

RESEARCH ARTICLE

Improved resolution of cave weta diversity (Orthoptera: Rhaphidophoridae): ecological implications for Te Pahi, Far North, New Zealand

JL Fitness^a, M Morgan-Richards^a, OJ-P Ball^b, AJR Godfrey^c and SA Trewick^{a*}

^aEcology Group, Institute of Agriculture and Environment, Massey University, Palmerston North, New Zealand;

^bNorthTec, Applied and Environmental Sciences Department, Whangarei, New Zealand; ^cInstitute of Fundamental Sciences, Massey University, Palmerston North, New Zealand

(Received 27 February 2014; accepted 29 October 2014)

The New Zealand cave weta fauna is large and diverse but poorly described. This study aimed to improve the strategies for cave weta identification and, in doing so, build an understanding of population dynamics and distribution of the taxon across three habitat types in the Te Pahi Ecological District. Species identification used morphological traits and metric analysis of specimens in pitfall traps. Although nearly half the individuals were juveniles (< 10 mm long) that could not readily be distinguished from one another, four species were identified from the larger specimens. Capture rates of cave weta varied by species, habitat, month and the interactions of these variables. Nearly half of all identified cave weta individuals in our sample were *Neonetus variegatus*, which was abundant across all three habitats (pine forest, native forest and shrubland) throughout the year, but were caught in pitfall traps in the greatest numbers in some pine forest sites. A species of *Pachyrhamma* was also abundant and showed seasonal variation in capture rate, but no adults were captured by pitfall traps. *Talitropsis* sp. and *Pallidoplectron* sp. were least frequent in our sample. Taxonomic resolution improves ecological inference, but, as with other invertebrates, trapping method and design influence sampling outcome among species.

Keywords: biodiversity; cave cricket; cave weta; *Neonetus*; *Pachyrhamma*; *Pallidoplectron*; Rhaphidophoridae; *Talitropsis*

Introduction

Invertebrates provide a huge range of ecosystem services and functions that are largely unknown to the public or policy makers (Cardoso et al. 2011). Deficiency of ecological information is due in part to inadequate species discovery and classification reliant on scant information from different collecting locations and taxa being confounded. In New Zealand, where species-level endemism is high (Trewick & Morgan-Richards 2009) and invertebrate diversity is inadequately characterised (Gordon 2010), studies of the distribution and abundance of forest invertebrates is impeded by lack of taxonomic resolution (Giangrande 2003; Ward &

Larivière 2004). It is common practice in studies seeking to contrast biodiversity across habitats or time to taxonomically round-up to family and order level, discarding potentially informative ecological information about habitats, seasons and species (Moeed & Meads 1992; Crisp et al. 1998; Bowie et al. 2006; Ruscoe et al. 2013). Inadequate taxonomic discrimination can influence all types of downstream biodiversity assessments (Whittaker 1972).

A primary use of biodiversity data is in the establishment of conservation criteria for habitats and areas (Kremen et al. 1993). It is generally assumed that diversity of native invertebrate species

*Corresponding author. Email: s.trewick@massey.ac.nz

is greatest in the least modified areas, where the highest diversity of indigenous plants exists (Crisp et al. 1998), but determining the biodiversity of any area, whether natural or modified, is currently intractable at the species level for many invertebrate groups. Similarly, estimation of ecosystem function or community health tends to be dependent on few readily recognised species rather than on the most relevant taxa (Hilty & Merenlender 2000). For example, Australian ants are often used as bio-indicators to assess effects of habitat disturbance (Hoffmann & Andersen 2003), and tree weta (*Hemideina thoracica* [White, 1846]) abundance to assess the impact of predator control in New Zealand (Ruscoe et al. 2013).

Cave weta (Orthoptera: Rhabdophoridae) are abundant, widespread and diverse in most terrestrial New Zealand habitats, but few species have been considered in detailed ecological analyses. This is largely because their inadequate taxonomy currently limits their value in comparing regional biodiversity or assessing the effects of habitat modification on biodiversity. There are 55 described New Zealand Rhabdophoridae species assigned to 16 genera (Eades et al. 2013). Additional diversity certainly exists, with many new species awaiting description. At the same time, genus- and species-level taxonomy needs revision and will involve some synonymy. For example, two genera have recently been discarded (Cook et al. 2010), and this attrition continues a long tradition within the New Zealand literature of revision and synonymy for invertebrates. Most taxonomic work has relied on few individuals from single locations, and the collection of Rhabdophoridae in general has been limited. In part this is due to the expectation that cave weta occupy caves. The scarce, locally distributed, large-bodied cave-dwelling species (mostly genus *Pachyrhamma* Brunner von Wattenwyl, 1888) dominate the literature at the expense of the majority, which are relatively small, abundant, cryptic forest-dwelling species (e.g. Hutton 1897; Richards 1959, 1960; see also www.wetageta.massey.ac.nz). In fact, various cave weta species occupy almost all terrestrial and arboreal habitats in New Zealand from bogs to alpine scree fields,

but in most cases this is the limit of our understanding of their biology. Their light-shy nocturnal habit, sexual dimorphism and incomplete metamorphosis all impede taxonomic resolution, but our recent (unpublished) observations indicate that forests in central New Zealand are typically occupied by about six different cave weta species.

The first task for efficient progress with the taxonomy and complementary ecological analysis of cave weta is to identify characters and strategies that are useful in detecting differences between taxa. Clarification of terminology is essential to make such tools usable. Here we approach the general problem by explicitly examining how best to detect distinct taxa with the assumption of no prior information about the taxa at a location. Using cave weta from an extensive sampling programme in Te Paki Ecological District (Far North, New Zealand), we set out to establish an approach to distinguish putative species, determine what taxa exist in the area, and use this information to explore their seasonal distribution and abundance among habitat types and sites.

Methods

Study region and sampling

Te Paki Ecological District in Northland (Fig. 1) is regarded as a biodiversity hotspot within New Zealand, with a high number of endemic species including herbaceous plants (de Lange 2008), lizards (Chapple et al. 2008), insects (Winterbourn 2009; Buckley & Bradler 2010) and land snail species (Sherley 1996; Lux et al. 2009). The area has a high proportion of native vegetation, but most of this is regenerating after anthropogenic fire and agricultural modification (Lux et al. 2009). The range of native habitat types includes kauri (*Agathis australis*) forest, mixed broadleaf-podocarp forest, coastal forest, wetlands, gumlands and shrublands. There are also extensive plantations of introduced pine (*Pinus radiata*).

