Habitat associations and detectability of the endemic Te Paki ground beetle *Mecodema tenaki* (Coleoptera: Carabidae)

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Abstract: Te Paki Ecological District in Northland is regarded as a New Zealand biodiversity hotspot, but habitat loss and forest fragmentation have adversely affected many of its endemic species. We investigated the distribution and habitat associations of *Mecodema tenaki* (Coleoptera: Carabidae), a Te Paki endemic ground beetle whose threat status was recently changed from 'Nationally Critical' to 'Declining'. Manual searching and pitfall trapping (live-capture and lethal) were used to detect the species at 46 sites in three habitat types: native forest, pine plantation and shrubland. Between 2006 and 2010, 41 individuals were found at five locations in the east of the district, significantly increasing individual and locality records for the species. Efficacy of both forms of pitfall trapping for determining presence/absence of *M. tenaki* was extremely high, whereas manual searching had lower sensitivity. Beetles were only found in structurally heterogeneous native forest with a closed canopy, including edge zones. All beetles were found at sites underlain by rocks of the Parengarenga Group (mainly Kaurahoupo Conglomerate); however, neither forest community composition nor soil properties were good predictors of beetle presence. The most important factor influencing the present distribution of *M. tenaki* is likely to have been anthropogenic habitat disturbance. Our study shows that lethal trapping methods are not essential for studying or monitoring this threatened species. It also shows that retaining and managing even very small native forest fragments within its historical range may be important for the protection of the species, and that a site-based rather than a single-species approach is likely to be the most effective management strategy. The possibility of relocating beetles to suitable, presently unoccupied locations should not be discounted. Our results indicate that a threat ranking of 'Nationally Vulnerable' rather than 'Declining' may be more appropriate for the species.

Keywords: fragmentation; pitfall trapping; search effort; threatened species

Introduction

Due to its long history of geological isolation, New Zealand's biota is distinctive. It is characterised by high levels of endemism, with many higher taxa also being under- or over-represented (Daugherty et al. 1993). A large-bodied, flightless and very species-rich insect taxon endemic to New Zealand is the ground beetle genus *Mecodema* Blanchard (Coleoptera: Carabidae). Larochelle and Larivière (2007) recognised 60 species of *Mecodema* as well as six subspecies, around 30% of which are listed as threatened (Hitchmough et al. 2007). A recent revision of the *Mecodema curvidens* group has led to the formal description of the previously tag-named *Mecodema* "Te Paki" as *Mecodema tenaki* Seldon and Leschen 2011 (Seldon & Leschen 2011). *Mecodema tenaki* (henceforth *M. tenaki*) is endemic to Te Paki Ecological District and was, until recently, listed as 'Nationally Critical' (Hitchmough et al. 2007). This has since been revised to 'Declining' (Leschen et al. 2012). Very little is known about the species, and formal and informal records exist for only eight individuals. The first individual was collected in 1956, but accompanying label data do not make it possible to identify the precise location of collection. The remaining individuals were collected or reported from Unuwhao (1957 and 1986), Whareana (1967 and 2003) and the lower Akura Stream area (1999). Exact coordinates are only available for the records at the lower Akura Stream and Whareana. Consequently, little is known of the precise distribution of the species.

New Zealand's status as a biodiversity hotspot is well known (Myers et al. 2000), and Te Paki Ecological District is recognised in this country as a hotspot for several taxa including plants (Cameron & Jones 1996), molluscs (Goulstone et al. 1993), and spiders (Ball & Fitzgerald 2011). Although most of the ecological diversity of Te Paki Ecological District is contained within protected areas, much of the district has been highly disturbed and modified by human activity over the past few centuries. Most of the district was covered in native forest but this habitat now covers only about 3% of the area (Lux et al. 2009). Habitat loss and forest fragmentation have been identified as among the most serious threats to the maintenance of biodiversity in general (Tilman et al. 1994; Dobson et al. 1997), and concern is heightened when they occur within nationally significant biodiversity hotspots such as Te Paki. Although many insects have been found to be sensitive to the effects of habitat loss and fragmentation, their responses vary (Didham et al. 1998; Harris & Burns 2000; Barbosa & Marquet 2002; Schnitzler et al. 2011). Carabids have been used as indicators of environmental health and of habitat or

landscape modification (Lövei & Sunderland 1996; Rainio & Niemelä 2003).

Our aim was to investigate the distribution of adult *M. tenaki* within Te Paki Ecological District and identify and describe the habitat associations of the species. Specific habitat associations investigated were habitat type, plant species composition, leaf litter depth, ambient temperature, physiography and other landscape variables, parent rock type, and soil chemistry. We also examined the efficacy of three detection methods for *M. tenaki*: manual searching, live-capture pitfall trapping and lethal pitfall trapping. Our findings should enable managers to monitor the conservation status of the species more accurately and determine appropriate field-based management strategies.

Methods

Study area

The study was carried out within Te Paki Ecological District (c. 309 km^2), Northland, New Zealand. The region is characterised by warm humid summers and relatively mild winters. Mean annual rainfall at the Cape Reinga AWS (automatic weather station) between 1984 and 2010 was 980 mm (K. McGill, NIWA, pers. comm.) although most other parts of the ecological district receive between 1200 and 1400 mm per year (Lux et al. 2009). Mean annual temperature at the Cape Reinga AWS between 1999 and 2010 was 15.7°C, and mean maximum daily temperatures of the warmest (February) and coldest (July) months were 22.6°C and 14.8°C, respectively.

Most of Te Paki Ecological District is dissected hill country rising to 310 m a.s.l., and several major rock types are represented (New Zealand Geological Survey 1989). An allochthonous ophiolite, the Tangihua Complex, consisting largely of Cretaceous basalt, dolerite, gabbro and siliceous mudstone (Whangakea Volcanics), is present over much of the district. The ophiolite suite on the North Cape headland also includes cumulate gabbro (Murimotu Intrusives) and serpentinised harzburgite and iherzolite (Surville Serpentinite) of Cretaceous age. Younger (Oligocene to Miocene) rocks of the Parengarenga Group are extensive in the eastern part of the district. These consist of Kaurahoupo Conglomerate (igneous conglomerate with minor sandstone), Paratoetoe Formation (sandstone, mudstone and conglomerate) and Tom Bowling Formation (calcareous muddy sandstone and volcaniclastic deposits). Dune and alluvial deposits of Pleistocene and Holocene ages are also present on the west coast and some northern and eastern coasts.

