

Life cycle, survival rates and longevity of an alpine weta *Hemideina maori* (Orthoptera: Anostostomatidae) determined using mark-recapture analysis

Paul T. Leisnham^{1,3}, Claire Cameron² and Ian G. Jamieson^{1,*}

¹Ecology, Conservation and Biodiversity Research Group, Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

²Department of Mathematics and Statistics, University of Otago, P.O. Box 56, Dunedin, New Zealand

³Present address: Ecology and Health Research Centre, Wellington School of Medicine, Department of Public Health, P.O. Box 7343, Wellington, New Zealand

*Corresponding author (E-mail: ian.jamieson@stonebow.otago.ac.nz)

Abstract: Although reproductive and behavioural studies have been conducted on captive tree weta, there have been very few ecological field studies of any of the weta species involving free-ranging, marked individuals. The mountain stone weta (*Hemideina maori*) is a tree weta that lives on rock tors in the alpine region of the South Island of New Zealand. Over three seasons each of 480 adults and 789 juveniles was individually marked on four large and 14 small tors to gather baseline information on aspects of *H. maori*'s life cycle and life history. Seasonal patterns were seen in the appearance of the smallest nymphs, moulting, and in the survival and recruitment of adults. Some marked juveniles were recaptured after 10 or more months, with a maximum interval of 14.1 months, indicating that instar intervals can be exceptionally long. Adult males and females had similar survival rates and often lived for 2 or 3 breeding seasons. Relatively high recapture rates (~60–70%) and long life spans make adult *H. maori* amenable to modern mark-recapture analyses using the programme MARK. We believe this research will be a useful template for further mark-recapture studies such as those to verify life history characteristics of endangered species of weta or the effects of secondary poisoning on invertebrates.

Keywords: insect life histories; mark-recapture; New Zealand; Stenopelmatidae; survival; tree weta.

Introduction

Weta are a group of flightless, nocturnal orthopterans, some of which are among the largest insects in the world (Gibbs, 1998a; Field, 2001). Many of the larger species of weta are endangered because of their vulnerability to predation and habitat loss (Gibbs, 1998b). The high profile of these large, unique insects makes them 'flagship' species for New Zealand invertebrate conservation (Gibbs, 1998b; Sherley, 2001).

Of the five genera of weta, the sexually dimorphic tree weta group *Hemideina* has been the most studied, possibly because of its abundance and aggressive behaviour (Gibbs, 1998a; Field, 2001). Tree weta have become recognised as good subjects for behavioural work in captivity (Field and Sandlant, 1983; Barrett, 1991; Ordish, 1992; Field, 1993) and for ecological studies in the wild (Moller, 1985; Jamieson *et al.*, 2000; Jamieson, 2002). However, there is little

verification of some life history attributes, including aspects of egg laying, hatching, growth, survival and longevity (Trewick and Morgan-Richards, 1995; Jamieson *et al.*, 2000).

The mountain stone weta *Hemideina maori* is unusual for a tree weta because of its alpine distribution (Meads, 1990; Gibbs, 1998a). *Hemideina maori* shelters under rock slabs that have broken off rock outcrops called tors (King *et al.*, 1996; Jamieson *et al.*, 2000). In this study, mark and recapture methods were used to examine the phenology, survival and longevity of this species in the expectation that adaptation to the alpine environment might have resulted in some differences compared with the lowland *Hemideina* species. This information was also sought for concurrent studies on the mating system (Jamieson, 2002; Leisnham and Jamieson, in press) and meta-population biology (Leisnham and Jamieson, 2002) of *H. maori*. We also sought to provide a useful template for future mark-recapture studies of other endangered species of weta.

Methods

Study site

The study site was in the Rock and Pillar Range, located 60 km north-west of the city of Dunedin in the South Island of New Zealand. The study site was located in the southern part of the range, about 1 km east of McPhee's Rock (1250 m a.s.l.) (45°28'S 170°02'E). The vegetation on the range consists mainly of cushion-herbfield and is described in detail by Bliss and Mark (1974). The landscape is studded with numerous rock tors which *H. maori* inhabit (Leisnham and Jamieson, 2002). In the context of weta habitat, tor size is defined by the number of loose rocks under which weta can potentially take refuge rather than by the area of the tor itself. Tors can vary in size, from one or two loose rock slabs on a relatively small rock column to more than 30 rock slabs spread among four to five large columns. For the purposes of this study, tor size reflected the number of rocks and number of weta inhabitants. 'Small' tors on our study site were arbitrarily defined as containing 1–12 loose rocks and from 0–12 weta. 'Large' tors contained 30–40 rocks and 20–70 weta. There were four large and 14 small tors within the study site. Although there were no tors within the study site with an intermediate number of rocks, the two patch sizes in this study represent opposite ends of a continuum of naturally occurring tor sizes (I. Jamieson, *unpubl. data*).

Ageing, sexing and marking of weta

Weta were classified into sex and age classes (adult or juvenile) on the basis of genitalia (see Gibbs, 1998a; Stringer and Carey, 2001). The youngest juvenile weta that had no detectable genitalia, and therefore could not be sexed, were referred to as nymphs.

