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New Zealand Entomologist

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnze20>

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Published online: 10 Apr 2014.

To cite this article: E. M. Chappell, D. S. Webb & J. D. Tonkin (2014): Notes on sexual size dimorphism, sex ratio and movements of adult ground weta *Hemiandrus maculifrons* (Walker) (Orthoptera: Anostostomatidae), *New Zealand Entomologist*

To link to this article: <http://dx.doi.org/10.1080/00779962.2013.856377>

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Notes on sexual size dimorphism, sex ratio and movements of adult ground weta *Hemiandrus maculifrons* (Walker) (Orthoptera: Anostomatidae)

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The ground weta (*Hemiandrus maculifrons*) is an apparently abundant species with a New Zealand-wide distribution. Despite this, there is a paucity of ecological and biological information concerning this species. We aimed to gain new information about movement patterns, capture rates and body size differences by tagging individuals and conducting nightly surveys of a single *H. maculifrons* population in the Otanewainuku Forest, Bay of Plenty, New Zealand. Over a 26-night period between March and April 2012, we tagged 53 females and 78 males with queen bee tags and small reflector strips and recorded the location of animals that were subsequently re-sighted. Adult females were significantly larger than males, but capture and re-sight rates suggested males were the more abundant sex during the study period. Female weta moved further over consecutive nights than males (average distance moved, 1.57 m vs. 1.01 m, respectively); however, the tagging method, time of year and study area may have resulted in underestimates. These results indicate areas for further research into aspects of sexual selection, such as potentially biased sex ratios, sexual size dimorphism and mate competition, within *H. maculifrons*.

Keywords: abundance; invertebrate tracking; mark-recapture; New Zealand; queen bee tags

Introduction

New Zealand weta are nocturnal, flightless orthopterans comprising two families: Anostomatidae (tree, giant, tusked and ground weta) and Rhaphidophoridae (cave weta). Within the anostomatids, ground weta (*Hemiandrus* spp.) are the most speciose group, with eleven described and c. 30 undescribed species (Johns 1997, 2001; Jewell 2007; Taylor Smith et al. 2013). They are the only non-endemic genus of weta in New Zealand (approximately 10 species occur in Australia; Johns 1997).

Ground weta are an important component of the New Zealand forest ecosystem (Gibbs 1998). They form part of the diet of many native species, including the morepork (*Ninox novaeseelandiae*), wattle birds (Callaeidae spp.), the kiwi (*Apteryx* spp.), tuatara (*Sphenodon punctatus*), and one of New Zealand's only native land mammals, the short-tailed bat (*Mystacina tuberculata*) (Reid et al. 1982;

Colbourne et al. 1990; Gibbs 1998; Pierre 2000). Additionally, introduced rodents (*Rattus* spp.), mustelids (*Mustela* spp.), hedgehogs (*Erinaceus europaeus occidentalis*) and cats (*Felis catus*) (Karl & Best 1982; Jones et al. 2005; Smith et al. 2005; Wilson & Lee 2010) also predate on ground weta. Despite this predation pressure, ground weta species such as *Hemiandrus pallitarsis* (Walker) and *H. maculifrons* (Walker) are relatively abundant across New Zealand and can be found in a range of modified as well as natural habitats (Johns 2001; Chappell et al. 2012).

Hemiandrus species are also the smallest weta in terms of body size, ranging from 12–45 mm (Jewell 2007) and weighing 1–3 g (giant weta weigh 7.4–32.2 g; McIntyre 2001). Unlike their larger relatives, the tree weta and tusked weta, *Hemiandrus* do not exhibit sexual dimorphism in the form of male weaponry. However, it appears that ground weta may be sexually size dimorphic

with the males being smaller (Wyngaarden 1995; Johns 1997; Jewell 2007; Chappell et al. 2012), although whether there is selection for large females, as a result of increased fecundity, or selection for small males, is unknown.

Possibly due to their small size, nocturnal behaviour and soil-burrowing habit, few studies have investigated ecological and behavioural aspects of ground weta. Although patterns of movements and population structure have been determined for other weta (e.g. tree weta, Moller 1985; stone weta, Jamieson et al. 2000; tusked weta, Stringer & Chappell 2008; and giant weta, Watts et al. 2012), no research has been conducted on *Hemiandrus* species. This study uses a simple and inexpensive tagging method in combination with nightly observations, to determine sexual size dimorphism, and gain new information regarding sex ratios, capture and re-sighting rates and travel distances of *H. maculifrons*.