Indigenous vegetation covers over 75% of Te Paki Ecological District, although most is in a state of regeneration following extensive human-induced disturbance (Lux et al. 2009). Most of the indigenous vegetation cover therefore consists of shrubland, although sedgelands, freshwater wetlands (including gumlands), and dunelands are also represented. Native forest (kauri–podocarp–broadleaved or coastal-broadleaved), although present, has been reduced to small, isolated remnants in gullies. At 230 ha, Unuwhao (Fig. 1) is by far the largest native forest remnant. Other large native forest remnants range from 22 to 65 ha (Lux et al. 2009). Most of the remaining land cover consists of pine forest (*Pinus radiata*) plantations, of variable age, and improved pasture. Sampling in our study was undertaken mainly in native forest, but shrubland (which included elements of sedgeland and gumland) and pine plantation habitats were also included.

Beetle sampling

Three methods were used to detect *M. tenaki*: manual searching, lethal pitfall trapping and live-capture pitfall trapping. A total of 46 sites were surveyed using either one or two of the sampling methods. Sites where lethal trapping was conducted were randomly selected, whereas sites subjected to manual searching alone, or to a combination of live-capture trapping and manual searching, were chosen non-randomly.

Manual searching

Manual searching involved looking under logs and stones and rummaging through leaf litter. Due to the difficult nature of the terrain and the large amount of time taken to reach many

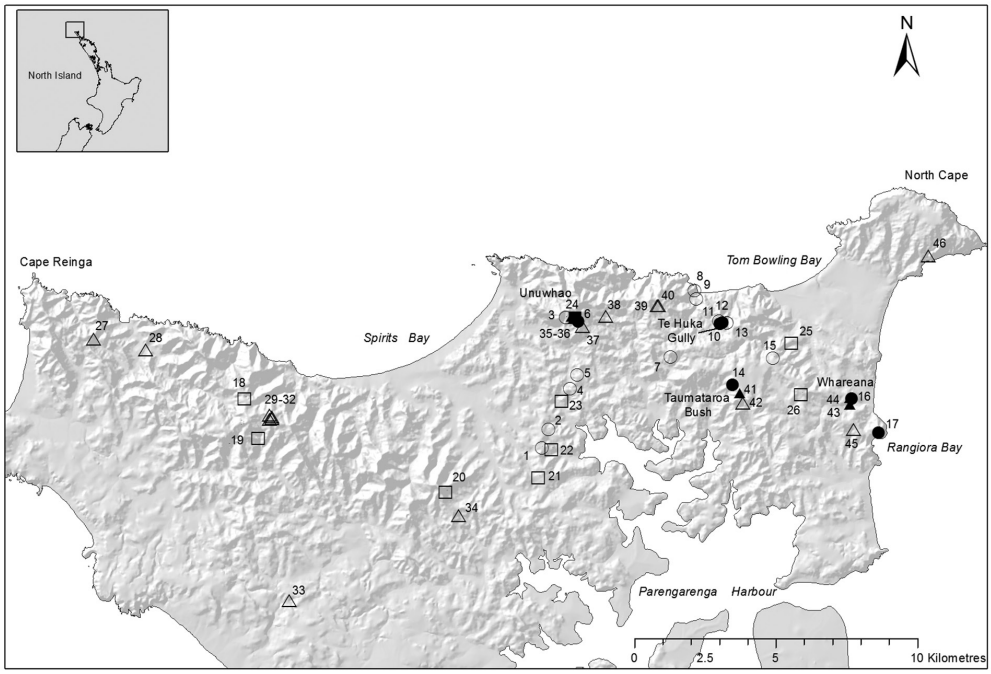

Figure 1. Map of Te Paki Ecological District showing locations of all survey sites. Circles = sites where manual searches only were conducted; squares = lethal trapping sites; triangles = live-capture trapping sites. Filled symbols indicate presence of *M. tenaki*; open symbols indicate *M. tenaki* not detected. See Appendices 1 and 2 for site codes.

of the sites, total search times varied between sites, although all native forest sites were searched for a minimum of 20 min. For sites that had been selected for live-capture pitfall trapping (see below), a 20-min manual search was conducted prior to the deployment of the traps. If the species was detected at this stage, traps were not deployed and no further surveys were conducted at the site. If the species was not detected, traps were deployed and additional short manual searches were conducted, time permitting, during the live-capture pitfall trapping surveys. Both manual searching and live-capture trapping were discontinued at a site on first detection of *M. tenaki*. Other criteria used to subjectively determine the locations of the manual search sites were the presence of sufficient refuges (e.g. logs and rocks), the presence of diverse vegetation with significant cover and a mean top height greater than 5 m (i.e. pine plantation forest, tall shrubland and native forest only), whether *M. tenaki* had been detected at nearby sites (in order to investigate the extent of area occupied), or whether there were large areas in the district that had not been sampled (to achieve greater coverage). Manual searching was the only method of detection used at 17 sites (Sites 1–17); it was also used in conjunction with live-capture pitfall trapping at a further 20 sites (Sites 27–46) (Fig. 1, Appendices 1 and 2).

Lethal pitfall trapping

Traps consisted of a polyvinyl chloride (PVC) sleeve (diameter 110 × 110 mm) sunk to just below ground level, inside which a plastic cup (diameter 100 × 110 mm) was placed. A protective plywood cover (200 × 200 × 12 mm), held approximately 30 mm above the ground by wooden legs, was secured firmly over the trap using wire pegs. Approximately 100 ml of 100% propylene glycol was used as the killing and preserving agent in each trap.

The lethal-trapping survey was undertaken between July 2006 and July 2007 at nine sites (Sites 18–26). At each site, a cluster of eight traps (two rows of four traps, with all traps and rows 10 m apart) was deployed. Traps were emptied and reset monthly throughout the study. Sampling was stratified across three habitat types: native forest, pine plantation and shrubland–sedgeland–gumland (hereafter called shrubland). Three sites in each habitat type were therefore surveyed (Fig. 1, Appendix 2). Trees at the three pine plantation sites were 10–11 years (Sites 22 and 23) and 23–24 years (Site 25) at the time of the survey. In order to lessen beetle mortality, trapping effort at a site was reduced if *M. tenaki* was detected at any point. In such instances, trapping was conducted every third month at intervals corresponding with winter, spring, summer and autumn, and coinciding with sampling at the other lethal-pitfall-trapping sites.

