Survival of adult mountain stone weta *Hemideina maori* (Orthoptera: Anostostomatidae) along an altitude gradient as determined by mark-recapture

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Abstract: The mountain stone weta *Hemideina maori*, a tree weta, is a cold-adapted New Zealand insect that shows increasing body size with increasing altitude and decreasing temperature. This study modelled the monthly survival probability of adult weta at three sites (high, medium and low altitude) in the Rock and Pillar Range, Otago. Survival was predicted to be lowest at the low elevation site where weta are at the lower limit of their current altitudinal range. A total of 504 adult weta were marked and released at all three sites between November 1999 and May 2002. Mark-recapture analysis showed that survival varied over time, being lowest during the summer months. Survival also differed between the sexes, with females having a higher probability of survival than males, but there was no difference in survival between altitudes. Our findings that body size varied significantly with elevation but that survival was similar between sites, suggest that body size at each altitude might be adapted to the local environment. It would be of interest in a longer term study to model survival of *Hemideina maori* as a function of variation in average summer temperatures, to test predictions about the effects of climate change on populations of alpine ectothermic animals.

Keywords: altitude; body size; mark recapture; survival; weta.

Introduction

Variation in life histories can result from differences in genotypes or from environmentally-induced differences among individuals of a given genotype (Roff, 1992). This latter phenomenon, termed phenotypic plasticity, is one way for an organism to overcome the problem of living in a heterogeneous environment (Mousseau *et al.*, 2000). In ectotherms, growth rate tends to be slower and maturation delayed by development at cool temperatures. As a result, adult ectotherms attain larger body sizes at high altitudes and latitudes (Atkinson, 1994; Partridge and Coyne, 1996; Atkinson and Sibly, 1997; Arnett and Gotelli, 1999). Because body size is an important ecological parameter, there is a need to understand both the effects of temperature on body size and how body size ultimately relates to survival (Atkinson and Sibly, 1997). This is particularly relevant given current ecological interest in climate change, and that 99% of the world's animal species are ectothermic (Atkinson and Sibly, 1997).

It has been shown both theoretically and empirically that survival probability is a major determinant of life history evolution (Charlesworth, 1980; Roff, 1992). Adult survival probability can vary with sex and body size and also as a function of environmental variables (Lebreton *et al.*, 1992). The mountain stone weta *Hemideina maori* (Orthoptera: Anostostomatidae) is a New Zealand insect that shows increasing body size in association with increasing altitude and decreasing temperature in the Rock and Pillar Range, Central Otago (Dowsett, 2000; Koning and Jamieson, 2001). However, little is known about the life history traits of *Hemideina maori*, and in particular how variation in body size and environmental temperature influence survival probability.

To estimate survival probability in the field under natural conditions, it is necessary to follow individually marked animals through time (Lebreton *et al.*, 1992). *Hemideina maori* is suited for mark-recapture studies because individuals are large and flightless, meaning they can be easily tagged and monitored. Also, their habit of taking refuge under rock slabs during the day makes recapturing weta relatively easy (Jamieson *et al.*, 2000; Leisnham and Jamieson, 2002; Leisnham *et al.*, 2003). *Hemideina maori* lives in an alpine environment, is freeze tolerant (Ramløv, 1992; Sinclair *et al.*, 1999), and occurs between 1000 and 1500 m a.s.l. (King *et al.*, 1996). Weta are nocturnal and most active during the summer months. In the Rock and

Pillar Range summer night-time temperatures are on average 4°C higher at 1100 m than at 1450 m (summit elevation) (I. Jamieson, *unpubl. data*), and adult weta found at lower altitudes have smaller adult body sizes than those found near the summit (Koning and Jamieson, 2001). Little is known about the underlying factors causing this variation in body size and whether there are any associated differences in survival.