Tors were surveyed approximately every two weeks from November to May for three seasons (1997/98, 1998/99 and 1999/2000) and November to January of a fourth season (2000/01). On each of the study tors, all liftable rocks that were considered suitable refuge sites for adult weta were numbered during initial surveys. During a survey, each numbered rock was lifted, weta were removed and placed in plastic containers, and the rock carefully placed back in its original position. For each unmarked weta, the sex, age class and location were recorded, and head width, head length, pronotum length, right femur length and ovipositor (if female) were measured using dial calipers. Adults were marked with a three-digit (001–999) waterproof tag glued onto the pronotum using 10-second drying Selleys Supa Glue™ (Selleys Chemical Co. Pty. Ltd.) (Jamieson *et al.*, 2000). Larger juveniles were marked with smaller sized tags (J001–J999). For a concurrent study on dispersal (Leisnham and Jamieson, 2002), smaller

juveniles and nymphs were also marked with a water-based non-toxic paint applied to a leg. All weta were released under the edge of the rock from which they came and they were watched until they had moved freely back into their cavity.

Juveniles and nymphs could only be marked temporarily; once they moulted the tag or paint was lost from the individual along with the old cuticle. Therefore, they could not be tracked for any length of time with as much certainty as adults. All juveniles that were thought to have reached the penultimate moult before adulthood (i.e. sub-adults) were marked on large and small tors. All juveniles and nymphs were also marked on small tors, but not on large tors, where only a proportion of juveniles within a designated area on large tors (representing about one third of the tor) were marked.

Survival and longevity analysis of mark-recapture data

Modelling adult recapture and survival rates

MARK 1.9 software package was used to construct reduced-parameter variations of the Cormack-Jolly-Seber model (CJS) (Lebreton *et al.*, 1992; <http://www.phidot.org/software/mark/docs/book/>) to estimate adult survival (ϕ) and recapture (p) probabilities on the four largest tors. This is an open population model that takes into account all individuals captured at least once. The effects of time and sex were tested on ϕ and p (Table 1).

The survival term ϕ is the probability that an individual remains in the local population. Because death and emigration can not be separated in open populations, 'survival' is not always an appropriate term to use (Tabashnik, 1980; Knight *et al.*, 1999). However, because there is low adult dispersal between local populations (<4% of re-sighted weta; Leisnham

Table 1. Notation for either daily survival (ϕ) or recapture (p) probability parameters in the Cormack-Jolly-Seber (CJS) models of the adult populations on each of the four large tors. A complete CJS model examines the effect of sex and time on both p and ϕ . The most parameterized CJS model is $\phi_{\text{sex*time}}p_{\text{sex*time}}$.

Notation	Model description
ϕ/p	Constant ϕ/p
ϕ/p_{sex}	ϕ/p varies between sexes
ϕ/p_{time}	ϕ/p varies over time
$\phi/p_{\text{time+sex}}$	ϕ/p varies with time and between sexes with a constant difference between sexes
$\phi/p_{\text{time*sex}}$	ϕ/p varies with time and between sexes without a constant difference between sexes

and Jamieson, 2002) any differences in ϕ would be primarily due to survival, and therefore the term survival is warranted in this study.

The model that best estimated recapture and survival rates from the model set for each tor was evaluated using Akaike's Information Criteria, adjusted for sample size (AICc) (Burnham and Anderson, 1998). AICc values were used to select models with the fewest parameters. Lower AICc values indicate better fitting models. As a general guideline, AICc values differing by >2 are a good indication that the model with the lower AICc value is preferable, whereas models with AICc values differing by <2 are reasonably similar regardless of magnitudes involved (White and Burnham, 1999). Components of the AICc models from each tor were pooled to select the model that best fit the overall data (from the four largest tors). Model fitting using AICc has been used in a number of recent mark-recapture studies (e.g. Armstrong and Ewen, 2001; Armstrong *et al.*, 2001).

Tests of model assumptions

Open population mark-recapture models such as CJS assume that the capture-history data support four assumptions: (1) every marked individual has the same probability of recapture; (2) every marked individual immediately after time i has the same probability of surviving to time $i+1$; (3) marks are not lost or missed, and (4) all samples are instantaneous relative to the periods between samples (White and Burnham, 1999). To check whether assumptions 1 and 2 were supported, we tested the Goodness of Fit of the most complex model used for factors affecting time and sex (i.e. $\phi_{\text{time} \times \text{sex}} P_{\text{time} \times \text{sex}}$) with the programme RELEASE (available within MARK) (Pollock *et al.*, 1990). The Goodness of Fit tests supported assumptions 1 and 2 (Leisnham, 2001). Assumption 3 was met (see Jamieson *et al.*, 2000) and, as with most mark-recapture studies, assumption 4 was assumed to be met.

Estimating adult lifespan

The lifespan of adult weta was calculated using the mean minimum lifespan (MML) method (Ehrlich and Gilbert, 1973; Knight *et al.*, 1999). First, weta that were not recaptured were eliminated from the dataset, and then only those adults from the large tors L1, L2 and L6 that were caught for the first time between the fourth survey in December 1997 and the end of the first field season in April 1997 were included in the analysis. Tor L3 data were excluded since it was only surveyed twice in 1998/99. It was assumed that unmarked individuals caught after the third survey in 1997 had recently moulted to the adult stage (i.e. had not overwintered as adults) and would live their natural lifetimes within the study period, up until early summer in

2000/01. For comparative purposes, mean adult lifespan was also derived from the daily survival estimates produced from the CJS model and calculated as $-\ln(\phi)^{-1}$ (Cook *et al.*, 1967; Lawrence, 1988), with standard errors (SE) given as $\ln(\phi)^{-2} \text{se}(\phi)/\phi$ (i.e. the invariance property of the maximum likelihood estimates).

