Population expansion by Cook Strait giant wētā, *Deinacrida rugosa* (Orthoptera: Anostostomatidae), following translocation to Matiu/Somes Island, New Zealand, and subsequent changes in abundance

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Abstract

Wētā, large wingless anostostomatid orthopterans, have been the most frequently translocated insects in New Zealand. Until recently, such translocations were only monitored intermittently to confirm presence. We investigate the spread of Cook Strait giant wētā (*Deinacrida rugosa* Buller, 1871) after its release on Matiu/Somes Island, Wellington, New Zealand, in 1996. Adult wētā were surveyed from 2008 to 2016 using footprint tracking tunnels and/or searching with spotlights at night. The population underwent a reversal in distributional abundance after 2008. In 2008, they were abundant in the north and rare in the south but by 2013 and 2015 they were relatively less abundant in the north and common in the south. Why they diminished in the north remains unknown but possible causes are predation on juvenile wētā by nocturnal geckos (detected in the north and east but not in the south), by some habitat change (mostly reduction of some lawn), or by a combination of these together with removal of wētā from the north for translocation elsewhere. Further research is required to confirm which of these factors affect wētā abundance, if there are other causes, and if any further change in distributional abundance occurs.

Key words

conservation, footprint tracking tunnels, gecko, skink, threatened species

Introduction

Translocation, the deliberate movement of living organisms from one area to another (IUCN/SCC 2013), is an important tool in conservation management and restoration. Most faunal translocations focused on vertebrates, such as birds and mammals (Fischer and Lindenmayer 2000) whereas invertebrates were less frequently translocated even though they comprise a significant proportion of biodiversity and have critical ecosystem functions such as pollination and nutrient cycling. For example, Seddon et al. (2005) reported that 9% of 699 species of plant and animal reintroductions involved invertebrates. This is despite invertebrates being ideal candidates for translocations because of their small size, high reproductive output, and small spatial requirements (Pearce-Kelly et al. 1998). There are few documented examples of invertebrate translocations, other than for Lepidoptera in the Northern Hemisphere (New et al. 1995 and references therein, Witkowski et al. 1997) and Orthoptera in New Zealand (Watts et al. 2008a, Watts and Thornburrow 2009, Watts et al. 2009, 2012).

In New Zealand, the flightless and often large bodied anostostomatid Orthoptera colloquially known as wētā, evolved since the Cretaceous in the absence of terrestrial mammals except for bats. Some species of wētā undoubtedly disappeared during the widespread local extinctions that occurred after the arrival of kiore (*Rattus exulans*) with Polynesians ca. 1300 years ago and after other rodents and predatory mammals were introduced by Europeans (Wilmshurst et al. 2008, Watts et al. 2008b). However, 11 species of giant wētā (genus *Deinacrida*) survived: six are alpine or sub-alpine, *Deinacrida mahoenui* avoided mammalian predators by moving into gorse (*Ulex europaeus*) planted by early European settlers and four other species survived on islands (Sherley and Hayes 1993, Watts et al. 2008a). Conservation interventions applied to ensure long-term persistence of giant wētā most frequently involved translocations to islands or to fenced sanctuaries on the mainland where mammals had been eradicated or kept at low densities (Watts et al. 2008a). Giant wētā and tree wētā (genus *Hemideina*) were the most frequently (71%) translocated insects in New Zealand and until recently, such translocations have only been monitored by intermittent surveys to confirm presence (Sherley et al. 2010).

Here, we investigate the spread of the Cook Strait giant wētā, *Deinacrida rugosa* Buller, 1871, after 62 individuals were released on Matiu/Somes Island, Wellington, New Zealand, in 1996 (Gascoigne 1996; Fig. 1). *D. rugosa*, with a body length of up to ca. 70 mm, is the largest of three anostostomatid species present on Matiu/Somes Island. The others are the slightly smaller Wellington tree wētā (*Hemideina crassidens* (Blanchard, 1851)) which was also translocated onto the island in 1996 and 1997 (Watts et al. 2009), and a small ground wētā (*Hemiandrus pallitarsis* (Walker, 1869)) that survived when the island's forest was replaced with pasture. All three wētā are nocturnally active and primarily herbivorous but they will eat other invertebrates whenever they can. Juveniles of *D. rugosa* are arboreal but generally found within 1 m of the ground, whereas adults live primarily on the ground, lay their eggs in soil and roost in dense low-lying vegetation or under piles of sticks or leaf litter. This wētā has a protracted life cycle (ca. 3 years) with adults being present from about September to July but they are easiest to find during the warmest months of December to March (Ramsay 1955, Watts et al. 2009). This is the second detailed description of how a threatened New Zealand invertebrate has spread geographically after it was translocated (Watts et al. 2008a, Sherley et al. 2010, Stringer et al. 2014).

During the course of this research we also acquired incidental observations on lizard distributions and include the results because of the possibility that predation by lizards may have contributed to changes in distributional abundance of *D. rugosa* on Matiu/Somes Island. We acknowledge that our methods for surveying wētā may not have been ideal for surveying lizards so we consider these results are only indicative.

Three geckos (*Woodworthia maculata* (Gray, 1845), *Mokopirirakau granulatus* (Gray, 1845), *Naultinus elegans* Gray, 1842) and four skinks (*Oligosoma aeneum* (Girard, 1858), *O. kokowai* Melzer, Bell & Patterson, 2017, *O. nigriplantare* (Peters, 1874), *O. polychroma* (Patterson & Daugherty, 1990)) were present on Matiu/Somes. *W. maculata*, *O. aeneum*, *O. nigriplantare* and *O. polychroma* survived the habitat changes on the island whereas the other lizards were released there between 1999 and 2007 (Sherley et al. 2010, Romijn and Hartley 2016). *M. granulatus* and *W. maculata* are potential predators of small juvenile wētā because they hunt insects at night. *M. granulatus* is primarily arboreal whereas *W. maculata* is found on trees, shrubs and on the ground (Robb 1980, Whitaker 1982). All four species of skink and *N. elegans* are diurnally active and feed primarily on moving invertebrates so they are unlikely to prey on juvenile giant wētā which hide while roosting during the daytime.

