
Actual male increase	63	61	58	35

Departures	Periods A and B	Period C	Period D
Total observations where male decrease could occur	323	127	156
Actual male decrease	107	33	58
Total observations where female decrease could occur	723	152	178
Actual female decrease	133	56	78

Figure 3. Departure rates (with 1.4*SE error bars) from artificial cavities for Auckland tree weta (*Hemideina thoracica*). The rate is divided by number of days since last visit, to reduce the effect of difference in days between counts, and is thus identified as a daily departure rate. If error bars overlap on the same day, females and males are slightly offset for clarity. The departure rates may be considered different in an approximate significance test where error bars do not overlap.

Figure 4. Seasonal pattern of harem formation in Auckland tree weta (*Hemideina thoracica*) as seen by proportions of occupied artificial cavities with both males and females in an urban forest fragment, Hamilton City, New Zealand, throughout a 16-month period.

Figure 5. Proportion of male and female subadult Auckland tree weta (*Hemideina thoracica*) recorded in artificial cavities over a 16-month period. The percentage of the total sample that was subadult is presented above each monthly bar, all other weta using the cavities were sexually mature.

in both time periods, and if the time periods are combined, the significance of these results is strengthened (odds ratio = 0.232, p-value = 0.021 for males leaving harems and odds ratio = 7.29, p-value = 0.000 for males leaving other males). Otherwise, male departures were not significantly different between different habitation types in summer or autumn–winter. Analysis of Period C and Period D data shows no significant patterns in female departures.

Sex ratio and age structure

There were more females than males in every daily and monthly count throughout the research period. The average ratio of females to males was 2.5:1 in the first 28 days and 2.1:1 from May 2007 through to July 2008. The proportion of occupied cavities containing weta of both sexes changed markedly through the year (Fig. 4), but sex ratio did not. Few immature weta were present in artificial cavities during the first few months of colonisation (3.9% of total in April, and 6.1% in June 2008; Fig. 5), but immature weta numbers increased in autumn 2009 (14–17% of total). Immature males outnumbered immature females.

Discussion

For the first time, we show changes in tree weta aggregation and movement patterns associated with occupancy of diurnal refuge cavities through the seasons. A clear change in aggregation patterns was observed in early summer when increased numbers of male and female weta were recorded together in cavities. This contrasts with the high proportion of cavities with single weta observed in the previous winter and spring. The formation of harems appears to result both from female weta no longer avoiding other female weta and from males moving into cavities with one or more female weta. Our data show that males occupied cavities with a female present more often than either empty cavities or cavities with another male present, both during the initial colonisation and in the summer. This result is consistent with cavity choice experiments in *Hemideina crassidens* (Kelly 2006c) where males search for mates, as might be expected in a polygynous species where sperm competition is likely occurring (Kokko & Wong 2007; Kelly 2008a). However, patterns of female occupancy also demonstrate that, throughout the year, females joined cavities more often than by chance where a prior male occupant had been recorded. If female movement patterns are associated with the search for mates, this suggests that females also make choices about prospective mates (Spencer 1995), and that co-habitation with males may not lead to the high costs that occur in *Hemideina crassidens* (Kelly 2006c). Although female tree weta do not receive a nuptial gift, males might control access to the daytime refuge that is a resource requirement, and therefore contribute to female searching or movement patterns. The female arrival and departure patterns apparent here contrast with behaviour patterns recorded in *Hemideina crassidens* that indicate females are more sedentary than males, but agree with findings that both females and males are mobile, and that polygynandry might be a better descriptor of the mating system than polygyny (Kelly 2006c).

We emphasise that we make no claims about the behaviour of individual or 'typical' weta. Instead, we focus on changes in occupancy patterns, and our conclusions pertain to weta (plural) as a population rather than to individual weta. Thus,

although the same individual weta might be using a cavity where occupant age and sex are unchanged between monthly observations (Spurr & Berben 2004; PMW unpubl. data), our results do not rely on this assumption. The data clearly demonstrate that changes in cavity occupancy numbers for males and females show significant dependency on initial occupancy of the cavity. This leaves some uncertainty as to how the dependency works at the individual level; for example, occupancy change in a cavity between visits may not necessarily come about in the simplest possible way, such as through the arrival or departure of a single weta, although this may in fact be the case. Nonetheless, the existence of the effects themselves on the occupancy pattern of the population is evident.

