

Dramatic increases in weta (Orthoptera) following mammal eradication on Maungatautari – evidence from pitfalls and tracking tunnels

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Abstract: Opportunities now exist to establish pest-free areas on the mainland of New Zealand by eradicating introduced mammals from within predator-proof-fenced areas. This has increased opportunities to investigate how the native insect fauna responds to the eradication of introduced mammals. We examined the response of weta populations to mammal eradication in a before-after-control-impact (BACI) experiment within the southern enclosure on Maungatautari. A novel monitoring technique (footprint tracking tunnels) was used in combination with a conventional technique (lethal pitfall traps) to monitor weta populations. Within 2 years after mammal eradication, there were dramatic increases in weta pitfall captures, weta tracking rates and the incidence of weta footprinting per tracking card (proportion squares tracked out of 100). The mean number of weta per pitfall increased 12-fold (95% credible interval 7–20) after mammal eradication for adult *Hemideina thoracica* and 52-fold (95% credible interval 30–89) for other weta. Before and immediately after mammal eradication approximately equal proportions of juveniles, subadult and adult weta were caught in the pitfall traps. The age structure of weta caught in pitfall traps changed after mammal eradication, with the percentage of adult weta in the samples increasing markedly from 30% in summer 2004/05 to 66% in summer 2008/09. The sex ratio of weta caught also changed, the percentage of females in pitfall traps increasing from 25% in summer 2004/05 to 55% in summer 2008/09. The two monitoring techniques have different advantages and disadvantages, which are discussed, but key advantages of tracking tunnels are that they are non-lethal and time-efficient. Counting squares tracked per card gave a more sensitive and precise indicator of response to mammal eradication than simply recording presence and absence of tracks, but required much more processing time.

Keywords: artificial weta roosts; conservation; predation

Introduction

New Zealand's native invertebrate fauna has largely evolved in the absence of mammalian predators and competitors. Most evidence on impacts of mammals on invertebrate populations has come from rodent eradications on islands (Green 2002; Rufaut & Gibbs 2003; Sinclair et al. 2005). This research has been complemented by studies investigating the effects of rat control on the mainland (Spurr 1996; Hunt et al. 1998; King 2007), including several studies examining the potential adverse effects resulting from rodent poisoning (Spurr & Berben 2004; Powlesland et al. 2005). Eradication of mammals (particularly rodents) has resulted in altered invertebrate abundance (Green 2002; CHW unpubl. data), species richness (Sinclair et al. 2005), and diversity (Hutcheson 1999), as well as increased adult activity (Rufaut & Gibbs 2003). Such responses have not always been increases (Craddock 1997; Sinclair et al. 2005; CHW unpubl. data) and many invertebrate groups have shown no response to rodent control.

The native New Zealand invertebrate fauna is characterised by a high proportion of species that are large-bodied, long-lived, flightless, often ground-dwelling, and nocturnal (Gibbs 2010). For example, the two families of weta (Orthoptera: Anostomatidae and Rhabdophoridae) form a distinctive iconic component of the fauna. There are four New Zealand genera within the family Anostomatidae: *Deinacrida* are commonly known as giant weta; *Hemideina* are tree weta; *Hemianthus* are ground weta; and *Anisoura* and *Motuweta*

are the tussock weta. The cave weta belong to the family Rhabdophoridae and are both more speciose and less well described. These large wingless orthopterans have unfortunately often succumbed to the invasion of mammals in New Zealand (Watts et al. 2008a). Small introduced mammals, particularly rodents, are considered the main predators of weta in New Zealand forests (Innes 1979; Jones & Sanders 2005; King & Murphy 2005; Ruscoe & Murphy 2005). Weta, for example, were found in 39–76% of ship rat (*Rattus rattus*) stomachs (Innes 2005), and the density and behaviour of *Hemideina crassidens* is apparently detrimentally affected by introduced predators (Rufaut 1995). In addition, *Hemideina* species are both relatively common and large in size, and they are being used as indicator species for monitoring the 'health' of native forests and the impact of poisoning programmes targeting introduced mammals (Spurr & Drew 1999). Despite this, monitoring weta behaviour and population dynamics in the wild is difficult, particularly as they are nocturnal and often arboreal (Trewick & Morgan-Richards 2000).

A variety of monitoring methods, such as pitfall and Malaise traps, have been used to monitor the impacts of mammals on invertebrate populations in New Zealand (Hutcheson 1999; Green 2002; Sinclair et al. 2005; CHW unpubl. data), depending on the invertebrate group selected for study, but no standard technique has emerged. These methods guarantee rapid acquisition of considerable collections and provide researchers with specimens. However, lethal trapping is not suitable in locations where there are taxa of conservation significance

(Spear 2004; Bowie et al. 2006). These are inappropriate for monitoring large insects like weta and particularly when they are rare or threatened. Existing non-lethal techniques used to monitor weta include spotlighting at night, which takes considerable effort (Watts et al. 2008b), and the use of artificial weta roosts for monitoring *Hemideina* species (Trewick & Morgan-Richards 2000; Green 2005; Bowie et al. 2006; Kelly 2006). Recently, Watts et al. (2008b) reported that footprint tracking tunnels could be used effectively to detect the adults of the giant weta *Deinacrida heteracantha* and to distinguish their presence from other weta species. Footprints were detected in 72% of tracking tunnels over three consecutive nights and 89% of these appeared during the first night. Results also suggested that using peanut butter as an attractant bait increased the detection rate of adult *Deinacrida heteracantha* (Watts et al. 2008b).

Mammals (mainly rodents) have now been eradicated from many large offshore islands (Towns & Broome 2003; Ombler 2004) and increasing numbers of mammal-free areas are being created on the mainland using predator-proof fences to exclude mammals. This has increased the number of places for investigating how the native invertebrate fauna changes and responds to the removal of mammals. In addition, tracking tunnels set for rodents are routinely used in fenced sanctuaries, for detecting the presence and density of small mammals (Brown et al. 1996; Blackwell et al. 2002; Gillies & Williams 2002; Speedy et al. 2007) and so we took the opportunity to make an additional use of the tracking tunnels at Maungatautari in the central Waikato to detect weta footprints and compare the results with weta caught in lethal pitfall traps. The Maungatautari Ecological Island Trust (MEIT) has a vision 'to remove forever, introduced mammalian pests and predators from Maungatautari, and restore to the forest a healthy diversity of indigenous plants and animals not seen [there] in our lifetime' (MEIT website www.maungatrust.org).

