Estimating abundance, age structure and sex ratio of a recently discovered New Zealand tusked weta *Motuweta riparia* (Orthoptera, Anostostomatidae), using mark-recapture analysis.

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Abstract: Estimates of abundance, age structure and sex ratio are essential for monitoring the status of populations. We report the first attempt to reliably estimate these parameters in a population of the recently discovered Raukumara tusked weta (*Motuweta riparia*), which is found almost entirely near streams. On two occasions we searched a 211-m section of creek for 4–5 successive nights and individually marked all weta. We estimated abundance of adults and juveniles using closed-population mark-recapture analysis. The choice of mark-recapture model made a substantial difference to the estimated abundance (116–238) and proportion of juveniles (32–72%). However, no single model was clearly better supported than any other. We therefore used model averaging to account for uncertainty in model choice, giving an estimate of 142 (95% CI 105–231) weta including 56 (95% CI 41–234) adults and 77 (95% CI 46–209) juveniles. This corresponds to a density of 0.11 (95% CI 0.08–0.18) weta per m^2, assuming 3 m of habitat on either side of the creek. Recapture probability was much lower for adults (n = 2) than juveniles (n = 10), possibly caused by a difference in handling (adults were held overnight whereas juveniles were not). Slightly more juvenile males (n = 22) were caught than juvenile females (n = 21), but more adult females (n = 51) were caught than adult males (n = 31), suggesting a potentially higher mortality in males. An initial assessment of population size is crucial when considering the conservation status and management strategy of rare animals, such as the highly endangered Middle Island tusked weta. The immediate practical benefit of the methods developed here is therefore clear. In the long-term, these methods also have important implications for the continued monitoring of trends in other threatened invertebrate populations.

Keywords: age structure; density; invertebrate conservation; mark-recapture analysis; New Zealand; sex ratio.

Introduction

A new species of large tusked weta was recently discovered in the Raukumara Ranges of New Zealand (Gibbs, 1998a). Described as the Raukumara tusked weta (*Motuweta riparia* Gibbs, Orthoptera: Anostostomatidae) (Gibbs, 2002), it is one of three endemic tusked weta and is most closely related to the endangered Middle Island tusked weta (*Motuweta isolata* Johns) (Johns, 1997). *Motuweta riparia* are typically only found within a few metres of small streams, and often jump into the water when disturbed (Gibbs, 1998a; McIntyre, 1998). This behaviour may explain its survival on the mainland given that large terrestrial invertebrates have largely been extirpated by introduced mammals, such as rats, cats and stoats (Moller, 1978; Moors *et al.*, 1992; Sherley, 1998, 2001; Gibbs, 1998b).

Motuweta riparia is currently considered 'secure in the medium term', meaning no immediate conservation action is required (Sherley, 1998). Although its distribution has probably diminished due to deforestation (Sherley, 1998), *M. riparia* has now been reported from at least 25 locations and is believed to exist in large numbers over a wide area (Gibbs, 2002; J. McCartney, pers. obs.). A wide distribution and assumed resilience has led to the conclusion that the Raukumara tusked weta is locally abundant (Burge, 2002). However, the status of local populations is unknown, as research to date has been restricted to a handful of field observations (Gibbs, 1998a, 2002; McIntyre, 1998), and two studies on behaviour and reproductive biology (Burge, 2002, 2005).

In this paper we use mark-recapture analysis to obtain the first reliable estimates of population density, sex ratio and age structure for a Raukumara tusked weta population. Such estimates are needed for monitoring future trends in population structure (or health), and provide the first step toward developing models that can be used to predict populations' responses to management. While this research is relevant to the population under study, it also provides methods that can be extrapolated to other populations of the same or related species. In particular, methods developed here may be utilized to assess and monitor primary or translocated populations of rare species such as the highly endangered Middle Island tusked weta.