Methods

Matiu/Somes Island (24.9 ha) was completely cleared of native forest when it was an animal quarantine station. Extensive restoration began in 1981 and about 14 ha of the island are now covered in the early stages of regenerating coastal forest and scrub. Tree species include karaka (*Corynocarpus laevigatus*), mahoe (*Melicytus ramiflorus*), broadleaf (*Griselinia littoralis*), lemonwood (*Pittosporum eugeniodes*) and coastal tree daisy (*Olearia solandri*), and shrubs include taupata (*Coprosma repens*), tauhinu (*Ozothamnus leptophyllus*) and flax (*Phormium tenax*). Approximately 11 ha (44%) of this vegetation at the northern end of the island is >4 m tall. Pasture and grass still cover about 1.8 ha, mostly towards the centre of the island and alongside some pathways, while the remainder is seashore, road paving and buildings (Hector 2011).

Data were obtained using footprint tracking tunnels and visual searches during visits to Matiu/Somes Island on 11–15 February 2013, 14–18 February 2015. On 3–4 February 2016, no tracking tunnels were set and only searching was carried out. Differences in research effort followed from constraints in funding and the availability of field assistants. The distribution of *D. rugosa* from 12–15 February 2008 (3 nights) was published previously by Watts et al. (2009, 2011) and the data are included here as the initial record for comparative purposes.

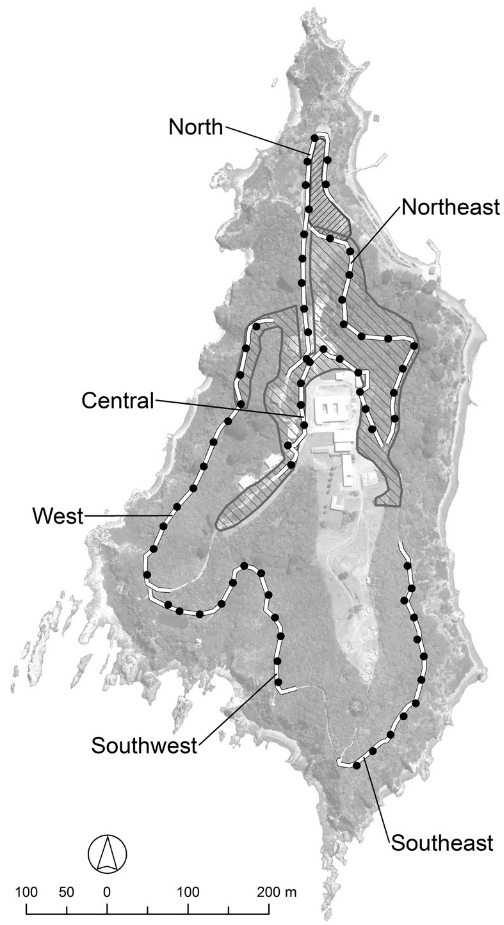

Fig. 1. Arrangement of tracking tunnel transects (shown in white) along the footpaths on Matiu-Somes Island. Each circle indicates the location of a tracking tunnel. The dark hatched area indicates where *Deinacrida rugosa* were released in 1996. The light hatched area shows where 186 adult *D. rugosa* were taken for translocation in 2007 and 2008. Note that no wētā were removed from the North transect.

Footprint tracking tunnels.—Six transects, each consisting of a series of tracking tunnels ('Black Trakka': Gotcha Traps™, www.gotchatraps.co.nz) spaced 30 m apart, were set out on existing footpaths. Three transects were positioned near each other at the north end of the island and three were spaced elsewhere around the footpath that circumnavigated the island (Fig. 1). This arrangement was chosen in 2007 to concentrate monitoring effort where sightings of giant wētā had been most frequently reported by Department of Conservation staff (Watts et al. 2009, 2011) and it was retained in subsequent visits so results in succeeding years would be comparable. Each tracking tunnel was a square-section plastic tube 100 mm × 100 mm × 500 mm long. Cardboard cards, each with a central strip of slow-drying ink, were used to obtain footprints of anything that walked through the tunnel. Five transects (North, Central, Southeast, Southwest, West) each comprised 12 tunnels and the Northeast transect had 11 tunnels (total number of tunnels = 71; Fig. 1). These were set up on 11 February 2013 and 14 February 2015 then baited with ca. 4 g of peanut butter applied to the middle of the inked area for four nights. Tracking tunnels baited with peanut butter as an attractant are suitable for monitoring wētā (Watts et al. 2008c) but their use for monitoring lizards is still under investigation. Geckos and skinks are attracted to peanut butter although there are better baits, and preliminary evidence indicates that tracking tunnels may be suitable for monitoring skink abundance (Siyam 2006, Lettink and Monks 2016). The tracking cards with fresh peanut butter were placed in the tunnels just before dusk each evening and removed soon after dawn. This minimized the number of footprints from diurnally active skinks which would otherwise be so dense as to obscure all other footprints.

The footprints of anostostomatid wētā are readily recognisable (e.g. Watts et al. 2008c, 2011). Protarsal, mesotarsal, and metatarsal prints longer than 4.1, 4.4, and 5.1 mm, respectively, indicated the presence of adult Cook Strait giant wētā (Watts et al. 2009, 2011). Smaller footprints were not recorded because they may have originated from juvenile *D. rugosa*, or from one of the other smaller wētā species present on the island (Wellington tree wētā and a ground wētā).

Footprints of geckos and skinks are also clearly identifiable (Jarvie and Monks 2014). However, we used the tracking tunnel cards primarily for monitoring *D. rugosa* and we include data on gecko tracking to confirm our observations on their distribution. We include data on the distribution of skinks even though we minimized our use of tracking tunnels during daylight in order to reduce tracking by skinks.