This study assesses whether monthly survival probability of adult weta varies significantly across high, medium and low altitudes in the Rock and Pillar Range. Given that *Hemideina maori* is a cold-adapted insect, we predicted its survival rate would be lowest at low altitudes, where they are living at the lower limit of their altitudinal range and where they frequently experience what we assumed to be sub-optimal conditions such as warm temperatures.

Methods

Study sites

The Rock and Pillar Range is located in Central Otago, 53 km inland from the east coast of the South Island of New Zealand (45°28'S, 170°02'E). The range runs SW to NE for 23 km and is 1450 metres a.s.l. at its highest point. Environmental conditions are harsh, with persistent strong winds and low air and soil temperatures (Bliss and Mark, 1974). Characteristic of the range are the schist outcrops (tors), which *Hemideina maori* inhabits. Tors can range in size from one rock a few metres wide to several rock columns up to 30 m in diameter (Jamieson *et al.*, 2000; Leisnham and Jamieson, 2002). Weta are found primarily under rock slabs that have broken off tors and that can be lifted relatively easily (King *et al.*, 1996; Jamieson *et al.*, 2000).

The three sites for this study were located along the gently rising southern slope of the range, on an altitudinal gradient (Fig. 1). Site A was at 1400 m a.s.l. (Infomap 260 H43 804380), Site B was 6 km south west of Site A at 1250 m a.s.l. (Infomap 260 H43 765213) and Site C was 7 km south west of site B at 1100 m a.s.l. (Infomap 260 H43 756132). Site C is also at the lowest altitude that weta have been found in the Rock and Pillars (I. Jamieson, *unpubl. data*). Study tors at each site were chosen because of their relative isolation from surrounding tors. Leisnham and Jamieson (2002) marked all adult weta at Site B over a four year period to examine dispersal patterns. They found no marked weta outside the study area and dispersal rates between tors within the study area were relatively low (< 4% of marked adult weta, *n* = 480). Therefore, we assumed for this study that few, if any, tagged weta moved outside the study areas during the course of the research.
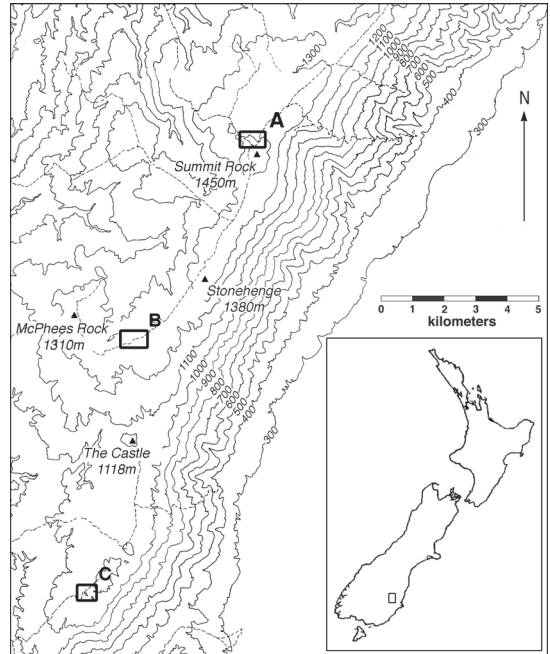
Figure 1. Location of the three study sites on the southern slope of the Rock and Pillar Range. Dashed lines indicate four-wheel drive tracks.

Site A (upper) 1400 m

Vegetation at the summit consists of low-lying cushion plants and herbfields (Bliss and Mark, 1974), and is leasehold farmland lightly grazed by sheep. The study site had three large tors approximately 750 m apart, with 19, 38 and 46 rocks on and around each respectively that were large enough for an adult weta to take shelter under.

Site B (middle) 1250 m

Vegetation at Site B is similar to that at the summit, with herb-fields and cushion plants between the tors. The area is also leasehold farmland lightly grazed by sheep. The study site had three large tors with 34, 38 and 39 rocks on and around each of them, and one small tor with 13 rocks. Tors were at least 300 m apart.