Other statistical analyses

Monthly differences in the proportions of captures that included newly moulted weta and differences in the proportion of adult males and females surviving across seasons were analysed as contingency tables using Chi-square tests, applying Yates' Correction for Continuity where appropriate. Means \pm standard errors are presented throughout unless otherwise stated. All tests were two-tailed and significance was assigned at the 5% level.

Results

Nymph appearance, moulting pattern and instar interval length

Observations during the 1997/98 season indicated that the smallest nymphs often take refuge under much smaller rocks (i.e. <10 mm thick) than those under which juveniles and adults are found. During the 1998/99 and 1999/2000 seasons most of the small, flat rocks on the study tors were also turned over during each survey to determine when nymphs first emerged. The mean number of nymphs per monthly period shows a clear seasonal pattern on both larger and small tors, rising to a peak in January or February, then declining (Fig. 1).

The timing of moult was determined for 50 weta, based primarily on the pale colour of newly moulted individuals (Gibbs, 1998a). Thirty-seven (74%) of these moultings occurred in January and only one occurred outside of the summer period (November). The percentage of captures of juveniles and adults that involved a newly moulted individual rose sharply to a peak in January, then declined thereafter in all three field seasons (Fig. 2) ($\chi^2 = 66.0$, d.f. = 6, $P < 0.001$, pooled data).

In all, 1269 weta (1006 tagged and 263 painted) were marked on the study tors over the three full field seasons from November 1997 to April 2000 (Table 2). Recapture rates for nymphs marked with paint were low (2.9%) compared with small juveniles marked with paint (34.6%) or larger juveniles marked with tags (46.8%) (Table 2). This was most likely due to nymphs having a shorter instar interval, but their smaller surface area for the paint to adhere to (the paint wears off with time) could also have contributed to the

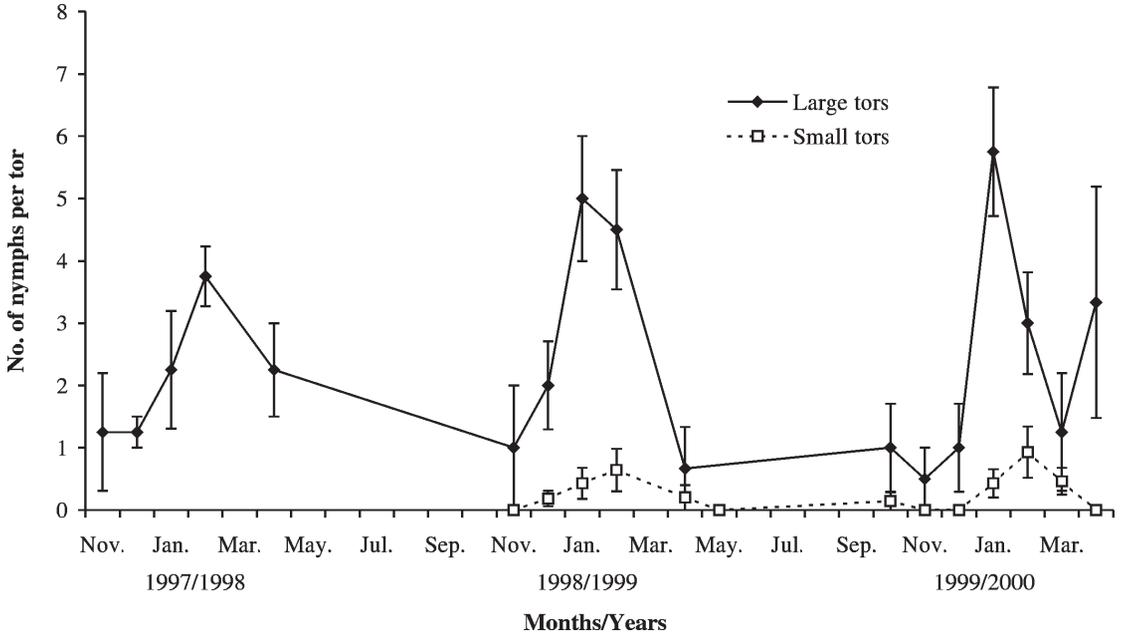


Figure 1. Mean (\pm SE) estimated number of nymphs appearing per month per tor ($n=2-5$) over three field seasons from November 1997 to April 2000.

