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On the distribution of tree weta in the North Island, New Zealand.

Steven A. Trewick* & Mary Morgan-Richards*‡

The distribution in the North Island of three species of tree weta (*Hemideina thoracica*, *H. crassidens* and *H. trewicki*) is described from field surveys. The two most widespread species (*H. thoracica* and *H. crassidens*) were generally parapatric but the boundary between the two was rather complex with a number of disjunctions. Most notable were the relict populations of *H. crassidens* isolated on Mt Ruapehu (39°17'S) and Mt Taranaki (39°17'S). The main boundary between these two species crosses the North Island at approximately 40° 20' S. A recently described species (*H. trewicki*), found only in the Hawkes Bay region, is sympatric with *H. thoracica* over much of its range. These weta probably developed into separate species after they became isolated by geophysical processes, and their subsequent distribution has been the result of recent climate-related dispersal.

Keywords: *Hemideina*; tree weta; distribution; North Island; biogeography; stenopelmatidae

INTRODUCTION

Seven species of tree weta (Stenopelmatidae: *Hemideina*) are known in New Zealand (Ramsay & Bigelow 1978; Morgan-Richards 1995), of which three are recorded in the North Island. *Hemideina crassidens* (the Wellington weta) is found in the north and west of the South Island as well as in the south of the North Island, whilst *H. thoracica* (the Auckland weta) is confined to the northern and central regions of the North Island as far south as Levin (Meads 1990). These two species are easily differentiated by external colouring; *H. crassidens* is distinctly marked with transverse yellow and black/brown tergital bands, and generally has a dark brown pronotum, whilst *H. thoracica* has a more uniform brown abdomen and a pale pronotum with dark hieroglyph-like markings (Karny 1934; Ramsay & Bigelow 1978; Meads 1990). A third North Island *Hemideina* species, possessing a combination of these characters has recently been described from Hawkes Bay (Morgan-Richards 1995).

Little is known about the ecology of tree weta despite their being so abundant and frequently encountered. Tree weta generally inhabit forest or scrub and feed at night principally on the leaves of woody and herbaceous plants. They roost by day in holes in living and dead trees, under bark or in similar confined dark recesses. No behavioural or ecological differences between the three North Island species have been empirically demonstrated.

We present the results of a detailed survey of the distribution of North Island tree weta, in which we have paid special attention to the interaction of the species wherever their ranges are adjacent or sympatric.

METHODS

Potential weta habitats were surveyed throughout the North Island. We examined suitable roost holes in both living and dead timber, extracted individual weta, then identified and released them. We concentrated on the area between latitudes 39° and 41°S, the zone in

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which the two dominant species meet, according to Meads (1990). We examined several individuals at each site and took care to locate these in a number of different trees and branches in order to increase the chances of finding individuals of both species, if present. In addition, we examined preserved specimens held at the Museum of New Zealand Te Papa Tongarewa, Wellington. Specimens with suitable data were included on the distribution maps, although most recorded sites were revisited during this survey. Grid references were taken from McKenzie (1987) and altitudes from maps in the Department of Survey and Land Information Parkmap series. Some specimens of weta were collected at sites that were new locations for a species. These were preserved and will be lodged at the Museum of New Zealand Te Papa Tongarewa.

RESULTS

Figure 1 shows a distribution map for the three species in the North Island of New Zealand. Of particular interest is the approximate boundary zone of *H. crassidens* and *H. thoracica* and the local discontinuities along it. Most sites with suitable habitat that were searched contained weta, although density of individuals varied considerably among sites. At almost all sites only a single species of tree weta was found. *H. crassidens* was located further north than previously documented by Meads (1990), with outlying populations in Taranaki, Ruapehu, Taihape and Dannevirke. *H. crassidens* was distributed east across the Wairarapa to Weber, and on either side and presumably throughout the Tararua Range. On the Ruahine Mountains only *H. thoracica* was found, although a continuation of the *H. crassidens* range extends north along the west flank of these mountains up to Taihape (175°51'E, 39°31'S). Nearer to the west coast the range of *H. crassidens* extends north to Marton (175°22'E, 40°04'S).