Site C (lower) 1100 m

Vegetation at Site C differs from that of Sites A and B, being predominantly tussock grassland with scattered shrubs; the land is also more heavily grazed by sheep and cattle. The common gecko *Hoplodactylus maculatus*, which can prey on juvenile but not adult weta (Toynbee, 2002), is also present at this site but not the other two sites. Site C had three small tors, two of

which had 13 rocks and were 100 m apart; the third tor had three rocks and was 400 m from the other two. Weta are much less common in the vicinity of Site C than Sites A and B, and as mentioned previously, are on the edge of their lower altitudinal range (I. Jamieson, *unpubl. data*).

Data collection

Data were collected from December to May over three successive breeding seasons (1999/2000, 2000/2001 and 2001/2002). During the 1999/2000 season and the 2001/2002 season, sampling was undertaken once every six weeks at each site. During the 2000/2001 season, sampling also occurred every six weeks, but surveys were conducted over three consecutive days. The sampling regime was modified in this way during the 2000/2001 season to obtain estimates of population size for each site, but for the purpose of this study, the three days are treated as one sampling session. Each site had a total of 11 sampling sessions between December 1999 and May 2002. Differences in sampling effort were taken into account in the modelling process.

At each tor, rocks were lifted carefully, weta placed in holding containers and the rocks replaced in their original positions. Weta were identified as being juvenile or adult and sexed (Jamieson *et al*., 2000). Measurements of head width and right hind femur length [indicators of body size (Koning and Jamieson, 2001)] of adult weta were made using Vernier calipers. Weta were weighed using electronic scales to the nearest 0.01 g. Small alpha-numeric tags were glued to the pronota of adult weta as described by Jamieson *et al*. (2000) and Leisnham and Jamieson (2002). After processing, weta were released under the rock from which they came.

Data analysis

Histograms and normal probability plots were used to check that morphological measurements were approximately normally distributed at each site and within each sex. A general linear model (GLM) was used to compare differences in the mean head and body measurements among the three sites and between males and females. The residuals of the GLM were checked for homoscedasticity to ensure variation in morphological measurements at each site was approximately the same. These analyses were carried out using Minitab 8.2 (Minitab Inc., 1991).

We analysed the mark-recapture data using MARK 2.1 (White and Burnham, 1999; a software package available from http://www.cnr.colostate.edu/~gwhite/mark/mark.htm). The Cormack-Jolly-Seber model (CJS) (Lebreton *et al*., 1992) was used to obtain estimates for survival and recapture probability. The fully parameterised CJS model can be written as $\{\phi_{(group*time)} \ p_{(group*time)}\}$, where ϕ and p represent survival and recapture probability, respectively. This model allows survival and recapture probabilities to be different between groups for each time interval, i.e., an interaction between the two factors. For this study there were six groups; three sites, with two sexes at each site. Data from 11 sampling sessions were used in the analysis and there were 10 time intervals corresponding to the periods between each session. Weta survived the interval between each session with a probability of $\phi_{(ij)}$ and had a probability of being re-captured at each session of $p_{(ij)}$, where i indexes time and j indexes group.

Program RELEASE (available within MARK) was used to assess the goodness-of-fit of the CJS model described above, as a global starting model. More specifically, RELEASE compares the observed data with data expected under the assumption of the CJS model, that every marked animal present in the group at $time_{(i)}$ has the same probability of recapture and the same probability of surviving to $time_{(i+1)}$ (White and Burnham, 1999). Two further assumptions that also need to be satisfied when using the CJS model are: 1) all samples are instantaneous relative to the interval between occasion *i* and *i*+1, and 2) tags are not lost or missed. Sampling in the current study was effectively instantaneous, and a previous pilot study showed that tag loss was unlikely to occur (I. Jamieson, *unpubl. data*). If occasional tag loss does occur, the proportion of lost tags is unlikely to differ between the three sites, and therefore would not influence the overall aim of the study.