The research on Maungatautari had three objectives. The first was to determine how weta populations responded to mammal eradication in a lagged before-after-control-impact (BACI) experiment within the southern enclosure on Maungatautari. The BACI experiment gave an initial estimate of the response of weta populations to mammal eradication for the first two years within the southern enclosure, and then mammal removal occurred within the adjacent forest, giving an opportunity to test whether that area showed similar effects with the predicted 2-year lag. The second objective was to compare tracking tunnels as a non-lethal technique for monitoring weta populations with the more commonly used but lethal pitfall trapping. The third objective was to determine if, using the lengths of their footprints alone, *Hemideina thoracica* could be distinguished from the other three weta species also present on Maungatautari – *Hemiandrus pallitarsis*, *Gymnoplectron acanthocerum* and *Gymnoplectron* sp. 1.

Methods

Study area and species

Maungatautari (3400 ha) is an extinct andesitic volcanic cone covered with a range of native forest from lowland rimu-tawa (*Dacrydium cupressinum*, *Beilschmiedia tawa*) forest to montane forest dominated by tawari-kamahi (*Ixerba brexioides*, *Weinmannia racemosa*) and tawheowheo (*Quintinia serrata*), and is surrounded entirely by farmland

(Clarkson 2002). MEIT completed a 47-km Xcluder™ pest-proof fence (www.xcluder.co.nz) around Maungatautari and then attempted to eradicate pest mammals from within the fenced area. As a pilot for mammal eradication on the larger mountain, two smaller enclosures were constructed and the mammals removed from the 35-ha (northern) and 65-ha (southern) enclosures.

During September–October 2004, 13 mammal species (ship rat, mouse, cat, stoat, weasel, ferret, hedgehog, rabbit, hare, possum, red deer, goat and pig) were targeted for eradication using brodifacoum-laced bait spread aerially during two operations across the fenced enclosures (Speedy et al. 2007). In the southern enclosure, a total of four ship rats (all female) and five mice (*Mus musculus*) were detected using tracking tunnels and removed by trapping in the 20 months following the second bait application, although further mice were almost certainly poisoned by brodifacoum baits in bait stations deployed in March 2006 to specifically target increasing mouse detections (Speedy et al. 2007). No other mammal species are known to have survived the two aerial bait applications and the southern enclosure, the focus of our study, has been considered completely pest-free since July 2006 (Speedy et al. 2007). Aerial poisoning to eradicate mammals from the main Maungatautari reserve adjacent to the southern enclosure began on 1 November 2006.

Distinguishing weta species apart from their footprints

Four species (*Hemideina thoracica*, *Hemiandrus pallitarsis*, *Gymnoplectron acanthocerum* and *Gymnoplectron* sp. 1) of weta are commonly found on Maungatautari. Therefore, these weta species were chosen for footprinting and individuals were captured on Maungatautari and held in captivity overnight while their footprints were recorded. Footprints were recorded for adult (9–10th instar), subadult (5–8th instar), and juvenile (<5th instar) age classes. The footprints of *Gymnoplectron acanthocerum* and *Gymnoplectron* sp. 1 were combined into 'Gymnoplectron species' due to their similar small-sized footprints. Footprints were examined for a total of eight individuals of each of *Hemideina thoracica*, *Hemiandrus pallitarsis* and *Gymnoplectron* species per age class. The size (mm) of their tarsal pad prints was recorded after they had walked over tracking cards in controlled conditions. This was repeated five times for each weta and the two cards with the clearest prints were used to obtain average tarsal print length from up to five prints per card. Footprints of the protarsal, mesotarsal and metatarsal pads can be distinguished from each other as they are each distinctively shaped and the orientation of the pads in relation to other each is characteristic. The length (mm) of the tarsal pad from the right leg of each weta was also measured and a record made of the species, sex and age class. Means \pm 95% confidence intervals were calculated for the length of the right protarsal, mesotarsal and metatarsal pads and the associated right tarsal pad prints for each species and age class of weta so that differences between species and age class were apparent by inspection.

Sampling weta using tracking tunnels

'Black Trakka' tunnels (500 \times 100 \times 100 mm; Gotcha Traps, 2 Young Street, RD2, Warkworth, NZ) were placed within the southern enclosure. These were primarily to detect introduced mammals after the eradication, but we examined the tracking cards retrospectively for weta footprints. Each tunnel contained a card pre-inked using a specially formulated ink (Gotcha Traps)

that improves the definition of footprints and baited with peanut butter. The tunnels were placed at 50-m spacing on parallel lines 50 m apart with a varying number of tunnels per line, and cards were collected weekly from 14 October 2004 to 2 November 2006 (cards collected after that date were not kept). For analysis we used the 13 lines with >10 tunnels, and used data for four sampling occasions in October–November for each of the three years (2004, 2005 and 2006), giving a total of 2388 cards from 199 tunnels over 12 sampling occasions.

Each card was first examined by CW for the presence of weta footprints. To determine whether the incidence of weta footprints per tracked card increased with time since mammal eradication, CW also recorded the proportion of 100 squares tracked on each card. To do this, a piece of transparency film with 100 15 × 15 mm squares in four randomly placed groups of 25 (covering 75% of tracking card area) was placed over the tracking card, and each square examined for weta footprints.

Sampling weta using pitfall traps

Ten pitfall traps were placed at 5-m intervals along each of four 50-m transects, two within the southern enclosure and two outside the enclosure. The transects were about 600 m apart, and were all in similar rimu–tawa forest. Pitfall traps consisted of 100-mm-deep plastic cups containing 100 ml of 50% monopropylene glycol, and were left for one month on each sampling occasion. The weta were stored in 70% ethanol and later counted and identified. We collected pitfall samples on three occasions from November to February in each of four summers (2004/05, 2006/07, 2007/08 and 2008/09), giving 12 sampling occasions. Initial sampling began immediately after the mammal eradication in the southern enclosure, so gives a BACI design where weta numbers were expected to increase in the southern enclosure with the other two transect lines serving as a control. Sampling after November 2006, when eradication was done on the whole mountain, allowed us to assess whether a similar increase then occurred on the other lines, giving us greater power to distinguish the effect of the eradication from other possible changes in conditions over time.

We also attempted to determine ages of weta caught to assess how introduced predators affected age structure. However, even distinguishing adults is complicated by the occurrence of size polymorphism in adult males, particularly in *Hemideina thoracica*. Adult females, which are in their 10th instar, can be distinguished from subadults by ovipositor length. In contrast, males can become sexually mature at the 8th instar or later so age was estimated from the development of their anal cerci (Gibbs 2001). Weta were scored as adult (8–10th instar), subadult (5–7th instar) and juvenile (<5th instar) based on relative size and the degree of development of the abdominal terminalia (as above). The age structure of the weta sampled is presented as the proportion of adult, subadult and juvenile weta in the sample caught over the 3-month trapping period each year. In addition, the sexes of adult and subadult weta were recorded.

Modelling changes in abundance indices

We modelled changes over time in three parameters: the mean number of weta caught per pitfall (N); the probability of a card being tracked by a weta (p); and the mean proportion of squares tracked on tracked cards (θ). The product $p\theta$ gives the probability of an individual square being tracked, hence p

and $p\theta$ are alternative indices of weta density/activity obtained from the tracking cards. We did separate analyses for two categories of weta, adult *Hemideina thoracica* and all other weta, as this was the only clear distinction that could be made from tracking cards (see Results).