Near Levin, *H. thoracica* was abundant in a small reserve of regenerating bush (175°17'E, 40°39'S) and also present towards the west coast (175°15'E, 40°37'S), near Otaki (175°09'E, 40°45'S), and Manakau (175°14'E, 40°44'S). These populations seem to be discrete and monospecific, but only *H. crassidens* was located at all neighbouring sites.

The opposite scenario was found in the vicinity of Mt Taranaki (Fig. 2) where a population of *H. crassidens* was isolated within a region dominated by *H. thoracica*. *H. crassidens* was found at higher altitudes than *H. thoracica* along all three access roads up the mountain. The bush on Mt Taranaki is continuous, so it is possible to locate the zone where the two species meet. This contact zone appears to be relatively narrow (a matter of a few hundreds of metres between 650 and 900 m asl) and to all intents and purposes the two species are parapatric (having a non overlapping geographic contact) on Mt Taranaki. However, in the zone of interaction the two species were found sharing the habitat, and in one case a mixed species harem (Moller 1985) of one male *H. crassidens* and three female *H. thoracica* was encountered in a large roost hole. *H. crassidens* and *H. thoracica* from Mt Taranaki were included in a genetic investigation (Morgan-Richards, Daugherty & Gibbs 1995), which found no evidence of genetic introgression, nor were there any morphologically intermediate (hybrid) forms at the three boundary sites searched around Mt Taranaki. *H. crassidens* extended to lower altitudes (650 m) on the south side of the mountain. The range of *H. crassidens* on Mt Taranaki includes the subalpine vegetation (>950 m) where it lives at high density among the leatherwood (*Olearia colensoi*) that dominates that vegetation zone.

The same pattern of distribution was found on Mt Ruapehu (*H. crassidens* at higher altitude surrounded by *H. thoracica*), though here the extent of the *H. crassidens* range was greater. There was a boundary between *H. crassidens* and *H. thoracica* at about 920–1000 m asl along the Ohakune Mountain Road (175°28'E, 39°21'S), but to the north-west *H. crassidens* lives below 880 m asl near the Mangahua stream (175°28'E, 39°10'S). To the north of Mt Ruapehu, *H. crassidens* was found at 1460 m asl at the edge of the tree line (175°32'E, 39°12'S) above Whakapapa village. *H. thoracica* reappeared on the Central Plateau, to the north, along the Ketatahi track (175°40'E, 39°04'S), but has not been found elsewhere on the Central Plateau. Mangahua was the northern-most recorded locality of *H. crassidens*.

Near Palmerston North in the western foothills of the Tararua Range (174°40'E, 40°25'S)