Sampling was carried out in three habitat types: native forest (coastal broadleaf and conifer broadleaf); pine plantation; and shrubland. The latter is dominated by mānuka (*Leptospermum scoparium*)

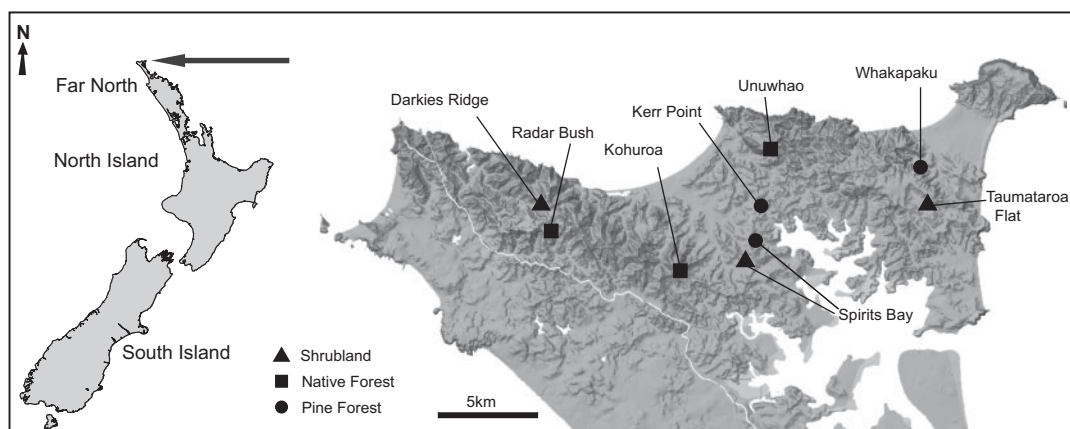


Figure 1 Study location in Te Pahi Ecological District, Far North, New Zealand, showing location of pitfall trap sites, in native forest, shrubland and pine forest habitat.

and kānuka (*Kunzea ericoides*), but includes sedge-land and gumland elements. Cave weta and other invertebrates were collected as part of a larger study of Te Pahi biodiversity using a stratified design comprising three randomly selected sites in each of the three habitat types. Lethal pitfall trapping at each site involved a cluster of eight traps placed in two rows of four with each trap 10 m from its neighbour. Our sampling sites correspond to sites 18–26 of Ball et al. (2013). The traps consisted of a plastic sleeve 110 mm in diameter sunk to just below ground level, inside of which was placed a snug-fitting plastic collecting cup (100 mm deep). Approximately 100 ml of 100% propylene glycol was used as the killing and preserving agent in each trap. Each trap had a plywood cover (200 mm × 200 mm × 12 mm) raised approximately 30 mm above the ground on wooden legs. Traps were reset monthly throughout the survey period from July 2006 until June 2007. The invertebrate samples were rinsed and stored in 80% ethanol and later sorted to family or order. At one site (Unuwahao A), where the rare beetle *Mecodema tenaki* (Seldon & Leschen 2011) was encountered, the sampling was reduced to once every three months to minimise adverse impact on that species.

Morphology and identification

Cave weta from each site were initially sorted into two groups based on size so that attention could

be focused on the morphology of the larger individuals that were more likely to be adult. Most weta species descriptions rely on characteristics of adults and currently there are no reliable data on morphological variation among juvenile stages within and between species. Our experience and available species descriptions indicate that adult cave weta are rarely less than about 10 mm long (frons to posterior tip of abdomen) so we examined and gathered data from the larger individuals in all time periods and habitats. We expected to encounter large juveniles as well as adults because there is a high degree of variation in adult size among New Zealand cave weta taxa. Distinguishing between adults and large juveniles relied on the darker sclerotised bodies and fully formed external genitalic structures of the former. In particular the pigmentation, shape and sharpness of ovipositors, subgenital plates and cerci were informative about developmental stage, although these features differ subtly between adults and subadults (the penultimate instar).

Examination of putative adults allowed us to formulate hypotheses about which morphological characters could be used to characterise and distinguish the different taxa present. We subsequently returned to the group of small (< c. 10 mm) individuals in order to determine whether any of these could be classified into one of the putative species inferred from larger specimens.

Table 1 Apical spines used for diagnosis of species and a summary of the presence and absence of the four putative species of cave weta TPA, TPB, TPC and TPD from Te Pahi Ecological District.

Spine code	Fore Femur		Mid Femur		Hind Femur		Fore Tibia		Mid Tibia		Hind Tibia		Fore Tibia		Mid Tibia		Hind Tibia		Fore Tibia		Mid Tibia		Hind Tibia		Fore Tibia		Mid Tibia		Hind Tibia						
	Pro.	Retro.	Pro.	Retro.	Pro.	Retro.	Pro.	Retro.	Superior	Pro.	Superior	Pro.	Retro.	Superior	Pro.	Retro.	Superior	Pro.	Retro.	Superior	Pro.	Retro.	Superior	Pro.	Retro.	Superior	Pro.	Retro.	Superior	Pro.	Retro.				
TPA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
TPB	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
TPC	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
TPD	1	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0

1, present; 0, absent.

Specimens were assessed using morphological characters that have previously been considered in cave weta taxonomy or have been found to be informative in similar arthropods. These characters included the combination of apical spines on the fore, mid, and hind femora and tibiae, and shape of subgenital plate. Altogether, presence/absence of each of 22 apical spines was recorded from one side of the body, although both sides were examined if there was any uncertainty about the absence of a spine, which might have been lost during handling (Table 1, Fig. 2). Measurements were made of pronotum length (Pro), hind femur length (HF) and hind tibia length (HT) using electronic callipers. Leg measurements were taken from the side that had the most complete legs still attached to the body to ensure correct allocation. Pronotum length was preferable to body length, which is variable in living and preserved specimens. The subgenital plates of males and females were examined and classified into readily recognised types. Pigmentation and pilosity (hairiness) were considered but both are altered or difficult to assess in wet glycol-preserved specimens.

Morphometric data for comparative analysis were obtained from a subsample of specimens that represented the range of shapes, sizes and sex of specimens. Most of these were adults or large juveniles and we noted the presence of many males and females that were not adult but were nevertheless large compared to the mean size of cave weta in our sample. All statistical analyses used R v3.0 (R Core Team 2013). Exploratory analysis used principal component analysis (PCA) in the ‘vegan’: Community Ecology Package (Oksanen et al. 2013). This analysis included the categorical apical spine and metric data to help determine whether taxa could be separated on the basis of these characters. PCA also examined whether juveniles could be matched to their adult counterparts using this morphological information, and which, if any, of these traits corresponded on males and females.

With data from adults and large juveniles (i.e. near adults in the case of one morphotype), *t*-tests