We assessed the significance of mammal eradication by comparing models where: (1) parameters were constant over time; (2) parameters varied randomly among years; and (3) parameters changed as a function of time since mammal eradication (Table 1). For pitfalls, we considered alternative models where changes over time followed an exponential function or a logistic function, the latter indicating density dependence. Because all datasets had repeated samples from individual sampling sites (pitfalls or tunnels) nested within transect lines, we included random effects of transect lines and sampling sites in all models. Year was included as a random effect in type 2 models, and individual sampling occasion as a random effect in type 2–3 models. Models were coded in WinBUGS 1.4 and fitted to the data using Bayesian updating (Spiegelhalter et al. 2003). We compared models based on DIC (Spiegelhalter et al. 2002), and removed random effects that did not improve the models.

Except for logistic models, all models considered were generalised linear mixed models (Table 1). Pitfall data were modelled using a Poisson error term and log link function as is standard for abundance data. Tracking presence-absence data were modelled using a Bernoulli error term and a log(–log) link function. Data on proportions of squares tracked on marked cards were arcsin square root transformed, as is standard for proportional data (Sokal & Rohlf 1981), then modelled using a normal error term and linear link function. Random effects were taken to be normally distributed.

Assuming numbers captured in pitfalls are proportional to abundance, the log-linear relationship with time since eradication (t) is expected under exponential growth, as $\log(N_t) = \log(N_0) + rt$, where N_0 is initial abundance and r is population growth rate. Under the logistic growth model

$$N_t = \frac{K}{1 + \left(\frac{K - N_0}{N_0}\right) e^{-rt}}$$

where K is carrying capacity (Ricklefs 1973). This can be converted to the function $\log(N_t) = \alpha + \log(\beta) + \log(1 + (\beta - 1)e^{-t})$ (Table 1) where $\alpha = \log(N_0)$ and $\beta = K/N_0$. The log(–log)-linear relationship between tracking probability and time since eradication (Table 1) is also expected under exponential growth if the effective encounter area around each device (Leslie & Davis 1939) is assumed to stay constant with respect to density, hence we refer to this as an ‘exponential model’ in Tables 2–3. We also found that the log(–log) link consistently gave a better fit to the tracking data than the standard logit link.

Results

Distinguishing between footprints of adult *Hemideina thoracica* and other weta

Adult *Hemideina thoracica* had significantly larger protarsal, mesotarsal and metatarsal pad lengths than any other weta species and age class measured (Fig. 1). There was no difference between subadult *Hemideina thoracica*, adult *Hemiandrus pallitarsis*, and adult *Gymnoplectron* species

Table 1. Comparison of models fitted to data on (a) numbers of weta in pitfall traps; (b) presence of weta marks on tracking cards; and (c) intensity of marking on tracked cards (measured by dividing cards into 100 quadrats and noting the number of squares marked by weta). Exponential and arcsin-linear models assume continuous increases in weta density (or activity) after mammals were eradicated; the logistic model assumes a density-dependent increase; year models assume random annual variation; and constant models assume no changes over time. All models initially incorporated hierarchical random variation among transect lines (4 pitfall lines, 13 tracking lines) and individual devices (40 pitfalls, 199 tracking tunnels), and random variation among sampling occasions within years (3 for pitfalls, 4 for tracking). However, these effects were removed if the variance was insignificant.

Data	Model name	Structure ¹	Adult tree weta				Other weta			
			\bar{D}^2	\hat{D}^3	pD^4	DIC^5	\bar{D}^2	\hat{D}^3	pD^4	DIC^5
(a)										
Pitfalls	Logistic	$\log(N) = \alpha + \mu_D + \log(\beta(1 + (\beta - 1)e^{-rt}))$	1024.0	1012.8	11.2	1035.1	1309.8	1287.3	22.4	1332.2
	Exponential	$\log(N) = \alpha + rt + \mu_L + \mu_D$	1063.5	1050.5	13.0	1076.4	1430.2	1407.2	22.9	1453.1
	Year	$\log(N) = \alpha + \mu_Y + \mu_L + \mu_D$	1044.2	1028.5	15.7	1059.9	1353.8	1328.5	25.3	1379.0
	Constant	$\log(N) = \alpha + \mu_L + \mu_D$	1168.6	1156.3	12.3	1180.9	1775.3	1753.5	21.8	1797.1
(b)										
Tracking	Exponential	$\log(-\log(1-p)) = \alpha + rt + \mu_D$	2966.3	2865.3	101.0	3067.3	2548.6	2453.1	95.5	2644.1
	Year	$\log(-\log(1-p)) = \alpha + \mu_Y + \mu_D$	2969.2	2867.4	101.8	3071.0	2544.7	2449.3	95.4	2640.1
	Constant	$\log(-\log(1-p)) = \alpha + \mu_D$	3142.1	3054.4	87.7	3229.8	2850.0	2770.0	80.0	2929.9
(c)										
Intensity	Arcsin-linear	$\sin^{-1}\sqrt{\theta} = \alpha + rt + \mu_L + \mu_D + \mu_T + \epsilon$	-1128.0	-1178.3	50.3	-1077.6	-1157.2	-1286.2	129.0	-1028.3
	Year	$\sin^{-1}\sqrt{\theta} = \alpha + \mu_Y + \mu_L + \mu_D + \mu_T + \epsilon$	-1130.9	-1183.6	52.7	-1078.2	-1157.8	-1287.1	129.3	-1028.6
	Constant	$\sin^{-1}\sqrt{\theta} = \alpha + \mu_Y + \mu_L + \mu_D + \mu_T + \epsilon$	934.7	928.7	6.0	940.7	1290.7	1274.9	15.9	1306.6

¹ N , mean number of weta per pitfall; p , probability of a tracking card being tracked; θ , mean intensity of marking per tracked card; α , intercept terms; r , growth rates with time; β , ratio of carrying capacity to initial density; μ_L , random effect of transect line; μ_D , random effect of individual device (pitfall or tracking tunnel); μ_Y , random effect of year; μ_T , random effect of sampling occasion; ϵ , residual sampling error.

²Posterior mean of the deviances.

³Deviance with nodes set at their posterior means.