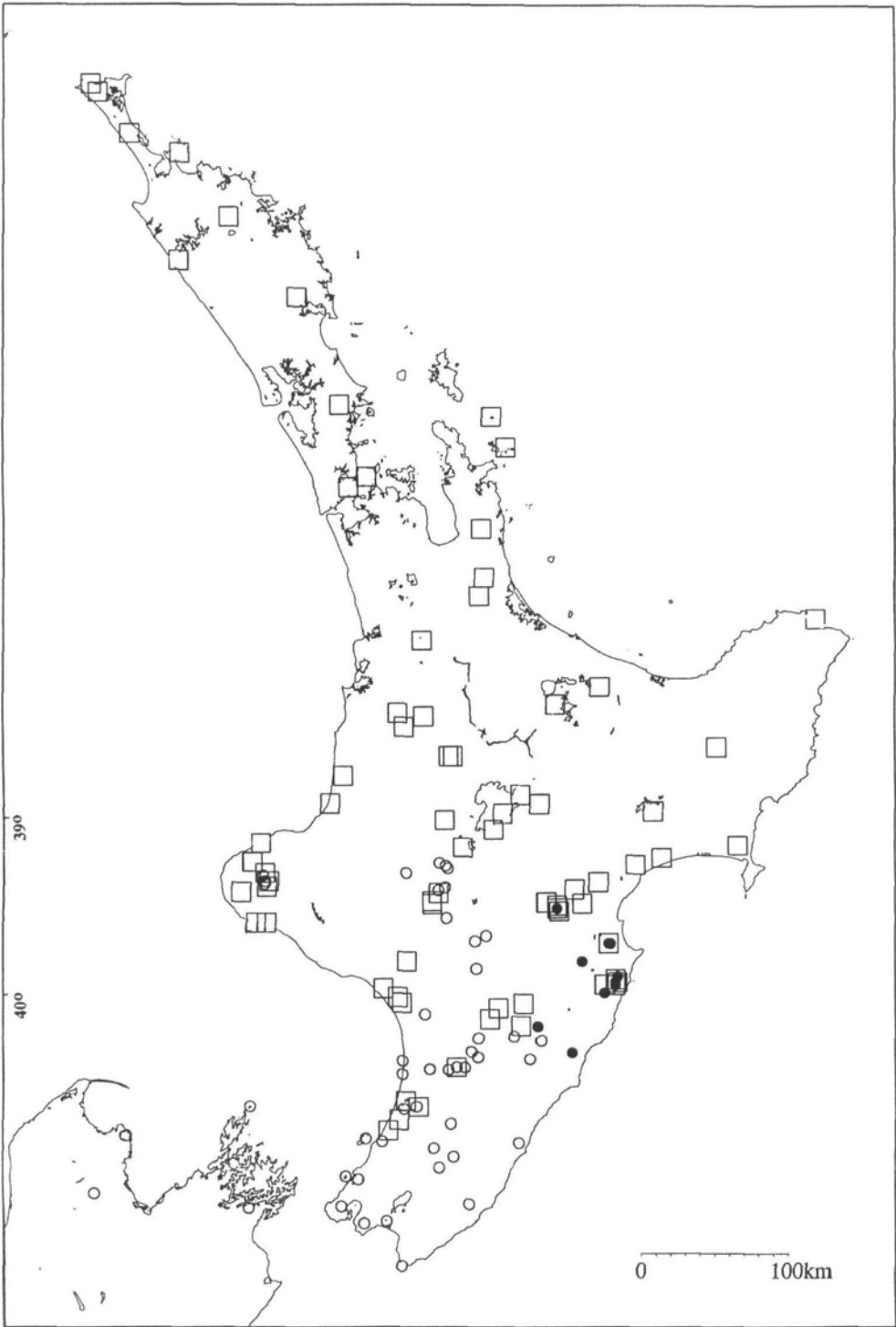


Fig. 1 – Distribution of tree weta in the North Island of New Zealand. Open squares: *Hemideina thoracica*. Open circles: *H. crassidens*. Filled circles: *H. trewicki*.