Methods

Study species

Hemiandrus maculifrons is the only species within the genus that is found in both the North and South Islands of New Zealand (although it is likely a species complex; B. Taylor Smith, Massey University, pers. comm. 2013). This species has a long-ovipositor and is characterised by a dark brown pronotum and upper abdomen, and a mottled femur. Observations suggest both male and female *H. maculifrons*, like several other *Hemiandrus* species, produce pre-copulatory vibratory sounds by 'drumming' their abdomen on the substrate, usually a leaf surface (Gwynne 2004).

Study site

The research was conducted at the Otanewainuku Forest, 25 km south of Tauranga in the Bay of Plenty, North Island, New Zealand (176.206922° E, 37.893569° S). Surveying was undertaken at 440 m a.s.l along the first 500 m of the Rimu Track at the north end of the Department of Conservation car park. The area searched included the gravel track and approximately one metre of vegetation either side of the track. This range was limited by difficulties in sighting weta in dense vegetation. The track runs through indigenous

forest consisting of tawa (*Beilschmiedia tawa*), kāmahi (*Weinmannia racemosa*) and rewarewa (*Knightia excelsa*) with rimu (*Dacrydium cupressinum*) emergents. Common understorey species include kanono (*Coprosma grandifolia*), filmy fern (*Hymenophyllum* spp.), and other fern species (e.g. *Blechnum discolor*, *Asplenium bulbiferum*).

Survey technique

The area was surveyed every night from 14 March until 9 April 2012 with the exception of the night of 2 April; in total 26 nights. Every 10 m along the track to the 500-m endpoint a numbered strip of reflective tape (DOT-C2) was attached to a small galvanised peg pushed into the side of the track. These markers were used for measuring from when weta were captured and for recording location upon re-sighting. Daily surveys started between 1900 and 2100 (c. 30 minutes after sunset) and took approximately 45 minutes to two hours to complete. The track was searched by two people using headlamps, one starting from each end and meeting in the middle, or starting from the same end and searching one side of the track each. Adult female *H. maculifrons* were identified by a fully developed ovipositor and adult males were distinguished by the falci on the last tergite which form blackened hooks in the last instar (Johns 2001).

Capture, marking and re-sighting

The first night of the study was spent tagging weta, seven subsequent nights were spent tagging new weta and re-sighting previously tagged weta, and the last 18 nights were spent re-sighting tagged individuals and counting non-tagged weta along the track. Weta were captured by hand and placed into clear plastic ziplock bags with a uniquely numbered tag. A corresponding tag was attached to a galvanised peg and inserted into the track to mark the capture site. The distance and bearing to the nearest track marker was recorded for each tagged weta.

After searching the entire length of the track, each weta was measured, marked and released at the site of its capture. Digital vernier callipers (resolution: 0.01 ± 0.02 mm; Prograde, USA) were used to measure the lengths of the metafemur, metatibia and pronotum. The ratio of femur length to pronotum length was calculated to determine an

approximate body size to leg ratio. An individually numbered queen bee tag was attached to the pronotum using the non-toxic glue supplied with the tags. In addition, a 2.5-mm piece of reflector tape (DOT-C2) was glued using the same non-toxic glue to the pronotum in order to increase visibility for re-sighting.

When a marked weta was re-sighted the tag number and sex of the weta, and the distance and bearing from the original marker were recorded, unless the weta was more than 15 m away when these measurements were taken from the nearest marker. Additional information such as time sighted, what the weta was found on, and height above ground were also recorded. The numbers of captured and re-sighted weta were converted to per hour values to account for the variation in the times of the daily searches.

The final point-to-point distance moved from the first sighting, when two or more re-sightings were made on consecutive nights, was calculated as the straight-line distance using the following equation:

$$c^2 = a^2 + b^2 - 2ab \cos C$$

where c = distance travelled, a = first recorded distance to track marker, b = second recorded distance to track marker, and C = angle between the two consecutive measurements (i.e. the absolute value of the difference between the two bearings). Non-consecutive night re-sightings were not used for calculating point-to-point distances moved. In cases where weta were re-sighted more than 15 m from the original capture location, the total point-to-point distance travelled could not be calculated accurately. Instead, the distance from the weta to the nearest marker on each re-sighting occasion was summed. This value was then added to and subtracted from the total distance between the two markers to get an estimate of potential distance travelled.