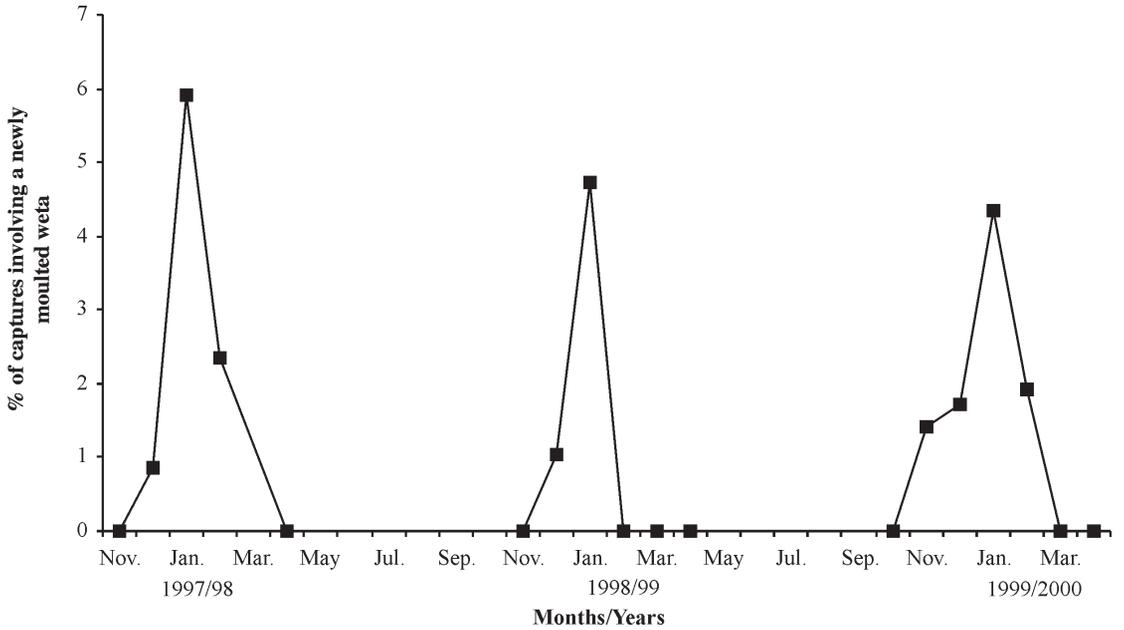


Figure 2. Percentage of the total number of juvenile and adult weta captured per month that involved a newly moulted individual over three field seasons from November 1997 to April 2000.

Table 2. Summary of mark-recapture data of *H. maori* over three field seasons between November 1997 to April 2000.

	Tagged			Painted			Total	
	Males	Females	Males	Females	Unknown	Males	Females	Unknown
Marked individuals								
Adults	234	246	0	0	0	234	246	0
Juveniles ¹	282	244	93	66	0	375	310	0
Nymphs	0	0	0	0	104	0	0	104
Total	516	490	93	66	104	609	556	104
Recaptured individuals								
Adults	142	158	0	0	0	142	158	0
Juveniles	142	104	25	30	0	167	134	0
Nymphs	0	0	0	0	3	0	0	3
Total	284	262	25	30	3	309	292	3
Recapture events								
Adults	445	631	0	0	0	445	631	0
Juveniles	279	213	25	30	0	304	243	0
Nymphs	0	0	0	0	3	0	0	3
Total	724	844	25	30	3	749	874	3

¹Some juveniles are likely to have been marked more than once because they lose their mark when they moult.

low recapture rates.

Some marked juveniles were recaptured with the same tag after an interval of 10 or more months, with a maximum interval of 14.1 months (Fig. 3). We were able to track two juveniles (both about 20% of average adult size) across two of their moults to obtain a more accurate instar interval length. One instar spanned from 10 February to 15 April (just over two months), while the other lasted from 4 February to 10 February the following year (12.4 months).

Adult recapture, survival and longevity estimates

We marked 480 adult weta on the study tors over the three field seasons (Table 2). Of the adults marked in the first season (1997/98), 72% ($n = 229$) were recaptured at some point in the study. Overall, 63% of all adults marked in the study were recaptured. On average, $52 \pm 4\%$ of female and $40 \pm 6\%$ of male weta that were marked and still alive were likely to be recaptured during any one survey of a tor, as derived from the MARK model $\phi_{\text{sex}+\text{time}P}$.

The best-fit model for the combined data set was $\phi_{\text{time}P_{\text{sex}}}$ with over five times better support than the next best model (Table 3). Females had a higher daily recapture rate than males on all of the four largest tors (note the higher number of recapture events for adult females in Table 2) suggesting that they were less likely than males to move from rock slabs into cracks and crevices in the tor column where they could go undetected. Although females had a higher daily recapture rate than males, a similar proportion of marked adult females (64%) and males (61%) were

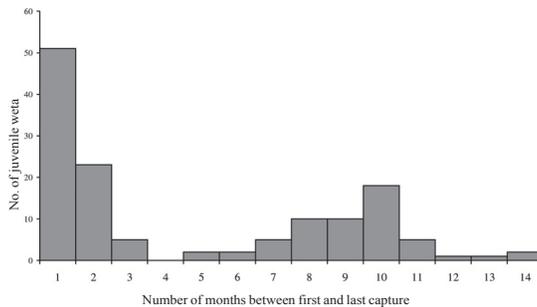


Figure 3. Frequency distribution of minimum instar interval (i.e. number of months between first and last capture of a marked juvenile) on Tors L1, L2 and L6 combined, for juvenile weta marked in 1997/98 ($n = 135$). Minimum instar intervals less than one month were not included.

recaptured at least once over the duration of the study.

The best-fit model indicated that survival varied through time (meaning across the sampling intervals), but was constant between males and females. To determine whether there was a seasonal effect on survival the best fitting time-dependent model ($\phi_{\text{time}P_{\text{sex}}}$) was compared with models in which estimates of survival were grouped into years ($\phi_{\text{year}P_{\text{sex}}}$) and months ($\phi_{\text{month}P_{\text{sex}}}$). The survival model ϕ_{time} ($\text{AICc} = 3444.70$) was still the best compared with ϕ_{month} ($\text{AICc} = 3452.24$) and ϕ_{year} ($\text{AICc} = 3515.10$) for the composite data and all four tors analysed separately (data not shown). This finding indicated that seasonal effects on survival did