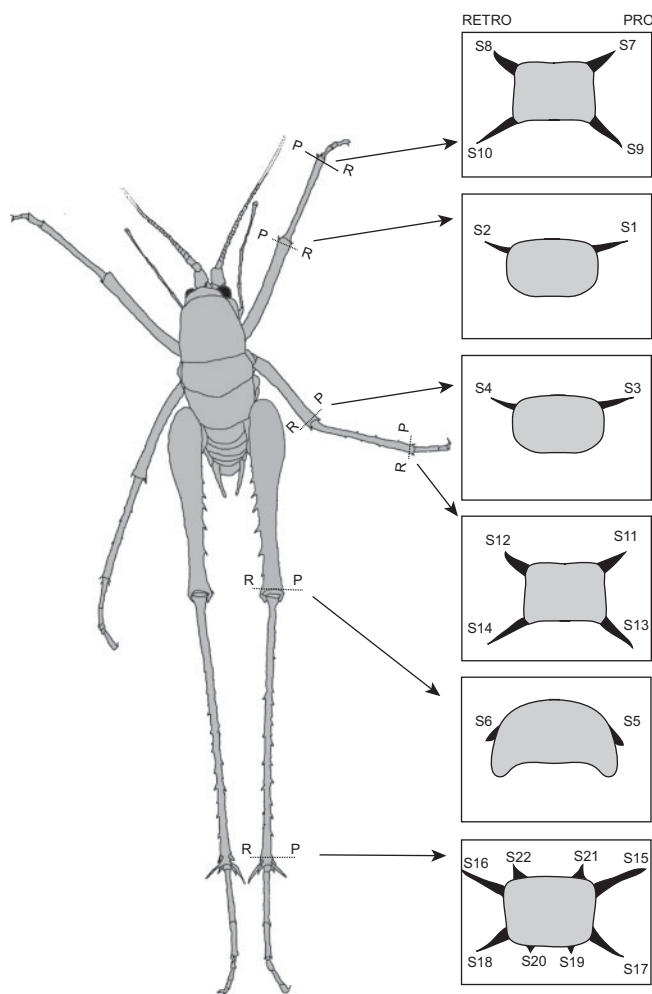


Figure 2 Dorsal view of cave weta showing the location of apical spines. S1) Fore femur prolateral; S2) fore femur retrolateral; S3) mid femur prolateral; S4) mid femur retrolateral; S5) hind femur prolateral; S6) hind femur retrolateral; S7) fore tibia superior prolateral; S8) fore tibia superior retrolateral; S9) fore tibia inferior prolateral; S10) fore tibia inferior retrolateral; S11) mid tibia superior prolateral; S12) mid tibia superior retrolateral; S13) mid tibia inferior prolateral; S14) mid tibia inferior retrolateral; S15) hind tibia superior prolateral; S17) hind tibia inferior prolateral; S19) hind tibia inferior subapical prolateral; S21) hind tibia superior subapical prolateral. Spines S15, S17, S19 and S21 are paired with the retrolateral spines S16, S18, S20 and S22, respectively.

were used to compare size differences between the sexes and the putative species. ANOVA with a Tukey HSD test was used to compare different measured traits among putative taxa. We applied PCA to the metric data (Pro, HF, HT) on their own to assess morphological variation among individuals within the large specimen set. We identified a combination of characters that diagnosed a

number of putative species. Alignment of the Te Pahi taxa to the existing described cave weta fauna involved judicious use of existing literature as detailed below.

Abundance

Total counts of all identifiable and unidentified juvenile cave weta from each sample enabled us to

analyse their relative abundance over space and time. All statistical analyses used R v3.0 (R Core Team 2013). We used generalised linear modelling (GLM) assuming a Poisson distribution of count data to compare cave weta abundance over time. Site and habitat are nested variables. Strictly, 'site' is a random effect but was not fitted in this way because we wanted to determine whether there was additional site–site variation, and so we added terms sequentially into the model. In general, the number of trap-days was constant for all sites in a given month and variation among months was accommodated by including month as a factor in the models. Zero counts were inserted where traps were in use but caught no cave weta, while traps not in use for a particular month were coded as NA. We modelled cave weta abundance with and without data for the unidentified juveniles as a fifth taxon. The response variable was the count for each species. The explanatory variables were site, habitat type (native forest, pine or shrubland) and time (month of the year trapped), and all possible interactions of these variables were considered.

Results

Using the larger cave weta that were either adults or near adults, we identified four morphotypes from their spination, overall size and appearance. Males and females could be reliably paired based on spine counts and overall size. Despite their size, it was apparent that the largest individuals, all of which were assignable to taxon TPB, included no adults. Females, for instance, had relatively soft, pale and blunt ovipositors, whereas adult Rhabdophoridae ovipositors are sclerotised, dark and pointed, often with fine serrations. The size range of the TPB specimens was greater than the adults of TPA, suggesting that a number of instars were included among the TPB sample. TPC and TPD were paler than TPA and TPB, and each had a unique spine combination (Table 1). TPC was similar in size to TPA and was initially overlooked because its pallid colouration and delicate form made it look like a juvenile of another species. The fourth phenotype, TPD, was

the smallest of all of the putative taxa and this species also had a pale, juvenile-like appearance. Careful examination of the ovipositors in the females of TPD specimens revealed otherwise. The unique spine combinations of all four taxa reinforced our hypothesis that they were different species and not just variants of the first morphotypes encountered (Fig. 3).

Discriminating morphotypes

Initial assessment of the reliability of classifying juveniles into one of the four morphotypes indicated that it was prudent to exclude small juveniles (< c. 10 mm) from subsequent morphological analysis. There was no clear discrimination of juveniles based on size into one of the four putative species (Fig. 4A). We also found the presence/absence of some spines to be more variable among the small juveniles than adults, suggesting an ontogenetic component to spine development. Juvenile females could usually be distinguished readily from their respective adults by their pale, soft and blunt ovipositors lacking serrations. Juvenile males were less readily distinguished as late instars were very similar to adults. However, juveniles tended to be smaller, paler, with fewer apical and lateral spines on the legs, and the genitalia were underdeveloped and often difficult to see. Distinguishing penultimate and last instar individuals was the most difficult and in many cases impractical, but also may not be necessary except when secondary sexual characters are expressed only in the final instar. In order for species diagnosis to be as robust as possible we removed all small juvenile and uncertain individuals from the sample sets for each morphotype, excepting those large but not adult individuals of TPB, which could always be reliably distinguished from the other morphotypes.

Males and females within the same species had very different subgenital plates associated with their different genital structure and function. From examination of adult specimens (and near adult TPB individuals) collected in this study we were able to identify eight distinct subgenital plate shapes, four relating to females and four to males

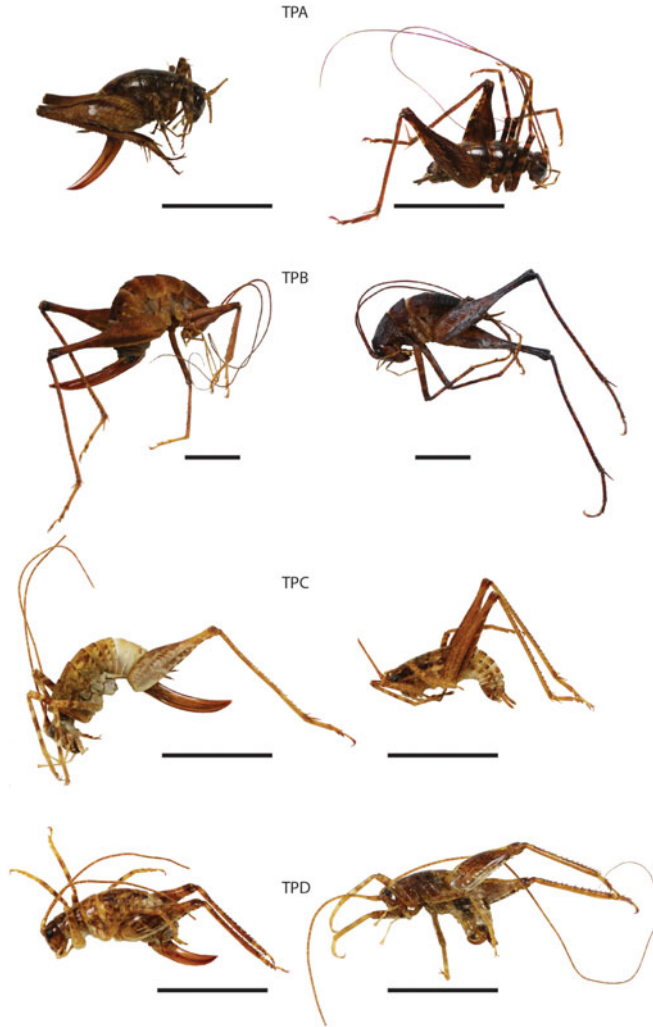


Figure 3 Four species of cave weta identified from Te Paki Ecological District, females on left, males on right.