⁴Effective number of nodes, given by $\bar{D} - \hat{D}$

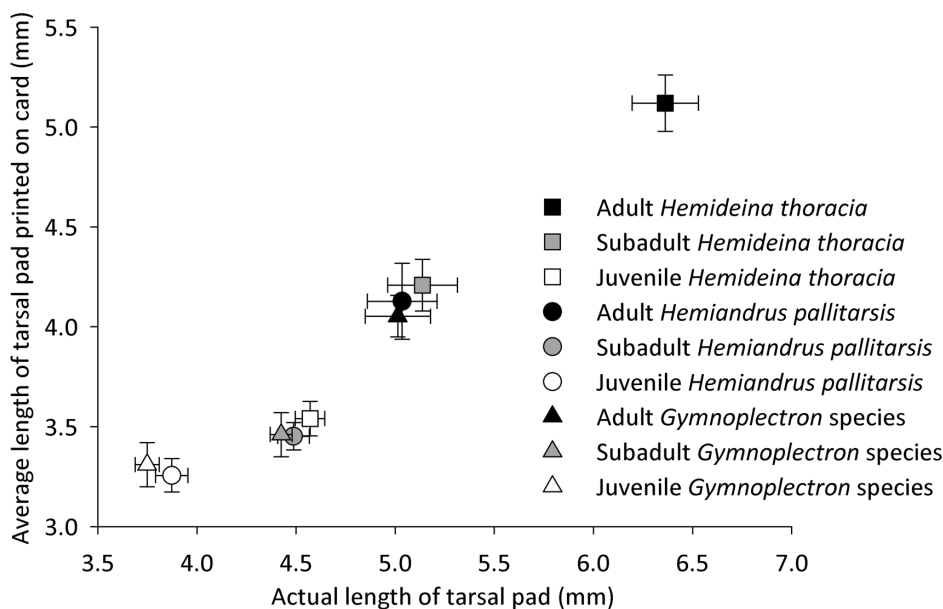
⁵Deviance Information Criterion (given by $\hat{D} + 2pD$), with lower DIC indicating better models.

Table 2. Estimates and 95% credible limits for nodes (parameters) in models for changes in weta pitfall capture rates and tracking rates after eradication of mammals. Model structures are shown in Table 1, and modelled trends over time are shown in Figs 2–3.

Data	Node	Adult tree weta				Other weta			
		Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%
Pitfalls (logistic)	α	-2.27	0.27	-2.87	-1.81	-2.99	0.28	-3.59	-2.47
	r	0.24	0.06	0.15	0.39	0.34	0.04	0.27	0.44
	β	11.99	3.37	7.43	20.15	51.71	14.77	30.08	88.98
	σ_D	0.15	0.09	0.01	0.34	0.24	0.06	0.13	0.36
Tracking (exponential)	α	-0.75	0.06	-0.88	-0.63	-0.40	0.05	-0.51	-0.30
	r	0.036	0.003	0.030	0.042	0.044	0.003	0.039	0.050
	σ_D	0.42	0.04	0.33	0.51	0.37	0.04	0.30	0.47
Intensity (arcsin-linear)	α	0.35	0.02	0.30	0.40	0.46	0.06	0.36	0.58
	r	0.030	0.001	0.027	0.033	0.030	0.003	0.024	0.036
	σ_L	0.006	0.006	0.000	0.020	0.053	0.015	0.030	0.090
	σ_D	0.157	0.003	0.150	0.163	0.170	0.003	0.164	0.177
	σ_T	0.048	0.014	0.027	0.084	0.107	0.030	0.066	0.181
	σ_E	0.029	0.008	0.011	0.044	0.069	0.007	0.056	0.082

Table 3. Comparison of the four different techniques for monitoring weta. No further time is required to set and collect cards from tracking tunnels for weta monitoring if tunnels are already set to monitor mammals.

Monitoring technique	Minutes taken to set out in the field	Minutes taken to collect data from field	Lab analysis	Total time involved	Dependent on weta activity	Specimen obtained	Lethal	Bait	Chemicals
Weta footprints in 10 tracking tunnels					Yes				
– Scoring as presence-absence on card	70	35	15	120		No	No	Yes	Yes (ink)
– Scoring as squares tracked per card	70	35	60	165					
10 lethal pitfall traps	180	90	330	600	Yes	Yes	Yes	No	Yes
10 hours of spotlight searching at night	-	600	60	660	Yes	Yes	No	No	No
10 artificial roosts for tree weta	60	200	-	260	Yes	Yes	No	No	No

**Figure 1.** Relationship between actual length of tarsal pad and average length of tarsal pad printed on a tracking card ($n = 8$). Adult *Hemideina thoracica* prints were significantly larger than ‘other weta’ prints recorded. Bars show 95% confidence intervals. Note that results for metatarsal pad only are presented; data showed similar trends for protarsal and mesotarsal pads.

(Fig. 1). The footprints of juvenile *Hemideina thoracica*, subadult *Hemiandrus pallitarsis*, and subadult *Gymnoplectron* species were not distinguishable from each other (Fig. 1). Juvenile *Hemiandrus pallitarsis* and *Gymnoplectron* species had substantially smaller footprints than any other age class measured (Fig. 1).

The lengths of tarsal pads were larger than their footprints on the card for all 72 weta examined, regardless of species, sex or age class. On average, the prints for protarsal, mesotarsal and metatarsal pads on the cards were 55% ($\pm 1.4\%$), 67% ($\pm 1.7\%$) and 82% ($\pm 1.0\%$) of the actual lengths of the footprints.

Changes in tracking rates after mammal eradication

The probability of a card being tracked clearly increased after mammal eradication, and the trends are explained well by the exponential model (Tables 1–2, Fig. 2). Under this model, the probability of tracking increased from 0.38 (95% credible interval 0.34–0.41) at the time of the eradication to 0.70 (0.66–0.73) 26 months later for both adult *Hemideina*

thoracica, and from 0.49 (95% credible interval 0.46–0.53) to 0.88 (0.86–0.90) for other weta. If we assume the logarithm of tracking probability to be directly proportional to population density, as is expected under the exponential model, then the proportional increase in density at any time t is given by $\log(p_t)/\log(p_0)$. This gives 2.5- and 3.2-fold increases in density for adult *Hemideina thoracica* and other weta respectively over the 26 months, and these are much smaller increases than suggested by the pitfall data (see below).

Taking the number of squares tracked suggests more dramatic increases, and also gives estimates with greater precision. The arcsin-linear model gave a reasonable fit to the increasing proportion of squares tracked per card over time (Table 1), and when multiplied by the probability of a card being tracked, gave a reasonable fit to the probability of a square being tracked (Fig. 2). Under these models (Table 2), the probability of an individual square being tracked increased from 0.05 (95% credible interval 0.04–0.07) to 0.59 (0.55–0.63) for *Hemideina thoracica* and from 0.11 (0.08–0.16) to 0.82 (0.76–0.87) for other weta (Fig. 2).