Live-capture pitfall trapping

Live-capture pitfall trapping was initially employed only at the most ecologically sensitive sites (i.e. small stock-fenced native bush fragments managed for the large land snails *Placostylus ambagiosus* and *Paryphanta watti*). Although live-capture trapping limited the number of trap days that could be accumulated, mortality of threatened or rare invertebrate species, including of *M. tenaki*, was avoided. As the study progressed, it became clear that live-capture pitfall trapping was extremely effective at detecting *M. tenaki*, and as a consequence, this method replaced lethal trapping as the preferred trapping method.

Initially, 23 sites in native forest or tall shrubland were selected for live-capture pitfall trapping, using similar criteria to those used for manual searching (see above). Short manual searches were conducted at each site prior to the deployment of traps. At three sites (Sites 14, 16 and 17), *M. tenaki* was detected on the initial manual search, negating the need for trapping. Consequently, live trapping was conducted at the remaining 20 sites. Nine sites were sampled between July 2006 and June 2007 (Sites 29–32, 35, 36, 39, 40 and 44), and 11 sites between November 2007 and February 2010 (Sites 27, 28, 33, 34, 37, 38, 41–43, 45 and 46) (Fig. 1, Appendix 2). The same traps and trap configuration used in the lethal-trapping survey were employed (clusters of eight traps, except at Sites 29, 31 and 32 where only six traps were deployed due to topographical constraints). Small stones and leaf litter were placed in the bottom of the traps as cover and two small (3-mm diameter) holes were drilled through the base of the cups to allow water to drain away. Traps were left for seven continuous days, after which they were checked and closed (= one trapping cycle). For the nine sites sampled between July 2006 and June 2007, trapping was conducted on a monthly basis and only ceased if presence of *M. tenaki* was confirmed, or if no individuals were captured after 12 trapping cycles. For the 11 sites sampled between November 2007 and February 2010, trapping was carried out at different times of the year and at irregular intervals at each site. Trapping at these 11 sites concluded following detection, or after only six rounds of non-detection. All *M. tenaki* caught by live-capture trapping were released within 2 m of the trap. Where possible, trapping at all 20 live-capture sites was timed to coincide with the dark lunar phase in order to standardise methods and avoid possible confounding factors of increased nocturnal light on beetle activity (Thiele 1977).

Environmental measurements

At all sites surveyed by lethal or live-capture pitfall trapping, vegetation cover within an area approximately 30 m in diameter centred in the middle of the trap cluster was assessed in five tiers using the Reconnaissance (Recce) method (Allen 1992). At sites where *M. tenaki* was detected by manual searching, the same vegetation survey method was used but the plot was centred at the point where the beetle was found. Average depth of leaf litter was also assessed around each of the eight pitfall traps (or at eight similarly spaced points at manual search sites with *M. tenaki*) by taking four measurements (1.5–2 m apart) from the four main compass bearings. Eight soil cores (diameter c. 120 × 25 mm) were taken with an auger (two rows of four cores, 10 m apart) from all trapping sites and from manual search sites where *M. tenaki* had been detected. Cores from each site were pooled, air-dried in the laboratory at ambient temperature, and ground to pass through a 2-mm mesh. Phosphorus, potassium, calcium, magnesium, sodium, and available nitrogen concentrations, as well as organic matter content and pH were analysed using standard procedures by a commercial laboratory (Hill Laboratories, Hamilton, New Zealand). No environmental variables were assessed at manual search sites where *M. tenaki* was not detected.

Ambient air temperature was recorded at 30-min intervals, using data loggers (Hobo H8 Pro Series), at all lethal-trapping sites (Sites 18–26) between August 2006 and July 2007. Ambient air temperature was also recorded between July 2008 and June 2009 using loggers (Hobo Pro v2) set at 60-min intervals at seven of the live-capture trapping sites (Sites 27, 28, 33, 34, 39, 42 and 46), and at three other sites (Sites 16, 24 and 41) where presence of *M. tenaki* had been confirmed earlier in the study. Individual data loggers were placed in the

shade about 1 m above the ground within the area sampled at each site. All data loggers used in a particular year were calibrated with each other and appropriate correction factors applied to data obtained.

Data analysis

To ensure our trapping methods were robust enough to establish absence of *M. tenaki* with confidence, a simple probability of detection function was calculated using data from live-capture trapping. Data from all sites where *M. tenaki* was detected by live-capture trapping were combined to calculate the probability of one trap in a cluster catching at least one beetle, given that *M. tenaki* were known to be present. The probability that at least one trap in a cluster would catch one or more beetles per sampling cycle was then calculated using the binomial probability distribution. This approach required one major assumption, namely that absence was correctly ascertained at sites where beetles were not found after extensive trapping. It is also important to note that this method averages across any seasonal and site differences in probability of capture. We compared the detection rates of manual searching with those of live-capture trapping across the 23 sites selected for manual search prior to live trapping. The probability of detecting *M. tenaki* with a specified level of manual search effort was calculated by fitting an exponential (i.e. constant decay-rate) time-to-event regression model to the search times employed at all sites where *M. tenaki* was present (whether discovered by the initial manual search or subsequent pitfall trapping). The exponential detection probability was calculated from the slope of a linear regression fitted to the baseline hazard function of a Cox's proportional hazard model (Hosmer et al. 2008) generated from the 'coxph' and 'basehaz' functions of the survival package in the statistical and computing program R v2.12.1 (R Development Core Team 2010).

Similarity of plant community composition at all native forest sites subjected to pitfall trapping, and native forest sites subjected to manual searching where *M. tenaki* was detected, was calculated with the Bray–Curtis dissimilarity measure, and visualised using principal coordinates analysis (PCoA) unconstrained ordination in the statistical and computing program R v2.12.1 (R Development Core Team 2010), using the labdsv package (Roberts 2010). Principal coordinates analysis, also called metric multidimensional scaling (MDS), is appropriate for non-Euclidean distance measures such as the Bray–Curtis dissimilarity measure. Principal coordinates analysis attempts to preserve the relative distances between sites in the multidimensional environmental space, as opposed to non-metric multidimensional scaling (NMDS), which focuses on preserving rank-order relationships. In practice, the outputs of both methods are often very similar. Abundances of species were calculated from the ordinal abundance of each plant species recorded in each of the five structural tiers of the Recce plot methodology (i.e. the sum of five values each ranging from 0 (0% cover) to 6 (>75% cover)). A second PCoA was performed using abiotic soil properties (pH, P, K, Ca, Mg, Na, organic matter, available N) and leaf litter depth at each of these same sites.