Environmental measurements

Ambient air temperature and relative humidity were recorded using a HOBO Pro v2 waterproof data logger attached to a tree 1.5 m above ground level, midway along the surveyed distance. Soil temperature was measured using a dial thermometer and taken mid-way along the track at the

beginning of each survey. The following subjective environmental variables were recorded at the beginning of each survey: wind strength, 1 = weak to 4 = strong; rainfall, 1 = nil to 3 = moderate; leaf litter dampness, 1 = dry to 3 = wet; cloud cover, 1 = clear to 3 = overcast; and moonlight, 1 = light to 3 = dark.

Statistical analyses

All statistical analyses were performed using R version 2.15.2 (R Development Core Team 2013). For comparisons between male and female measurements, all data were analysed using non-parametric Mann-Whitney tests with the `wilcox.test` function because the data remained non-normally distributed after log transformation.

Principal component analysis (PCA) was used on normalised environmental data to reduce the number of dimensions to three components using the `princomp` function. The following environmental variables were used in the PCA: average relative humidity; average, evening, minimum and maximum air temperature; daily air temperature range; soil temperature; cloud cover; dampness; moonlight; rain; and wind. These three principal components were used to determine whether captures (total number of individuals found, including re-sights) and re-sight rates per hour of males, females and all individuals, body size (mean male and female pronotum, femur and body ratio measurements), and sex ratios (i.e. proportion of males) could be explained by the environmental conditions. Three separate PCAs were performed due to different data being present for the capture/re-sight, sex ratios and body size. For instance, where no captures were made, sex ratios could not be calculated despite being a data point for the capture/re-sight data. Each of the measurements was then regressed against each of the first three principal components using simple linear regression with the `lm` function.

Results

Body size

The pronotum of adult females was on average 0.59 mm, or 1.14 times, larger than that of adult male weta and the femur length was also significantly longer in females compared to males

(Table 1). The pronotum to femur ratio, however, was larger in male weta, indicating that males have longer legs relative to their pronotum than females (Table 1).

Sex ratio

Of the 222 weta found (including re-sights) over 25 nights of searching, 65 were female and 157 were male (on 18 March, the number of search hours was not recorded but 71 individuals were found including re-sights, 31 females and 40 males). In total, male weta were found more often per hour than female weta (Table 1, Figure 1). This resulted in an observed male-biased sex ratio of approximately 2.45 males/h to every female/h. Although the number of female weta found decreased over the study period ($r^2 = 0.26$, $F_{1,23} = 8.03$, $p = 0.009$, $y = 4.52 - 0.18x$), the number of male weta did not ($r^2 = 0.07$, $F_{1,23} = 1.70$, $p = 0.21$) and neither did the proportion of males (i.e. the number of males as a proportion of the total number of animals found) over the study period ($r^2 = 0.001$, $F_{1,23} = 0.02$, $p = 0.89$) (Figure 1).

Capture and re-sightings

A total of 131 weta were tagged, including 53 females and 78 males. Of the 131 tagged weta, 50 (38.2%) were re-sighted at least once over the 25-night search period. Of those, a further 23 (17.6%) were re-sighted a second time, 15 (11.5%) a third time, and eight (6.1%) were re-sighted on four occasions (Table 1, Figure 2). Overall, the number of times tagged male and female weta were re-sighted did not differ (median number of times re-sighted = 0 for both sexes; Table 1); however, of the weta re-sighted at least once, males were re-sighted more often than females (male median = 2, female median = 1; Table 1). There was no difference in the average number of days between re-sights for males and females (Table 1, Figure 3). The longest period between re-sightings for weta was 13 days for males and 10 days for females (Table 1, Figure 3). A total of 16 weta were re-sighted using the reflector strip but with missing tags (it was unknown if any of these were the same weta spotted on different occasions).

Table 1. Body measurements, number of captures and re-sightings, sex ratio and distance travelled over consecutive nights for adult male and female ground weta, *Hemidrachus maculifrons*, in Otanewainuku Forest, Bay of Plenty, New Zealand, between March and April 2012. N = number of animals (for sex ratio and distance moved N = number of nights sampled), SE = standard error, W = Mann-Whitney test statistic.