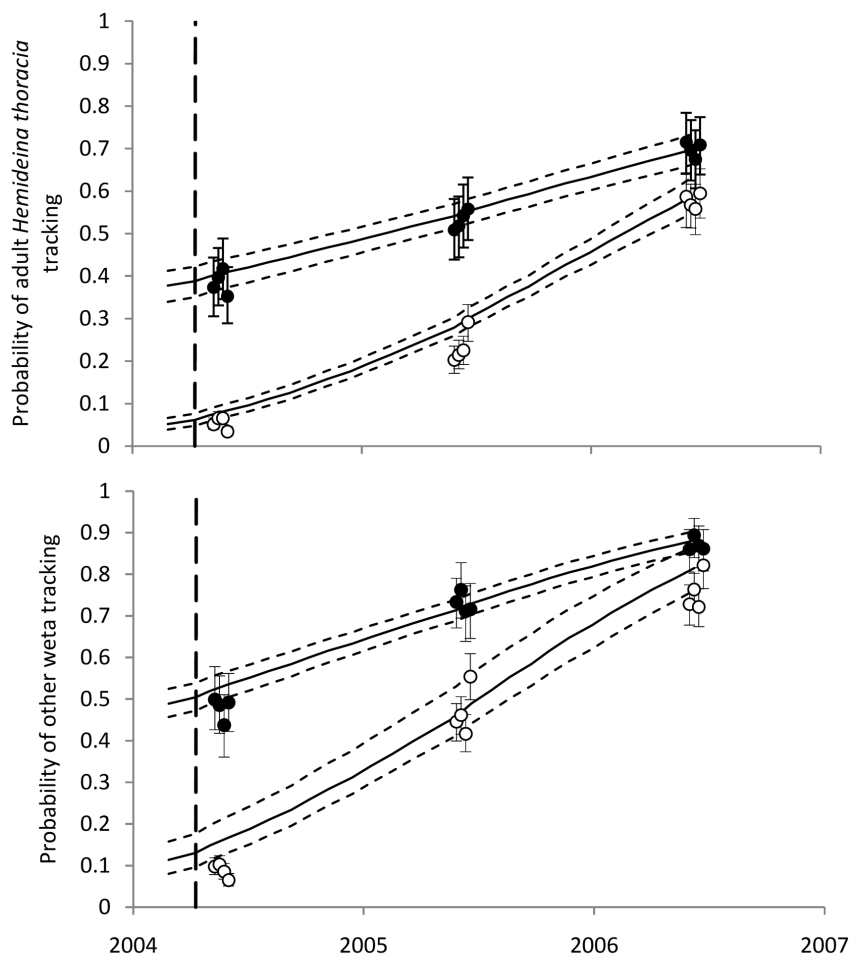


Figure 2. Changes in tracking rates of weta after mammal eradication in the southern enclosure on Maungatautari. Time of mammal eradication is shown with the dashed vertical line for the southern enclosure. Closed circles show the probability of a card being tracked and open circles show the probability of an individual square being tracked (100 squares were scored per card). Solid curve lines show means predicted from models fitted to the data, with dotted lines showing 95% credible limits. Probabilities of cards being tracked are based on the exponential model (Tables 1–2). Probabilities of individual squares being tracked are obtained by multiplying the probability of a card being tracked by the predicted proportion of squares tracked as estimated by the arcsin-linear model (Tables 1–2).

With only 3 years of data we could not exclude the possibility that the trends were due to random yearly variation, as DIC values for random-year and time-trend models are similar (Table 1). However, it is clear from the high DIC of the ‘constant’ model that there were highly significant changes over time. There was substantial variation among individual tracking tunnels in both tracking probability and incidence of tracking per tracked card, and with the latter there was also significant variation among transect lines and individual sampling occasions (Table 2); hence it is important to account for these effects.

Changes in pitfall capture rates after mammal eradication

A total of 1126 *Hemideina thoracica*, *Hemiandrus pallitarsis*, *Gymnoplectron acanthocerum* and *Gymnoplectron* sp. 1 were captured over the trapping period. The most common weta caught were subadult and juvenile *Gymnoplectron acanthocerum*.

The number of weta per pitfall increased dramatically in the first 1–2 years after mammal eradication in the southern enclosure in 2004, and similarly after mammal eradication outside the enclosure (Fig. 3). Trends were similar for adult *Hemideina thoracica* and other weta. However, the rate of increase clearly slowed over time in all cases, suggesting density dependence. Consequently, the data were best explained by logistic growth models, which gave a good fit to the data and had far lower DIC values than the other models considered

(Table 1). The distributions for the parameters in the models are shown in Table 2, and indicate that the number of adult *Hemideina thoracica* per pitfall increased 12-fold (95% credible interval 7–20) after mammal eradication, and the number of other weta per pitfall increased 52-fold (30–89) (Fig. 3). There was no significant variation among transect lines, individual pitfalls or sampling occasions for adult *H. thoracica*, but there was significant variation among individual pitfalls for other weta (Table 2).

Changes in sex and age structure after mammal eradication

The age structure of all weta species combined changed with time after mammal eradication (Fig. 4). Before and immediately after mammal eradication approximately equal percentages of juveniles, subadult and adult weta were caught (Fig. 4). In the southern enclosure, subadults were dominant 2 years after eradication (summer 2006/07), and in the 3rd and 4th years after eradication adults dominated the southern enclosure catch (60% in 2007/08 and 66% in 2008/09; Fig. 4a). One year after eradication of mammals from Maungatautari, juvenile weta dominated (73%) pitfall trap catches and subadults were dominant (67%; Fig. 4b) the following summer (2008/09).

The sex ratio of adult to subadult of all weta species caught in the pitfall traps differed with time after mammal eradication (Fig. 5). When the mammals were being eradicated males dominated the samples (72–78%; Fig. 5), whereas in the southern enclosure, 2 years after mammal eradication,