Methods

Study site

The study site is in indigenous bush on private land in the Wairata area of the Waioeka Gorge Road, at the South Western edge of the Raukumara Ranges, Bay of Plenty, North Island, New Zealand (38° 18'S, 177° 20'E). We restricted the study site to 3 m from the stream (at normal flow) because previous studies (Gibbs, 1998a; McIntyre, 1998) indicated that weta were unlikely to be found further away.

Our site was centred on Weta Creek, a previously unnamed first/second order tributary to the Wairata Stream, and extended 3 m from the creek on each side. The stream is in a narrow valley, with near-vertical sides 0–4 m from the stream's edge. From its junction with Wairata Stream, Weta Creek runs for 211 m before it reaches a large 4-m tall waterfall, which we deemed the upper limit of our site. The defined study area is therefore 1266 m^2 excluding the stream itself.

The area around the stream consists of broadleaf forest, similar to other sites where tusked weta are found (Gibbs, 1998a; McIntyre, 1998; Burge, 2002), and the stream has unstable slopes and small flood terraces similar to those described by Burge (2002) and Gibbs (2002). The stream has an average gradient of about 5°.

Field surveys

We visited the study area from 15–19 May 2002 and 11–14 June 2002. Each night we started searching at the base of Weta Creek and worked our way to the waterfall. Searches started between 1800 and 1900 (1–2 h after dusk), irrespective of weather conditions, and took about 3–4 h. We carefully scanned the banks and surrounding vegetation using headlamps, with one observer on each side of the stream. We were also careful to scan isolated rocks in the stream, and looked as far from the stream as we could without straying more than 3 m from its edge. We were careful not to disturb the area, and tried to focus our lights no more than a few metres in front of us. Every 5 m we looked back for weta that may have been missed. We placed a marker (labelled flagging tape on a 30 cm galvanised steel peg) every 5 m along the stream, and used these to define the searched area.

Capture, marking and re-sighting

We captured weta by grasping the pronotum or by placing a container over the weta and scooping it up. Newly found juveniles were held in a cloth, measured and marked (see below for details), and then released where they were found. Adults were more difficult to process than juveniles (due to the precision required for measuring secondary sexual organs) so we collected them into small plastic aerated containers containing some damp fern or moss. We inserted a galvanised steel peg into the ground where each new weta was captured or sighted and marked each weta's identification number on a label and attached it to the peg. The pegs had two functions: they were used to ensure weta were released exactly where captured and also as marking points to measure movement distances for when weta were later recaptured. The adult weta were then taken back to our hut (shearing quarters at Wairata Forest Farm) where they were marked and measured the following day.

For marking weta, we used a 'White Out' pen to cover a substantial area of the pronotum (Trewick and Morgan-Richards, 2000; Christensen, 2003) with white correcting fluid. When dry, we wrote an identification number on the white patch with a fine black permanent marker. Only one weta from 11 had been recaptured between field trips (21 days) and although the label seemed undamaged we subsequently tested the marking technique in the laboratory on five captive tusked weta (three females and two males). The environment was reconstructed realistically with gravel and stones from the actual field site and a flowing river. We found that labels lasts at least three months without visible damage to either the weta or marking (J. McCartney, unpubl. data).

Additionally, we recorded the age (adult/juvenile) and sex of each weta (see Gibbs, 1998a; McIntyre, 1998; and Stringer and Carey, 2001, for characteristics), and released them that night at their exact capture locations. When a marked weta was encountered, its identity was recorded along with the date and location, but it was not disturbed. They were therefore "recaptured" in terms of mark-recapture analysis but were not literally recaptured.

Analysis

We used closed-population mark-recapture analysis to estimate the number of adults and juveniles within the study area, and then divided by the area to obtain population densities. A closed population analysis should be reliable for our system, as it is highly unlikely that there would be movements to or from the site [see Efford (2004) for a method for estimating density when such movements take place]. To ensure a closed population (no births, deaths, immigration or emigration), we only used the data from 15–19 May 2002 when estimating population size and age structure. There were too few data to consider both sex and age in this analysis. We therefore simply measured the sex ratios of weta captured, combining data from May and June, and did not estimate sex-specific capture probability.