	Male			Female			W	p		
	N	Mean (SE)	Median	Range	N	Mean (SE)			Median	Range
Body measurements										
Pronotum (mm)	84	4.12 (0.03)	4.12	3.69–4.70	54	4.71 (0.03)	4.75	4.23–5.36	202.5	<0.0001
Femur (mm)	84	10.87 (0.05)	10.92	9.01–12.19	54	12.14 (0.08)	12.29	10.30–13.01	227	<0.0001
Femur/pronotum	84	2.64 (0.02)	2.63	2.28–3.03	54	2.58 (0.02)	2.56	2.31–2.89	2.5	0.014
Captures/re-sightings										
No. marked	78				53					
Re-sighted at least once	31	2.23 (0.22)	2	1–4	19	1.42 (0.19)	1	1–4	403	0.018
Total no. of times re-sighted	78	0.88 (0.15)	0	1–4	53	0.51 (0.12)	1	1–4	2256	0.309
Time between re-sights (days)	69	2.90 (0.30)	2	1–13	27	2.90 (0.45)	2	1–10	1013	0.923
Sex ratio										
Total no. weta/hr	25	5.21 (1.06)	3.75	0–19.60	25	2.12 (0.53)	1.45	0–10.24	424.5	0.028
Distance moved										
Av. distance travelled/night (m)	25	1.01 (0.20)	1.24	0.03–3.78	11	1.57 (0.19)	1.56	0.36–2.41	72	0.024

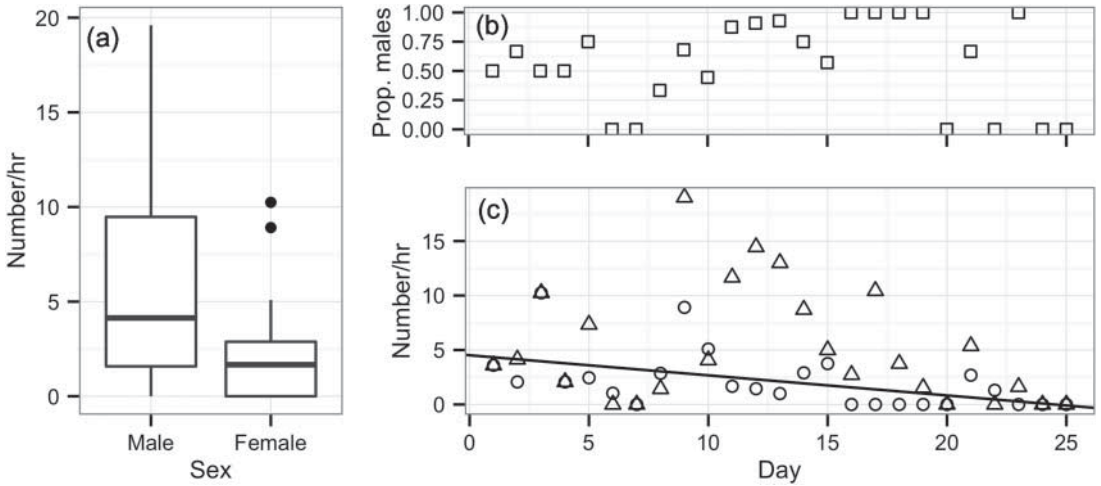


Figure 1. Capture data for male and female ground weta (*Hemiandrus maculifrons*) found in Otanewainuku Forest, Bay of Plenty, New Zealand, between March and April 2012. (a) Boxplot showing median and upper and lower quartiles for adult male and female weta found per hour, including re-sights. (b) The proportion of males found each night during the study period. A value of 0.5 represents an even sex ratio; values above indicate male-biased ratios while values below show female-bias. (c) Mean number of adult male (Δ) and adult female (\circ) weta found per hour over the study period. Black line shows regression of females with time, $r^2 = 0.26$, $y = 4.52 - 0.18x$.

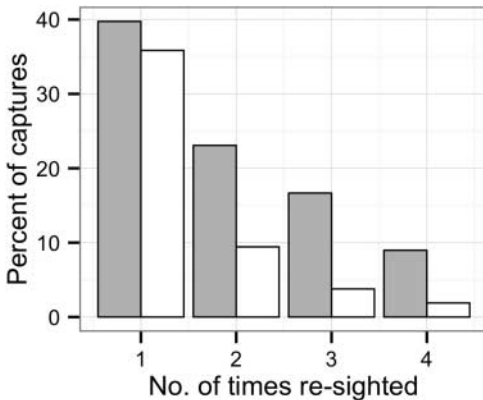


Figure 2. The maximum number of times each marked adult ground weta, *Hemiandrus maculifrons*, was re-sighted during nightly searches in Otanewainuku Forest, Bay of Plenty, New Zealand, between March and April 2012. Grey bars = male, white bars = female.