Reduced parameter models for recapture were selected using the most complex survival model, and alternative models for survival were selected using the most parsimonious recapture model. As we were interested in finding out whether monthly survival probability varied between sites in association with body size, the three best models that included either site or time, or both, as parameters were re-run, with the covariate right femur length also included. To assess whether differences in sampling effort between seasons influenced recapture probability, a model in which recapture was allowed to vary between seasons was compared with a model in which recapture was constant between seasons.

AICc values [Akaike's Information Criterion adjusted for small-sample bias (White and Burnham, 1999) were used to select the best model, with lower AICc values indicating a better fitting model. To determine how much support the best model had compared with alternative models, the difference between the AICc value of the candidate model and AICc value of the best model (ΔAICc) was reported. If the ΔAICc of a candidate model is less than 2.0 then it can be considered to have reasonable support.

a

b
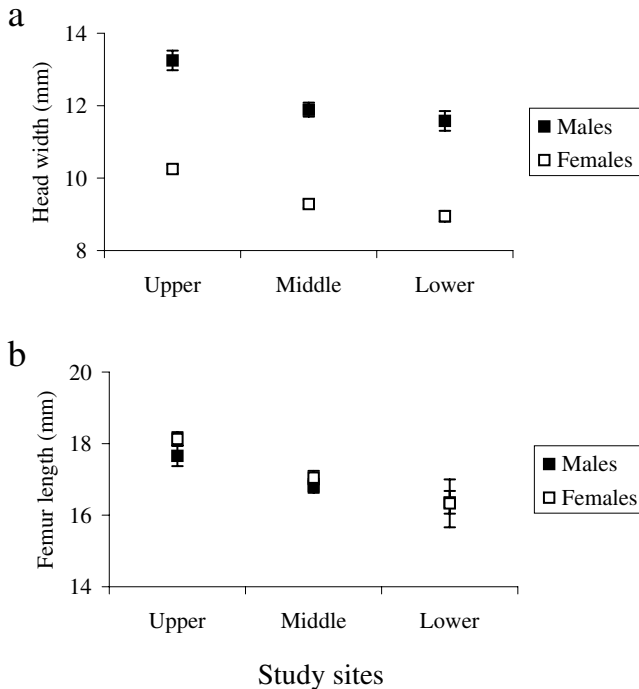
Study sites

Figure 2. Mean head width (a) and femur length (b) for male and female adult weta marked at each of the three study sites in three seasons (1999/2000, 2000/2001 and 2001/2002). Solid squares represent males, open squares females and vertical bars are 95% confidence intervals. The sample of measured weta included individuals from tors that were surveyed in addition to those used in the mark-recapture analysis. Sample sizes were: Upper site males $n = 106$, females $n = 132$; Middle site males $n = 122$, females $n = 116$; Lower site males $n = 23$, females $n = 42$.

Table 1. Results from the overall goodness of fit test in program RELEASE. Observed data are compared with data expected under the assumptions of the CJS model.

Group	Chi-square	d.f.	P
Upper site males	8.224	17	0.962
Upper site females	5.615	19	0.999
Middle site males	14.318	21	0.856
Middle site females	29.002	23	0.180
Lower site males	1.872	7	0.967
Lower site females	3.196	12	0.994
Total	62.227	99	0.999

Table 2. Analysis to determine whether survival rates of adult weta in the Rock and Pillar Range varied with altitude, over three breeding seasons and two winters (December 1999 to May 2002).