Visual searches.—A visual search using spotlights was made once along each of the six transects each night for four consecutive nights in 2013 and 2015 starting approximately 1 hour after sunset from 2120 to 0130 hours. On 3 and 4 February 2016, a search was made each night of the six transects but tracking tunnels were not set. Each search was extended 30 m beyond the first and last tracking tunnel (i.e. five searches were 420 m long and one was 390 m long). The path and up to ca. 1 m on both sides, together with vegetation up to ca. 2 m high, were systematically and thoroughly searched by a group of three people without disturbing the vegetation. Two people side by side at the front searched the path and the ground and low vegetation on their side of the path and the third person followed searching taller trees and shrubs. To reduce potential search bias we followed procedures outlined in Watts et al. (2009, 2011) with minor variations depending on the number of searchers available. This involved exchanging people between the search positions, changing the order in which transects where searched on different nights, and changing the direction they were searched. In 2008, 2013 and 2015 the searches used a pool of between four to six different people whereas in 2016 the same three people were used for both searches.

Each time a wētā was found, its position was taken with a GPS (estimated accuracy usually <5 m) and the wētā was marked with small individually numbered labels. The GPS positions enabled us to count the number of wētā found within distances of 15 m along the transects from each tracking tunnel position. Information obtained from marking was not used in the present investigation but is published elsewhere (Watts et al. 2009, 2011, in press).

Finally, we counted the number of geckos seen on the paths during the last search (night of 4 February 2016) after we noticed that they were subjectively more abundant on paths where few adult *D. rugosa* were found during a search on the night of 3 February 2016. Geckos were not counted during previous years because the weather was cooler and they were rarely seen on paths.

Temperature and humidity.—Temperature and humidity were recorded with an Escort iLog EI-HS-D-32-L data logger set just above ground level under dense shrubs. This continuously recorded data for the duration of each survey except 2016. A ventilated plastic cover shielded the data logger from dappled sunlight. Temperature and humidity recordings were averaged for each search period.

Analysis.—The potential spatial and temporal changes in adult *D. rugosa* distribution were investigated using two sample z tests for proportions by comparing the percent of tunnels tracked per transect pairwise between years 2008, 2013 and 2015. Furthermore, a maximum likelihood chi-square test for association was used to assess whether the relative percentages of tracked tunnels per transect had changed over time. A contingency table permutation test, with the chi-square statistic calculated by maximum likelihood and 4999 random permutes, was used to test whether the relative frequency of wētā observed along the six transects differed between 2008, 2013, 2015, and 2016. The contingency table permutation test was also used to compare just the 2013 and 2015 data.

The effect of median temperature and median vapour pressure deficit (VPD) during the search period on the total number of adult *D. rugosa* found per night by searching six transects in 2008, 2013 and 2015 was assessed using simple linear regression. The effects of median VPD and median temperature on the percent of tunnels tracked by adult *D. rugosa* per night in 2008, 2013 and 2015 were also assessed using simple linear regression.

The 2008, 2013 and 2015 tracking data were used to investigate the relationship between the presence of lizards and adult *D. rugosa*. Separate linear regressions were used to assess whether the percent of tunnels tracked by wētā per transect per year was related to the percent tracked by i) skink and ii) gecko. For gecko, but not for skink, there was statistical evidence that the regression lines should differ between years ($p<0.05$). An analogous analysis was used to assess the relationship between the presence of lizards and other wētā (not adult giant wētā). For both skink and gecko, as there was no statistical evidence that the regression lines should differ between years ($p>0.05$), a common line was fitted to data over all years.

For all linear regressions, the residual diagnostic plots provided no evidence of any departure from the assumption of independent normally distributed residuals with constant variance.

All analyses were conducted in Genstat 18 (VSN International 2014).

Results

Changes in both distribution and abundance.—In both 2013 and 2015, adult *D. rugosa* were most frequently found along the paths and on mowed lawn at the southern end of the island (Southwest transect).The lowest numbers were found in the north (North transect) and along the eastern side of the island (Northeast and Southeast transects). This contrasted with the distribution in 2008 when most were found along transects in the north (Central, North and Northeast transects; Table 1, Fig. 2). Analysis of all available search data (2008, 2013, 2015 and 2016) provides strong evidence that the relative frequencies of adult *D. rugosa* found along the six transects changed over time (contingency table permutation test: likelihood $\chi^2=197.36$, range of values from 4999 permutations 2.67–45.10, $p<0.001$; Table 1).

The distribution of tracking tunnels with adult *D. rugosa* footprints present followed the same overall pattern of adult wētā observed by searching: in 2013 and 2015 adults were most often detected using tracking tunnels along transects at the southern and south-eastern end of the island whereas fewer were detected along