We estimated abundance using the "closed captures" model in Program MARK 2.1 (White and Burnham, 1999). The encounter history for each individual showed when it was captured or re-sighted (indicated by 1), or not detected (indicated by 0), over the five nights from 15–19 May 2002. Individuals were divided into six groups in the encounter histories file, with juveniles constituting one group, and adults divided into five groups, according to the night on which they were first captured. The division of adults into these groups was necessitated by the fact that adults were not released until about 24 h after capture, meaning they were unavailable for re-sighting on the next night. To allow for this, the re-sighting probability for each group of adults was fixed to zero for the night after capture.

We considered three factors that could affect the probability of a weta being captured or detected: age, *a* (adults or juvenile); time, *t* (differences among nights); and behaviour, *b*. In this case behaviour refers to the effect of capture on subsequent detection, in other words, the probability of initial capture is different from the probability of recapture (Otis *et al.*, 1978). In our study, capture might directly result in changes in a weta's behaviour due to the previous capture/marking event. For example, weta may have a lower tolerance to head-lamps after an initial capture, promoting greater aversion behaviour during future recapture attempts. Initial capture may also indirectly affect recapture probability, for example, due to the white patch on the pronotum. We considered the possibility that the effect of capture might occur only in adults (b_{ad}), given that adults were held much longer than juveniles, but also considered the possibility that it would have the same effect in both ages (a+b), or would have different degrees of effect ($a\times b$). We considered ten different models in total for the factors affecting capture probability (Table 1), and compared these models using Akaike's Information Criterion corrected for small sample bias (AICc) (e.g. Burnham and Anderson, 2002).

Under each of these models, MARK gives separate estimates for the number of weta in each group. These values can be added to obtain estimates of the total number of adults or the total population. However, obtaining confidence limits for these totals is more complicated. We first obtain confidence intervals for $\beta_.$, where $\beta_.$ is the natural logarithm of $U_.$, the total number of animals that were never caught. Using the

Table 1. Number of *Motuweta riparia* at Weta Creek estimated by 10 different closed-capture models fitted to data collected from 15–19 May 2002. Factors assumed to affect capture and re-sighting probability under different candidate models include: a = age (adult or juvenile); b = behaviour (recapture probability different from initial capture probability, where b_{ad} means this effect applies only to adults); t = time (night of survey); × indicates interactions between factors, whereas + indicates additive effects only. The number of parameters (K) in each model is given and ΔAIC_c is the difference in AIC_c value from the best model. Akaike weights (w_i) indicate the relative support for the models ($w_i = e^{-\Delta_i/2} / \sum e^{-\Delta_i/2}$) and $\hat{N}$ is an estimate of population size of juveniles ($\hat{N}_{juv}$) and adults ($\hat{N}_{ad}$) within the searched area. $\hat{N}_{juv}/\hat{N}$ is the proportion of adults in the observed population. Overall estimates based on model averaging are given as the average.

Model	K	Δ_i	w_i	$\hat{N}_{juv}$ (95% CI)	$\hat{N}_{ad}$ (95% CI)	$\hat{N}$ (95% CI)	$\hat{N}_{juv}/\hat{N}$
$a+b_{ad}$	9	0.00	0.35	76 (53–136)	46 (41–92)	122 (109–141)	0.62
b_{ad}	8	0.72	0.24	68 (49–114)	71 (54–109)	139 (108–199)	0.49
$a\times b$	10	1.84	0.14	118 (39–3391)	46 (41–92)	164 (141–197)	0.72
t	11	3.25	0.07	85 (58–147)	90 (77–109)	176 (154–203)	0.48
.	7	3.96	0.05	89 (61–156)	95 (81–114)	185 (163–213)	0.48
$a+t$	12	4.12	0.04	75 (52–133)	142 (109–190)	216 (181–263)	0.35
b	8	4.33	0.04	57 (42–118)	59 (48–85)	116 (97–155)	0.49
a	8	4.33	0.04	76 (53–136)	162 (126–213)	238 (200–288)	0.32
$a+b$	9	5.82	0.02	56 (41–137)	79 (54–145)	135 (103–205)	0.41
$a\times t$	16	8.56	0.00	74 (51–131)	143 (110–192)	217 (141–197)	0.34
Average				77 (46–209)	56 (41–234)	142 (105–231)	0.58