Point-to-point distances travelled

In total, 36 records of weta positions over consecutive nights were recorded from 25 weta (18 males, seven females). Straight-line point-to-point distances over consecutive nights were longer for females (mean = 1.57 m; median = 1.56 m) than for males (mean = 1.01 m; median = 1.24 m; Table 1). Consecutive-night distances travelled

ranged from 0.03 to 3.78 m (Table 1), however several weta were re-sighted at markers at least 70 m away from the original capture location on non-consecutive nights (G01 moved a minimum of 49.95–60.05 m in two nights; G48 moved 68.74–71.26 m in two nights; G94 moved 60.6–79.4 m in three nights; and G95 moved 17.4–22.6 m in two nights).

Multivariate analyses

The first three components of each of the three PCAs (Eigenvalues > 1.0) relating to capture/re-sight, body size and sex ratio explained near identical percentages in variation of the environmental data (PC1: 45.6–47.3%; PC2: 18.3–20.6%; PC3: 8.7–11.5%; Appendix 1 – Online Supporting Information). All environmental variables loaded negatively on the first component (PC1) of all three PCAs except for temperature range, but there was no link with the biological data. The second component (PC2) better differentiated the variables along the component, but only explained between 18.3% and 20.6% variation. PC2 for captures/re-sight and sex ratio were similar with average relative humidity, dampness and rain contributing the highest negative loadings, whereas maximum temperature

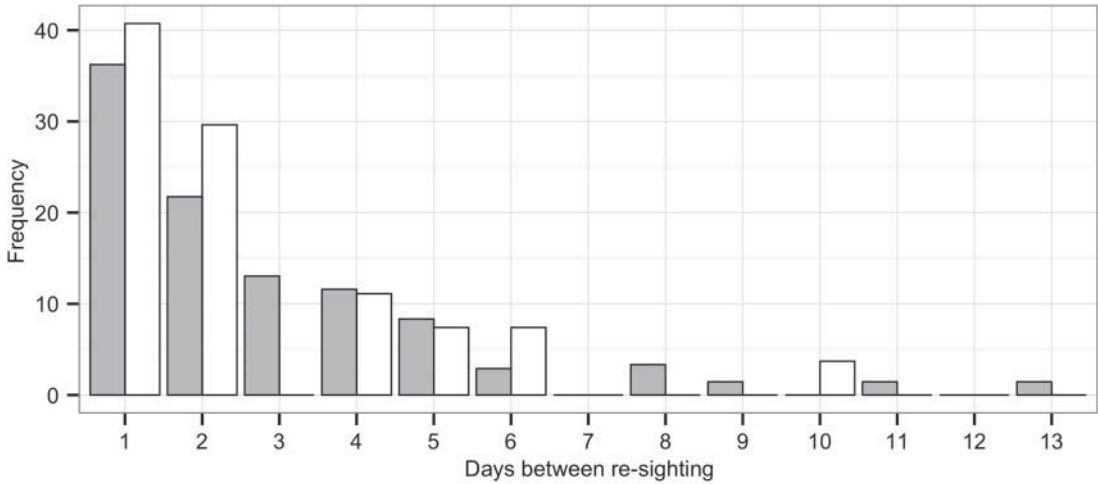


Figure 3. Frequency distribution of the number of days between re-sightings of marked adult ground weta, *Hemian-drus maculifrons*, in Otanewainuku Forest, Bay of Plenty, New Zealand, between March and April 2012. Grey bars = male, white bars = female.

had the greatest positive loading. On PC2 for the body size data, maximum temperature and soil temperature loaded the most negatively and cloud cover, dampness and rain were the variables with the highest positive loadings (Appendix 1 – Online Supporting Information).

Female pronotum size increased significantly with PC2 of the body-size PCA ($F_{1,12} = 8.23$, $p = 0.014$, $r^2 = 0.41$, $y = 4.7 + 0.062x$). Both male ($F_{1,23} = 5.16$, $p = 0.032$, $r^2 = 0.18$, $y = 2.3 - 0.780x$) and total ($F_{1,23} = 5.05$, $p = 0.034$, $r^2 = 0.18$, $y = 2.8 - 0.872x$) re-sightings declined with PC2 of the capture/re-sight PCA. No other variables in the body size, captures/re-sightings or sex ratio datasets showed any relationship with any of the three PCs (Appendix 2 – Online Supporting Information).