The odds ratios for a female moving into a cavity occupied by one or more females (compared with a vacant cavity) suggest that female weta avoid other females for most of the year. However, in early summer, this pattern changed. Factors influencing female departure rates are not clear, but from our data it seems unlikely that males evict females after mating (cf. Kelly 2008b), as estimated male departure rate was similar to female departure rate (Table 2). During the summer most adult females were observed in harem groups, and about 64% of females recorded in one visit were present in that cavity in the next visit. Female eviction thus seems unlikely. The odds ratios indicate which observed patterns of arrival differ significantly from random (and indicate attraction where they are greater than 1). In cases where a small sample size occurs for an initial population state, confidence intervals can be wide. However, in most cases, confidence intervals did not fall below 1, and thus indicate the findings are robust.

We have no evidence that male departures from artificial cavities in the first six months of cavity colonisation were influenced by previous cavity occupancy. However, during the summer–autumn period males were more likely to stay if a female harem of more than two females was present, and leave (or be evicted) if a second male was present. These findings are consistent with expectations of male–male competition where female defence polygyny is a feature of social organisation (Emlen & Oring 1977; Field & Sandlant 1982; Moller 1985; Field 1993; Gibbs 1998; Kelly 2006c), but where small satellite males may adopt a sneak and wander strategy that increases their mating success (Emlen & Oring 1977; Field & Jarman 2001). This strategy has been documented in other tree weta species (Kelly 2008a).

Harems were the most common occupancy pattern observed for several months over the summer, and weta aggregations appeared stable over this period. There were few changes to male occupancy records when males were associated with harems, in contrast to the related species *Hemideina crassidens* where males are thought to abandon cavities as soon as they have mated with all available females (Kelly 2006b, c). Nonetheless, many cavities had single females, and groups of females without a male. Cavity size did not appear to limit harem size as has been observed in studies in related species (Field & Sandlant 1983, 2001; Kelly 2006a), without reaching maxima observed in *Hemideina crassidens* (12 females and one male; MM-R pers. obs.).

In this population, the adult sex ratio data appear female skewed. However, a recent meta-analysis of adult sex ratio across 58 populations and 6 species of tree weta found that adult sex ratio did not differ significantly from unity (Wehi et al. 2011). Counting method (including night observations, day-time collections, and use of artificial cavities) did not

influence observed sex ratio, and instead indicated that sex ratio skew seen in individual populations (such as in this study) most likely arose through small sample size (Wehi et al. 2011).

Our results demonstrate that patterns of cavity occupancy by tree weta within this urban, mature forest patch are structured by seasonal change. Seasonal fluctuations in occupancy numbers, with a peak in late summer, and lows in midwinter and spring, are consistent with Ordish's (1992) study of *Hemideina crassidens*, although others report less seasonality to movement (Spurr & Berben 2004). Male and female occupancy patterns, and the preponderance of adult weta, are at odds with other studies (*Hemideina thoracica* – Powlesland et al. 2005; *Hemideina crassidens* – Ordish 1992). Nonetheless, an influx of immature weta was evident in autumn, with most approximately half-grown, concurring with the observations of Gibbs (1998). Greater male mobility in winter (compared with females) could result in increased juvenile male occupancy, and is probably associated with dispersal, not mate searching. Chromosomal and mitochondrial DNA evidence supports greater male than female dispersal, with estimates of dispersal per generation of at least 100 m for *Hemideina thoracica* (Morgan-Richards et al. 2000; Morgan-Richards & Wallis 2003).

In conclusion, we found that strong changes in male and female occupancy patterns occur seasonally. Contrary to general expectations that male movements, associated with mate searching, would dominate in this orthopteran species, males had higher departure rates than females in winter and spring. Although most tree weta inhabited cavities singly at this urban forest location, arrival and departure patterns for males and females are consistent with polygynandry where both sexes are mobile in the mating season (Kelly 2006c). It is unclear why females appear to avoid other females for much of the year. However, there may be costs to co-habiting with conspecific females that outweigh the benefits, except during the mating season. Occupancy patterns for both male and female *Hemideina thoracica* were thus distinct, and appear to be influenced by the presence and sex of other occupants in the artificial cavities, and by the time of the year.

Acknowledgements

References

Acharya L 1995. Sex-biased predation on moths by insectivorous bats. Animal Behaviour 49: 1461–1468.