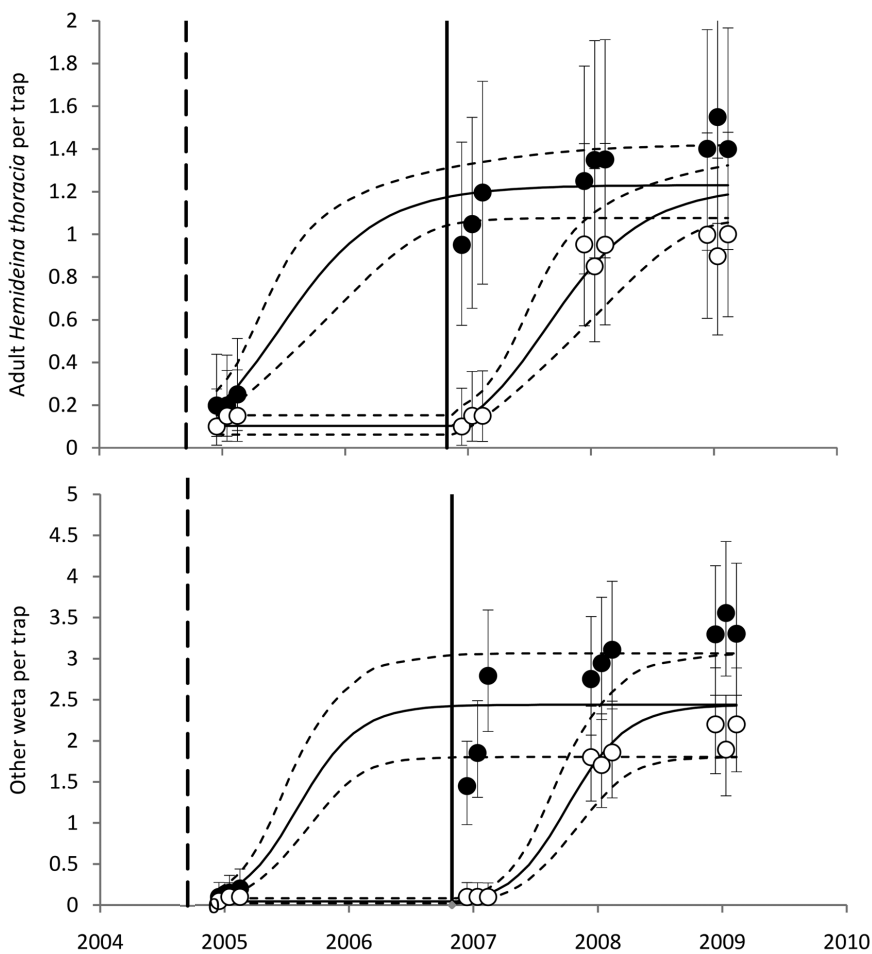


Figure 3. Changes in pitfall capture rates of weta after mammal eradication in a lagged before-after-control-impact (BACI) experiment within the southern enclosure and in the adjacent forest on Maungatautari. Bars show 95% credible intervals based on samples from 20 lethal-pitfall traps. Closed circles show weta caught inside the southern enclosure and open circles show weta caught in the adjacent forest on Maungatautari. Time of mammal eradication is shown with the dashed vertical line for the southern enclosure and the solid vertical line for the adjacent forest on Maungatautari. Solid curve lines show the fitted logistic model and the dotted lines show 95% credible limits around the relationship.

female subadults and adults increased to 49% and by summer 2008/09 accounted for 55% of the catches (Fig. 5). An increase in the percentage of female weta present in the samples was also observed 2 years after mammal eradication from the comparative area of Maungatautari (Fig. 5). Percentages increased from 26% in the summer of 2004/05 and 22% in the summer of 2006/07, to 53% in the summer of 2008/09.

Discussion

Response of weta to introduced mammal eradication

With the rapid increase throughout New Zealand in the establishment of conservation projects focused on maintaining mammal-free sanctuaries using pest-proof fences, the results presented here provide an important step in understanding how weta respond to mammal removal. This study showed a dramatic increase in weta pitfall captures, weta tracking rates and incidence of weta footprints per tracking card within 2 years after mammal eradication. This may simply reflect increases in weta abundance following mammal eradication but they could also reflect behavioural changes. The latter follows because tree weta were reported to spend more time on the ground when mammalian predators were absent (Rufaut & Gibbs 2003; Moller 1985). These results could, of course, also be caused by a combination of these effects. Data presented here are indices of density and/or activity, and research giving absolute estimates of abundance (e.g. through closed mark-

recapture; McCartney et al. 2006) is required to distinguish between these effects.

The age structure of weta caught in pitfall traps on Maungatautari changed after mammal eradication from having approximately equal percentages of all age classes to being dominated by subadults in the summer of 2006/07 and finally to adult domination 2 and 3 years after mammal eradication in summers 2007/08 and 2008/09. It is unknown whether predators, particularly rodents, target larger size classes such as adults but Rufaut and Gibbs (2003) also observed a change in age structure of *Hemideina crassidens* on Nukuwaiata (Chetwode Islands), and reported that the percentage of adults increased markedly from 33% in 1994 to 65% in 1998 after the relaxation of predation pressure from kiore (*Rattus exulans*). Large invertebrate species are more vulnerable to predation by introduced mammals, particularly rodents (Gibbs 1998). Therefore, larger individuals of some species are likely to be strongly impacted by mammal predation. The dominance of adults in the weta population 2–3 years after mammal eradication reflects the life cycle of most weta species, which have a total lifespan of 2–3 years and show a distinct seasonal developmental pattern, although there is usually some overlap between generations. However, *Hemiandrus* species show particularly poor seasonal synchronisation and all developmental stages occur throughout the year (Stringer & Cary 2001). Cary (1983) suggested that this lack of seasonality probably related to the carnivorous diet of the weta he studied.

