

SHORT COMMUNICATION

Mark-recapture study of mountain stone weta *Hemideina maori* (Orthoptera: Anostostomatidae) on rock tor 'islands'Ian G. Jamieson, Mark R. Forbes¹ and E. Brooke McKnight

Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand (E-mail: ian.jamieson@stonebow.otago.ac.nz)

¹Department of Biology, 2240 Herzberg Laboratories, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6

Abstract: Mountain stone weta (*Hemideina maori*) on the Rock and Pillar Range in the South Island, New Zealand, are found primarily in cavities under flat rocks on isolated outcrops or 'tors'. We marked 66 adult weta on one tor and 30 adults on an adjacent tor and recorded their location during the summer and for the following three years to obtain baseline data on survival, longevity, dispersal, and movement within tors. It was not uncommon for adult weta to live for two to three years. Most marked weta were resighted at least once, usually under the same rock. Few weta moved further than the rock adjacent to where they were first captured and only one dispersed to a neighbouring tor. On one tor, a relatively stable group of 6–8 females and 2 males was resighted during most of the summer period under one large rock. An analysis of our mark-recapture methodology and results indicates that *H. maori* may be an appropriate species for investigating population structure in a metapopulation context as well as local mate competition.

Key words: survival; longevity; dispersal; Stenopelmatidae; New Zealand.

Introduction

Weta are a group of nocturnal, flightless Orthopterans, some of which are among the largest insects in the world (Gibbs, 1998). All seven species of the tree weta genus *Hemideina* (Orthoptera: Anostostomatidae, formerly Stenopelmatidae) are endemic to New Zealand (Morgan-Richards, 1995; Johns, 1997). All but one of these species have pronounced sexual dimorphism for cephalic weaponry; the head and jaws of adult males are twice the size of those of adult females (Meads, 1990; Gibbs, 1998). This appears to be the result of sexual selection for males to defend aggressively a group of reproductive females in a refuge site such as in a tree or rock cavity (Field and Sandlant, 1983; Moller, 1985; Gwynne and Jamieson, 1998).

Tree weta are common around homes and gardens in many parts of New Zealand (Gibbs, 1998), yet few if any detailed ecological field studies involving marked individuals have been carried out on them. Although reproductive and behavioural studies have been conducted on captive animals (Field and Sandlant, 1983; Barrett, 1991; Ordish, 1992; Field, 1993), very

little is known about survival, longevity, dispersal, and social organisation of tree weta in the wild (Trewick and Morgan-Richards, 1995). Their relatively large size for an insect allows tree weta to be easily tagged. This, plus their flightlessness, potentially makes them ideal species for mark-recapture studies.

The mountain stone weta, *Hemideina maori* (Pictet and Saussure), is unusual for a tree weta in that it occupies a treeless environment. In the Rock and Pillar Range, they are found primarily in cavities under rock slabs which have broken off from schist outcrops or 'tors' (Meads, 1990; King *et al.*, 1996; Gwynne and Jamieson, 1998). Tors range in size from a single rock a few metres in width to three to four large rock columns 20–30 m in diameter. Tors are separated by alpine meadows where there are no rocks and presumably no weta. Therefore each rock tor could essentially represent an island habitat, but we presently do not know the degree of isolation between such islands. Further, Gwynne and Jamieson (1998) measured weta on several of these tors and found a positive correlation between male head size and harem size. However, the time individual males or females

remained resident in these groups was not determined because the weta were unmarked.

As part of a long term study of the ecology and behaviour of *H. maori*, we marked adult weta on two tors and recorded their location during the summer period as well as over the following three years. The objectives were to collect baseline life history information of adult male and female survival, longevity (i.e. length of life after initial marking as an adult), degree of isolation between tors, and movement within tors. We also assess our mark-recapture methodology and data for its eventual use in a metapopulation analysis (Hanski and Gilpin, 1997) of spatial variation amongst 'island' populations of an alpine weta.