Barron DG, Brawn JD, Weatherhead PJ 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods in Ecology and Evolution 1: 180–187.

Bateman AJ 1948. Intra-sexual selection in *Drosophila*. Heredity 2: 349–368.

Bates D, Maechler M 2010. lme4: Linear mixed-effects models using S4 classes. In R package version 0.999375-37. http://CRAN.R-project.org/package=lme4.

Boiteau G, Meloche F, Vincent C, Leskey TC 2009. Effectiveness of glues used for harmonic radar tag attachment and impact on survival and behavior of three insect pests. Environmental Entomology 38: 168–175.

Darwin C 1874. The descent of man and selection in relation to sex. 2nd edn. London, John Murray. 688 p.

Davis TM, Ovaska K 2001. Individual recognition of amphibians: effects of toe clipping and fluorescent tagging on the salamander *Plethodon vehiculum*. Journal of Herpetology 35: 217–225.

Emlen ST, Oring LW 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215–223.

Field LH 1993. Observations on stridulatory, agonistic, and mating behaviour of *Hemideina ricta* (Stenopelmatidae: Orthoptera), the rare Banks Peninsula weta. New Zealand Entomologist 16: 68–74.

Field LH, Jarman TH 2001. Mating behaviour. In: Field LH ed. The biology of wetas, king crickets and their allies. Wallingford, UK, CABI. Pp. 317–332.

Field LH, Sandlant G 1983. Aggression and mating behaviour in the Stenopelmatidae (Orthoptera, Ensifera), with reference to New Zealand wetas. In: Gwynne DT, Morris GK eds Orthopteran mating systems – sexual competition in a diverse group of insects. Boulder, CO, Westview Press. Pp. 120–146.

Field LH, Sandlant GR 2001. The gallery-related ecology of New Zealand tree wetas, *Hemideina femorata* and *Hemideina crassidens* (Orthoptera, Anostostomatidae). In: Field LH ed. The biology of wetas, king crickets and their allies. Wallingford, UK, CABI. Pp. 243–257.

Gibbs GW 1998. Why are some weta (Orthoptera: Stenopelmatidae) vulnerable yet others are common? Journal of Insect Conservation 2: 161–166.

Gwynne DT 1987. Sex-biased predation and the risky mate-locating behaviour of male tick-tock cicadas (Homoptera: Cicadidae). Animal Behaviour 35: 571–576.

Gwynne D 1991. Sexual competition among females: what causes courtship-role reversal? Trends in Ecology and Evolution 6: 118–121.

Gwynne DT 1995. Phylogeny of the Ensifera (Orthoptera): a hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. Journal of Orthoptera Research 4: 203–218.

Hammerstein P, Parker GA 1987. Sexual selection: games between the sexes. In: Bradbury JW, Andersson MB eds Sexual selection: testing the alternatives. Chichester, UK, John Wiley. Pp. 119–142.

Jamieson IG, Forbes MR, McKnight EB 2000. Mark-recapture study of mountain stone weta *Hemideina maori* (Orthoptera: Anostostomatidae) on rock 'tor' islands. New Zealand Journal of Ecology 24: 209–214.

Kelly CD 2006a. Movement patterns and gallery use by the sexually dimorphic Wellington tree weta. New Zealand Journal of Ecology 30: 273–278.

Kelly CD 2006b. The relationship between resource control, association with females and male weapon size in a male dominance insect. Ethology 112: 362–369.

Kelly CD 2006c. Resource quality or harem size: what influences male tenure at refuge sites in tree weta (Orthoptera: Anostostomatidae)? Behavioral Ecology and Sociobiology 60: 175–183.

Kelly CD 2008a. Sperm investment in relation to weapon size in a male trimorphic insect? Behavioral Ecology 19: 1018–1024.

Kelly CD 2008b. Why do male tree weta aggressively evict females from galleries after mating? Ethology 114: 203–208.

Kokko H, Wong BBM 2007. What determines sex roles in mate searching? Evolution 61: 1162–1175.

Lehmann L, Perrin N 2003. Inbreeding avoidance through kin recognition: choosy females boost male dispersal. American Naturalist 162: 638–652.

Leisnham PT, Jamieson IG 2002. Metapopulation dynamics of a flightless alpine insect *Hemideina maori* in a naturally fragmented habitat. Ecological Entomology 27: 574–580.