To test for an association between (1) plant community composition, or (2) multivariate soil properties, with the presence/absence of *M. tenaki*, we looked for separate clusters of the presence and absence sites across PCoA space. Statistical significance of clustering was tested with the permutation-based 'ordtest' function of the labdsv package with N = 10 000 iterations. This test compares the sum of within-set pairwise distances to a distribution of sums obtained from randomised reclassifications of the points; the probability of the observed level of clustering being calculated with reference to the percentiles of the randomised classifications (Roberts 2010). A multiple logistic regression (i.e. a generalised linear model with binomial error structure) was also performed to further test the ability of abiotic soil properties to predict the presence/absence of *M. tenaki* across sites, each site being equally weighted irrespective of sampling effort.

Mean annual temperature, mean maximum daily temperature, and mean daily temperature range of the warmest and coldest months were calculated for sites where data loggers had been deployed.

Results

Distribution and habitat associations

Using a combination of methods, *M. tenaki* was recorded at a total of 12 sites north of the Parengarenga Harbour within an area approximately 5 × 11 km (Fig. 1). All sites where *M. tenaki* was detected were in native forest, although the beetle found at Te Huka Gully (B) (Site 11) was at the junction between native forest and pine plantation forest where the leaf litter was a mixture of the two types. The specimen at Whareana (A) (Site 16) was found under a rotting karaka (*Corynocarpus laevigatus*) log. Apart from the individual at Unuwhao (F) (Site 6), which was found under a rock, all other beetles were found under decaying logs; however, their advanced states of decay meant it was not possible to confirm the tree species of origin.

Manual searching

Total time spent manually searching for *M. tenaki* was 22.5 person-hours spread over 37 sites (Appendices 1 and 2) and resulted in the species being detected at six sites (Fig. 1; Appendix 1). Brief manual searches, of 20 min each, failed to detect *M. tenaki* at five live-capture trapping sites where the species was subsequently detected by pitfall trapping (Appendix 2).

Pitfall trapping

Total lethal trapping time at the nine sites in 2006–2007 was 24 560 trap-days (Appendix 2). No *M. tenaki* were captured at any pine or shrubland sites, and of the three native forest sites, the species was detected only at Unuwhao (A) (Site 24) (Fig. 1; Appendix 2). Presence of *M. tenaki* was confirmed at this site within the first month of sampling and on all three subsequent sampling dates. Fourteen individuals were trapped at this site: three in winter (July–August 2006), three in spring (October–November 2006), seven in summer (January–February 2007), and one in autumn (April–May 2007).

At the 20 live-capture trapping sites, total trap-time was 6832 trap-days. A total of 21 *M. tenaki* were detected at five of these sites, all in native forest (Fig. 1; Appendix 2). In all instances, presence was confirmed within the first week of sampling, negating the need for further surveys.

Evaluation of detection methods

The average probability of a single live-capture trap catching at least one beetle, at any site where detection was confirmed, was 0.25. Assuming independent captures, the probability of catching one or more beetles in at least one out of eight traps per sampling event was 0.90 ($1 - 0.75^8$). Over six sampling

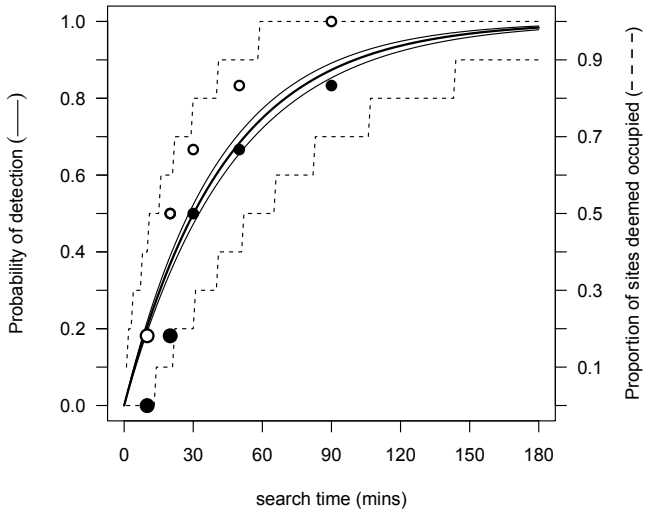

Figure 2. Estimated probability of detecting *M. tenaki* with a specified level of manual search effort assuming a constant rate of detection (smooth solid line = mean ± 2SE). Dots represent empirical data for the proportion of sites at which the species was detected, where the lower value at time *t* is based on the proportion of sites yielding detections immediately prior to *t* (filled symbol), and the upper value is based on the proportion immediately after detection at time *t* (open symbol). Symbol sizes are proportional to the number of sites (n = 11 for t < 20 min, thereafter n = 6 because searching was abandoned after being unsuccessful at five sites after 20 min). Dashed lines represent the 5th and 95th percentiles of simulated discovery rates across 10 occupied sites, based on the corresponding time-dependent detection probability and a binomial distribution of successes.

events, the probability of detecting at least one beetle (if the species was present at similar densities to other occupied sites) was therefore over 99.99%. The false-negative rate of six live-capture events was therefore estimated to be less than 0.01%.

Of the 23 sites due to be assessed by live-capture pitfall trapping, *M. tenaki* were discovered at three of these by short (10–50 min) manual searches prior to placement of the traps. Of the remaining 20 sites where they were not detected by an initial manual search, live-capture pitfall-trapping subsequently revealed the presence of *M. tenaki* at five sites. This indicates that short manual searches had a false-negative rate of 25% and a true-positive rate (or sensitivity) of 37.5%. (When *M. tenaki* was detected by manual searching, we assume it would also have been detected by live-capture pitfall trapping due to the very low (<0.01%) false-negative rate calculated for the latter.)

The constant probability of detection from manual searching was estimated at 0.37 (0.35–0.39, 95% CI) per 20 min of search effort. This equates to a mean time to detection (when present) of 43.5 min. With 60 min of search effort, the expected probability of detection rises to 0.75 (0.72–0.77, 95% CI), while just over 130 min of manual searching would be necessary to exceed a 0.95 probability of detection at sites where the beetle is actually present (Fig. 2). The relatively high false-negative rate was the reason that manual-search sites where the beetle was not detected were excluded from the multivariate analyses examining the association between presence/absence of *M. tenaki* and the measured environmental variables.