Study Area and Methods

The study was conducted in the Rock and Pillar Range (1450 m asl) northwest of Dunedin. The study site was approximately 1 km east of McPhee's Rock (Infomap 260-H43, 748220) in the southern part of the range. For a general description of the habitat and vegetation, see Bliss and Mark (1974).

We selected a tor which had approximately 25 loose rocks and was known from previous surveys to have numerous weta (T. King, University of Otago, Dunedin, N.Z., *pers. comm.*), as the main study site (Tor 1). All liftable rocks on the tor were numbered and adult weta were marked from late spring (23 November), 1995. Frequent surveys (6 to 21 days between visits) were carried out until 30 January 1996, with one further one in autumn (2 May), 1996. Two surveys were conducted the following season on 28 November 1996 and 18 March 1997, and then biweekly throughout spring and summer in 1997-98 and 1998-99, as part of another larger study. During our second trip to the study area (29 November 1995), we initiated marking on an adjacent tor (Tor 2) 200 m away from Tor 1, but only managed to mark weta under about half of the available rocks. All rocks on Tor 2 were surveyed in subsequent years, which allowed us to estimate annual survival of the weta we marked, but not their movements within tors.

Adult females were identified by their long, upward curved and pointed ovipositor and adult males by their long, inward curved cerci. Immatures had shorter, straighter ovipositors and cerci respectively, in females and males. During surveys, rocks were carefully lifted, all weta removed and placed in plastic containers, and then the rock placed back in the same position. The sex and maturity of the weta were recorded and the head width of males was measured using Vernier calipers. Adults were marked by first lightly abrading the waxy cuticle in the centre of the pronotum with an emery board. A tag was then attached with a small drop of

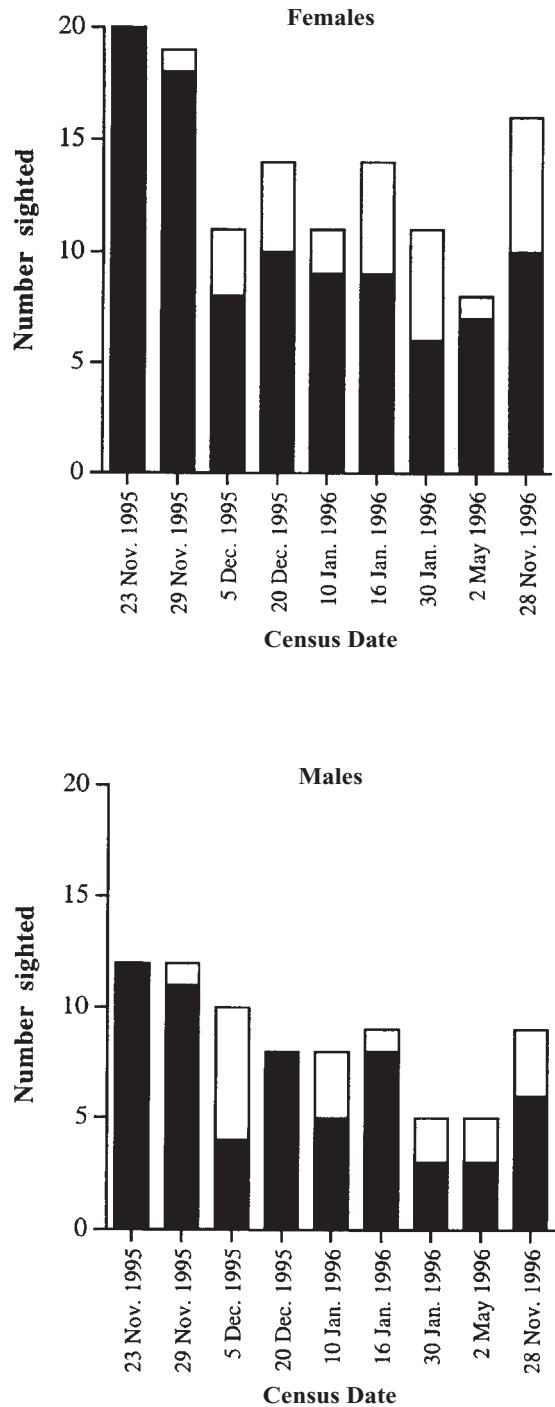


Figure 1. Total number of adult female and male weta sighted under rocks over nine census periods. Open portion of bar indicates the number of new (unmarked) weta.