Leisnham PT, Cameron C, Jamieson IG 2003. Life cycle, survival rates and longevity of an alpine weta *Hemideina maori* (Orthoptera: Anostostomatidae) determined using mark-recapture analysis. New Zealand Journal of Ecology 27: 191–200.

McIntyre M 2001. The ecology of some large weta species in New Zealand. In: Field LH ed. The biology of wetas, king crickets and their allies. Wallingford, UK, CABI. P. 540.

Moller H 1985. Tree wetas (*Hemideina crassicruris*) (Orthoptera: Stenopelmatidae) of Stephens Island, Cook Strait. New Zealand Journal of Zoology 12: 55–69.

Morgan DKJ, Waas JR, Innes J 2009. An inventory of mammalian pests in a New Zealand city. New Zealand Journal of Zoology 36: 23–33.

Morgan-Richards M, Wallis GP 2003. A comparison of five hybrid zones of the weta *Hemideina thoracica* (Orthoptera: Anostostomatidae): Degree of cytogenetic differentiation fails to predict zone width. Evolution 57: 849–861.

Morgan-Richards M, Trewick SA, Wallis GP 2000. Characterization of a hybrid zone between two chromosomal races of the weta *Hemideina thoracica* following a geologically recent volcanic eruption. Heredity 85: 586–592.

Ordish RG 1992. Aggregation and communication of the Wellington tree weta *Hemideina crassidens* (Blanchard) (Orthoptera: Stenopelmatidae). New Zealand Entomologist 15: 1–8.

Powlesland RG, Stringer IAN, Hedderley DI 2005. Effects of an aerial 1080 possum poison operation using carrot baits on invertebrates in artificial refuges at Whirinaki Forest Park, 1999–2002. New Zealand Journal of Ecology 29: 193–205.

R Development Core Team 2010. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing. http://www.r-project.org/

Reichard M, Jurajda P, Smith C 2004. Male–male interference competition decreases spawning rate in the European bitterling (*Rhodeus sericeus*). Behavioral Ecology and Sociobiology 56: 34–41.

Saraux C, Le Bohec C, Durant JM, Viblanc VA, Gauthier-Clerc M, Beaune D, Park Y-H, Yoccoz NG, Stenseth NC, Le Maho Y 2011. Reliability of flipper-banded penguins as indicators of climate change. Nature 469: 203–206.

Shuster SM, Wade MJ 2003. Mating systems and strategies. Princeton University Press.

Spencer AM 1995. Sexual maturity in the male tree weta *Hemideina crassidens* (Orthoptera: Stenopelmatidae). Unpublished MSc thesis, Victoria University of Wellington, Wellington, New Zealand. 85 p.

Spurr EB, Berben PH 2004. Assessment of non-target impact of 1080-poisoning for vertebrate pest control on weta (Orthoptera: Anostostomatidae and Rhaphidophoridae) and other invertebrates in artificial refuges. New Zealand Journal of Ecology 28: 63–72.

Stringer IAN 2001. The reproductive biology and the eggs of New Zealand Anostostomatidae. In: Field LH ed The biology of wetas, king crickets and their allies. Wallingford, UK, CABI. Pp. 379–397.

Trewick SA, Morgan-Richards M 1995. On the distribution of tree weta in the North Island, New Zealand. Journal of the Royal Society of New Zealand 25: 485–493.

Trewick SA, Morgan-Richards M 2000. Artificial weta roosts: A technique for ecological study and population monitoring of tree weta (*Hemideina*) and other invertebrates. New Zealand Journal of Ecology 24: 201–208.

Trivers R 1972. Parental investment and sexual selection. In: Campbell BG ed. Sexual selection and the descent of man, 1871–1971. Chicago, Aldine-Atherton. Pp. 136–179.

Trivers R 1985. Social evolution. Menlo Park, CA, Benjamin Cummings. 480 p.

Vittinghoff E, Shiboski SC, Glidden DV, McCulloch CE 2005. Regression methods in biostatistics: linear, logistic, survival, and repeated measures models. New York, Springer.

Wehi PM, Nakagawa S, Trewick SA, Morgan-Richards M 2011. Does predation result in adult sex ratio skew in a sexually dimorphic insect genus? Journal of Evolutionary Biology 24: 2321–2328.