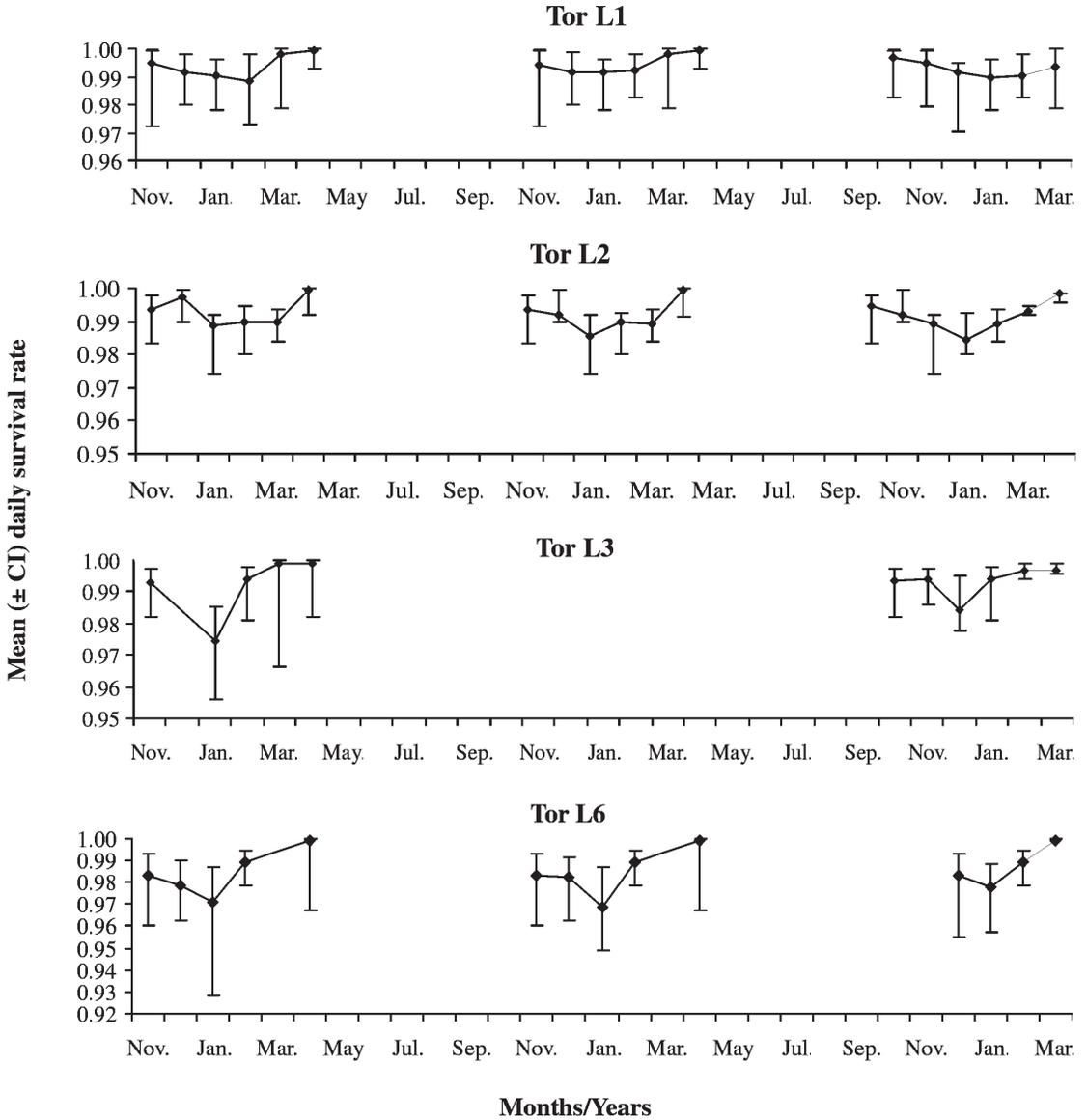


Figure 4. The daily survival rate (ϕ) (\pm 95% CI) of adult weta on the four large tors, when estimates are grouped into months. The value of ϕ could not be estimated in 1998/99 on Tor L3 because of sparse data.

not explain variation in survival better than those of actual sampling intervals, although sampling intervals and monthly intervals did overlap to some extent. Indeed, although there were large confidence intervals around the monthly and yearly estimates, survival appeared to decline slightly to a minimum in summer (January and February) then rise, a pattern seen in each

of the three field seasons on each tor (Fig. 4). The lower survival during January and February appears to be offset by increased rates of recruitment of newly moulted adults at this time (see Fig. 2).

Figure 5 shows the percentage of adult male and female weta that lived for a certain number of months. The distributions were not significantly different, when

Table 3. Results of the mark-recapture analysis using the programme MARK for the initial model set of the composite data. The lowest AICc score indicates the best model. For model notation, see Table 1.