superglue [10 second drying Selleys Supa Glue (Selleys Chemical Co. Pty. Ltd.)]. Tags were paper with a three-digit number (001–999) printed on them, which were covered with clear waterproof epoxy glue. Marking and measuring of each weta took approximately 15 min., after which it was released under the edge of the same rock from which it came and observed until it had moved freely back into its cavity.

Results

We marked a total of 40 adult female and 26 adult male weta on Tor 1 during seven sampling trips between 23 November 1995 and 30 January 1996. This represents a female to male sex ratio of 1.5:1 which is not significantly different from 1:1 ($\chi^2=2.97$, 1 d.f., $0.05 < P < 0.10$). The trend toward slightly more adult females remained throughout the summer period and into the following year (Figure 1). The average ratio of immature females to males was 0.78:1 ($\chi^2=0.50$, 1 d.f., $P > 0.10$). The greatest proportion of adult males (48%) and adult females (50%) were marked during the first survey. Fewer than 50% of these were known to be still alive by 20 December 1995 and 30 January 1996, respectively (Figure 2). Although females appeared to have a higher survival rate than males, further analysis, using the programme ‘Mark’ (White and Burnham, 1999), of all individuals tagged during the study period revealed large confidence intervals around the survival estimates, with the effect of being female increasing the probability of survival from 0.69 (31%) to 2.31 (131%).

We continued to survey Tor 1 and Tor 2 for marked weta for the following three summers. The data

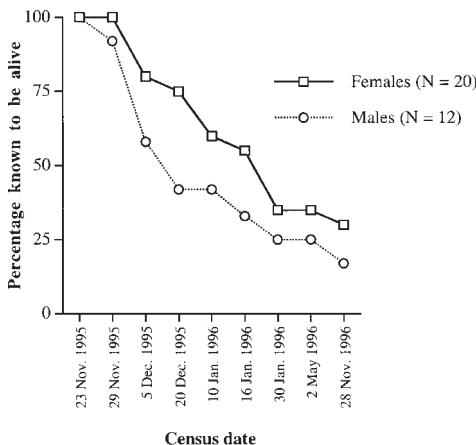


Figure 2. Percentage of the total number of adult female and male weta known to be alive after being marked during the first survey period.

from these two tors indicated that it is not uncommon for adults to survive for two to three breeding seasons (Figure 3). One female on Tor 2 was resighted over four breeding seasons. The proportion of females and males that survived to the second or third breeding seasons were not significantly different on either tor (range of Z values = 0.07–1.19, all P values > 0.10). The proportion of the adults marked on Tor 1 in November: 8/34; December: 3/13; and January: 9/19 that were still alive in the second breeding season did not differ significantly ($\chi^2=3.71$, 3 d.f., $P > 0.10$). The corresponding values for Tor 2 were November: 1/10; December: 1/9; and