Environmental variables

The mean number (±SE) of vascular plant species recorded at all sites where *M. tenaki* was found (39.6 ± 2.8, n = 12) was similar to that for species at native forest sites where *M. tenaki* was not detected by pitfall trapping (42.4 ± 2.8, n = 14). Eight species of vascular plant[1] were present at all sites with *M. tenaki*: taraire (*Beilschmiedia tarairi*), pūriri (*Vitex lucens*), karaka, kohekohe (*Dysoxylum spectabile*), houhere (*Hoheria populnea*), māhoe (*Melicytus ramiflorus*), hangehange (*Geniostoma rupestre*) and basket grass (*Oplismenus hirtellus*). Another six taxa were present at all but one of the sites with *M. tenaki*: nīkau (*Rhopalostylis sapida*), rangiora (*Brachyglottis repanda*), sedges (*Carex* spp.), common maidenhair (*Adiantum cunninghamii*), hounds tongue fern (*Microsorum pustulatum*) and rasp fern (*Doodia australis*). These species were also present at all or most of the sites classed as native forest where *M. tenaki* was not detected by pitfall trapping. The unconstrained ordination (PCoA) of sites based on plant abundance showed no significant difference in plant community composition between sites with and without *M. tenaki* (ordtest: P = 0.293) (Fig. 3a).

Mecodema tenaki was only found at sites underlain by two parent rock types, Kaurahoupo Conglomerate and Tom Bowling Formation, both of the Parengarenga Group (Table 1; Fig. 4; Appendices 1 and 2). However, a PCoA indicated that soil chemistry (and leaf litter depth) did not explain the presence/absence of *M. tenaki* (ordtest: P = 0.925) (Fig. 3b). Furthermore, logistic regression showed no significant differences in soil properties (pH, P, K, Ca, Mg, Na, organic matter, available N and leaf litter depth) between sites with and without *M. tenaki* (all P > 0.2).

Mean annual air temperatures measured at the lethal trapping sites during 2006–2007 ranged from 14.0° to 14.3°C in native forest, 15.1° to 15.5°C in pine plantation, and 14.9° to 15.3°C in shrubland. Mean daily temperature ranges of the warmest month were lowest in native forest (3.4°–4.9°C), highest in shrubland (9.0°–15.1°C), and intermediate in pine plantation (4.9°–11.8°C). The trend was similar, though less pronounced, for mean daily temperature ranges of the coldest month. Only the mature pine forest site (Site 25) had similar temperature profiles to the native forest sites. Temperature variables measured between July 2008 and June 2009 at the 10 native forest sites were similar. Thus, there were no clear differences in temperature between native forest sites with *M. tenaki* and sites where the species was not detected by trapping.

Discussion

Forty-one *M. tenaki* were found during the course of the study, 6 by manual searching and 35 by pitfall trapping. Beetles were detected at 12 sites in five general locations: Unuwhao, Te Huka Gully, Taumataroa Bush, Whareana and Rangiora Bay (Fig. 4). The total represents a large increase in the number of recorded individuals of the species. *M. tenaki* was last recorded at Unuwhao in 1986 and was found at Whareana in 2003; it had not been reported previously from the other three areas. Our results also show that adult beetles are present and active year-round.

[1] Plant names follow the New Zealand Plant Names database (Allan Herbarium 2000).

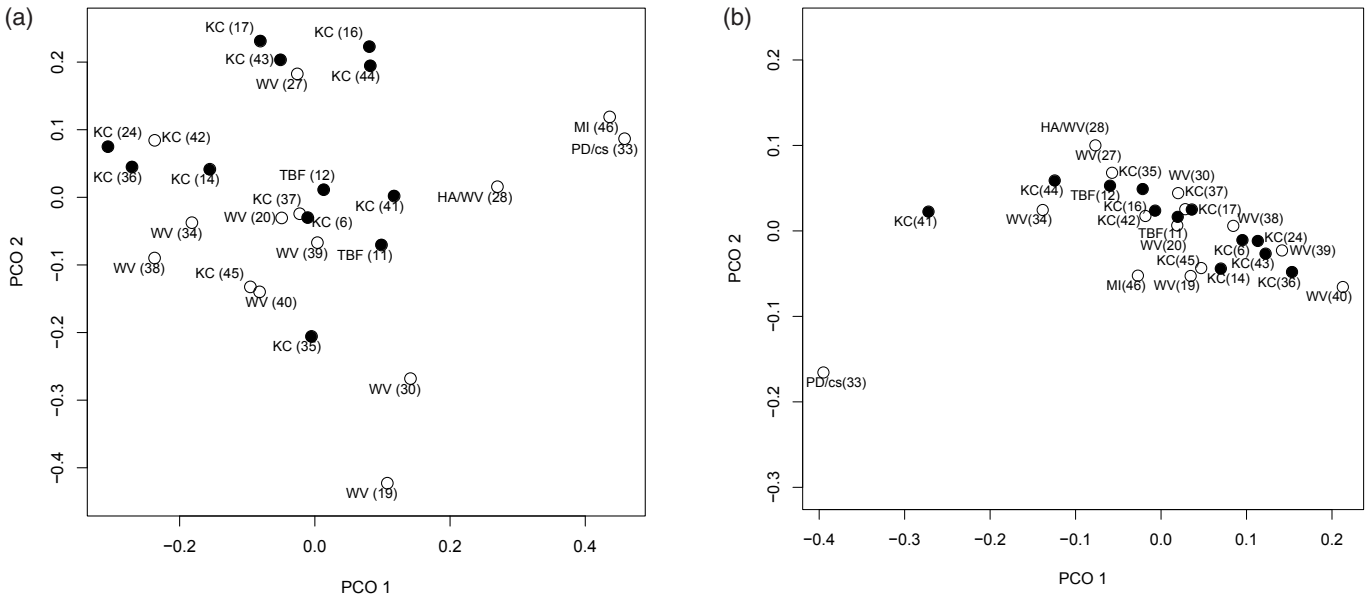

Figure 3. Ordination (principal coordinates analysis; PCoA) based on (a) plant community composition and (b) soil properties, of all native forest sites subjected to pitfall trapping, and native forest sites subjected to manual searching where *M. tenaki* was detected. The first two axes encompass (PCO 1) 46% of the total variation and (PCO 1+2) 92.4% of the total variation. Filled circles = sites where *M. tenaki* was detected; open circles = sites where *M. tenaki* was not detected (site numbers in parentheses). Labels indicate geological environment, where: KC = Kaurahoupo Conglomerate; TBF = Tom Bowling Formation; WV = Whangakea Volcanics; MI = Murimotu Intrusives; PD/cs = Pleistocene Deposits with consolidated sand; HA/WV = Holocene Alluvium over Whangakea Volcanics.