delta method (Seber, 1982), the standard error of $\beta_.$ is approximated by

$$SE\left(\hat{\beta}_.\right)=\frac{1}{\hat{U}_.}\sqrt{\left\{\sum_{i=1}^{k}\hat{U}_i^2 SE\left(\hat{\beta}_i\right)^2+2\sum_{i=1}^{k}\sum_{j=1+1}^{k}\hat{U}_i\hat{U}_j Cov(\hat{\beta}_i\hat{\beta}_j)\right\}}$$

where $\hat{U}_i$ and $\hat{\beta}_i$ are the estimates for each of *k* groups, and $Cov(\hat{\beta}_i\hat{\beta}_j)$ is the covariance among estimates for different groups (all of these estimates are available from the MARK output). The approximate 95% confidence limits are given by $\hat{\beta}_. \pm 2SE(\hat{\beta}_.)$, and these are back transformed to obtain confidence intervals for $U_.$. These are then added to $n_.$, the number of individuals caught, to obtain a 95% confidence interval for $N_.$, the total population size.

The estimated population size depends on the model used. The best estimates come from the model with the lowest AICc, but the choice of model is ambiguous if two or more models have similar AICc values. We therefore used model averaging (Buckland *et al.*, 1997) to obtain estimates and confidence intervals that took uncertainty in model selection into account. We again start by obtaining an estimate and standard error for β, then back transform to get the estimate and 95% confidence interval for *N*. The averaged estimate for β is given by

$$\hat{\beta}_{ave}=\sum w_i\hat{\beta}_i$$

where w_i is the weight given to model *i* based on its AICc (Table 1) and $\hat{\beta}_i$ is the estimate under that model and $SE(\hat{\beta}_i)$ the model-based standard error. The unconditional standard error is given by

$$SE\left(\hat{\beta}_{ave}\right)=\sum\left\{w_i\sqrt{SE(\hat{\beta}_i)^2+\left(\hat{\beta}_i-\hat{\beta}_{ave}\right)^2}\right\}$$

This value not only averages the standard errors among models, but also accounts for uncertainty in parameter estimation due to ambiguity of model choice.

Results

We captured, weighed and marked 125 weta, including 82 adults and 43 juveniles. Three additional juveniles were captured, but one escaped before marking and two were too small to identify their sex with certainty.

Density and age structure

Over the five consecutive nights used for closed-capture abundance estimation, we caught 77 weta comprising 40 adults and 37 juveniles. There were a total of 12 recaptures over this period, including two adults that were recaptured once, eight juveniles that were recaptured once, and one juvenile that was recaptured twice.

The estimated number of weta in the study area ranges from 116 to 238 depending on the closed-capture model used, and the estimated proportion of juveniles in the population ranges from 0.32 to 0.72 (Table 1). However, the higher population estimates come from models that poorly explain the data, and therefore have little support. Based on model averaging, which takes the support of the models into account, the study area is estimated to have 142 (CI 95% 105–231) weta, with 77 (58%) of these being juveniles (95% CI 46–209), and 56 (95% CI 41–234) being adults. Dividing this estimate by 1266 m^2 (the area sampled) gives an estimated density of 0.11 (95% CI 0.08–0.18) weta per m^2.