(Fig. 5). To pair the males and females of the same species we used the apical leg spines.

In the TPA specimens, females had a subgenital plate that was small and triangular, with a notch at the apex, whilst in males it was curved distally with a double keel separated by a shallow groove. TPB females had a triangular subgenital plate but the males had a long, narrow tongue-like structure indented on the ventral surface. The TPC females' subgenital plate was broad with parallel sides and two distal lobes, while in males it was slightly curved upwards distally with no keel. The

female TPD subgenital plate was broad and short, with the distal margin toothed, and in the male it was narrow at its base but widening as it curved upwards (Fig. 5).

Four main permutations of apical spines were identified (Table 1). In addition we found that the hind femur retrolateral apical spine was sometimes present and sometimes absent in specimens of TPA. This variation showed no consistent pattern in space or time, and was therefore considered to be polymorphic within this species. The three other apical spine combinations were unvarying

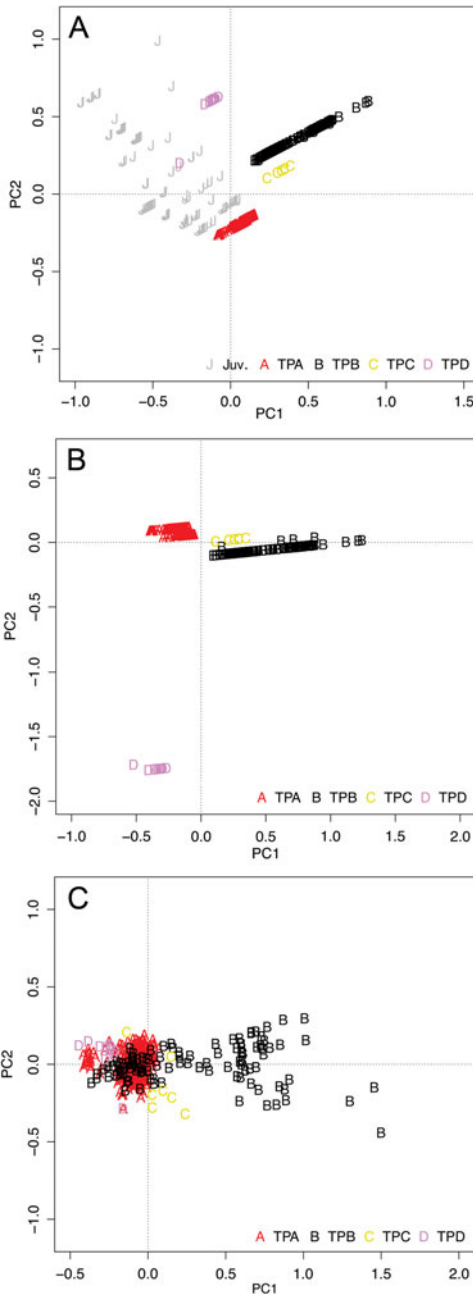


Figure 4 Principal component analysis of Te Paki cave weta morphology. **A**, All taxa and juveniles using spine and metric data; **B**, four diagnosed taxa using spine and metric data (data from unidentified juveniles excluded); **C**, four diagnosed taxa using only metric data. *J*, juveniles < 10 mm long; *A*, TPA; *B*, TPB; *C*, TPC; *D*, TPD.

among individuals of the same morphogroup, including males and females, which allowed them to be matched. Presence/absence of six apical spines varied consistently among the four species: fore femur retrolateral apical spine, mid femur prolateral apical spine, fore tibia superior prolateral apical spine, mid tibia superior prolateral apical spine, hind tibia inferior subapical prolateral spine and hind tibia inferior subapical retrolateral spine (Table 1, Fig. 2). Together, these provide a combination of character states that consistently and reliably diagnosed adults and near adults of the four taxa encountered.

Metric analysis

Data from 319 adult TPA, TPC and TPD, 104 large TPB pre-adults and 154 other unidentified small juveniles were used in metric analysis to compare shape and size between sexes and among the four taxa. Only for TPA did we find any significant size difference between the means of adult males and females (*t*-test, $P < 0.05$, Table 2). Although males and females of the other putative species did not differ significantly in size we note that there were quantitative differences between sexes. For instance, the hind femur of male TPC specimens was longer than the females' (Fig. 3). Adult TPB may well differ but this could not be tested with the present sample.

Tukey HSD comparison tests showed there were significant differences in size of all three metric variables measured between TPA and TPB (P -value < 0.0001), and between TPB and TPD (P -value < 0.0001). In all cases, TPB was the largest even though no adults of this taxon were present in the sample. However, size alone was not reliable for distinguishing all taxa and the use of spine combination characters and subgenital plate shape was essential (Table 3).

Including all spine data and the three metric variables (P , HF and HT) PCA resolved numerous clusters when unidentified juveniles were included (Fig. 4A). TPA formed a cluster with a relatively large range in male and female sizes, but no discrete clusters indicative of instars or juveniles versus adults. TPB size variation was greatest,