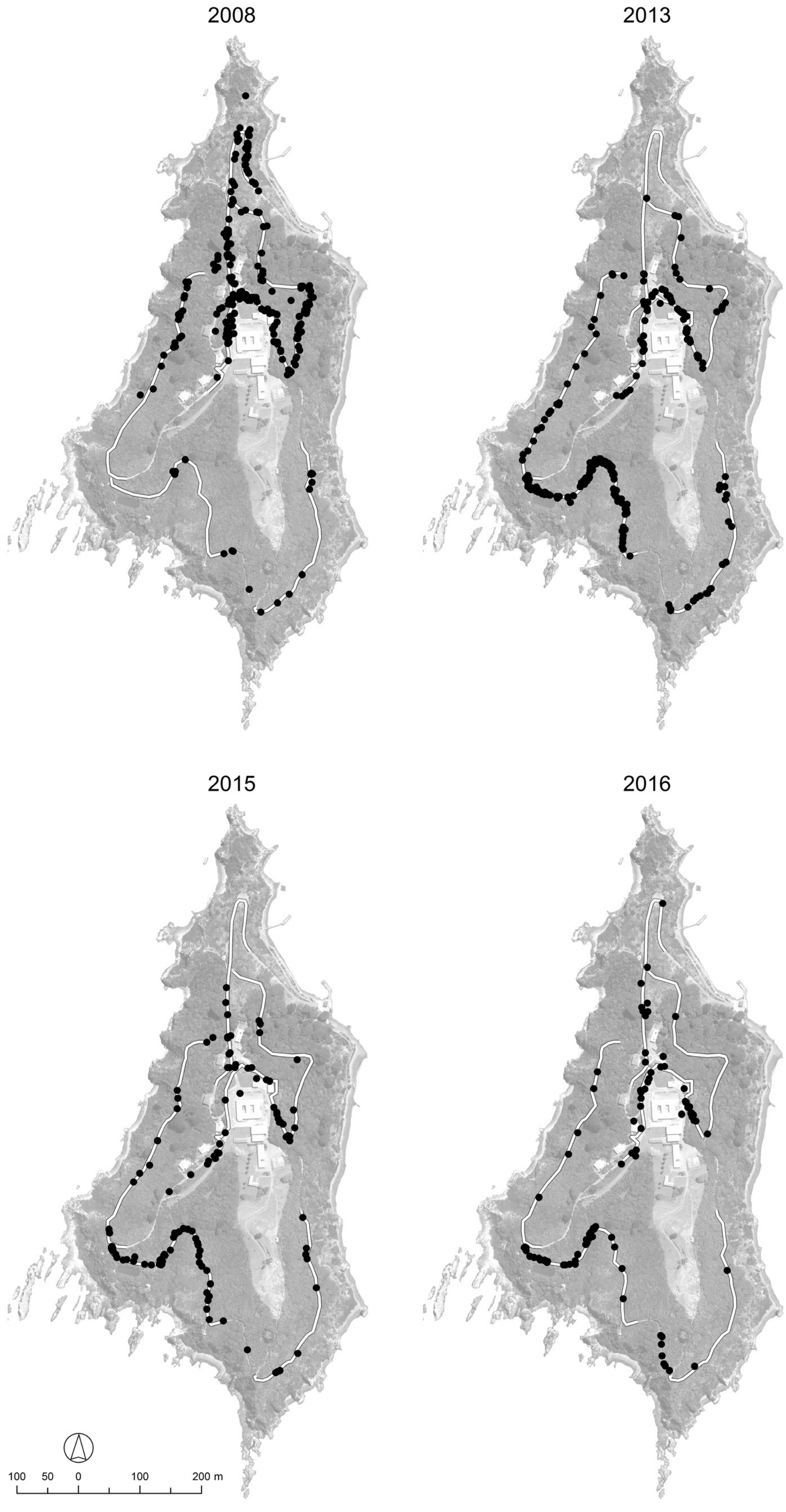

Fig. 2. Locations where all adult *Deinacrida rugosa* were found in 2008, 2013, 2015 and 2016. Tracking tunnel transects are indicated as white lines. 2008 data from Watts et al. (2009, 2011).

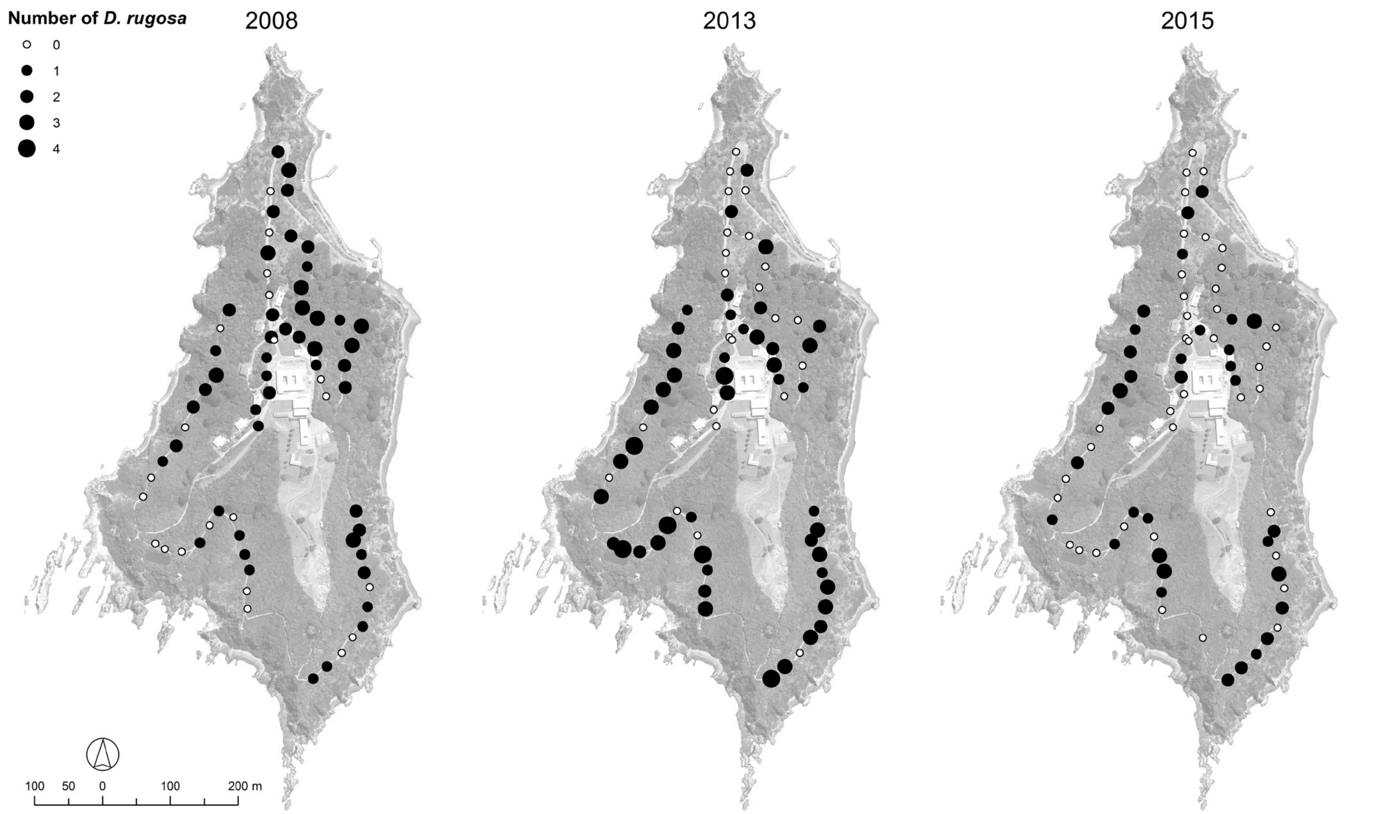

Fig. 3. Distribution of tracking tunnels with footprints of adult *Deinacrida rugosa* in 2008, 2013 and 2015. Cards were set over 3 nights in 2008 (Watts et al. (2009, 2011)) and over 4 nights in 2013 and 2015.