Model	K ¹	AICc ²	Δ _i ³	w _i ⁴
φ _{time} P _{sex}	104	3444.70	0	0.81
φ _{P_{sex}+time}	105	3448.24	3.54	0.14
φ _{time} P _{time}	186	3449.89	5.19	0.06
φ _{sex+time} P _.	104	3458.79	14.09	0.00
φ _{sex+time} P _{sex}	108	3460.20	15.50	0.00
φ _{sex} P _{sex+time}	109	3489.22	44.52	0.00
φ _{P_{time}}	101	3493.27	48.57	0.00
φ _{sex} P _{time}	105	3496.32	51.62	0.00
φ _{time} P _.	100	3501.76	57.06	0.00
φ _{sex} P _{sex}	16	3504.94	60.24	0.00
φ _{sex+time} P _{sex+time}	195	3506.51	61.81	0.00
φ _{sex+time} P _{time}	190	3509.58	64.88	0.00
φ _{P_{sex}}	12	3509.77	65.07	0.00
φ _{time} P _{sex+time}	190	3509.79	65.09	0.00
φ _{P_.}	8	3518.95	74.25	0.00
φ _{sex} P _.	12	3521.62	76.92	0.00
φ _{sex*time} P _{sex}	194	3592.03	147.33	0.00
φ _{sex*time} P _.	190	3594.25	149.55	0.00
φ _{P_{sex*time}}	198	3643.19	198.49	0.00
φ _{sex} P _{sex*time}	202	3647.51	202.81	0.00
φ _{time} P _{sex*time}	282	3682.57	237.87	0.00
φ _{sex+time} P _{sex*time}	287	3695.45	250.75	0.00
φ _{sex*time} P _{time}	280	3702.85	258.15	0.00
φ _{sex*time} P _{sex+time}	285	3710.50	265.80	0.00
φ _{sex*time} P _{sex*time}	361	4007.61	562.91	0.00

¹Number of parameters in model
²Akaike's Information Criterion, adjusted for sample size
³Difference in AICc value from the best model
⁴Akaike weight, indicating the relative support for the models (w_i=e^{-Δ_i/2}/Σe^{-Δ_i/2})

Table 4. Mean (± SE) adult lifespan of male and female weta on the four largest tors in the study site over three field seasons between November 1997 and April 2000, as derived from the daily survival estimates produced from the Cormack-Jolly-Seber models.

	Survival rate ¹	Lifespan (days)
Males	0.9959 ± 0.0006	243 ± 36
Females	0.9949 ± 0.0010	196 ± 38
Total	0.9953 ± 0.0007	212 ± 32

¹Survival rate is the probability that an individual in the tor population on any given day will be in the population on the following day.

the number of weta that were marked in 1997/98 and survived to the end of each season were compared ($\chi^2 = 0.80$, d.f. = 2, (third and fourth season combined), $P > 0.10$; Fig. 5). The average life span in days was 287 for females and 304 for males (297 for sexes combined), and some adults of each sex survived to a second or third breeding season (Fig. 5). One male and one female, on two different tors, were re-sighted in a fourth breeding season. The longest adult lifespan for was 1071 days (2.9 years) for a male and 1043 days (2.9 years) for a female. Average adult lifespans for males and females were also similar when based on daily survival estimates from the Cormack-Jolly-Seber models (Table 4).

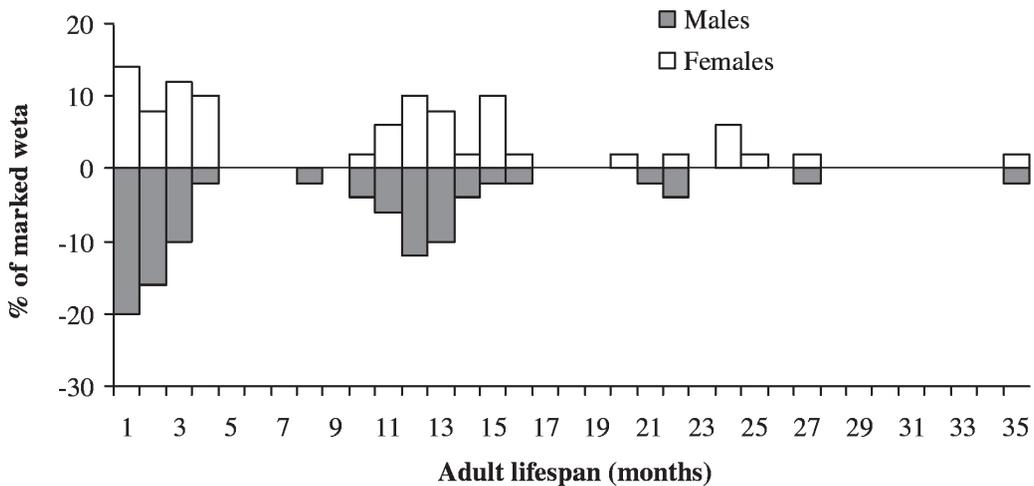


Figure 5. The proportional distribution of adult lifespans (measured in months), calculated by the mean minimum lifespan (MML) method, for adult female (n = 50) and male (n = 50) weta, first marked in 1997/98 on Tors L1, L2 and L6 combined, and subsequently re-sighted at least once.

Discussion

Life cycle of alpine weta

Insects are ectothermic (i.e. their body temperature is reliant on external heat sources), and therefore heat is the main factor driving development when food is not limiting (Gullan and Cranston, 2000). In this study, nymph emergence and moulting appeared to peak for *H. maori* during summer (January), the time when the air, soil and under-rock microhabitat temperatures in the Rock and Pillar Range are at their highest (Bliss and Mark, 1974). Although alpine ranges in the South Island can experience sub-zero temperatures and snow at any time of the year, hatching in January or February is presumably the optimal time in terms of nymphs maximising growth and development. Gravid females were found between February and April and are presumed to oviposit within this period, although ovipositing has not been observed in the wild. In contrast, nymph emergence and moulting in lowland species of tree weta occur over a wider period; females oviposit their eggs in autumn (April–May) and eggs usually hatch in spring (October–December) (Gibbs, 1998a; Stringer, 2001). There may be less selection pressure on lowland species to align growth and hatching with the peak summer temperatures since those species experience a more temperate climate year round.