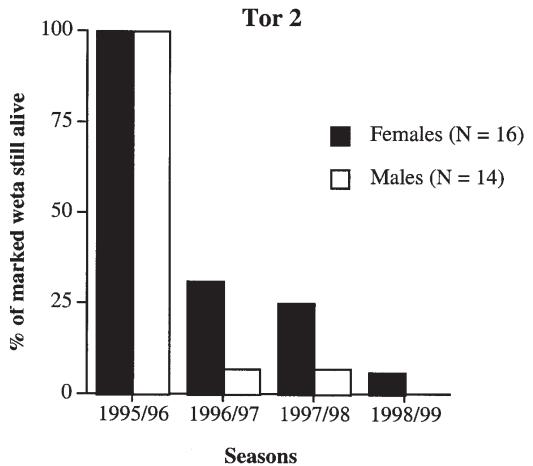
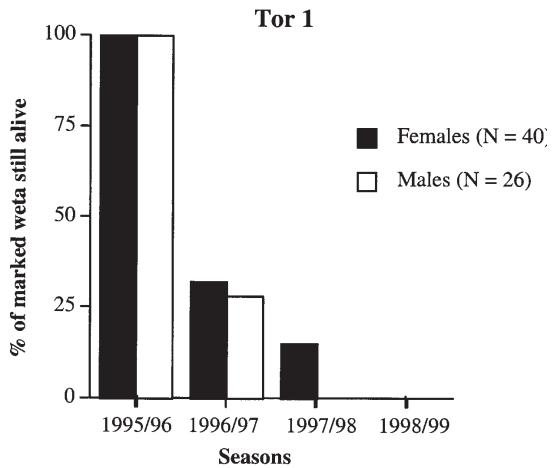


Figure 3. Percentage of adult female and male weta on Tor 1 and Tor 2 that were alive up to three years after being marked in 1995/96.

Table 1. The number of marked adult female and male weta that were resighted between 29 November 1995 and 30 January 1996 and either remained under the same rock, moved at least once to an adjacent rock, or moved at least once beyond an adjacent rock but still within the same tor.

Sex	Remained under same rock	Moved to adjacent rock	Moved within tor	Total resighted
Females	14 (56%)	8 (32%)	3 (12%)	25
Males	8 (47%)	5 (29%)	4 (24%)	17

January: 4/11; but sample sizes were too small for statistical comparison.

Most marked females (83%) and males (74%) were resighted at least once during the summer period (1995-96) and, in the majority of cases, were resighted under the same individual rock (Table 1). Approximately one third moved at least once to a nearby rock and fewer still moved a greater distance but still within the same tor complex. Despite occasional sampling of three smaller surrounding tors and intensive sampling of the closest large tor (Tor 2), only one marked weta (a female) had moved from Tor 1 to Tor 2 in the following summer.

The majority (63%) of the 25 rocks on Tor 1 that were turned over on any one survey had no weta, but one (Rock no. 3) had 6-8 adult females and 2-4 adult males. Several marked females were repeatedly found under Rock no. 3 from the beginning of the census

period, with four new adult females becoming resident from 10 January onwards (Table 2). For most of the census period, only two males (#628, #664) were present under Rock no. 3 (two other males (#629, #672) disappearing after 29 November, see Table 2). Two new males had taken over the rock by 30 January. One of the males that disappeared and was presumably evicted after 29 November (#672) had a larger head size (head width; 14.18 mm) than either #628 (11.86 mm) or #664 (12.52 mm) and was the largest male we marked. Interestingly, male #672 reappeared under Rock no. 3 in our autumn census in May.

Discussion

Tree weta are good subjects for mark and recapture studies because they do not have to be actively trapped and therefore are not subject to trapping bias or ineffective trapping techniques (Pollack *et al.*, 1990). Sampling and collecting tree weta from under rocks rather than in tree holes has its advantage in that the refugia does not need to be enlarged or destroyed to extract the weta (see Ordish, 1992; Townsend *et al.*, 1997). The one potential problem with surveying *H. maori*, however, is that some individuals could go undetected or disappear if they take shelter in cracks or crevices in the large rock tors. We suspect that male #672, which reappeared under Rock no. 3 in May 1996 after disappearing in November 1995, must have moved into a crevice in the main rock tor. We hope to determine

Table 2. Individual females and males that were found under Rock no. 3 for each census period in 1995/96. Tag numbers of individual females and males are indicated by the 3-digit numbers, unmarked individuals by 'UM', rock numbers where tagged individuals were found when not under Rock no. 3 are given in brackets; and individuals that were never seen again including in surveys from subsequent years are shown by a dash.