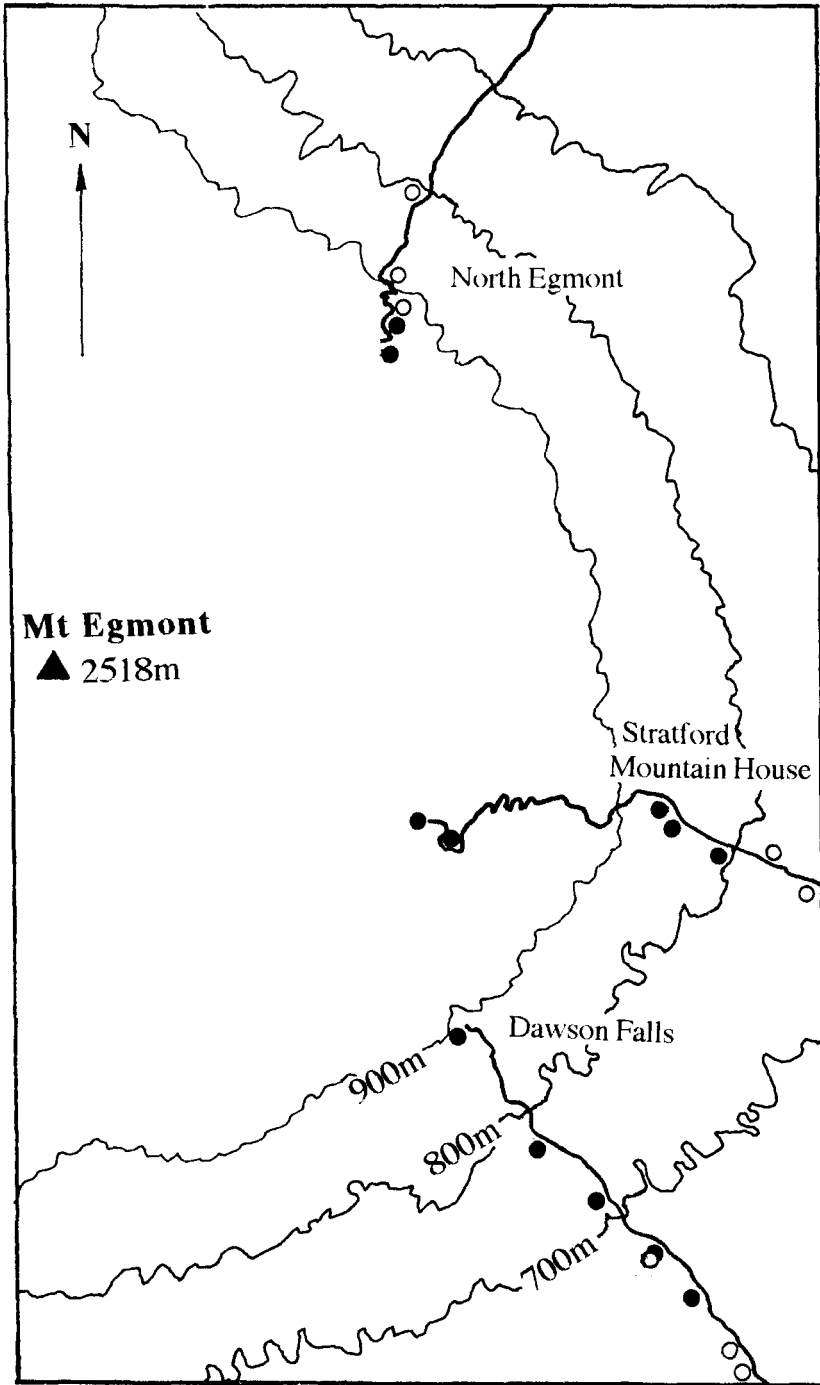


Fig. 2 – Distribution of tree weta on the eastern side of Mt Taranaki. Open circles: *H. thoracica*. Filled circles: *H. crassidens*. Overlapping symbols denotes both species in same roost. (Refer to Infomap Parkmap 273–09, Egmont National Park).

H. crassidens and *H. thoracica* were found in close proximity, and may be sympatric. The extent of this area of overlap is not clear and the apparent sympatry may be the result of marginal overlap of the two species amidst a mosaic of parapatric patches.

In the Hawkes Bay area around Hastings (176°51'E, 39°39'S), two species of tree weta were found at several sites surveyed (Fig. 3). One of these is *H. thoracica* but the other, despite morphological similarities, is not *H. crassidens* but a third and recently described species, *H. trewicki* (Morgan-Richards 1995). This species is distinguished from *H. crassidens* by means of fixed allozyme and chromosome differences, and although it bears similar abdominal bands to *H. crassidens* the colouring of the pronotum is like that of *H. thoracica*, so it can be distinguished in the field. Of all the *H. crassidens* examined as part of this survey, we found only one individual with a pale/hieroglyph pronotum, similar to that of *H. trewicki* and *H. thoracica*, at Mt Ruapehu. At four sites in the Hawkes Bay area, *H. trewicki* and *H. thoracica* are fully sympatric, often occupying the same roosts. We found only a single individual that was both morphologically and genetically intermediate between *H. trewicki* and *H. thoracica* at Mohi Bush (176°53'E, 39°51'S) (Morgan-Richards 1995). However, F1 hybrids are apparently sterile, as we found no evidence of introgression extending further than a single generation. A similar situation has been described for *H. ricta* and *H. femorata* which produce infertile F1 offspring on Banks Peninsula, South Island (Morgan-Richards & Townsend in press). As with *H. crassidens* and *H. thoracica* (in Taranaki and elsewhere), *H. thoracica* and *H. trewicki* are evidently not wholly conservative in their choice of mates, and observations of interspecific matings have been made in captivity.