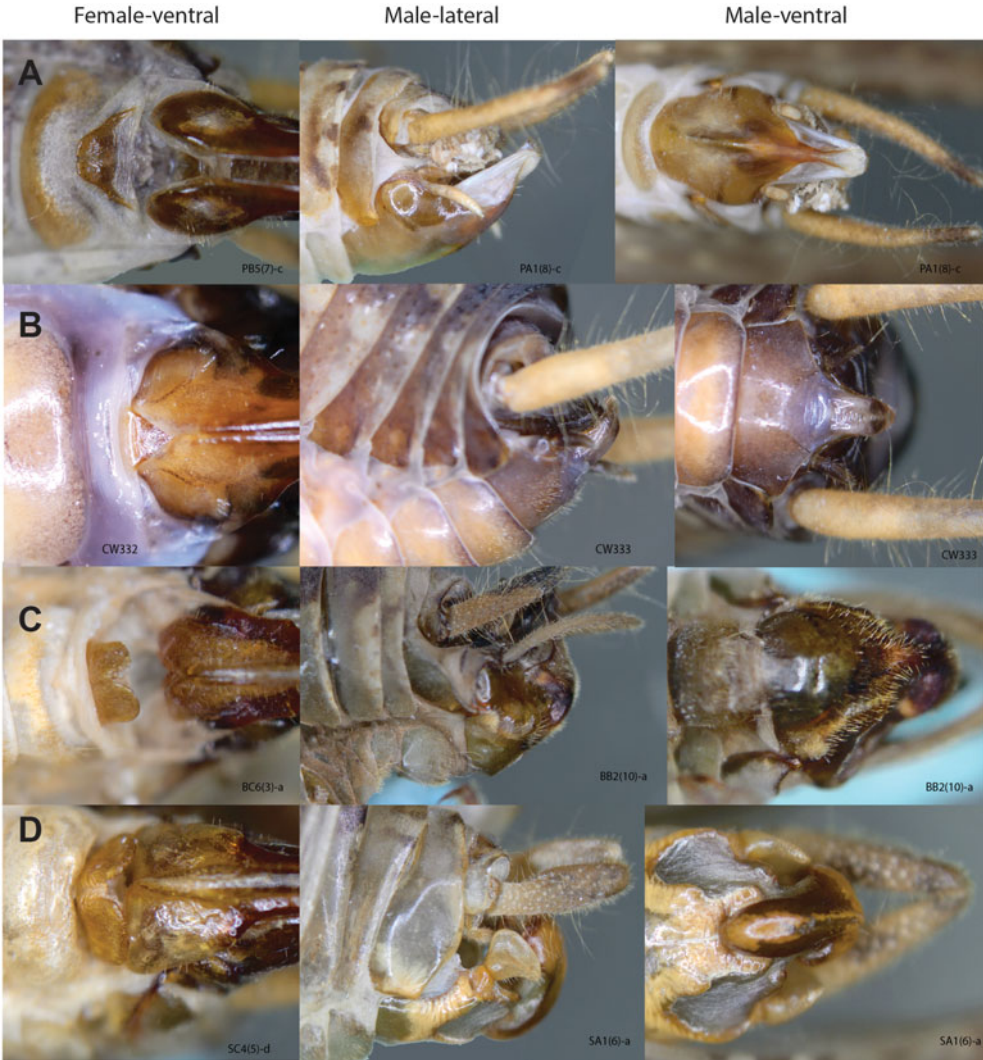


Figure 5 Subgenital plates of the four cave weta species identified from the Te Paki area. **A**, TPA (*Neonetes variegatus*); **B**, TPB (*Pachyrhamma* sp.); **C**, TPC (*Pallidoplectron* sp.); **D**, TPD (*Talitropsis* sp.).

which suggested the inclusion of several instars, but these overlapped in size. Excluding unidentified juveniles resulted in the four putative species forming separate arrays (Fig. 4B). The specimens representing TPA formed two adjacent clusters due to the variable presence/absence of the hind femur retrolateral apical spine. The close proximity of the two clusters strengthened our conclusion that these individuals were conspecific. When

spine data were removed from the analysis (Fig. 4C) we found that metric data alone were not sufficient to distinguish taxa.

Species abundances

We examined frequency of cave weta capture in pitfall traps using a GLM and found all explanatory variables significantly affected the fit of the

Table 2 Comparisons using *t*-tests of male and female mean sizes for three morphological traits in four cave weta species from Te Paki Ecological District.

Mean size in mm. (SEM)	<i>Neonetus variegatus</i> (TPA)		<i>Pachyrhamma</i> sp. (TPB)		<i>Pallidoplectron</i> sp. (TPC)		<i>Talitropsis</i> sp. (TPD)	
	Male <i>n</i> = 115	Female <i>n</i> = 182	Male <i>n</i> = 53	Female <i>n</i> = 51	Male <i>n</i> = 5	Female <i>n</i> = 2	Male <i>n</i> = 5	Female <i>n</i> = 6
Pronotum	2.69 (0.023)	2.980 (0.023)	3.906 (0.185)	4.358 (0.198)	3.19 (0.107)	3.275 (0.215)	2.45 (0.088)	2.384 (0.084)
Hind femora	8.63 (0.090)	8.927 (0.074)	12.61 (0.717)	13.293 (0.614)	16.7 (0.175)	10.04 (2.15)	7.12 (0.362)	7.409 (0.467)
Hind tibia	9.346 (0.099)	9.422 (0.078)	13.75 (0.740)	14.508 (0.638)	12.5 (0.196)	11.72 (3.45)	6.88 (0.423)	7.665 (0.679)

Bold, $P < 0.05$.

Table 3 Adjusted P values from Tukey HSD test comparing mean lengths of pronota, hind femura and hind tibiae of four cave weta species from Te Paki Ecological District pitfall traps.

	Pronotum length	Hind femur	Hind tibia
TPA vs TPB	0.000	0.000	0.000
TPA vs TPC	0.543	0.297	<u>0.025</u>
TPA vs TPD	0.174	0.095	<u>0.014</u>
TPB vs TPC	<u>0.014</u>	0.073	<u>0.284</u>
TPB vs TPD	0.000	0.000	0.000
TPC vs TPD	0.089	<u>0.023</u>	0.000

Significant differences are underlined ($P < 0.05$) or in bold ($P < 0.0001$). TPA (*Neonetus variegatus*), TPB (*Pachyrhamma* sp.), TPC (*Pallidoplectron* sp.), TPD (*Talitropsis* sp.).

GLM (Table 4). From the model we could infer that abundance of cave weta in pitfall traps depended on time of year, site, habitat, species and interactions of these effects. Including juveniles in the model resulted in the same variables being significant in determining abundance. In a

Table 4 Generalised linear model (Poisson, link: log) to explain the variation in cave weta abundance (response) in pitfall traps in Te Paki, New Zealand. Terms added sequentially (first to last). There were nine sites situated in one of three habitats (native forest, pine forest and scrub). Four cave weta species were identified and juveniles were excluded.

	<i>df</i>	Deviance	Resid. <i>df</i>	Resid. dev	Pr (> Chi)
NULL			431	6461	
Species	3	3177	428	3284	<0.001
Month	11	336	417	2948	<0.001
Habitat	2	1260	415	1688	<0.001
Site	6	448	409	1240	<0.001
Species:	33	260	376	979	<0.001
Month					
Species:	6	91	370	888	<0.001
Habitat					
Month:Habitat	22	105	348	783	<0.001
Species:	66	86	282	697	0.049
Month:					
Habitat					