The best three models do not differ greatly in their support (Δ_i <2), meaning all should be considered plausible (Table 1). The common factor in the three models is the inclusion of a behaviour effect in adults, i.e. recapture probability is different from initial capture probability (Table 2). The three models differ in whether initial capture probabilities are different for adults and juveniles and whether a behaviour effect is included for juveniles. The initial capture probabilities are lower in the juveniles than in the adults, except in the third model (b_{ad}) where they are the same. The recapture probabilities are consistently lower in the adults than the juveniles. When examining all three models, behaviour effect in juveniles is in the opposite direction as the adult effect, i.e. the probability of capturing a juvenile is either the same or increases after initial capture, whereas the probability of capturing an adult decreases (Table 2). The uncertainty about this effect creates uncertainty in our abundance estimate, i.e. estimating separate capture and recapture probabilities

Table 2. Estimated nightly probability of initial capture (*p*) and recapture (*c*) for juvenile and adult *Motuweta riparia* under the three best models, with 95% confidence intervals.

Model	$\hat{p}_{juv}$	$\hat{c}_{juv}$	$\hat{p}_{ad}$	$\hat{c}_{ad}$
$a+b_{ad}$	0.12 (0.07–0.21)	0.12 (0.07–0.21)	0.29 (0.15–0.49)	0.03 (0.01–0.13)
b_{ad}	0.14 (0.09–0.23)	0.14 (0.09–0.23)	0.14 (0.09–0.23)	0.03 (0.01–0.13)
$a \times b$	0.07 (0.01–0.65)	0.13 (0.07–0.23)	0.29 (0.15–0.49)	0.03 (0.01–0.13)

almost doubles the estimated number of juveniles, and greatly reduces the precision of this estimate ($M_{a \times b}$, Table 1).

Sex ratio

Of the 82 adults captured, 31 were male and 51 were female, giving a female-biased sex ratio (Z = -1.96, CI = 0.273–0.483). For the 43 juveniles captured, the sex ratio was nearly 1:1 with 22 males and 21 females (Z = -1.96, 95% CI = 0.362–0.661).

Discussion

An estimated 142 weta along a 211-m section of creek tentatively suggests a healthy population, consistent with Sherley's (1998) conclusion that *M. riparia* is secure in the medium term. A density of 0.11 weta per m^2 is lower than the maximum density noted for anostostomatid weta of similar body size. For example, Moller (1985) found about one tree weta (*Hemideina crassidens*) per m^2 on Stephens Island (New Zealand). *Motuweta riparia* might be expected to be at lower density, being a ground-dwelling species and therefore potentially having a smaller amount of habitat per m^2.

Gibbs (1998a) reported finding two *M. riparia* per person-hour of searching in the lower Mangatutara Stream which is less than half that found in our study of 4.2 weta per person-hour (125 weta in 15 h searching by two people). This could be interpreted to mean that the densities at the two sites were different with our site having more than twice as many weta as that of Gibbs' site. However, our mark-recapture analysis showed that detection rate could change substantially after initial capture, meaning catch-per-effort indices may be highly biased unless the search is restricted to a single night. Such indices will also be biased according to differences in habitat, conditions, and observer skill. We recommend that researchers should avoid such indices, and should use sampling methods that allow absolute estimates of abundance and can account for changes in detection probability (Borchers *et al.*, 2002).

Our results show that even when robust methods, such as closed-population mark-recapture, are used, attention must be paid to the appropriate model for estimating abundance. Model averaging is an effective method for dealing with uncertainty associated with model choice (Buckland *et al.*, 1997), but this applies only if the candidate models incorporate the key factors affecting capture and recapture probability. Our comparison of ten closed-capture models gave strong evidence that recapture probability was substantially lower than initial capture probability in adults and tentative evidence that the opposite effect occurred in juveniles. We also found tentative evidence that initial capture probability was higher in adults than in juveniles. The differences between adults and juveniles are most easily attributed to differences in handling regime and body size, i.e. only adults were held overnight, perhaps causing them to hide when they detect approaching light or to remain in their galleries for longer periods after release. The smaller body size of juveniles would be expected to make them harder to detect, and the increase in detection after initial capture may be due to the white patches on their backs for marking. A key issue in future research should be to reduce the uncertainty about these effects, since reduced ambiguity in model selection will allow greater precision in estimating abundance. If holding adults overnight does in fact substantially reduce their recapture probability, then avoiding this procedure would greatly improve our ability to estimate abundance.