Model		No. of Parameters	AICc[1]	ΔAICc[2]
Recapture:				
$\phi_{site*sex*time}$	$p_{site+time}$	72	1436.771	66.87
$\phi_{site*sex*time}$	P_{time}	68	1437.948	68.05
$\phi_{site*sex*time}$	$P_{sex+site+time}$	73	1439.250	69.35
$\phi_{site*sex*time}$	$P_{sex*site+time}$	75	1439.479	69.58
$\phi_{site*sex*time}$	P_{site}	62	144.057	74.16
$\phi_{site*sex*time}$	$P_{sex+time}$	71	1445.029	75.13
$\phi_{site*sex*time}$	$P_{sex+site}$	64	1448.854	78.96
$\phi_{site*sex*time}$	P_{sex}	61	1454.312	84.41
Survival:				
$\phi_{sex+time}$	$p_{site+time}$	23	1369.899	0.00
$\phi_{sex+site+time}$	$p_{site+time}$	25	1373.393	3.49
$\phi_{sex+site+time+femur}$	$p_{site+time}$	26	1373.945	4.05
ϕ_{time}	$p_{site+time}$	22	1375.017	5.12
$\phi_{time+femur}$	$p_{site+time}$	23	1376.059	6.16
$\phi_{site+time}$	$p_{site+time}$	24	1377.428	7.53
$\phi_{site+time+femur}$	$p_{site+time}$	25	1377.574	7.68
ϕ_{sex}	$p_{site+time}$	14	1390.165	20.27
ϕ_{site}	$p_{site+time}$	15	1395.589	25.69

[1] Akaike's Information Criterion corrected for bias; lower AICc values indicate better fitting models.
[2] Difference in AICc value from the best model; candidate models with ΔAICc values of less than 2.0 are considered to have reasonable support.

Results

Like most adult tree weta, *Hemideina maori* is sexually dimorphic with males having an enlarged head (Field and Deans, 2001). Consistent with earlier findings (Dowsett, 2000; Koning and Jamieson, 2001; I. Jamieson, *unpubl. data*), head width and femur length of both males and females were larger at the upper site and smaller at the lower site (Fig. 2).

A total of 504 adult weta were marked and released at all three sites between November 1999 and May 2002. A goodness of fit test indicated that the CJS model {$\phi_{(sex*site*time)}$ $p_{(sex*site*time)}$} showed no significant departures from the data (Table 1) and was

accepted as a suitable starting model. The best model for recapture was $p_{(site+time)}$ (Table 2), with the probability of an individual being recaptured (assuming it is in the population being sampled) varying by time and site, but with no interaction between the two. The upper site had the lowest probability of recapture and the lower site the highest, with the percentage of the total number of tagged weta at each site that were resighted at least once being 53% for the Lower Site ($n = 42$), 41% for the Middle Site ($n = 247$), and 24% for the Upper Site ($n = 215$).

The best model for survival was $\phi_{(sex+time)}$ (Table 2), with survival varying over time and between the sexes, but with no overall difference in survival between sites (Upper site $\phi = 0.88 \pm 0.02$ ($\pm$ SE); middle site $\phi = 0.89 \pm 0.11$ ($\pm$ SE); lower site $\phi = 0.90 \pm 0.02$ ($\pm$ SE)). Survival fluctuated over time, being highest during the winter months and lowest during mid-summer for both males and females (Fig. 3). Females had a higher monthly probability of surviving than did males (Fig. 3), with the odds of survival for a female being 1.5 ± 0.25 times that for a male (Table 3). Finally, models that included site and/or femur length in their structure were much less well supported than the model $\phi_{(sex+time)}$ (Table 2).

Discussion

This study was carried out to test whether survival of adult *Hemideina maori* varies along an altitudinal gradient in the Rock and Pillar Range. The results did not support the hypothesis that alpine weta living at the lower limit of their altitudinal range would have a lower survival probability than weta at higher elevations. Rather, the data indicated that monthly survival probability of alpine weta is similar at low, intermediate and high altitudes, but at each altitude females have a higher probability of survival than males. Weta also had lower recapture rates at the upper site, which might have been due to the greater amount of rocky habitat at this site (I. Jamieson, *unpubl. data*) or marked individuals taking shelter periodically in narrow crevices in the main tors (Leisnham *et al.*, 2003)