Date of census	Females →														
23 Nov.	665	625	644	660	641	627	634	[1]	[14]						
29 Nov.	665	625	644	660	641	627	634	[1]	[14]						
5 Dec.	665	625	[2]	660	641	[?]	[?]	643	645						
20 Dec.	665	625	644	660	641	[?]	[?]	643	645	[1]					
10 Jan.	665	625	644	[11]	-	[?]	[?]	643	645	003	010				
16 Jan.	665	625	[?]	-	-	[?]	[10]	643	645	003	010	022			
30 Jan.	665	-	[?]	-	-	[?]	-	[?]	-	003	010	[2]	224		
2 May	665	-	644	-	-	[?]	-	[?]	-	003	010	022	024	224	UM
	Males →														
23 Nov.	628	664	672	629		[12]									
29 Nov.	628	664	672	629		[12]									
5 Dec.	628	664	[?]	-	[2]	[?]									
20 Dec.	628	664	[?]	-	[8]	[12]									
10 Jan.	628	664	[?]	-	[?]	[?]									
16 Jan.	628	664	[?]	-	018	[11]									
30 Jan.	[?]	-	[?]	-	-	667	225								
2 May	628	-	672	-	-	[?]	225	UM							

the extent to which weta are using cracks and crevices by examining these with an endoscope, as well as occasionally surveying our study tors at night and recording the ratio of marked to unmarked adults seen out from under cover. During one overnight trip on 16 January 1996, we observed six adults out in the open between 12:30 – 1:30 am, and all were marked. Unmarked adult weta were found during almost all sampling periods (see Figure 1), and although a few of these could have been adults that were not found on our initial surveys, we suspect most had recently moulted from the last juvenile instar. We observed several teneral adults (as determined by a lack of pigment) and juveniles in the process of moulting during the overnight trip mentioned above. Even though we are unlikely to recapture all of the marked weta that were still alive during any one sampling trip, the results of our surveys show that rock slabs associated with tors are used extensively by weta, and monitoring this habitat over a long time should provide minimum estimates of survival of marked weta.

Our results also indicated that dispersal by adults between 'island' tors may be relatively uncommon. This, combined with the fact that they are relatively long-lived insects, meant that the probability of resighting marked adults was high. Although the weta undoubtedly become stressed when handled, several hours elapsed after they have been returned and released under their rock cavity and before they would normally become active after dusk. In addition, surveys were confined to at most once every six days. Therefore, handling is unlikely to have any short-term adverse effects on their movement or residency patterns. The repeated resightings of individuals under the same rocks supports that tagging and subsequent re-capture(s) did not appear to affect the behaviour of weta over the short or long term. In contrast, after marking a group of Wellington tree weta *H. crassidens* (Blanchard) in a tree cavity with paint, Ordish (1992) noted that all members of the group vacated the cavity.

Although the proportion of marked males and females that were known to be still alive in the next breeding season were similar, adult males on Tor 1 appeared to disappear at a faster rate during the summer and tended to be less abundant than adult females. Observation of *H. maori* under laboratory conditions indicated that males can injure and sometimes kill opponents in fights over possession of rocks with adult females (Fache, 1998). Therefore the lower resighting rate of males, at least under the rock slabs, may be the result of intrasexual competition.

Competition among males for access to reproductive females is a consequence of females aggregating under relatively few rocks (Gwynne and Jamieson, 1998). Gwynne and Jamieson (1998) found

a significant positive correlation between male head size and harem size, but the relationship was relatively weak on several tors (r_s values between 0.22–0.45). In our sample from Tor 1, the male with the largest head size was not a long-term resident under the rock with the largest harem during the breeding period. We are now in the process of collecting tissue samples from adults that reside under rocks with large harems, and from the nymphs occupying the smaller rocks surrounding the harem, for parentage analyses to determine if the period of residency is a good predictor of offspring paternity.