Discussion

Female-biased sexual size dimorphism

Within the sampled population of *H. maculifrons*, measurements of pronotum and hind femur length indicate that adult females were significantly larger than adult males. Female-biased sexual size dimorphism (SSD) is normal among many invertebrate groups, in particular insects (Blankenhorn et al. 2007; Esperk et al. 2007), and is dominant among orthopterans (Hochkirch & Gröning 2008). Within the Ensifera suborder (which includes the

Anostomatidae), females are on average 1.09 times larger than males (although size differences between sexes are more pronounced within the Caelifera suborder; Hochkirch & Gröning 2008). Female-biased SSD has also been documented within some New Zealand weta, for example, *Deinacrida* spp. and *Hemiandrus* spp. (Gibbs 1998; Kelly et al. 2008; Chappell et al. 2012).

In orthopterans, increased female body size, in comparison to male body size, can be correlated with an increased number of developmental instars and/or increased developmental time (Esperk et al. 2007). For example, Cary (1981), found female *H. maculifrons* had more instars than males (9 vs. 7), and also took a longer time to develop (although this was not tested statistically). In contrast, some other ground weta species, such as *H. furoviarius*, exhibit more instars in the smaller sex (males) (Wyngaarden 1995). Investigating aspects such as intraspecific competition and life-history strategies is required to explain the observed female-biased SSD in these ground weta species (Hochkirch & Gröning 2008).

Of interest was the finding that male ground weta had a greater leg to pronotum length ratio than females. One hypothesis, the ‘mobility hypothesis’, provides the explanation that where females are the larger sex, there may be sexual selection for more mobile males (Blankenhorn 2005). Some evidence for this was reported in the Cook

Strait giant weta (*Deinacrida rugosa*) where males with longer legs and smaller bodies moved greater distances and were reproductively more successful (Kelly et al. 2008). Although we found no support for long-legged *H. maculifrons* males travelling greater distances than short-legged males, the mobility hypothesis remains a potential explanation for the observed sexual size difference in these weta and remains an area for future research.

Sex ratio and re-sighting rates

During this study adult male ground weta were observed almost 2.5 times more often than adult females. Additionally, when an animal was re-sighted at least once, males were re-sighted more often than their female counterparts. However, this apparent male-biased sex ratio is likely due to the temporal scale of the sampling; only a single population of a single species was observed for approximately three weeks. Previous surveys of a related ground weta species (*H. pallitarsis*), on Middle Island in the Mercury Group, found a biased sex ratio in only two months of the year (in April only males were found and in October only females were found; Stringer 2006). Additionally, a 1:1 sex ratio was also found when sampling *H. maculifrons* over a 16-month period (Cary 1981). The importance of considering the time scale involved when analysing sex ratios is highlighted by Wehi et al. (2011), whose meta-analytical approach rejected the popular assumption that predation can result in a sex ratio bias in sexually dimorphic species.

Despite the temporal limitation of this study, seasonal variation may be an important component of any observed difference in operational sex ratio (OSR: the ratio of sexually receptive males to sexually receptive females; Kvarnemo & Ahnesjö 1996) within *H. maculifrons*. For example, female *H. maculifrons* may exhibit maternal care of eggs or young (an unusual trait for a long ovipositor species) as adult females have been observed ovipositing into the walls of underground brood chambers and remaining with them for several months (Cary 1981). Seasonal changes in sex ratio bias have been reported in a range of species, including the yellow dung fly (Otronen 1996), and katydids (Gwynne et al. 1998).

Further research could include, firstly, substantiating the sex ratio of ground weta using

mark-recapture analysis. This was not possible in our study as the assumption of equal detectability of marked and unmarked animals (Magle et al. 2007) was broken by using reflector strips. Secondly, investigating the reproductive strategies of males and how that may affect the OSR may be of interest in ground weta. For instance, male mate guarding behaviour, where a male can generally only guard a single female, reduces the male reproductive rate (Kokko & Rankin 2006). Additionally, resource availability can, if limited, affect spermatophylax production and therefore reduce the male sex ratio (e.g. Gwynne et al. 1998).