The rules used for calculating the size of the study site add an additional source of uncertainty to our density estimates. For example, our calculated area of 1266 m^2 would increase to 1802 m^2 if the stream was included. This could be justified given that some *M. riparia* were found on rocks in the centre of the creek. We excluded the creek area since *M. riparia* do not forage or nest under water. However, a less subjective measure might be to calculate the number of *M. riparia* per linear distance of stream edge (0.34 weta per m in our study).

The sex ratio of weta found was 1:1 for juveniles, but significantly female-biased for adults. The latter is similar to the female bias reported by Jamieson *et al.* (2000) and Leisnham *et al.* (2003) for the stone weta *Hemideina maori*. A more recent study of *H. maori* (Joyce *et al*., 2004) showed that female survival rate exceeded that of males over several seasons. These findings imply that there could be higher mortality in males, possibly due to male-male combat associated with the polygynous mating systems, of *Hemideina* species (Gwynne and Jamieson, 1998; Field and Deans, 2001; Field and Sandlant, 2001). Such a mating system probably also occurs in *M. riparia*, given that the tusks are only found in males. Alternatively, a harem defence mating system could result in a biased detection probability among males, with less dominant males tending to be more cryptic. This is consistent with the female bias of *H. maori* which also have a harem defence mating system (Leisnham *et al.,* 2003). It is therefore unclear at this point whether it is correct to assume that males and females have equal detection probabilities, indicating our data reflect a truly female-biased sex ratio, or whether the bias could be due to behavioural differences. This question could potentially be addressed with further mark-recapture data, although a substantial data set would be required to model the effect of sex and individual heterogeneity on capture probability.

Another issue to address is the assumption that *M. riparia* only occur near first and second order streams. New Zealand's fauna evolved in the absence of mammalian predators (except two bat species), naturally predisposing most native species to an inability to cope with the novel hunting strategies of adventive species (e.g. stoats, ferrets, rats and mice). The resilience of *M. riparia* has previously been attributed to its aquatic escape response (Gibbs, 1998a, 1998b, 2002). It is one of few Orthoptera known to submerge itself in water when disturbed (Gwynne 2001, pp 87-88 and references cited therein) and presumably evolved well before the introduction of exotic mammals. It is, however, currently unclear whether *M. riparia* are largely confined to stream edges due to deliberate habitat requirements, or because this is now the only environment where they can effectively escape mammalian predators.

McIntyre (1998) and Gibbs (1998a) concentrated their searches within a few metres of streams after finding few *M. riparia* elsewhere. We also confined our searching to within three metres of the water's edge, while visually scanning to a distance of about ten metres. Most weta found during searches were within three metres of the edge, and none more than four metres. However, away from our site, we found two other weta about 20 m and 50 m from the nearest stream. Although most recaptured weta were found within ten metres of their capture point, *M. riparia* are able to travel at least 80 m in one night (J. McCartney, unpubl. data) meaning the two weta found away from the stream may normally have been found by its edge. It is also possible, however, that *M. riparia* are found at considerable distances from stream edges but at densities difficult to detect. Mark-recapture methods could potentially be used to compare riparian and forest environments, but estimating extremely low densities would probably require an impractical level of effort.

Mainland restoration programmes (Saunders and Norton, 2001) may provide an opportunity to assess whether the distribution and/or abundance of *M. riparia* can be increased through control of introduced mammals. Regardless of whether *M. riparia* has declined due to introduced predators, some monitoring is needed to assess the status of local populations over time. Likewise, populations of rare invertebrates such the highly endangered Middle Island tusked weta, where original populations no longer exist in healthy numbers, will need monitoring if re-introduced into protected areas. Mark-recapture analysis provides an effective and relatively inexpensive way of accomplishing this.

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