Table 1. Percentages of the total numbers of adult *Deinacrida rugosa* found along six tracking tunnel transects during searches at night each year. Searches were made on successive nights: three in 2008, four each in 2013 and 2015, and two in 2016. (Data for 2008 from Watts et al. (2009, 2011) are included for comparison).

Transect	2008	2013	2015	2016
1 North	20.3	2.2	7.5	9.6
2 West	12.6	9.3	8.2	7.4
3 Southwest	2.8	55.1	48.9	40.4
4 Southeast	3.5	7.7	6.8	3.2
5 Northeast	19.6	3.4	6.0	3.2
6 Central	41.3	22.3	22.6	36.2
Total seen	143	323	133	94

Table 2. Average proportions (%) of all tracking tunnels set in each transect that contained footprints of adult *Deinacrida rugosa* wētā in February 2008, 2013 and 2015. All tracking cards were baited with peanut butter. Results are averaged over 3 nights in 2008 and 4 nights in 2013 and 2015 (Data for 2008 are from Watts et al. (2009, 2011) and are included for comparison).

Transect	2008	2013	2015
1 North	50.0	13.9	10.4
2 West	41.7	52.8	31.3
3 Southwest	13.9	50.0	20.8
4 Southeast	38.9	55.6	31.3
5 Northeast	75.8	21.2	9.1
6 Central	38.9	36.1	14.6
Overall	42.7	40.5	19.7

the North and Northeast transects. In 2008, in contrast, adult footprints were most often found in tracking tunnels in the northern half of the island (Table 2; Fig. 3). Analysis of the tracking tunnel data from 2008, 2013 and 2015 provided strong evidence that the relative percentage of tracked tunnels between transects changed over time (chi-square test of association: χ^2=94.49, 10 d.f., p<0.001; Table 2).

Overall, more adult wētā were found by searching per night in 2013 than in 2008 even though the temperatures in 2013 were slightly lower than in 2008 (Tables 1 and 3). In 2015, during a severe drought and when temperatures were generally cooler than in 2013, 59% fewer adult wētā were found per night (mean: 80.8 per night in 2013; 33.3 per night in 2015). However, there was no detectable change in the proportions of wētā found along each transect in 2013 and 2015 (Table 1; contingency table permutation test, *p*=0.119).

The shift in distribution is not as obvious when presence–absence of wētā is examined using data from each tracking tunnel position combined with wētā found by searching within 15 m of each tracking tunnel. When the results at each position were summed for all nights during each visit to the island

Table 3. Total numbers of adult *Deinacrida rugosa* found each night by searching along six tracking tunnel transects together with temperature and vapour pressure deficit (VPD) during the search periods. Data for 2008 are from Watts et al. (2009, 2011) and are included for comparative purposes.

Date		Number Wētā	Sex ratio (M:F)	Median temperature (°C) (range)	Median VPD (kPa) (range)
2008	13-Feb	34	0.21	18.3 (18.3–18.4)	0.36 (0.34–0.37)
	14-Feb	63	0.37	19.0 (18.8–19.1)	0.27 (0.26–0.30)
	15-Feb	45	0.22	19.4 (19.1–19.8)	0.91 0.86–0.95)
2013	11-Feb	61	0.27	17.8 (17.6–18.2)	0 (0)
	12-Feb	73	0.40	17.5 (16.6–19.7)	0.04 (0–0.11)
	13-Feb	98	0.53	16.2 (15.5–16.8)	0 (0)
	14-Feb	91	0.52	16.3 (14.9–19.3)	0.26 (0–0.82)
2015	14-Feb	16	0.33	13.2 (13.0–13.2)	1.06 (1.00–1.12)
	15-Feb	28	0.33	13.0 (12.8–13.3)	1.39 (1.35–1.43)
	16-Feb	51	0.46	13.7 (12.8–14.5)	1.44 (1.37–1.53)
	17-Feb	35	0.59	15.0 (14.4–16.1)	1.51 (1.39–1.64)
2016	3-Feb	45	0.41	22.7 (21.9–23.4)	0.98 (0.87–1.08)
	4-Feb	49	0.26	20.9 (19.2–22.6)	0.84 (0.56–1.12)

Table 4. Numbers of adult *Deinacrida rugosa* and geckos seen along the tracking tunnel transects on Matiu/Somes Island during the nights of 4 February 2016.

Transect	No. wētā	No. geckos
1 North	5	20
2 West	4	4
3 Southwest	24	0
4 Southeast	0	8
5 Northeast	1	24
6 Central	20	3
Overall	54	59

(Fig. 4) they show that in 2008 wētā were present in most locations (94%) along the three northern transects and present only at the northernmost positions on the three southern transects. By 2013, their distribution had changed so they were detected along the three southern transects and the Central transect, and were no longer found at some locations (39%) along the North and Northeast transects. In 2015, wētā had a similar distribution to 2013 except that they were detected at three fewer locations along each of the West and Southeast transects (Fig. 4). These summed results are not strictly comparable because searches were made during three nights in 2008 whereas they were made during four nights in both 2013 and 2015 (Fig. 4). Finally, single searches on two nights in February 2016 showed that adult wētā had a similar distribution to those in 2013 and 2015 except that relatively few wētā were found along the West and Northeast transects (Table 1).

Relationship between wētā detected and meteorological conditions.— Although meteorological conditions differed between nights and visits to the island (Table 3), both the total number of adult wētā found and the percent of tunnels tracked were inversely related to median vapour pressure deficit (simple linear regression; R^2=0.51, p=0.006 and R^2=0.56, p=0.008, respectively). In addition, the percent of tunnels tracked showed a positive relationship with the median temperature (simple linear regression; R^2=0.64, p=0.003) but there was no evidence of a relationship between the total number of adult wētā found and median temperature (simple linear regression; R^2=0.03, p=0.561).