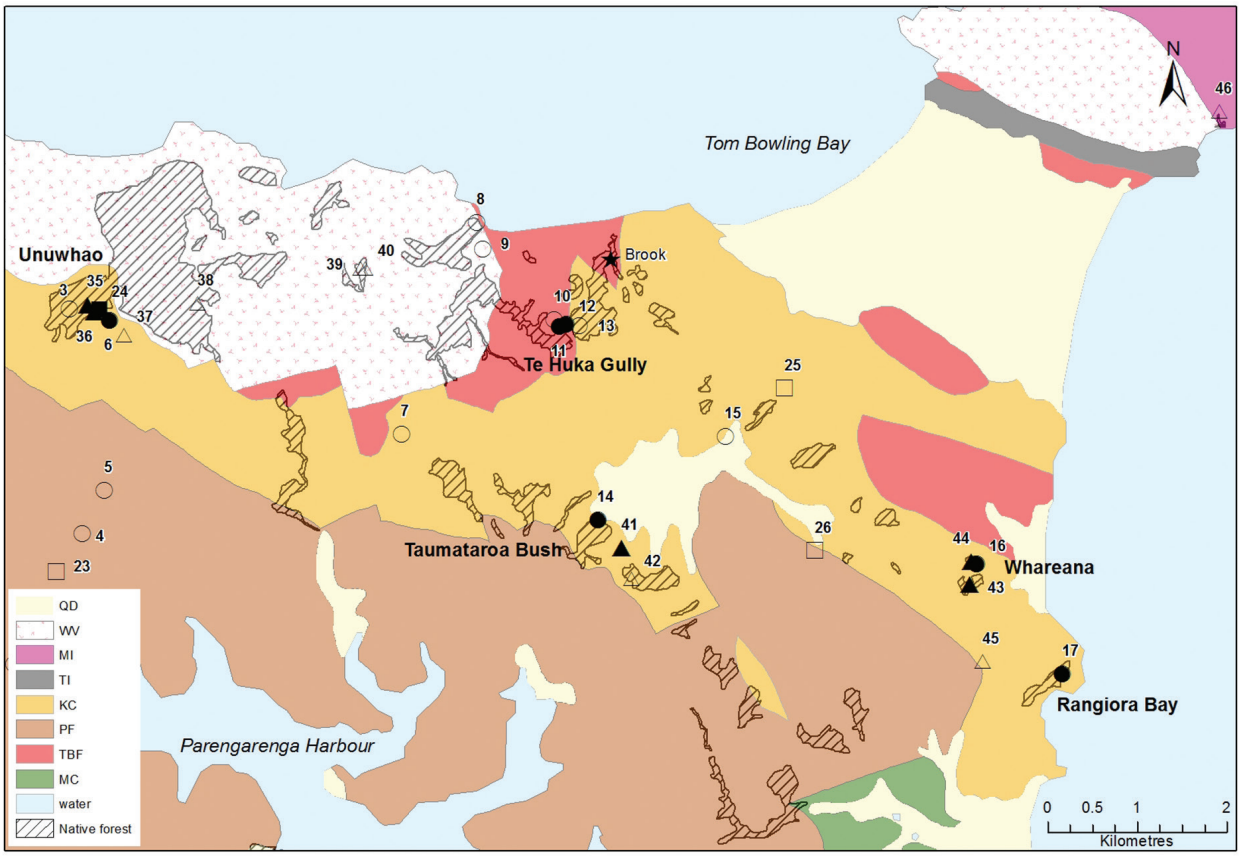

Figure 4. Map of the eastern part of Te Paki Ecological District showing the underlying geology and extent of remaining native forest cover in areas where *M. tenaki* was detected. Circles = sites where only manual searches were conducted; squares = lethal trapping sites; triangles = live-capture trapping sites. Filled symbols indicate presence of *M. tenaki*; open symbols indicate *M. tenaki* not detected. Filled star = historical (F. Brook, 1999) record of *M. tenaki*. See Appendices 1 and 2 for site codes. (QD = Quaternary deposits; WV = Whangakea Volcanics; MI = Murimotu Intrusives; TI = Tawakewake Intrusives; KC = Kaurahoupo Conglomerate; PF = Paratoetoe Formation; TBF = Tom Bowling Formation; MC = Maungakahia Complex).

Table 1. Number of sites where *M. tenaki* was found (numerator) out of the total number of sites searched or trapped (denominator) in each habitat and geology type.

Habitat type	Geology[1]					
	KC	TBF	WV	PF	Other	Total
Native forest	10/16	2/2	0/10	-	0/3	12/31
Shrubland and pine	0/1	0/1	0/4	0/7	0/2	0/15

[1]KC = Kaurahoupo Conglomerate; TBF = Tom Bowling Formation; WV = Whangakea Volcanics; PF = Paratoetoe Formation.

How successful were the sampling techniques used in this study? Although manual searching was used primarily on an ad hoc basis, this method detected the species for the first time at six sites. Searches of 20-min duration, however, failed to detect the beetle at a further five sites where presence was later confirmed by live trapping. Manual searching has been used in other studies of New Zealand carabids with varying degrees of success, and, unsurprisingly, appears to be more suited to relatively common, rather than rare species (Anderson et al. 2003, 2004; Brockerhoff et al. 2005; Hutchison 2007). Results from our study, as well as experience gained from incidental observations not reported here, indicate that 20–60 min of active searching was moderately effective at detecting *M. tenaki* (a probability of success of 0.37–0.75 respectively if the species was present). By comparison, where presence was confirmed, pitfall trapping detected *M. tenaki* on the first (live-capture trapping) or every (lethal trapping) trapping cycle, suggesting that pitfall trapping is a very effective method of detection. Following 6 or 12 clear trapping cycles, the likelihood that the species was truly absent from a site was therefore considered very high. Furthermore, live-capture trapping over a 7-day period appeared at least as effective at detecting *M. tenaki* as lethal trapping over a month-long period. Similar findings concerning the efficacy of live-capture pitfall trapping versus lethal pitfall trapping were reported by Seldon and Beggs (2010) for another *Mecodema* species. This is an important finding as it shows that lethal methods are not required in order to monitor or study the distribution and habitat associations of *M. tenaki*, which is, after all, a threatened species. As also suggested by Seldon and Beggs (2010), it would be useful to investigate whether live-capture trapping could be used in preference to lethal trapping for studying other threatened carabids or invertebrates in general. With this said, it is important to note that results from all types of pitfall-trapping studies are subject to a number of well-documented limitations (e.g. Greenslade 1964).