In terms of longevity, it was not uncommon for adult weta to live for two breeding seasons and a few may live three to four seasons. One female was resighted over a four-year period, but could have lived for at least five breeding seasons since she was initially marked in spring and thus may have over-wintered as an adult. Other lowland/forest species of tree weta take one or two years to reach adult stage (Barrett, 1991; Gibbs, 1998; M. Morgan-Richards, University of Otago, Dunedin, N.Z., *unpubl.*). Because mountain stone weta freeze solid during winter (Ramlov *et al.*, 1992; Sinclair *et al.*, 1999) and are probably inactive for at least five months of the year (B. Sinclair, University of Otago, Dunedin, N.Z., *pers. comm.*), they may take at least three to four years to reach sexual maturity.

In conclusion, these preliminary mark-recapture data provide a useful basis for initiating a long-term investigation of whether *H. maori* fit the criteria of a true metapopulation (Hanski and Gilpin, 1997), particularly in the context of the possible extinction and recolonisation of small tors.

Acknowledgements

We would like to thank Graham Wallis, Darryl Gwynne and Tania King for providing advice and helping with some of the preliminary weta surveys. Many people have assisted with the later surveys, and in particular we would like to thank Will Koning, Michelle Fache, Letisha Sheridan, Brent Sinclair, Paul Leisnham and Alvin Setiawan. Permission for access to the area and to carry out the work was provided by the Department of Conservation and Mr. W. Howell. Mary Morgan-Richards and Steve Trewick made helpful comments on a draft of the manuscript, and Richard Barker assisted with running the 'Mark' software programme. The University of Otago provided funding for the study and a travel grant to MRF. Further financial assistance to IGJ during the preparation of the manuscript was provided by Queen's University Biology Station and by a Natural Sciences and Engineering Research Council of Canada grant to MRF.

References

- 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.
- Fache, M.L. 1998. *Alternative mating strategies and male dimorphism in the alpine weta*, *Hemideina maori* (Orthoptera: Stenopelmatidae). B.Sc. (Honours) thesis, University of Otago, Dunedin, N.Z.
- 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.; 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, USA.
- Gibbs, G. 1998. *New Zealand weta*. Reed Books, Auckland, N.Z.
- Gwynne, D.T.; Jamieson, I.G. 1998. Sexual selection and sexual dimorphism in a harem-polygynous insect, the alpine weta (*Hemideina maori*, Orthoptera Stenopelmatidae). *Ethology and Ecology & Evolution* 10: 393-402.
- Hanski, I.; Gilpin, M.E. (Editors) 1997. *Metapopulation biology: Ecology, genetics and evolution*. Academic Press, London, UK.
- Johns, P. 1997. The Gondwanaland weta: Family Anostostomatidae (formerly in Stenopelmatidae, Hemicidae or Mimnermidae): Nomenclatural problems, world checklist, new genera and species. *Journal of Orthoptera Research* 6: 125-138.
- 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.
- Meads, M. 1990. *The weta book: A guide to the identification of wetas*. Department of Scientific and Industrial Research Land Resources, Lower Hutt, N.Z.
- Moller, H. 1985. Tree wetas (*Hemideina crassicuris*) (Orthoptera: Stenopelmatidae) of Stephens Island, Cook Strait. *New Zealand Journal of Zoology* 12: 55-69.
- Morgan-Richards, M. 1995. A new species of tree weta from the North Island of New Zealand (Hemideina: Stenopelmatidae: Orthoptera). *New Zealand Entomologist* 18: 15-23.
- Ordish, R.G. 1992. Aggregation and communication of the Wellington weta *Hemideina crassicuris* (Blanchard) (Orthoptera: Stenopelmatidae). *New Zealand Entomologist* 15: 1-8.
- Pollack, K.H.; Nichols, J.D.; Brownie, C.; Hines, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 1-97.
- Ramlov, 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.
- Sinclair, B.J.; Worland, M.R.; Wharton, D.A. 1999. Ice nucleation and freezing tolerance in New Zealand alpine and lowland weta, *Hemideina* spp. Hutton (Orthoptera: Stenopelmatidae). *Physiological Entomology* 24: 56-63.
- 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 (Supplement): 120-138.