Observed distributions of geckos and skinks on Matiu/Somes Island.— Gecko footprints were present on tracking tunnel cards mostly in the north of the island in 2008, 2013 and 2015 but some were also detected along the Southeast transect in 2015 (Fig. 5). Skink footprints in tracking tunnel cards were very variable from year to year but overall they were present in most locations except at the southwest of the island and in the middle of the northeast transect where the oldest forest was situated (Fig. 5).

Geckos were frequently observed on the northern transects during the night of 3 February 2016 whereas subjectively fewer were seen elsewhere. When counted during the night of the 4 February 2016, geckos were common along the North and Northeast transects where few wētā were found. Few geckos were found along the Central and southern transects where wētā were most frequently seen. Few geckos or wētā were observed along the West and Southeast transects (Table 4).

The percentage of tunnels tracked by adult *D. rugosa* had a negative linear relationship with the percentage of tracking tunnels tracked by geckos (linear regression with separate lines, R^2=0.71, p=0.005), but no relationship was detected between adult *D. rugosa* and skinks (linear regression with a common line for all years; R^2=0.07, p=0.305). Conversely, whilst there was no evidence of a relationship between the percentages of tunnels tracked by 'other' wētā and those with gecko footprints (linear regression with a common line for all years; R^2=0.08, p=0.265), those with footprints of 'other' wētā showed a negative linear relationship with tracking tunnels tracked by skinks (linear regression with a common line for all years; R^2=0.41, p=0.004).

Discussion

Population expansion and change in abundance.—Our observation that the population of *D. rugosa* expanded towards the south of Matiu/Somes Island between 2008 and 2013 confirms the suggestion by Watts et al. (2009) that this wētā was still in the process of establishing itself on the island in 2008. This wētā then took between 13 and 16 years to occupy the entire island, extending only 500–600 m from where they were released (Fig. 1). Meads and Notman (1992) also reported that *D. rugosa* released on Maud Island initially remained near their release site for seven years before expanding further afield. This species is capable of travelling much further than 600 m during their adult lifetime. Daily displacements between successive roosts of up to 44 m and 70 m for adult females and males, respectively, have been observed after

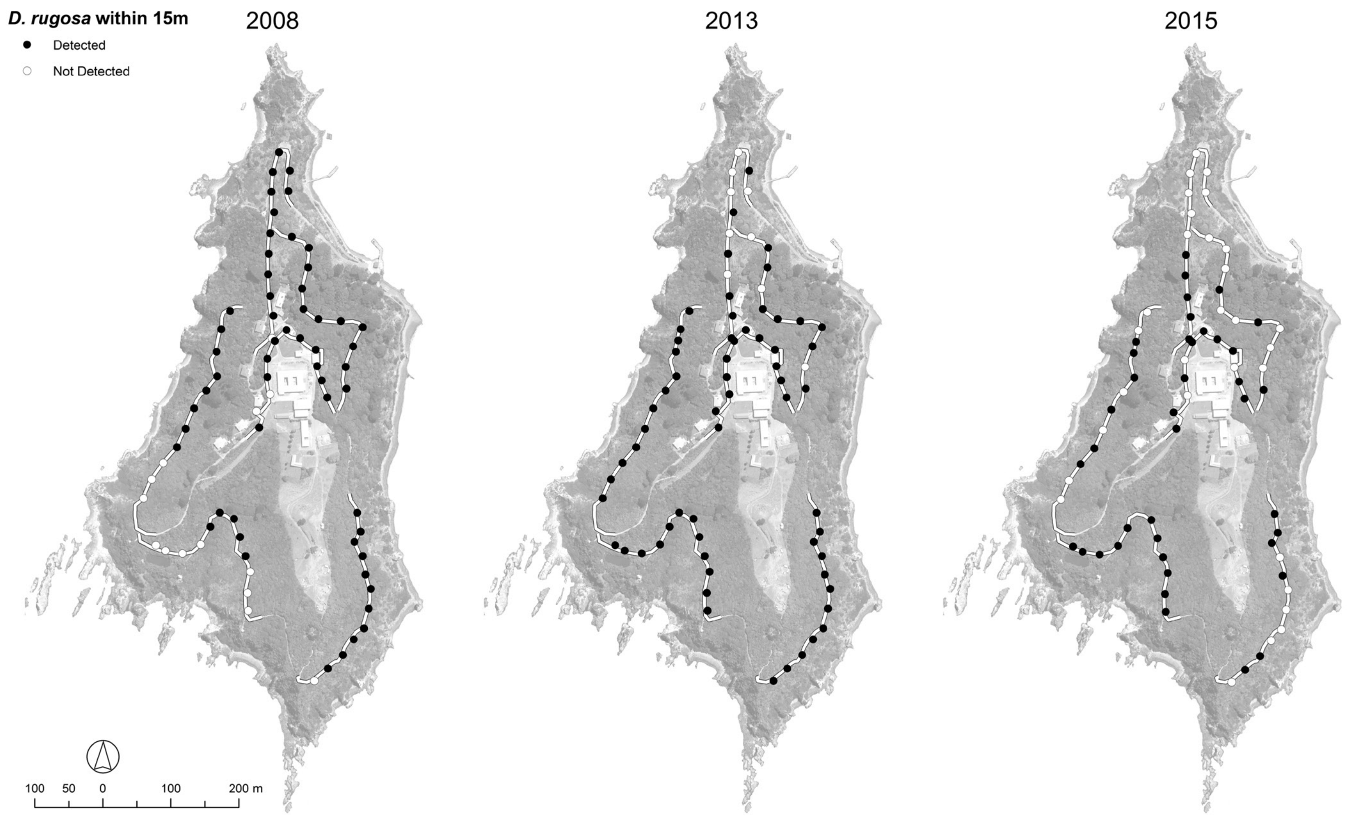

Fig. 4. Distribution of adult *Deinacrida rugosa* presence as evidenced by combining detection with tracking tunnels baited with peanut butter and finding them by searching at night. Searches extended 15 m from each tracking tunnel. Results are presence-absence derived from three searches over three nights in 2008, and four searches over four nights in both 2013 and 2015. Areas searched (tracking tunnel transects) are indicated as white lines. 2008 data from Watts et al. (2009, 2011).

translocation and *in situ* populations (McIntyre 1992, Kelly et al. 2008, Watts et al. 2011, 2012). Other factors must therefore be responsible for such a slow rate of spread over Matiu/Somes Island (Watts et al. 2009).