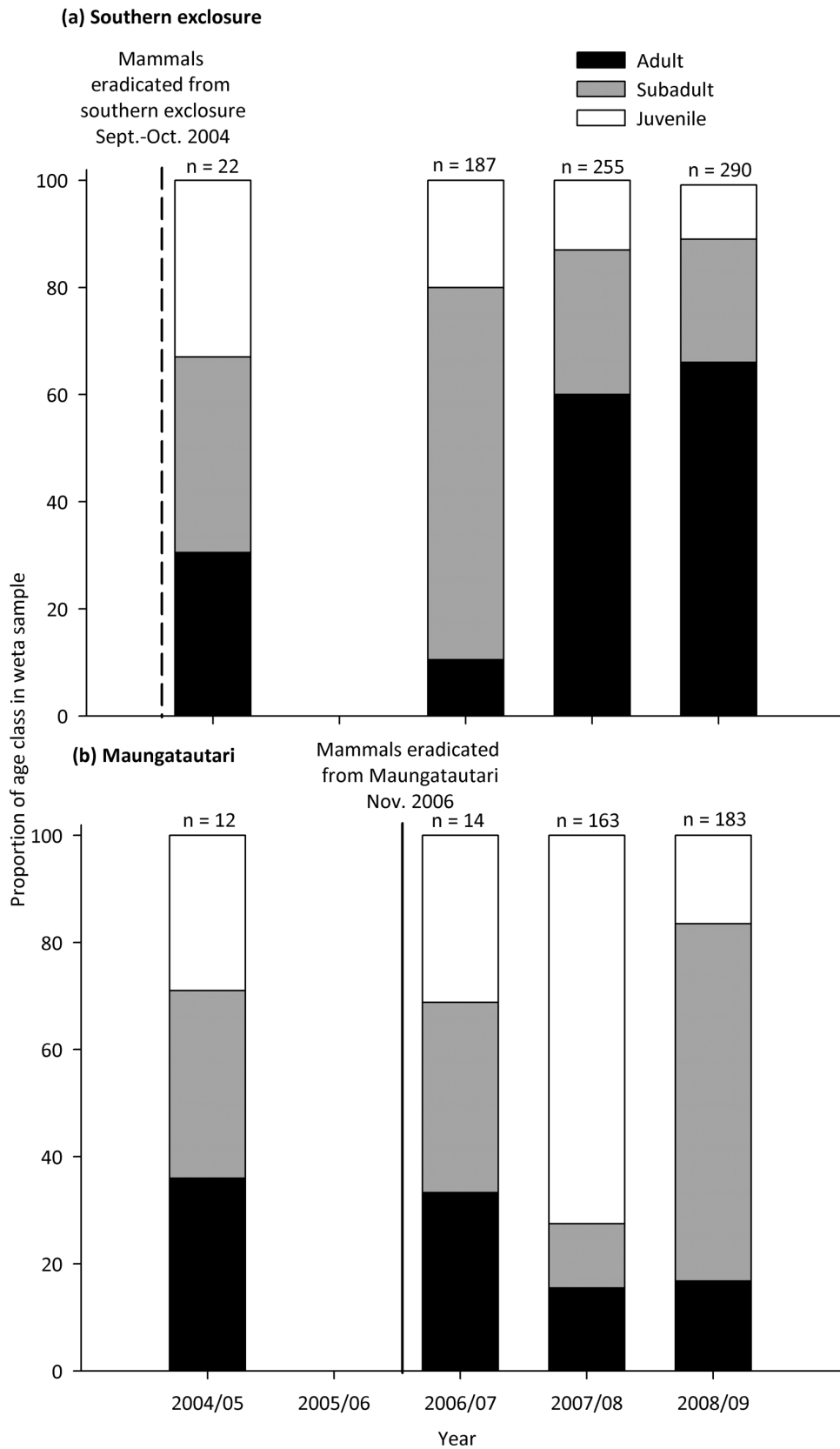


Figure 4. Changes in the percentages of adult, subadult and juvenile weta after mammal eradication in a lagged BACI experiment within (a) the southern enclosure and (b) in the adjacent forest on Maungatautari between 20 November and 24 February during each year of sampling. Samples sizes (*n*) noted on the top of each bar.

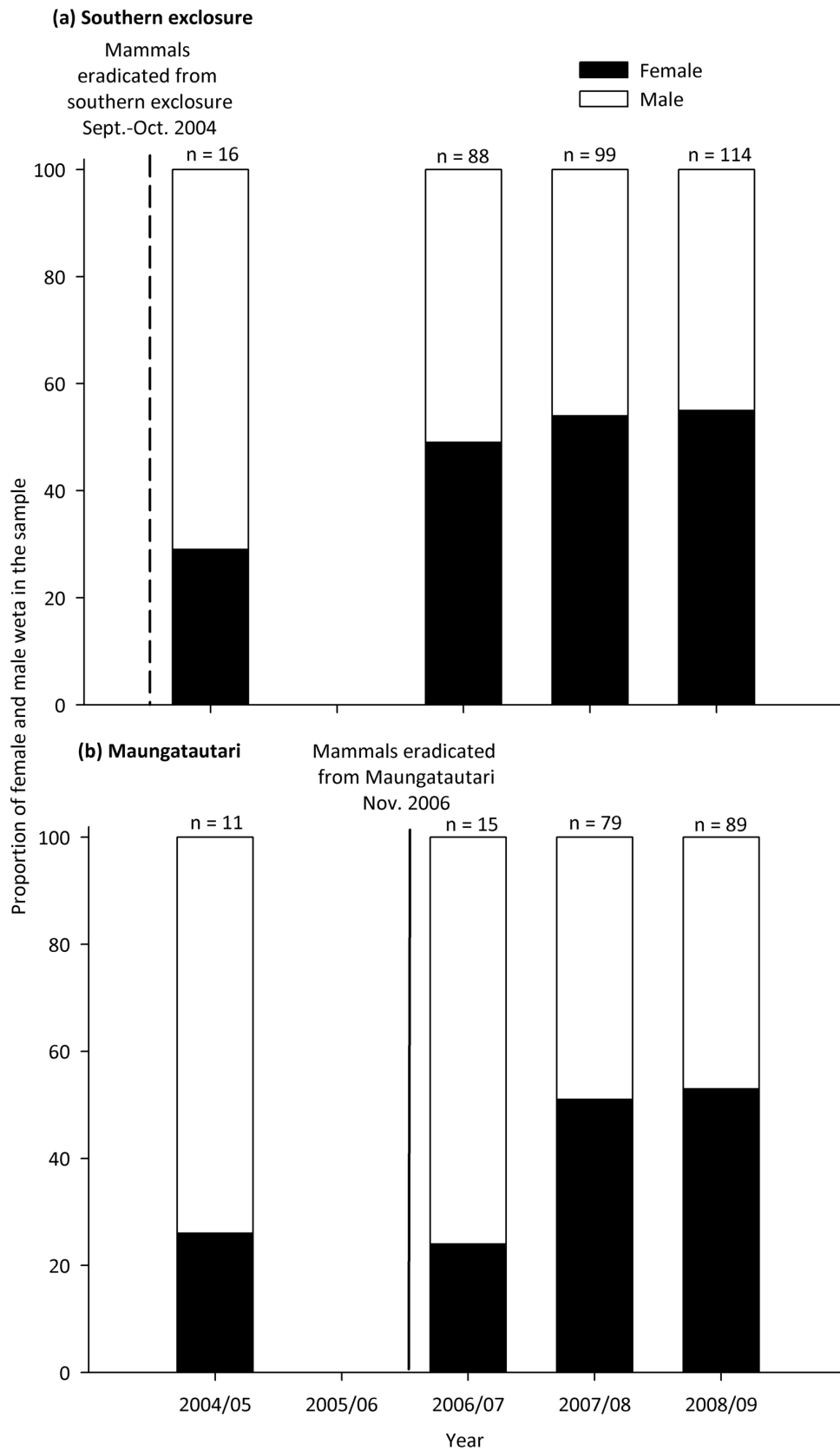


Figure 5. Changes in the percentages of female and male adult and subadult weta (all species combined) after mammal eradication in a lagged BACI experiment within (a) the southern enclosure and (b) in the adjacent forest on Maungatautari between 20 November and 24 February during each year of sampling. Samples sizes (*n*) noted on the top of each bar.

There was also a distinct change in the sex ratio of the adult and subadult weta following mammal eradication, with the percentages of females and larger instars (mainly adults) increasing markedly. Before and during mammal removal, the sex ratio was skewed towards males whereas after mammal eradication the sex ratio was relatively even. Moller (1985) investigated aspects of the ecology of *Hemideina crassidens* on mainland New Zealand and on predator-free islands and found that, on islands, large relatively unprotected galleries were occupied by large groups of *Hemideina crassidens*, in contrast to mainland situations where tree weta preferred small, inaccessible galleries. In addition, he proposed that female weta were vulnerable to mammal predation on the mainland because they were larger and had to visit the ground for considerable periods in order to oviposit. Moller (1985) also suggested his hypothesis be tested on islands before and after predator eradication and the present study has provided such an opportunity. Our results strongly suggest that the survival of adult *Hemideina thoracica*, particularly females, is enhanced by the removal of mammals.