Survival and longevity

As subjects for mark-recapture study, *H. maori* have an advantage over other *Hemideina* species living in trees because their refugia do not have to be destroyed or altered to extract the weta (see Ordish, 1992; Townsend *et al.*, 1997). However, one potential disadvantage with sampling alpine tree weta is that some individuals could go undetected if they take refuge in narrow crevices within large rock tors (Jamieson *et al.*, 2000). Thirty-nine crevices on the four large tors and seven on the small tors were sampled using an endoscope. We found that 77% ($n = 79$) of the adult weta (sexes undetermined) and 71% ($n = 7$) of the juvenile weta seen were marked. Our analysis revealed that males were less likely to be recaptured during normal surveys presumably because some were more likely to shelter in crevices rather than under flat rocks on the tors. Because *H. maori* show low rates of dispersal (4% of marked adults), only move short distances when they do disperse (361 m on average) (Leisnham and Jamieson, 2002), and are relatively long-lived (this study), the probability of resighting marked adults at least once is still high (63% for all marked weta and 72% for weta marked in the first study season), and comparable to what is found in mark-recapture studies of birds and mammals (see Pollock *et al.*, 1990; Lebreton *et al.*, 1992). Therefore,

as long as the sampling period is sufficiently long, monitoring of all suitably sized rocks on a tor should enable reliable survival estimates of adult weta.

Mark-recapture data from this study suggest adult *H. maori* might go through a seasonal die-off in mid-summer but this coincides with increased adult recruitment. There is no difference in survival between the sexes, and adults are long-lived for an insect; indeed they may be one of the longest-lived weta. It was not uncommon for larger tagged juveniles to be recaptured after 10 months, indicating the instar interval is extremely long. Since *H. maori* freeze solid during periods of very low temperature (Ramløv *et al.*, 1992; Sinclair *et al.*, 1999) and are likely to show little activity for five months of the year (B. Sinclair, University of Otago, Dunedin, N.Z., *pers. comm.*), they might take at least three or four years to reach sexual maturity and live for one, two, or possibly up to four breeding seasons as an adult. One female that was recaptured in 1998/99 had been marked in the spring of 1995/96 as part of an earlier study by Jamieson *et al.* (2000). If she had over-wintered as an adult before being marked she could have lived for at least five breeding seasons. Therefore from the time they hatch alpine tree weta might live on average four to five years and as long as seven to eight years.

In contrast to *H. maori*, most other lowland forest species of weta (giant and tree weta) are thought to have total life cycles of not more than two to three years (Stringer and Cary, 2001), although detailed mark-recapture studies have not been carried out to determine their true lifespan. It is assumed that most adult giant weta (genus *Deinacrida*) die at the end of their first breeding season (McIntyre, 2001; Stringer and Cary, 2001), although, to our knowledge, no mark-recapture studies on giant weta in the wild have been conducted to substantiate this aspect of life history. Lowland species of giant weta may not live as long as *H. maori*, but we would be surprised that an insect as large as a giant weta and with a relatively long development time (at least two years) would die after just one breeding season. In any case, there is a clear need for more mark-recapture studies on weta to determine longevity, especially for the endangered species that are being released on offshore island refuges.

In conclusion, this study has quantified the emergence time, instar interval, survival and longevity of a long-lived tree weta species, *H. maori*, using mark-recapture techniques. Such techniques have been used successfully in a concurrent study measuring dispersal and local extinction and colonization rates of *H. maori* on rock tors (Leisnham and Jamieson, 2002). We recommend that mark-recapture studies be conducted on other weta species. As Armstrong and Ewen (2001) and Armstrong *et al.* (2001) have demonstrated for birds, mark-recapture studies are of

particular interest in New Zealand for determining secondary poisoning effects in 1080 operations. Such studies should help determine survival rates and vulnerability of large invertebrates.