D. rugosa also underwent a population shift on Matiu/Somes Island while the population was expanding over the island between 2008 and 2013–2016, because their abundance subsequently declined in the north while it increased in the south. This was evidenced by the results from both searches at night and from tracking tunnels (Watts et al. 2009, 2011). The situation was complicated in 2015 when reduced numbers of wētā were seen and tracked during both a cold period and during a severe drought (Table 3) but the overall trend was unaffected. A similar population shift occurred after Wellington tree wētā were released at the north end of Matiu/Somes Island in 1996 and 1997 (Watts et al. 2009). These wētā were monitored from 2000 to 2006 using artificial retreats: they spread rapidly over the island to reach high densities in the south but, by 2005, their numbers had declined in the release area at the north of the Island (G.W. Gibbs, unpublished data).

Possible factors affecting the reduction of wētā abundance in the north.— It is not clear why numbers of *D. rugosa* diminished in the north after 2008 but habitat change, (particularly a reduction in available lawn area), harvesting for translocation elsewhere, predation by geckos or a combination of these may have been responsible. Another possibility suggested by G.W. Gibbs (pers. comm. 2015) to account for the population shift by *H. crassidens* is that some unknown nutritional factor higher in concentration in the south may be responsible, although Watts et al. (in press) detected no differences in chemical concentrations during a preliminary study of the plants most frequently eaten by *D. rugosa*. The suggestion by G.W. Gibbs followed from his observations that adult *H. crassidens* were larger in the south than in the north of Matiu/Somes Island and that size in adult male *H. crassidens* depends on the amount of animal protein the insect receives (G.W. Gibbs, unpublished data). Male *H. crassidens* can become adult between instars 9 and 12, and this largely determines their final size whereas *D. rugosa* is not known to have a variable number of instars (Stringer and Cary 2001). Watts et al. (in press) reported that adult male *D. rugosa* were slightly larger in the west than in the east but this was the only geographic variation in adult size they detected. This might indicate that there is geographic variation in an unknown nutritional component but it seems an unlikely explanation for why both species later became less abundant in the north.

Habitat change, particularly a reduction in lawn, was probably responsible for some reduction in abundance of *D. rugosa* in the north between 2008 and 2016. This follows because adults were most frequently found on lawn adjacent to shrubbery. We did not monitor habitat but did observe the following subjective changes. Lawn along about 40% of the North transect became reduced from a strip 1.5–2 m wide in 2008 to <0.2 m wide in 2016