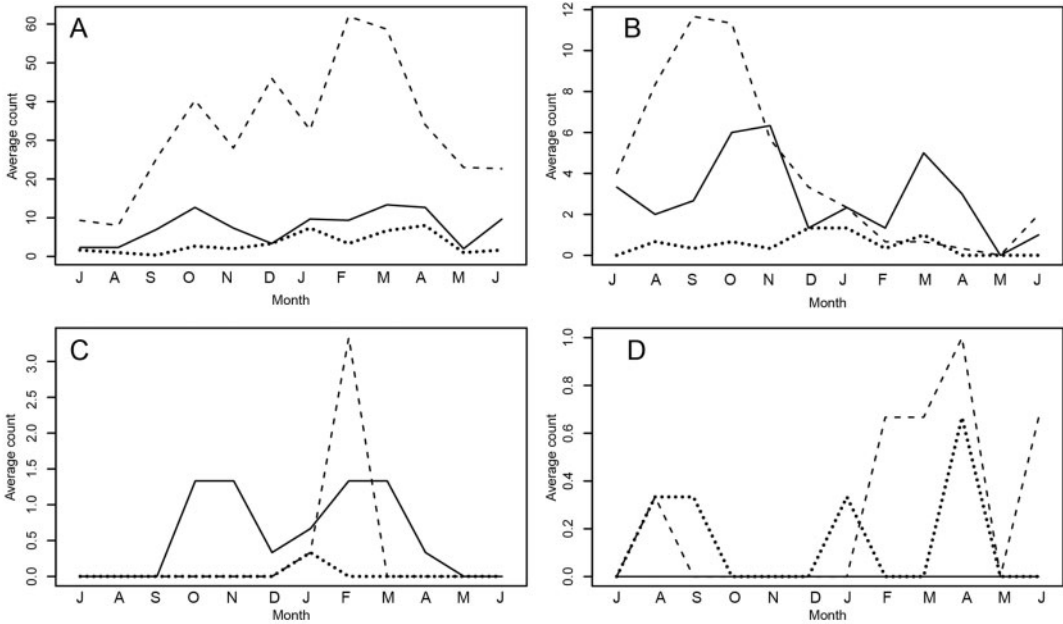


Figure 6 Mean monthly counts of four cave weta species in pitfall traps in Te Paki Ecological District between July 2006 and June 2007. **A**, TPA (*Neonetus*); **B**, TPB (*Pachyrhamma*); **C**, TPC (*Pallidoplectron*); **D**, TPD (*Talitropsis*). dashed line, pine forest; dotted line, native forest; —, shrubland. Note that y axis scales differ.

total sample of 3308 cave weta in our pitfall data, TPA constituted the majority of the 1880 that were classified into one of four taxa (83.1%). TPA occurred in all three habitat types sampled (Fig. 6A) and relative abundance was high in all months, including late winter (August, September) when > 100 individuals were caught. At all times of year the highest numbers of TPA were recorded from pine forest. TPB was the next most common species in our sample of cave weta large enough to be identified (14.4%), and was also found in all three habitats (Fig. 6B). TPB numbers in pine forest increased from June 2006 until the highest trapping rate in spring (September–October). This spring peak was not observed with the other three cave weta species, and might be an artefact of adult TPB being undersampled. So few TPC were found in the pitfall traps (< 2% of total), that no specimens of this species were caught between June and October (winter–mid-spring). Although TPC were collected from all three habitats only a single individual adult was collected from native

forest and, in total, more were sampled from shrubland than pine forest (Fig. 6C). TPD was also collected in low numbers (< 1%) in native forest and pine forest but not shrubland.

Significant interactions of species with month and habitat were detected, and we note significant variation among sites such that cave weta abundance within habitats was influenced by site. For example, most of the temporal variation in TPB numbers and differences among habitats appears to be derived from the pine forest sites at Kerr Point and Whakapaku. Thus, cave weta abundance at Te Paki requires identification and separate treatment of the four species.

Taxonomy

We reviewed existing descriptions of New Zealand Rhabdophoridae in relation to the apical spine data, subgenital plate shape, other morphological attributes (colour, pattern, hairs etc) and location information. This enabled us to confirm the genus

to which each morphotype belonged, and in one case the most likely species name. Thus, TPA, the most abundant species in the sample, was most likely *Neonetes variegatus* Brunner von Wattenyl, 1888 according to the description of Chopard (1923). The largest species, TPB, of which no adults were found in the pitfall traps, can readily be assigned to *Pachyrhamma* consistent with an adult pair of *Pachyrhamma* previously collected together in a hollow log at Unuwahao (Cook et al. 2010). Although the *Pachyrhamma* from the present study were not adults, their spine counts were consistent with known adult *Pachyrhamma* species from around New Zealand. TPC had numerous small retro and pro lateral spines on the hind femur similar to *Pallidoplectron* Richards, 1958. However, TPC was a much smaller species than the three *Pallidoplectron* currently described (Richards 1958, 1960). TPD was most similar to *Talitropsis* Bolivar, 1882, having a combination of spines, colour and glossy appearance very like *Talitropsis sedilloti* Bolivar, 1882, but the subgenital plates of males and females clearly distinguished it from that widespread and abundant mainland species.

Discussion

Species identification

We found that four species of cave weta detected in the Te Paki Ecological District could be distinguished just by the presence/absence of apical leg spines. Each spine permutation for adults of the four taxa was associated with a pair of subgenital plates (male and female). The pitfall trapping method appeared to capture most, if not all, instar stages of the four species, and adults of three of the four species, although we found instar sizes were not discrete. Adults of the large *Pachyrhamma* species (TPB) were apparently excluded by the pitfall sampling procedure. This might be due to the physical size of the traps or trap entrances being too small for the adult *Pachyrhamma* sp. to access, or a switch in microhabitat preferences between age classes. Although some species of *Pachyrhamma* are known to frequent caves, they are not limited to

this environment throughout their lifecycle, often coming out into the forest to forage on surrounding vegetation at night (Richards 1954; Cook et al. 2010). Furthermore, adults and juveniles have been observed together in caves (Richards 1962). The present study was limited by the single collection method used. Discovery of full cave weta diversity, population structure and behavioural shifts would probably be best achieved using a combination of sampling strategies.

It was possible to place the four cave weta species into genera even though many existing rhabdophorid descriptions are deficient. *Neonetes* was established by Brunner von Wattenwyl in 1888, but his original description is recognised as being rather vague with respect to species diagnosis (Chopard 1923). Redescription of *N. variegatus* by Chopard (1923) helped reconcile differences between Brunner von Wattenwyl's original description and that of Hutton (1897) and the specimens examined by Chopard (1923) himself. Hutton's description of *N. variegatus* is based on specimens from Auckland, whereas Chopard believed that Brunner's description of *N. variegatus* was closer to Hutton's *N. pilosus* from Wellington. Following Chopard's description, *N. variegatus* is the most likely candidate for the species TPA from Te Paki Ecological District.

Placement of TPB in the genus *Pachyrhamma* stems from particular spine combinations, especially the absence of both the fore femur retro-lateral apical spine and the hind femur prolateral apical spine (although in some *Pachyrhamma* this spine may be present), and the presence of all the other spines examined (Table 1). Geographically, the closest identified species *Pachyrhamma wai-puensis* Richards, 1960, was described from the Waipu caves area 280 km south of Te Paki (Richards 1960; Cook et al. 2010). It is possible that our pitfall traps caught an undescribed *Pachyrhamma* species. In order to establish the identity of *Pachyrhamma* sp. in this study we referred to an adult pair collected previously at Unuwahao and included in a phylogenetic study and taxonomic review of *Pachyrhamma* (Cook et al. 2010). The Te Paki specimens have the same spine configuration and subgenital plates as the

Unuwhao adult pair that are part of a distinct phylogenetic cluster within the *Pachyrhamma* clade. Neither morphology nor DNA data support the Te Paki *Pachyrhamma* taxon as *P. waipuenis* or any other named species.