H. trewicki was found in a narrow zone about 40 km wide and about 100 km in extent on the southern Hawkes Bay coast. The northern most location was at the edge of the Kaweka Forest (Blowhard Bush 175°25'E, 39°25'S), and the southern most near Porangahau (176°29'E, 40°16'S). There was a zone of sympatry with *H. thoracica* in the northern part of this range, and beyond this to the north, only *H. thoracica* was found. At the south of the range of *H. trewicki* we found no distinct parapatry or sympatry with *H. crassidens* (which was located nearby, at 176°16'E, 40°20'S), but there was morphological and genetic evidence (Morgan-Richards unpubl. data) of some introgression of these two species near Dannevirke (176°19'E, 40°12'S ; 176°17'E, 40°08'S). *H. thoracica* is also found near here (176°09'E, 40°08'S) but apparently not in mixed species populations.

DISCUSSION

Incidence and distribution

Most weta were located in holes in living and dry standing dead wood, although at some locations, they used holes in wetter and rotting logs on the forest floor. At one site a weta was seen to retreat into a hole filled with rain water, until completely submerged. We have taken the incidence of weta in roosts of varying "quality" to be an indication of weta density, such that the poorer roosts were used only when others were occupied. When there were no weta, even in what seemed to be potentially high quality roosts, we took this to indicate either very low density or complete absence of tree weta. During the survey, we found several small and localised sites without any weta, these tended to be very recent, open shrubland vegetation in farmland. Only in the Rangipo Desert did we find an extensive area without tree weta. In most secondary bush with a reasonably closed canopy, tree weta were abundant even when the vegetation consisted predominantly of an even aged single species stand, such as of mahoe (*Melycitus ramiflorus*) and kanuka/ manuka (*Leptospermum*). Large gaps in the map of North Island tree weta distribution (Fig. 1) such as in East Cape and Wanganui are the result of inaccessibility and do not indicate absence of weta. We presume that these unsurveyed regions contain *H. thoracica* in keeping with surrounding areas.

No-one knows to what extent the current distribution of weta has been affected by human activities. Fragmented and lost natural habitat is in some areas replaced by alternative artificial habitats around houses and in pine plantations etc, and in some localities at least, weta have evidently been able to recolonise or persist in areas cleared of forest that have