There are also shifts in invertebrate community composition after mammal removal. For example, a concurrent study suggested a 3-fold increase in abundance of ground-dwelling beetles 2 years after mammal eradication within the southern enclosure on Maungatautari but that the composition of the community differed (CHW unpubl. data). Temporal and spatial variation in invertebrate numbers may also obscure any treatment effect (e.g. van Aarde et al. 2004; Sinclair et al. 2005). Preliminary results from Karori Sanctuary suggested a decline in both abundance and species richness of beetles after mammal eradication, probably due to increased densities of mice and insectivorous birds in the sanctuary (CHW unpubl. data).

Few studies have examined responses of weta to mammal eradication. More *Deinacrida rugosa* were caught 3 years after mouse eradication on Mana Island (McIntyre 2001), whereas Rufaut and Gibbs (2003) found no marked increase in *Hemideina crassidens* density after eradication of kiore from Nukuwaiata (Chetwode Islands). However, they did note a change in the behaviour of adult *Hemideina crassidens* whereby tree weta roosted closer to the ground and were more active on Nukuwaiata 4 years after the eradication of kiore (Rufaut & Gibbs 2003). Thus the behaviour of weta in the southern enclosure on Maungatautari may have changed following mammal eradication as previously mentioned. There is also an indication that the behaviour of *Deinacrida heteracantha*, an arboreal giant weta species, may have changed after kiore were eradicated from Little Barrier Island and that these weta became more active on the ground (Watts et al. 2008b). A radiotracking study showed that adult *Deinacrida heteracantha* frequently walked and foraged on the ground 3 years after rats were eradicated (CHW & DT, unpubl. data) whereas a previous radiotracking study done when rats were present found that *D. heteracantha* never moved out of the canopy (Gibbs & McIntyre 1997).

Use of weta as indicator species for impacts of mammal control

Hemideina species are large common insects that are easily identified by non-experts and so they are being used as indicator species for monitoring both the 'health' of forest ecosystems and the impact of poisoning programmes that target introduced mammals (Spurr & Drew 1999; Spurr &

Berben 2004). However, data on the suitability of weta for this purpose are scarce. They form an important part of the diet of small introduced mammals, particularly rats, so they probably can be used as an indicator of rat abundance within native forests. In addition, monitoring indicator species, such as weta, appears more achievable than making overall insect community counts or biomass estimates, which takes considerably more effort. The development and application of non-lethal monitoring techniques, such as tracking tunnels and artificial roosts, are necessary prerequisites if weta are to be used as indicator species in conservation programmes.

What technique should be used for monitoring weta?

Currently three techniques are commonly used for monitoring weta, in addition to the new technique of using footprint tracking tunnels. Each has advantages and disadvantages (Table 3). Pitfall trapping has the advantage that specimens are obtained for further analysis, such as to determine population age structure, but this technique is time-consuming, the chemical liquid in the trap may act as a deterrent, and weta may escape from the traps. Research is required to investigate using non-lethal live pitfall traps to sample weta as discussed by Seldon and Beggs (2010) for *Mecodema*. Weta have also been surveyed by searching for them at night. For example, Rufaut and Gibbs (2003) detected an increase in the proportion of adult *Hemideina crassidens* active after rat eradication, using this technique. The advantages of searching at night are that it is non-lethal and specimens can be obtained, but it involves considerable time and effort.

Artificial weta roosts have been the most frequently used monitoring method for *Hemideina* species (e.g. Trewick & Morgan-Richards 2000; Green 2005; Bowie et al. 2006; Kelly 2006), because data are obtained quickly and easily. Only one preliminary study has compared the number of weta found in artificial roosts with those in the surrounding environment and this indicated that artificial roosts may provide an index of how many weta are present in the environment (Bleakley et al. 2006); however, opinions differ regarding the precision of the relationship (Trewick & Morgan-Richards 2000; Field & Sandlant 2001; Bowie et al. 2006). Artificial roosts also have the advantages of being non-lethal and data, such as age, can be obtained. They are also suitable for additional purposes such as mark-recapture estimates of the weta using them and for behavioural studies.

Tracking tunnels have the advantages of being time efficient and non-lethal so they are suitable for use where there are threatened species. The majority of forests where extensive predator control occurs, including fenced sanctuaries, already have tracking tunnels in place to monitor mammal densities or reinvasion so little additional work is required to use them to monitor weta populations. A subsample of cards could be scored annually from the same month to indicate changes over time. The ideal time of year to do this would be when weta are most active on the ground, which would be between March and May when mating and oviposition occur (Stringer & Cary 2001; Watts et al. 2008b). Scoring the incidence of weta footprints per square on tracking cards indicated a more dramatic increase in weta and there was a greater precision in the index than scoring the presence-absence of weta footprints per card. This suggests that this is a more sensitive method of detecting a response to mammal eradication. However, the effort involved in recording the incidence of weta footprints per tracked card is considerably greater than for scoring presence-

absence (Table 3). The disadvantages of using tracking tunnels are that only footprints are recorded and, with the exception of adults of the largest weta species present, different species or age classes cannot currently be identified. Weta are also attracted to peanut butter, which is the usual bait used in tracking tunnels for monitoring rodents, and as yet we do not know how much is consumed by the first animal that visits the tunnel and how this might affect the subsequent tracking rate. Thus the presence of bait may artificially inflate weta tracking rates after mammal eradication because weta are unlikely to consume it as fast as rodents and will not be in competition with mammals for the bait.

The different indices presented here lead to different conclusions about the magnitude of increase in weta. The pitfall trap results suggest a 12-fold increase for adult *Hemideina thoracica* and 50-fold for other weta. However, if we interpret tracking rates as density, this suggests 2.5- to 3-fold increases for both adult *Hemideina thoracica* and other weta. The probability of a square on a tracking card being tracked was more difficult to interpret, but this method suggests a more dramatic increase in weta and was consistent with pitfall trap results for adult *Hemideina thoracica*. In contrast to the pitfall trap results, the increase in tracking rates was consistent for adult *Hemideina thoracica* and other weta. Therefore, as mentioned above, density estimates need to be resolved.

We showed that when tracking tunnels are used to monitor weta they produce similar trends to using pitfall traps. However, weta are probably best monitored using a combination of techniques and a comparative study is required to determine which combination is the most suitable. Predictably, this will vary depending on particular objectives. While tracking tunnels seem to be the most time efficient and cheapest technique to cover a large area and not kill any weta, artificial weta roosts have the potential to provide additional information in relation to tracking tunnels. Both techniques could be used together, particularly as they are also easy and quick to use.

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