Movements of *Hemiandrus maculifrons*

The average consecutive-night distance moved by adult ground weta during this study was small; on average, males moved only 1.01 m over consecutive nights and females 1.57 m. Given this species appears to exhibit female-biased SSD, these distances provide no evidence for the male mobility hypothesis. However, there are several caveats with the methodology employed in tracking these weta. Firstly, the area monitored was linear, so any individuals moving away from the main path would not be re-sighted and therefore our reported point-to-point distances for *H. maculifrons* may have been underestimated. Several weta were, for example, found up to 70 m from their original capture location, indicating potential movement greater than has been found for the larger bodied giant weta (*Deinacrida heterocantha*; Watts & Thornburrow 2011). Secondly, data was lost due to the inefficiency of the tagging method (many tagged weta were re-sighted with only reflector strips attached). Thirdly, the linear study site design makes it difficult to differentiate animal activity between sexes. In particular, female ground weta are thought to spend extended periods within the burrow either ovipositing or tending eggs and hatchlings (Cary 1981; Wyngaarden 1995; Gwynne 2004). In this study we could not differentiate if female weta were: 1) inactive and remaining in their burrows; 2) actively moving out of the study area; or 3) not re-sighted due to increased predation pressure as a result of increased body size. Except for increased predation, each of these situations could result in an overestimation of the number of males. Resolving this issue would require employing a radio

transmitting system, which is problematic given their small size. Nonetheless, a possible monitoring solution could comprise a radio frequency identification (RFID) system such as that used by [Vinatier et al. \(2010\)](#).

Weta activity and environmental conditions

Our results indicate little relationship between weta metrics and environmental variables, which is not surprising given the length of sampling period and consequent limited range of environmental conditions. The only metrics showing relationships with the environmental variables were male and total re-sightings, and female pronotum size (both to the second principal component of their respective PCAs). These relationships indicate higher male/total re-sightings can be expected and larger females found when conditions are wetter, colder and more overcast. Although [Stringer \(2006\)](#) did not look at body size or distinguish sex, he found the number of ground weta (*H. pallitarsis*) observed was significantly correlated with mean soil moisture, mean soil temperature and mean air temperature, but was independent of rainfall and relative humidity. While of interest, the opposing trend we report here may be a function of the narrow range of conditions experienced, as indicated by the similarity of loadings on PC1. Moreover, it is important to recognise the low percentage variation explained by the second component, on which these links exist.

Conclusions

Our findings suggest *Hemiandrus maculifrons* is a female-biased SSD species that may exhibit a male-biased sex ratio depending on time of the year or stage of reproduction. Our study also suggests that there may be some differences in point-to-point travel distances between the two sexes. Although we found no clear relationship between the number of weta captured and environmental conditions, this research does provide some insight into *H. maculifrons* life-history dynamics, highlighting the need for a more in-depth study. Possible areas of interest could include, firstly, identifying the true sex-ratio, then identifying the underlying cause of a possible female-biased SSD and whether it can be explained by selection for small, mobile

males. We also need to understand how ground weta move within their environment and how this may be related to sexual selection and the different reproductive roles of each sex; aspects which may be answered through the use of novel tracking methods.

Supplementary data

Supplementary data available online at www.tandfonline.com/ <http://dx.doi.org/10.1080/00779962.2013.856377>

Appendix 1

(a) Eigenvectors and (b) environmental variable loadings for principal components (PC) PC1, PC2 and PC3 for the following datasets: capture/re-sights; body measurements; and proportion of males found per hour in Otanewainuku Forest, Bay of Plenty, New Zealand, between March and April 2012.

Appendix 2

Results of regression analysis of weta captures/h, re-sightings/h, sex ratio (proportion of males), and body measurements against (a) PC1, (b) PC2, and (c) PC3 of ground weta, *Hemiandrus maculifrons*, collected from Otanewainuku Forest, Bay of Plenty, New Zealand, between March and April 2012.

Acknowledgements

We would like to thank Adam Brown, Scott Lyon and Simon Holmes for assisting with field surveys. Permission to access the forest and conduct research on a native species was granted by the Department of Conservation, Mr. M. Tapsell and Mr. D. Flavell of the local iwi, Ngāti Ranginui. Two anonymous reviewers and Darren Ward provided useful comments to improve this manuscript.

Funding

This research was funded by the Bay of Plenty Polytechnic Taiorahau (Pacific Coast Applied Research Centre) Research Fund.

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