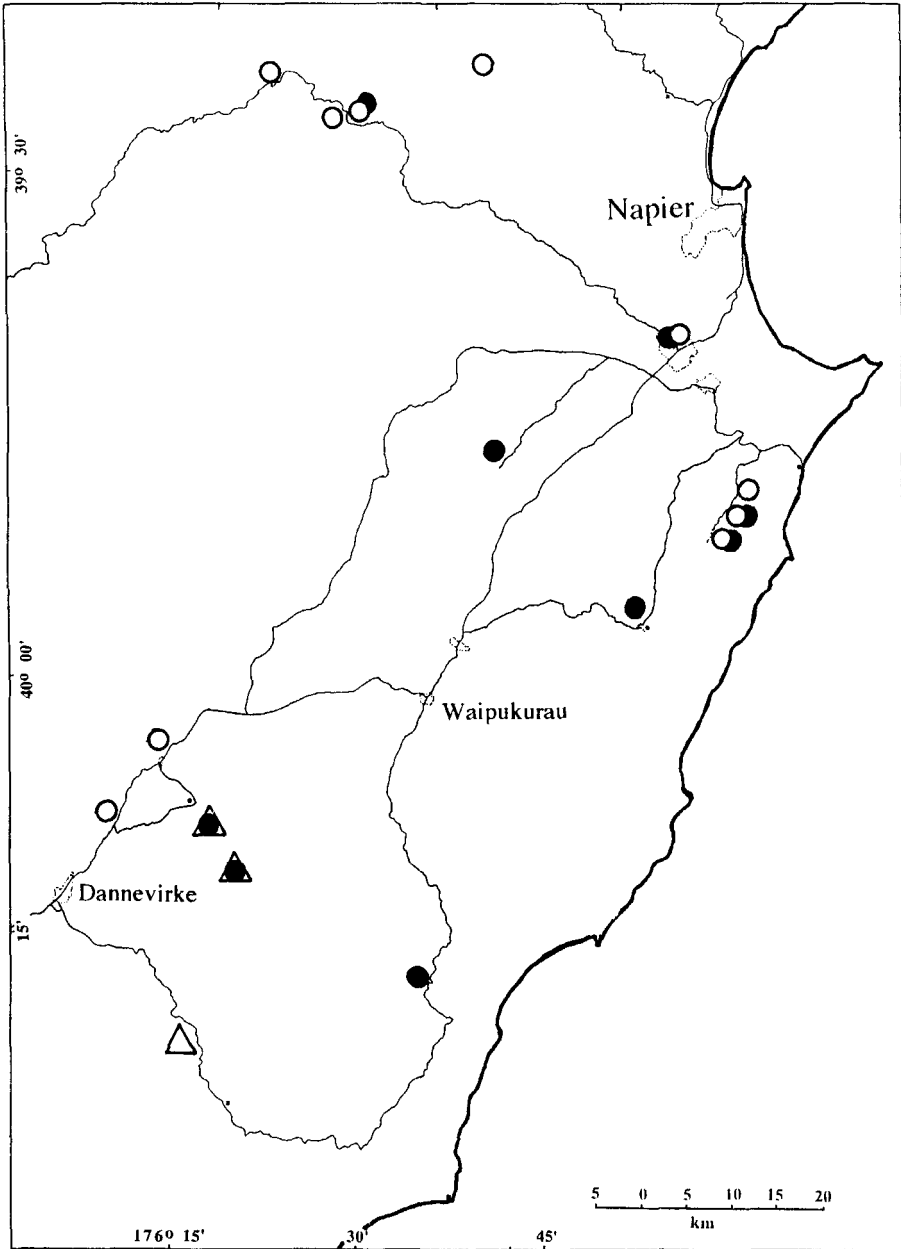


Fig. 3 – Distribution of tree weta in the Hawkes Bay/Wairarapa region. Open circles: *H. thoracica*. Open triangles: *H. Crassidens*. Filled circles: *H. trewicki*. Overlapping circles denote sympatric species (*H. thoracica* and *H. trewicki*), filled circle in triangle denotes location with hybrids (*H. crassidens* and *H. trewicki*)

subsequently revegetated. Little is known about the mobility of tree weta (but see Ordish 1992). Habitat fragmentation, which makes the location of suitable roost sites during survey work very difficult, may have caused weta to disperse further than usual in search of suitable habitat. Accidental transportation in timber and firewood has probably helped increase the

recent dispersal of tree weta, and the presence of *H. thoracica* amidst *H. crassidens* near Levin may be evidence of this. The effects of changes in the scale and type of predation on weta are not known although weta live at high density at Mohi Bush, where many native birds survive and possums and rats are controlled.

Parapatry vs sympatry

This survey has provided far more details on the distribution of tree weta in the North Island than previously available (Meads 1990). *H. crassidens* can be found further north than previously recorded and the interaction between the various species is rather complex. However, in most of their range, *H. crassidens* and *H. thoracica* are parapatric as indicated by previous observations of these tree weta (Meads 1990, Graeme Ramsay pers. com.). The same pattern of distribution apparently exists in northern South Island where *H. femorata* and *H. crassidens* meet (Graeme Ramsay Pers. Com.). Only at a few localities, such as at the boundary zone between *H. crassidens* and *H. thoracica* on Mt Taranaki, did we find the two species together, and this pattern is consistent with a distribution that is primarily parapatric.

Conversely, in Hawkes Bay we found two species together at several sites, and the geographic range over which these sites were found indicates that in this area the two species are truly sympatric. However, in Hawkes Bay the two species are *H. thoracica* and *H. trewicki* (Morgan-Richards 1995). *H. trewicki* is a new species, distinguished from *H. crassidens* (with which it has presumably been mistaken in the past, eg. by Moeed and Meads 1992) by both genetic and morphological features. The chief morphological diagnostic, pronotum colour, is polymorphic in *H. crassidens* although incidence of the *H. trewicki* (hieroglyph) type is very scarce in *H. crassidens*. We consider that sympatry of this new species with *H. thoracica* is a further diagnostic feature, which may assist the interpretation of the origin of the various tree weta species.

We found no evidence of local segregation within the habitat at any of the sites where two species of tree weta were sympatric. Two species frequently occupied neighbouring holes, or even, once, an adult breeding aggregation consisting of three female *H. thoracica* and one male *H. crassidens*. Tree weta are apparently either unable to distinguish other species, or they do not exclude one another purely on specific identity. Captive experiments have produced matings between all North Island species combinations, although no progeny were produced.