Some preliminary conclusions about the habitat associations of the species can be drawn from this study. *M. tenaki* was present in closed-canopy native forest sites, including sites with significant amounts of tall kānuka (*Kunzea ericoides*), which may be in the process of reverting back to broadleaved forest. It is likely that surface refuges (coarse woody debris and rocks) provide suitable habitat and are most likely to be present in forest. Most of the individuals located by manual searching were found under logs, but also one was found under a rock. Not surprisingly, an association between the abundance of logs and presence of another *Mecodema* species, *M. howitti*, was found on Banks Peninsula (Anderson et al. 2003). Further study is needed to determine whether *M. tenaki* is able to survive in more-disturbed habitats such as pine plantations and/or shorter shrublands, particularly where these are adjacent to native forest fragments inhabited by the species. However, differences in a range of environmental variables are likely to make their survival in such habitats more difficult. For example, mean daily air temperature ranges during 2006–2007, particularly during the warmest month, were considerably greater at the shrubland and young pine plantation sites than the native forest sites. If *M. tenaki* is highly silvicolous (forest-dwelling) and hygrophilous (moisture-loving), as most *Mecodema* species (especially in the *curvidens* group to which *M. tenaki* belongs) appear to be (Larochelle & Larivière 2001), this may exclude them from all habitats other than native forest and possibly well-established pine forest nearing harvest age.

There was little evidence that plant composition within native forest influenced the distribution of *M. tenaki*. Rather than plant species composition per se, several Northern Hemisphere studies have shown that factors such as vegetation structure, soil characteristics (e.g. pH, nutrient content, moisture content and organic content) and grazing, are important influences on carabids (Luff et al. 1989; Gardner 1991; Rushton et al. 1991; Holmes et al. 1993; McCracken 1994; Sanderson et al. 1995; Gardner et al. 1997; Ings & Hartley 1999). However, our results indicate that soil chemistry factors (and leaf litter depth) were poor predictors of the presence/absence of *M. tenaki*. Although all beetles were found at sites underlain by rocks of the Parengarenga Group (mainly Kaurahoupo Conglomerate, but also Tom Bowling Formation), we found no association between presence or absence of *M. tenaki* and measured soil chemistry at native forest sites.

Anthropogenic disturbance history is likely to have influenced the current distribution of *M. tenaki*. Much of Te Paki Ecological District was covered in kauri forest and mixed broadleaved forest, but, due to repeated burning, native forest is now highly fragmented and covers only 3.2% of the district (Lux et al. 2009). Being a relatively large beetle at 25–27 mm in length (Seldon & Leschen 2011) with probably quite poor dispersal abilities, *M. tenaki* would likely have experienced a significant anthropogenic range contraction as found for other carabids (Rainio & Niemelä 2003). Conditions required by larvae may also be important in determining the geographic distribution of *M. tenaki*, as the larva is often the most environmentally sensitive and vulnerable stage (Lövei & Sunderland 1996).

Using GIS, forest cover and parent rock material were used to estimate the likely area of occupancy and connectivity of the five subpopulations detected. The largest single area of occupancy (c. 25 ha) is most likely within the Unuwhao fragment. The Te Huka Gully – lower Akura Stream area (the latter represented by the single specimen found by Brook in 1999) and the Taumataroa Bush area likely sustain two additional subpopulations, c. 14.5 ha and c. 12.5 ha in size respectively. Given that they are surrounded by large areas of short shrubland, it is very unlikely that the Whareana (c. 4.3 ha) and Rangiora Bay (A) (c. 4.7 ha) sites represent anything other than two small isolated populations. The likely poor

dispersal abilities of *M. tenaki*, and the distances and obstacles involved, mean that it is probable that these five identified subpopulations do not operate as a metapopulation, but this aspect requires further investigation.

Even though the habitat associations observed for *M. tenaki* appear to be those of a habitat specialist, it has been able to persist in apparently small forest fragments and exploit their edge zones. Earlier studies have shown that some *Mecodema* species are also able to exploit edges, some of them in relatively small fragments, whereas others appear to be restricted to the core of large intact forests (Butcher & Emberson 1981; Anderson et al. 2003; Ewers & Didham 2004). If *M. tenaki* was a large-area specialist and an edge-avoider, it is unlikely to have survived to this point in these smaller fragments. The continued presence of *M. tenaki* at locations such as Whareana and Rangiora Bay (A) illustrates the importance of retaining even very small fragments of native forest within the historical range of the species, even though populations within small fragments will be smaller and more likely to decline to extinction more rapidly (Lövei & Sunderland 1996; Ewers & Didham 2006). Owing to its low dispersal ability, it is possible that *M. tenaki* has been able to avoid dispersal-related mortality as described for other species (see Ewers & Didham (2006) for a review). Also, if *M. tenaki* can make use of the resources in the matrix surrounding forest fragments, the intensity of the fragmentation effect might be reduced further (cf. Ewers & Didham 2006). From the habitat perspective, the future of the species would be more secure if a greater number of small native forest fragments were occupied, more core areas of larger native forests (e.g. Haupatoto or possibly Kohuroa) were occupied, and there was a greater degree of connectivity between fragments. Allowing the currently occupied fragments to expand through natural regeneration should assist the species.

It has been suggested that the greatest threat currently facing large carabids such as *M. tenaki* is predation from introduced mammalian predators (McGuinness 2007). Known introduced mammalian predators of carabids in the New Zealand region include the hedgehog (Campbell 1973), ship rat (Daniel 1973), cat (Fitzgerald & Karl 1979), stoat (King & Moody 1982) and probably the house mouse (Marris 2000; St Clair 2011). However, as McGuinness (2007) also highlights, little direct evidence for predator-mediated adverse effects on carabid populations can be found in the literature, and results are often equivocal or contradictory and are likely subject to complex confounding factors (Marris 2000; Sinclair et al. 2005; Ward-Smith et al. 2005; Watts 2007; Rate 2009).

Our study has helped clarify the threat status of *M. tenaki*. Assuming a requirement for native forest habitat, our results suggest that the total area of occupancy is probably less than 100 ha, even if, as is likely, not all subpopulations were detected. We also tentatively conclude that the population is currently relatively stable due to the persistence of the species in small fragments, and assume that it has been reduced to its current level by unnatural causes. Based on the criteria of Townsend et al. (2008), we therefore suggest that a threat ranking of 'Nationally Vulnerable $_{RR, Sp, St}$' (under criterion B3), rather than 'Declining', would be appropriate for *M. tenaki*. Site-based management that benefits a number of species at once would be recommended as the most appropriate management strategy, although relocation of beetles to uninhabited but suitable fragments, as proposed by Lövei and Cartellieri (2000) for carabids in general, could also be considered.

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Appendix 1. Identifiers and locations of sites at which the only method of detection of *M. tenaki* was manual searching. Total search times, habitat types and parent rock types at each site are also presented. Presence of *M. tenaki* indicated by + (highlighted in bold), non-detection by -. Sites are arranged in order from west to east.