The two remaining species of cave weta recorded in this study appear to be undescribed but are consistent with two existing genera. One can be assigned to *Pallidoplectron* due to the spine combination described by Richards (1958). This requires reinterpretation of Richards' use of the terms 'prolateral' and 'retrolateral', which appear to have been transposed in that description. The numerous lateral spines on the hind femur of TPC is a characteristic of this genus that we have recorded in specimens from other parts of the North Island (Josephine Fitness, Massey University, unpubl. data). The Te Paki taxon is smaller than the three described species: *Pallidoplectron turneri* Richards 1958, from the Waikato district near Waitomo; *P. peniculosum* Richards 1960, from the Waipu caves; and *P. subterraneum* Richards 1965, also from Waikato. Currently, there are no other published data on *Pallidoplectron* outside cave environments. The fourth species belongs to the genus *Talitropsis*, and is recognised as a member of this genus by the posterior face of the hind tibia being flattened and the hind femur possessing two small lateral spines on the retrolateral and prolateral sides. Another useful character to distinguish some *Talitropsis* species is that the hind femur is the same length or slightly longer than the hind tibia; the reverse is seen in most other genera. This may relate to the association of *Talitropsis* with small tree-hole roosts. The genitalia show that the Te Paki individuals are not *T. sedilloti*, which is widespread and abundant throughout New Zealand and has been the subject of some morphological and genetic analysis (Trewick 1999; Goldberg & Trewick 2011). There are two species endemic to the Chatham islands but only one other name has been applied to specimens from mainland New Zealand; *Talitropsis irregularis* Hutton, 1896 from Auckland. The brief description *T. irregularis* lacks clarity and no new material has come to light.

Variation in the presence/absence of spines and the size and shape of the cave weta revealed how challenging identification for this family can be. Initially, individuals of similar size were apparently indistinguishable, but closer inspection of numerous cave weta in the Te Paki sample revealed that spine counts alone were sufficient to distinguish four species (when adult or near adult). When dealing with the approximately 55 described species nationwide, apical spine combination will likely need to be combined with details of genitalia, size and geographic distribution (when better known). Apical spines were shown to be unreliable when dealing with juveniles. There are at least 16 genera of cave weta in New Zealand and although some revision is required this classification reflects substantial morphological variation. Although the presence/absence of a single spine has in the past been used for genus description, it is not sufficient. For example, *Turbottoplectron* Salmon, 1948 was distinguished from *Pachyrhamma* and *Gymnoplectron* Hutton, 1896 because it did not have the prolateral apical spine on the hind femur that was supposedly present in all species of the other two genera (Salmon 1948). Analysis of morphological and genetic information from representatives of these three genera justifies their synonymy as *Pachyrhamma* (Cook et al. 2010). We observed variation at one apical spine within *N. variegatus* from the Te Paki Ecological District in our study, showing that a single character can be misleading and the use of too few specimens in the establishment of cave weta taxonomy (as has frequently been the case) can overlook intra-specific and intra-population variation and result in unstable systematics.

In some orthopteran families, linear spines on leg elements may also be useful to distinguish between species. However, for cave weta, it has been shown that there is too much variation in these linear spines for them to be informative on their own (Richards 1959, 1960). Subgenital plates proved to be useful in the Te Paki sample. They differ for males and females but once matching pairs are identified using spination, subgenital plates prove to be the strongest candidate for

species distinction. In insect systematics, external genitalic structures are widely used for diagnostic characters as male parts are often more complex than the female equivalent (Eberhard 2010), and this is also true in Orthoptera (e.g. Usmani & Kumar 2011). However, the subgenital plates in male cave weta are structurally complex, and their three-dimensional shape is less readily described than the female structure, which can often be characterised in two dimensions.

Species abundance

At least four species of endemic cave weta are sympatric in the Te Paki region. Adults of *Neonetus variegatus* were caught in all three habitat types surveyed, although they were encountered more often in pine forest than native forest or shrubland. In contrast, adult *Talitropsis* were not caught in any of the shrubland traps, although the small sample size of this taxon precludes ecological inferences.

Trap capture rates may not accurately reflect true abundances, as differences including activity levels, trapping vulnerability and habitat heterogeneity, are likely to interact to yield final trapping rates. However, capture rates are species-dependent, and species capture rates were found to depend on both habitat and time of year. An interesting observation is that only in *Pachyrhamma* sp. (TPB) did we see a springtime increase in the capture rate. This suggests that when Rhabdiphoridae are combined into a single unit during an analysis, important information is likely to be lost. For example, studies aimed at recording the effects of predator control on cave weta abundance might produce misleading results when numerous species are treated as one (Ruscoe et al. 2013).

In considering regional biodiversity and its conservation, the quality of modified habitats and their capacity to support native species is important. In most instances, native species would be assumed to be more successful in native vegetation, but studies are increasingly showing that many native invertebrates can thrive in disturbed and modified habitats including urban areas (e.g.

Brockerhoff et al. 2001; Blanchon et al. 2011). Within *Pinus radiata* plantations at Te Paki we collected the same four species but detected significantly higher numbers of two cave weta species compared to the native forest or shrubland habitat, providing evidence of the important role pine forest can have in maintaining populations of endemic invertebrates (Maunder et al. 2005).

Conclusion

Even with an uncertain taxonomy, it is possible to increase resolution of biodiversity analyses using relatively few readily identified morphological characters. Careful treatment allows separation of adult (or near adult) individuals from juveniles, and segregation of distinct taxa among a pool of superficially similar individuals. This then provides the opportunity to glean much more information about spatial and temporal variation in abundance among the different taxa. Using a combination of apical spine and subgenital plate characters we were able to distinguish and identify four taxa of cave weta from the Te Paki Ecological District. Scrutiny of existing descriptions has allowed us to tentatively assign each of the four species to a genus and we consider three are likely to be new undescribed species. Morphological variation observed in *N. variegatus* spine data within populations confirms that some apical spination is not consistent within species. The high capture rate for this species enabled us to establish that this intra-specific variation was independent of sex, habitat or life stage.

With improved systematic resolution, the trapping data provides insight into the distribution of species and indicates species-specific spatial, temporal and habitat differences in relative abundances. This indicates that future studies of biodiversity will be more informative and meaningful because distinct taxa with distinct ecologies will each contribute to analyses. Disturbed environments appear not to impede the distribution of *Neonetus variegatus*, and pine forest appears to provide a valuable habitat for at least some endemic invertebrates. It is clear, however, that a single

trapping regime will not accurately capture all invertebrates or even all rhabdiphorid diversity.

Acknowledgements

We thank members of the Phoenix lab (evolves.massey.ac.nz), and Adam Sullivan, Shaun Neilsen, Lewis Fitness, Paul Barrett and Cleland Wallace for their assistance. Special thanks to Robin Ball for sorting weta from the samples. We are grateful to Muriwhenua Incorporation and Ngāti Kuri for their kind support throughout the project. This research was supported by NorthTec (Research Grant no. 2007–019), DoC (TIF-BIS WetaGeta.massey.ac.nz) and FRST (Te Tipu Pūtaiao Fellowship).