Given that body size varies with elevation, but survival is similar between sites, this suggests that body size at each altitude might be adapted to the local environment. In a concurrent study that examined whether body size variation in *Hemideina maori* is better explained by the influence of environmental temperature or site-specific genetic adaptation, it was found that juvenile weta exhibited countergradient variation in growth (Joyce, 2002). Countergradient variation occurs when genetic influences on a trait oppose environmental influences (Levins, 1968;
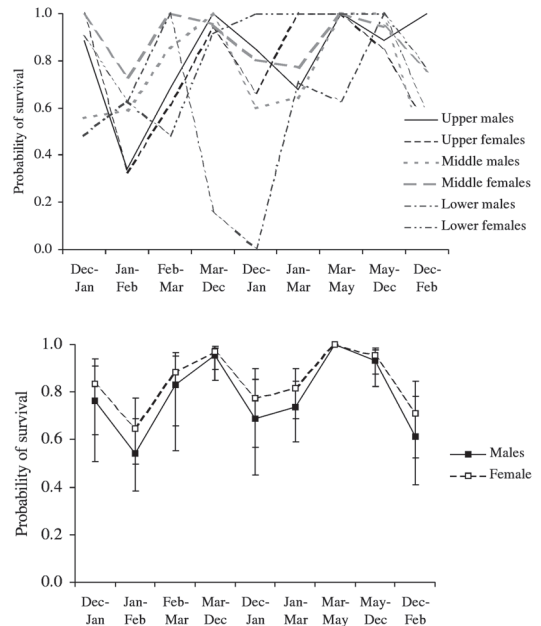
Figure 3. Monthly survival probabilities for adult weta between December 1999 and February 2002 at three sites in the Rock and Pillar Range. (a) The fully parameterised model $\phi_{(sex*site*time)} p_{(sex*site*time)}$. The estimate of zero survival for lower site males in December–January is because the one individual that was marked and released was not recaptured. The estimate of 1.0 for survival for lower site females between December 2000 and May 2001 is based on the release and recapture of four individuals and again is unreliable due to the small sample size. (b) The model $\phi_{(sex+time)} p_{(site+time)}$ best described the variation in the data. Because the model $\phi_{(sex+time)}$ is additive, the difference in survival between males and females is consistent, although it appears to vary in this figure because the values have been back-transformed from the logit scale. 95% confidence interval bars are shown.

Table 3. Beta values for male and female survival probabilities under the model $\phi_{(sex+time)} p_{(site+time)}$. Beta values are calculated on the logit scale and then back-transformed to give survival and recapture probabilities. Interpretation of the beta values can provide information on the magnitude of differences between males and females.

Beta	Value	SE	Description
β_{male}	1.174	0.582	Logit of male survival
β_{female}	0.443	0.167	Amount added to the logit of male survival to give the logit of female survival. Exp(0.443) = 1.5, therefore odds of survival for a female are 1.5 times greater than odds of survival for a male.

Conover and Shultz, 1995; Arnett and Gotelli, 1999), and suggests that body size in *Hemideina maori* is at least partly, locally adaptive. A cage experiment involving translocation of early instars of *Hemideina maori* between the summit and lower altitude sites is currently under way in the Rock and Pillar Range. Measurements of growth rate from this experiment should provide more conclusive evidence about the interactions among body size, environmental temperature and local genetic adaptation.

Hemideina maori is a cold-adapted species that is freeze tolerant (Ramløv, 1992; Sinclair *et al.*, 1999). Monthly survival was highest over winter and lowest over summer during the breeding period for both males and females in all three years. This could be due to the influence of warm temperature on a cool-adapted insect, stress and injury from breeding and mate competition, or a combination of these factors. It would be interesting to model survival as a function of local variation in average summer temperature recorded over a longer period of time, so that predictions about the effects of climate change on alpine ectothermic populations could be made.

Acknowledgements

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