Site no.	Site name	GPS location[1] East/North	Total search time (person-minutes)[2]	Habitat type[3]	Geology[4]	*M. tenaki* detected[5]
1	Spirits Bay (C)	1588530/6184995	20	PP	PF	-
2	Spirits Bay (D)	1588770/6185645	20	PP	PF	-
3	Unuwhao (G)	1589387/6189609	50	NF	KC	-
4	Kerr Point (B)	1589531/6187099	20	PP	PF	-
5	Blue Barn	1589778/6187579	10	PP	PF	-
6	**Unuwhao (F)**	**1589834/6189475**	**90**	**NF**	**KC**	**+(1)**
7	Waimahi Stream Gully	1593091/6188210	40	NF	KC	-
8	Te Huka Bay (A)	1593937/6190572	60	NF	WV	-
9	Te Huka Bay (B)	1593997/6190275	50	NF	WV	-
10	Te Huka Gully (C)	1594798/6189485	60	PP	TBF	-
11	**Te Huka Gully (B)**	**1594857/6189407**	**30**	**NF**	**TBF**	**+(1)**
12	**Te Huka Gully (A)**	**1594934/6189433**	**20**	**NF**	**TBF**	**+(1)**
13	Akura Stream	1595078/6189420	240	NF	KC	-
14	**Taumataroa Bush (B)**	**1595283/6187248**	**50**	**NF**	**KC**	**+(1)**
15	Waitangi	1596708/6188181	20	PP	PD/csp	-
16	**Whareana (A)**	**1599513/6186764**	**10**	**NF**	**KC**	**+(1)**
17	**Rangiora Bay (A)**	**1600467/6185537**	**50**	**NF**	**KC**	**+(1)**
			Total: 840			

[1]NZGD 2000, NZTM.
[2]Total search time is the cumulative amount of time spent searching at a site multiplied by the number of people searching.
[3]PP = pine plantation; NF = native forest.
[4]Underlying parent rock type and/or major soil influences: PF = Paratoetoe Formation; KC = Kaurahoupo Conglomerate; WV = Whangakea Volcanics; TBF = Tom Bowling Formation; PD/csp = Pleistocene deposits with consolidated sand and peat.
[5]Number of individuals caught, in parentheses.

Appendix 2. Identifiers and locations of all pitfall trapping sites across Te Paki Ecological District, and associated trapping efforts, total search times, habitat types and parent rock types. Presence of *M. tenaki* indicated by + (highlighted in bold), non-detection by -. In all cases, presence was initially confirmed by pitfall trapping. Sites are arranged in order from west to east for each of the two trapping methods.

Site no.	Site name	GPS location[1] East/North	Total trapping effort (trap -days)[2]	Total search time (person -minutes)[3]	Habitat type[4]	Geology[5]	*M. tenaki* detected (no. of individuals)[6]
Lethal trapping sites							
18	Darkies Ridge	1578009/6186761	2968	-	S	WV	-
19	Radar Bush	1578508/6185367	2968	-	NF	WV	-
20	Kohuroa (A)	1585119/6183457	2968	-	NF	WV	-
21	Spirits Bay (A)	1588403/6183958	2968	-	S	PF	-
22	Spirits Bay (B)	15888676184957	2840	-	PP	PF	-
23	Kerr Point (A)	1589242/6186677	2920	-	PP	PF	-
24	**Unuwhao (A)**	**1589724/6189608**	**992**	**-**	**NF**	**KC**	**+(14)**
25	Whakapaku	1597372/6188725	2968	-	PP	KC	-
26	Taumataroa Flat	1597711/6186910	2968	-	S	PD/csp/PF	-
			Total: 24 560				
Live-capture trapping sites							
27	Tapotupotu (A)	1572703/6188874	336	20	NF	WV	-
28	Tapotupotu (B)	1574538/6188484	336	20	NF	HA/WV	-
29	Te Paki Site D	1578931/6186182	504	20	TS	WV	-
30	Te Paki Site B	1578935/6186042	672	20	NF	WV	-
31	Te Paki Site A	1579011/6186064	504	20	TS	WV	-
32	Te Paki Site C	1579016/6186119	504	20	TS	WV	-
33	Shenstone Block	1579633/6179627	336	20	NF	PD/cs	-
34	Kohuroa (B)	1585611/6182616	336	20	NF	WV	-
35	**Unuwhao (C)**	**1589589/6189651**	**56**	**20**	**NF**	**KC**	**+(3)**
36	**Unuwhao (B)**	**1589665/6189571**	**56**	**20**	**NF**	**KC**	**+(4)**
37	Unuwhao (E)	1590003/6189317	336	25	NF	KC	-
38	Unuwhao (D)	1590823/6189675	336	35	NF	WV	-
39	Te Huka (B)	1592646/6190060	672	30	NF	WV	-
40	Te Huka (A)	1592696/6190058	672	20	NF	WV	-
41	**Taumataroa Bush (A)**	**1595550/6186941**	**56**	**20**	**NF**	**KC**	**+(5)**
42	Haupatoto	1595666/6186601	336	70	NF	KC	-
43	**Whareana (C)**	**1599435/6186534**	**56**	**20**	**NF**	**KC**	**+(8)**
44	**Whareana (B)**	**1599448/6186785**	**56**	**20**	**NF**	**KC**	**+(1)**
45	Rangiora Bay (B)	1599584/6185676	336	50	NF	KC	-
46	North Cape	1602231/6191815	336	20	NF	MI	-
			Total: 6832	**Total:** 510			

[1]NZGD 2000, NZTM.
[2]Total trapping effort = the number of traps multiplied by the number of days open.
[3]Total search time = the total time spent searching (time multiplied by number of people) until species detected by trapping or not detected at all.
[4]S = shrubland; NF = native forest; PP = pine plantation; TS = tall shrubland.
[5]Underlying parent rock type and/or major soil influences: WV = Whangakea Volcanics; PF = Paratoetoe Formation; KC = Kaurahoupo Conglomerate; PD/csp/PF = Pleistocene deposits with consolidated sand and peat over Paratoetoe Formation; HA/WV = Holocene Alluvium over Whangakea Volcanics; PD/cs = Pleistocene deposits with consolidated sand only; MI = Murimotu Intrusives.
[6]Number of individuals caught, in parentheses. For lethal trapping, number of individuals caught is the cumulative total over four trapping events; for live trapping, number caught = number of individuals captured on first (and only) detection.