References

- Ball O J-P, Whaley PT, Booth AM, Hartley S 2013. Habitat associations and detectability of the endemic Te Paki ground beetle *Mecodema tenaki* (Coleoptera: Carabidae). *New Zealand Journal of Ecology* 37: 84–94.
- Blanchon D, Pusateri J, Galbraith M, Thorpe S 2011. Sampling indigenous ground-living beetles in a stand of non-native tree privet (*Ligustrum lucidum*) in New Zealand raises new management questions. *Ecological Management & Restoration* 12: 234–236.
- Bowie MH, Hodge S, Banks JC, Vink CJ 2006. An appraisal of simple tree-mounted shelters for non-lethal monitoring of weta (Orthoptera: Anostomatidae and Rhabdiphoridae) in New Zealand nature reserves. *Journal of Insect Conservation* 10: 261–268.
- Brockerhoff EG, Ecroyd CE, Langer ER 2001. Biodiversity in New Zealand plantation forests: policy trends, incentives, and the state of our knowledge. *New Zealand Journal of Forestry* 46: 31–37.
- Buckley TR, Bradler S 2010. *Tepakiphasma ngatikuri*, a new genus and species of stick insect (Phasmatodea) from the Far North of New Zealand. *New Zealand Entomologist* 33: 118–126.
- Cardoso P, Erwin TL, Borges PAV, New TR 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 144: 2647–2655.
- Chapple DG, Patterson GB, Bell T, Daugherty CH 2008. Taxonomic revision of the New Zealand copper skink (*Cyclodina aenea*: Squamata: Scincidae) species complex, with descriptions of two new species. *Journal of Herpetology* 42: 437–452.
- Chopard L 1923. On some New Zealand Orthoptera. *Transactions of New Zealand Institute* 54: 230–239.
- Cook LD, Trewick SA, Morgan-Richards M, Johns PM 2010. Status of the New Zealand cave weta (Rhabdiphoridae) genera *Pachyrhamma*, *Gymnoplectron* and *Turbottoplectron*. *Invertebrate Systematics* 24: 131–138.
- Crisp PN, Dickinson KJM, Gibbs GW 1998. Does native invertebrate diversity reflect native plant diversity? A case study from New Zealand and implications for conservation. *Biological Conservation* 83: 209–220.
- de Lange PJ 2008. *Hebe saxicola* (Plantaginaceae)- a new threatened species from western Northland, North Island, New Zealand. *New Zealand Journal of Botany* 46: 531–545.
- Eades DC, Otte D, Cigliano MM, Braun H 2013. Orthoptera species file online, version 5.0/5.0. <http://orthoptera.speciesfile.org> (accessed 24 June 2013).
- Eberhard W 2010. Evolution of genitalia: theories, evidence, and new directions. *Genetica* 138: 5–18.
- Giangrande A 2003. Biodiversity, conservation, and the ‘taxonomic impediment’. *Aquatic Conservation-Marine and Freshwater Ecosystems* 13: 451–459.
- Goldberg J, Trewick SA. 2011. Exploring phylogeographic congruence in a continental island system. *Insects* 2: 369–399.
- Gordon DP 2010. The New Zealand inventory of biodiversity. Volume 2: Kingdom Animalia Chaetognatha, Exdysozoa, Ichnofossils. Christchurch, New Zealand, Canterbury University Press.
- Hilty J, Merenlender A 2000. Faunal indicator taxa selection for monitoring ecosystem health. *Biological Conservation* 92: 185–197.
- Hoffmann BD, Andersen AN 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* 28: 444–464.
- Hutton FW 1897. The Stenopelmatidae of New Zealand. *Transactions of New Zealand Institute* 29: 223–240.
- Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF, Sanjayan MA 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7: 796–808.
- Lux J, Holland W, Rate S, Beadel S 2009. Natural areas of Te Paki Ecological District. Whangarei, Department of Conservation.
- Maunder C, Shaw W, Pierce R 2005. Indigenous biodiversity and land use – what do exotic plantation forests contribute? *New Zealand Journal of Forestry* 49: 20–26.
- Moeed A, Meads MJ 1992. A survey of invertebrates in scrublands and forest Hawke’s Bay, New Zealand. *New Zealand Entomologist* 15: 63–71.
- Oksanen J, Guillaume BF, Kindt R, Legendre P, Minchin PR, O’Hara RB et al. 2013. Vegan: community ecology package. R package version 2.0–10.

- <http://CRAN.R-project.org/package=vegan> (accessed 11 December 2013).
- Richards AM 1954. Notes on food and cannibalism in *Macropathus filifer* Walker 1869 (Rhaphidophoridae, Orthoptera). Transactions of the Royal Society of New Zealand 82: 733–737.
- Richards AM 1958. Revision of the Rhaphidophoridae (Orthoptera) of New Zealand. Part III. The genera *Pachyrhamma* Brunner and *Pallidoplectron* n.g. Transactions of the Royal Society of New Zealand 85: 695–706.
- Richards AM 1959. Revision of the Rhaphidophoridae (Orthoptera) of New Zealand. Part VI. A new species belonging to the genus *Pachyrhamma* Brunner, 1888. Transactions of the Royal Society of New Zealand 87: 329–332.
- Richards AM 1960. Revision of the Rhaphidophoridae (Orthoptera) of New Zealand. Part VII. The Rhaphidophoridae of the Waipu Caves. Transactions of the Royal Society of New Zealand 88: 259–264.
- Richards AM 1962. Feeding behaviour and enemies of Rhaphidophoridae (Orthoptera) from Waitomo Caves, New Zealand. Transactions of the Royal Society of New Zealand, Zoology 2: 121–129.
- Ruscoe WA, Sweetapple PJ, Perry M, Duncan RP 2013. Effects of spatially extensive control of invasive rats on abundance of native invertebrates in mainland New Zealand forests. Conservation Biology 27: 74–82.
- Salmon JT 1948. New genera, species, and records of Orthoptera from the Three Kings Islands, New Zealand. Records of the Auckland Institute & Museum 3: 301–307.
- Sherley G 1996. Morphological variation in the shells of *Placostylus* species (Gastropoda: Bulimulidae) in New Zealand and implications for their conservation. New Zealand Journal of Zoology 23: 73–82.
- R Core Team 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/> (accessed 18 April 2013).
- Trewick SA. 1999. A new weta from the Chatham Islands (Orthoptera: Raphidophoridae). Journal of the Royal Society of New Zealand 29: 165–173.
- Trewick SA, Morgan-Richards M 2009. New Zealand biology. In: Gillespie RG, Clague DA eds. Encyclopedia of islands. Berkeley, University of California. Pp. 665–673.
- Usmani MK, Kumar H 2011. Female genitalia as a taxonomic tool in the classification of Indian Acridoidea (Orthoptera). Journal of Threatened Taxa 3: 2207.
- Ward DF, Larivière MC 2004. Terrestrial invertebrate surveys and rapid biodiversity assessment in New Zealand: lessons from Australia. New Zealand Journal of Ecology 28: 151–159.
- Whittaker RH 1972. Evolution and measurement of species diversity. Taxon 21: 213–251.
- Winterbourn MJ 2009. A new genus and species of *Leptophlebiidae* (Ephemeroptera) from northern New Zealand. New Zealand Journal of Zoology 36: 423–430.