There is no evidence of introgression beyond the first generation crosses of *H. thoracica* and *H. trewicki*. However, initial cytogenetics and examination of pronotum colour suggest that *H. trewicki* and *H. crassidens* can produce viable hybrid offspring. Extensive forest clearance has made the co-existence of *H. trewicki* and *H. crassidens* hard to investigate.

Allopatric speciation and biogeography

The general parapatry exhibited by most tree weta species, the apparent lack of species specific mate recognition systems, and the overlap in general autecology, all imply that the various modern forms arose by allopatric speciation. It is reasonable to assume that, for the most part, each of the modern species is found today in or near the area in which it evolved.

Genetic studies (Richards 1995) suggest that the species found on the North and South Islands form two main clades of tree weta (a third clade comprises a single non-typical species, *H. broughi*). *H. crassidens*, the only tree weta species with a distribution that bridges Cook Strait, is more similar to the other North Island species (*H. thoracica* and *H. trewicki*), than any of those confined to the South Island. This implies that the North and South Island clades are of ancient origin and the presence of *H. crassidens* in both islands is most simply ascribed to recent dispersal when the two islands were connected during the glacial stages of the Pleistocene (<2 million year b.p.).

We propose that during the last glacial period, when conditions across much of the North Island were more similar to those of the lower South Island today, *H. crassidens* was distributed extensively and further north in the North Island than at present. A relatively

recent connection between the two islands bridging the modern Cook Strait, as described by Fleming (1962), Stevens & Suggate (1978), and Lewis, Carter & Davey (1994), could have provided the opportunity for *H. crassidens* to migrate into the South Island.

Geophysical evidence suggests that during the late Miocene a continuous land mass ran through what is today the North and South islands. There were islands in the southern Hawkes Bay/ north Wairarapa region at that time and during the Pliocene (~6.5–2 million years b.p.) (Fleming 1962; Stevens & Suggate 1987), although it is not clear whether these islands emerged from the sea or were derived from early Miocene links with the main north/south land block (Fleming 1962). It is also probable that these islands persisted through time, and were later incorporated into a larger land mass running north/south to the east of the “Wairarapa” basin, which itself reached north through present day Hawkes Bay. Evidence of this basin still exists in the form of Te Aute swamp and in the pre-European swamp vegetation in this area (McLintock 1959). After the closing of the “Manawatu” strait at the end of the Pliocene, there was a continuous land mass of varying configurations throughout a series of Pleistocene glacial phases, during which Cook Strait developed for the first time (Lewis, Carter & Davey 1994). Connections between the two islands probably developed during later interglacial phases. Perhaps the present North Island weta are the product of allopatric speciation in the North Island during periods of isolation during the Miocene/Pliocene, followed by dispersal during Pleistocene glacial phases.

Mosaics, climate and distribution

H. crassidens tolerates lower temperatures than *H. thoracica*, as is evident from the marooned populations of *H. crassidens* at high altitude on Mt Taranaki and the Central Plateau. These disjunct *H. crassidens* populations, plus those of *H. thoracica* near Levin and the apparent species mosaic near Palmerston North, may be the consequence of range changes associated with climate fluctuations during glacial/interglacial episodes. Further changes may be continuing today.

The disjunction of *H. crassidens* on the peaks of both Mt Taranaki and Mt Ruapehu in latitudes (but not altitudes) that are otherwise solely occupied by *H. thoracica* implies that these populations are relicts of an earlier more widespread distribution. Both peaks support continuous bush habitat which allows the study of the local distributions of the two species, where they have remained undisturbed by human activities. To what extent their mutual exclusion is controlled by different physiological, and thus, demographic responses to local climate is not known, but this could be a fruitful area of future research. The suggestion that *H. crassidens* is tolerant of cooler climatic conditions is supported by the South Island distribution, which extends down the west coast to Lake McKerrow and the Hollyford River Valley (Graeme Ramsay pers. com.) and by its lower location on the southern (colder) flank of Mt Taranaki. *H. thoracica*'s northern distribution suggests that it is more successful in warmer conditions.

The interaction of *H. thoracica* and *H. crassidens* with *H. trewicki* presents a valuable opportunity to study the relative significance of biological and environmental features in determining the speciation and distribution of tree weta. With this in mind, a project to examine aspects of the population ecology of *H. trewicki* and *H. thoracica* at Mohi bush has been initiated.

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