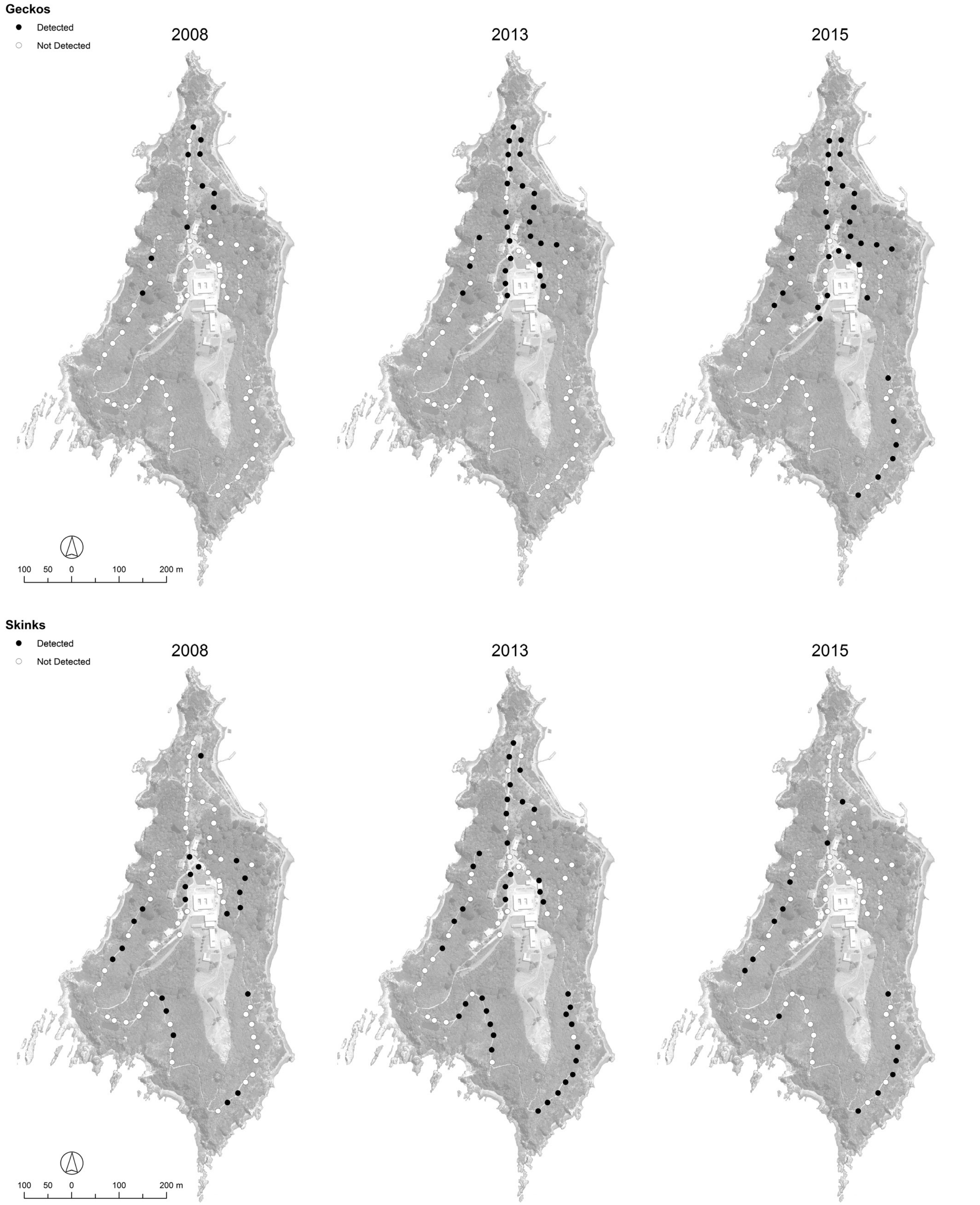

Fig. 5. Distribution of geckos and skinks as detected using tracking tunnels on Matiu/Somes Island. Data are combined presence-absence of footprints on cards from tracking tunnels baited with peanut butter during three nights in 2008 and four nights in both 2013 and 2015. 2008 data from Watts et al. (2009, 2011).

by overgrowth of adjacent shrubs. The increasing height of scrub reduced the size and numbers of scattered clumps of grass along the Northeast and West transects while bushes were progressively planted after 2008 in retired pasture at the eastern end of the Southwest transect. The latter formed an almost continuous low canopy by 2016 leaving only a fringe of grass alongside the path. We would have expected that habitat change would have favoured an increase in the abundance of *H. crassidens* in the north because continued growth of trees would result in increasing numbers of holes suitable for roosting.

Relationships between reptiles and wētā abundance.—The negative relationship detected between the numbers of nocturnally active geckos both seen and tracked in tracking tunnels does not demonstrate that these predators reduce the numbers of adult *D. rugosa* but it does indicate that further research is required to confirm this. *W. maculata* is the most abundant gecko on Matiu/Somes Island. It is known to be a generalist insectivore/frugivore which consumes large numbers of small invertebrates (Whitaker 1982). As such it is likely to opportunistically eat juvenile *D. rugosa* up to 20–30 mm in length (R.A. Hitchmough, Department of Conservation, pers. comm. 2017). The other nocturnally active gecko present, *M. granulatus* (Gray, 1845), was translocated onto the island in 2006 when 33 were released at the northern end but it is still uncommon (Sherley et al. 2010). We also acknowledge that our data on nocturnal geckos were obtained incidentally during surveys designed for giant wētā and not reptiles. The use of tracking tunnels for monitoring reptiles is still being investigated: both the tunnels and tracking cards may require modification for detecting reptiles and more attractive bait may be required, such as tinned pears or honey for geckos and fish-based tinned cat food for skinks (e.g. Whitaker 1967, Siyam 2006, Lettink and Monks 2016).

We detected no relationship between skinks and adult *D. rugosa* although our data on skink presence is unreliable because we tried to reduce their access to tracking tunnels during the daytime as described above. The skinks on Matiu/Somes Island are also primarily active on the ground during the day so they were unlikely to encounter juvenile *D. rugosa* which are nocturnally active.

Tuatara are known to eat large wētā (e.g. Walls 1981) and we observed one eating an adult *D. rugosa* in 2013 but their effect on the population of *D. rugosa* is unknown. Overall, we observed relatively few tuatara and most of these were along the Western transect where the original 50 were released in 1998 (Sherley et al. 2010) and around the western end of the Southwest transect. The number of wētā seen at these locations increased between 2008 and 2013 so this indicates that predation by tuatara was likely to have had a minor effect on wētā abundance.

Removal of wētā for translocation.—The removal of giant wētā for translocation between 2007 and 2010 is unlikely, by itself, to have contributed much to the reduction in the numbers of these insects in the north (Table 5) even though most were collected from along paths in the north and centre of the island (no wētā were removed from the North transect; Fig. 1). This is because the numbers removed probably represented a small proportion of the population. For example, the 64 adult female wētā removed in 2008 represented a maximum of 11.1% (approximate 95% CI range, 0.06–17.2%) of the 577 adult females (approximate 95% CI = 372–1108) estimated by mark-recapture (Watts et al. 2011). This proportion may have been even lower because we do not know the effective area assessed by that mark-recapture exercise. It is possible, for example, that the area assessed included only relatively narrow strips alongside the transects because adult female *D. rugosa* usually move <10 m between several successive daytime retreats before moving much larger distances (McIntyre 1992, 2001, Watts et al. 2011, 2012). We suggest that removing such a proportion of the adult population is unlikely to harm the overall population because large numbers of eggs are still likely to be laid by the remaining females (the only information on fecundity is by Ramsay (1955) who reported that one female laid 236 eggs). It is possible, however, that later small harvests of wētā (Table 5) may have had a large negative effect on the wētā population in the north because they were already less abundant but no robust population assessments were made when these wētā were removed.

Table 5. Numbers of *Deinacrida rugosa* collected from Matiu/Somes Island for release in Zealandia (Karori Wildlife Sanctuary), Wellington and Cape Sanctuary, Hawkes Bay. NR = not recorded. Data provided by R. Empson, K. Nakagawa.

Date removed	No. Male	No. female	Total
1 Feb 2007	25	75	100
Feb 2008	22	64	86
20 Jan 2010	12	30	42
30 Mar 2010	NR	NR	8
16 Mar 2013	15	26	41

Conclusions

Our results, together with those of Meads and Notman (1992), show that *D. rugosa* may take some years to occupy a large area of suitable habitat despite the distances that adults can travel. Such delays in occupancy may have resulted from the small numbers of founding individuals that were released (62 and 43 respectively) because results of the releases involving larger numbers of this wētā (Table 5) are not yet available.

Further research is required to confirm if predation by nocturnal geckos can reduce the abundance of *D. rugosa*. If predation by geckos explains the negative relationship between these species then it might also account for the southward population shifts experienced by both this wētā and *H. crassidens* on Matiu/Somes Island. We also recommend that *D. rugosa* and the reptiles present on Matiu/Somes Island be appropriately monitored at intervals of perhaps 5- or 10-years to document how their relative numbers and distributions change in case predation by reptiles is an important factor in establishing populations of this wētā elsewhere and in their long-term survival.

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