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References

- Armstrong, D.P.; Ewen, J.G. 2001. Estimating impacts of poison operations using mark-recapture analysis and population viability analysis: an example with New Zealand robins (*Petroica australis*). *New Zealand Journal of Ecology* 25(1): 29-38.
- Armstrong, D.P.; Perrot, J.K.; Castro, I. 2001. Estimating impacts of poison operations using mark-recapture analysis: hihi (*Notiomystis cincta*) on Mokoia Island. *New Zealand Journal of Ecology* 25(2): 49-54
- Barrett, P. 1991. *Keeping wetas in captivity*. Wellington Zoological Gardens, Wellington, N.Z.
- Bliss, L.C.; Mark, A.F. 1974. High-alpine environments and primary production on the Rock and Pillar Range, Central Otago, New Zealand. *New Zealand Journal of Botany* 12: 445-483.
- Burnham, K.P.; Anderson, D.R. 1998. *Model selection and inference*. Springer-Verlag, New York, U.S.A.
- Cook, L.M.; Brower, L.P.; Croze, H.J. 1967. The accuracy of a population estimation from multiple recapture data. *Journal of Animal Ecology* 36: 57-60.
- Ehrlich, P.R.; Gilbert, L.E. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. *Biotropica* 5: 69-82.
- Field, L.H. 1993. Observation on stridulatory, agonistic and mating behaviour of *Hemideina ricta* (Stenopelmatidae: Orthoptera), the rare Banks Peninsula tree weta. *New Zealand Entomologist* 16: 68-74.
- Field, L.H. 2001. *The biology of wetas, king crickets and their allies*. CAB International Publishers, Wallingford, U.K.
- Field, L.H.; Sandlant, G.R. 1983. Aggression and mating behaviour in the Stenopelmatidae (Orthoptera, Ensifera), with reference to New Zealand wetas. In: Gwynne, D.T.; Morris, G.K. (Editors), *Orthopteran mating systems: sexual competition in a diverse group of insects*, pp. 120-146. Westview Press, Boulder, U.S.A.
- Gibbs, G. 1998a. *New Zealand weta*. Reed Books, Auckland, N.Z.
- Gibbs, G. 1998b. Why are some weta (Orthoptera: Stenopelmatidae) vulnerable yet others are common? *Journal of Insect Conservation* 2: 161-166.
- Gullan, P.J.; Cranston, P.S. 2000. *The insects: an outline of entomology*. Second Edition. Blackwell Science Ltd., Oxford, U.K.
- Jamieson, I.G.; Forbes, M.R.; McKnight, E.B. 2000. Mark-recapture study of mountain stone weta *Hemideina maori* (Orthoptera: Anostostomatidae) on rock tor 'islands'. *New Zealand Journal of Ecology* 24: 209-214.
- Jamieson, I.G. 2002. The relationship between male head size and harem size in the sexually dimorphic mountain stone weta *Hemideina maori*. *Ecological Entomology* 27: 41-48.
- Knight, A.; Brower, L.P.; Williams, E.H. 1999. Spring remigration of the monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae) in north-central Florida: estimating population parameters using mark-recapture. *Biological Journal of the Linnean Society* 68: 531-556.
- King, T.M.; Wallis, G.P.; Hamilton, S.A.; Fraser, J.R. 1996. Identification of a hybrid zone between distinctive colour variants of the alpine weta *Hemideina maori* (Orthoptera: Stenopelmatidae) on the rock and pillar range, southern New Zealand. *Molecular Ecology* 5: 583-587.
- Lawrence, W.S. 1988. Movement ecology of the milkweed beetle in relation to patch size and structure. *Journal of Animal Ecology* 57: 21-35.
- Lebreton, J.D.; Burnham, K.P.; Clobert, J.; Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67-118.
- Leishnam, P.T. 2001. *Meta-population dynamics of alpine weta*. M.Sc. thesis, University of Otago, Dunedin, N.Z.
- Leishnam, P.T.; Jamieson, I.G. (in press) 2004. The relationship between male head size and mating opportunity in the harem defence, polygynous tree weta *Hemideina maori* (Orthoptera: Anostostomatidae). *New Zealand Journal of Ecology* 28.

- Leisnham, P.T.; Jamieson, I.G. 2002. Meta-population dynamics of a flightless alpine insect *Hemideina maori* (Orthoptera: Anostostomatidae) in a naturally fragmented habitat. *Ecological Entomology* 27: 574-580.
- McIntyre, M. 2001. The ecology of some large weta species in New Zealand. In: Field, L.H. (Editor), *The biology of wetas, king crickets and their allies*, pp. 225-242. CAB International Publishers, Wallingford, U.K.
- Meads, M. 1990. *The weta book: a guide to the identification of wetas*. DSIR Publishing, Wellington, N.Z.
- Moller, H. 1985. Tree wetas (*Hemideina crassicuris*) (Orthoptera: Stenopelmatidae) of Stephens Island, Cook Strait. *New Zealand Journal of Zoology* 12: 55-69.
- Ordish, R.G. 1992. Aggregation and communication of the Wellington weta *Hemideina crassidens* (Blanchard) (Orthoptera: Stenopelmatidae). *New Zealand Entomologist* 15: 1-8.
- Pollock, K.H.; Nichols, J.D.; Brownie, C.; Hines, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 1-97.
- Ramløv, K.H.; Bedford, J.; Leader, J. 1992. Freezing tolerance of the New Zealand alpine weta *Hemideina maori*, Hutton (Orthoptera: Stenopelmatidae). *Journal of Thermal Biology* 17: 51-54.
- Sherley, G. 2001. Conservation of threatened species of weta (Orthoptera: Anostostomatidae) in New Zealand. In: Field, L.H. (Editor), *The biology of wetas, king crickets and their allies*, pp. 521-527. CAB International Publishers, Wallingford, U.K.
- Sinclair, B.J.; Worland, M.R.; Wharton, D.A. 1999. Ice nucleation and freezing tolerance in New Zealand alpine weta and lowland weta, *Hemideina* spp. Hutton (Orthoptera: Stenopelmatidae). *Physiological Entomology* 24: 56-63.
- Stringer, I.A.N. 2001. Reproductive biology and the eggs of New Zealand Anostostomatidae. In: Field, L.H. (Editor), *The biology of wetas, king crickets and their allies*. CAB International Publishers, Wallingford, U.K.
- Stringer, I.A.N.; Cary, P.R.L. 2001. Postembryonic development in tree and giant wetas of N.Z. In: Field, L.H. (Editor), *The biology of wetas, king crickets and their allies*, pp. 398-426. CAB International Publishers, Wallingford, U.K.
- Tabashnik, B.E. 1980. Population structure of Pierid butterflies. *Oecologia* 47: 175-183.
- Townsend, J.A.; Brown, B.; Stringer, I.A.N.; Potter, M.A. 1997. Distribution, habitat and conservation status of *Hemideina ricta* and *H. femorata* on Banks Peninsula, New Zealand. *New Zealand Journal of Ecology* 21: 43-49.
- Trewick, S.; 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.
- White, G.C.; Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: (Suppl.) 120-138.

Editorial Board member: Kay Clapperton