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Habitat use, behavior and movement patterns of a threatened New Zealand giant weta, *Deinacrida heteracantha* (Anostomatidae: Orthoptera)

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Abstract

Wetapunga (*Deinacrida heteracantha*), New Zealand's largest insect, were formerly abundant in forests of northern New Zealand. However, they are now restricted to one population on mammal-free Little Barrier Island (3083 ha). This study investigated the movements, habitat use and behavior of 22 adult wetapunga fitted with miniature radiotransmitters for up to 18 nights. Adult wetapunga appeared to be quite mobile, with males (16 m per night) moving further than females (8 m per night). Differences in the distances travelled by adult male and female wetapunga between daytime refuges appear due to differences in reproductive behavior. Wetapunga were associated with silverfern, nikau palm, kanuka, and kohekohe within second-growth coastal forest on Little Barrier Island. The majority of wetapunga were found above ground level, but were also occasionally found moving on the ground. In addition, adult wetapunga were found in relatively open sites with little or no cover and were clearly visible by day. Wetapunga were generally solitary and the majority of their activities, such as feeding, movements and oviposition, occurred at night. The one exception is mating (actual copulation and pre-, post-copulatory behavior), which usually occurred during daylight after weta had paired during the previous night. During the study, one male wetapunga was eaten by an unknown avian predator. Radiotelemetry has extended our knowledge of adult wetapunga behavior and this monitoring technique could be readily applied to other large invertebrates.

Key words

conservation, wetapunga, radiotracking, monitoring tool

Introduction

The human colonization of isolated archipelagos usually results in a wave of extinctions in the native biota (James 1995, Blackburn & Gaston 2005). The widespread invasive rodents (*Rattus* spp.) that accompany humans have been implicated in the decline and extinctions of many island endemic vertebrates and invertebrates (Townsend *et al.* 2006, Gibbs 2009). Many larger-bodied insects are now rare or threatened following the introduction of rodents to New Zealand (St Clair 2011). This is particularly true of the 11 species of endemic giant weta (*Deinacrida*, Anostomatidae), several of which are of high conservation value (Gibbs 1998).

Wetapunga (*Deinacrida heteracantha*, Fig. 1) are New Zealand's largest insect with adult males and females respectively ~ 52-57 mm and 60-73 mm body length, weighing ~9 g and 35 g (McIntyre 2001). They were formerly abundant in forests of northern New Zealand including Northland, Auckland, and Great Barrier Island (Watt 1963). However, they are now restricted to Little Barrier Island (Hauraki Gulf, North Island, New Zealand), a 3083-ha nature reserve that is free of introduced mammalian predators. Wetapunga numbers were thought to be declining (Gibbs & McIntyre 1997), but are now slowly increasing following the eradication of kiore

(*Rattus exulans*) in 2004 (Green *et al.* in press).

Wetapunga are considered an arboreal forest species that spend most of their time above ground, roosting in epiphytes and cavities during the day, and feeding mostly on fresh foliage at night (Gibbs 2001). Richards (1973) found adults under mats of *Muehlenbeckia complexa* on the ground on Little Barrier Island, while Gibbs & McIntyre (1997) found them above ground under loose bark of kanuka and inside cavities in mahoe (*Melicactus ramiflorus*) and pohutukawa (*Metrosideros excelsa*).

Past surveys of wetapunga have involved searching through habitat during the day or spotlighting at night, but this is time consuming and the results depend on the skill of the searcher. A method that involves systematically searching habitat was developed to estimate populations of Mahoenui giant weta (*D. mahoenui*) using site-occupancy modelling (MacKenzie 2003); artificial wooden refuges attached to trees have also been used to monitor tree weta (*Hemideina* species.), which roost in cavities in trees (Trewick & Morgan-Richards 2000, Green 2005, Kelly 2006). Recently, Watts *et al.* (2008) reported that footprint-tracking tunnels, similar to those used for monitoring small mammals, could be used effectively to detect the adults of wetapunga and to distinguish their presence from other weta species. In that study, footprints were detected in 72% of tracking tunnels over three consecutive nights and 89% of these appeared during the first night. While this technique is a breakthrough in detecting the presence of adult wetapunga, its value in monitoring population density has yet to be established. In studies with a ground-dwelling species of giant weta, Watts *et al.* (2011a) found strong indications that both baited and unbaited tracking tunnels could be used to estimate the number of adult Cook Strait giant weta (*D. rugosa*) present, but this probably depends on their responses to meteorological conditions, which are yet to be clarified.

Wetapunga are found in the canopy of second-growth forest, which, combined with their cryptic appearance, makes them difficult to locate and observe. Radiotelemetry is a valuable tool for collecting data on the ecology and behavior of animals that are difficult to follow and observe. The continued reduction in transmitter and battery size and increase in transmitter range has meant it is feasible to attach them to invertebrates including spiders (Janowski-Bell & Horner 1999), beetles (Hedin & Ranius 2002) and tettigoniids (Lorch *et al.* 2005).

Transmitters have previously been used to monitor the ecology and behavior of three species of giant weta in New Zealand: Mahoenui giant weta (*D. mahoenui*, Richards 1994), Cook Strait giant weta (*D. rugosa*; McIntyre 2001, Kelly *et al.* 2008, Watts *et al.* 2011) and wetapunga (Gibbs & McIntyre 1997). The last-mentioned authors followed four subadult and one adult wetapunga for 2-12 days on Little Barrier Island and described sedentary behavior, with short



Fig. 1. Female wetapunga (*D. heteracantha*) found in second-growth forest on Little Barrier Island, New Zealand. The body length of this female was 71 mm and she weighed 36.5 g. For color version, see Plate VIII.

movements to and from feeding sites close to refuge sites (Gibbs & McIntyre 1997). Since then, technology has greatly improved the size, range, and battery life of transmitters while reducing their cost.

We carried out a pilot study in May 2008, during which we radiotracked 6 adult wetapunga (3 female and 3 male) and found that a larger telemetry study involving more wetapunga was feasible. We therefore attached radiotransmitters to another 16 adult wetapunga (8 female and 8 male) in May 2009 to (1) obtain autoecology information about wetapunga, (2) evaluate the feasibility of using radiotransmitters to monitor wetapunga after their planned translocation to other islands, and (3) determine whether current monitoring techniques are effective. Estimations of how far wetapunga move each night should provide a basis to determine the spacing of tracking tunnels that will reduce the probability of an

individual wetapunga being tracked in multiple tunnels.

We present new data from these two studies on the movements, habitat use and behavior of adult wetapunga on Little Barrier Island and discuss the implications for monitoring this species.

Materials and methods

Radiotracking study.—Adult wetapunga were captured during the day when sheltering in above-ground refuge sites within regenerating kanuka-broadleaf forest on Little Barrier Island. Their locations were recorded with a GPS (Garmin 60CSX) and each weta weighed using a Pesola balance. Radiotransmitters (Model BD-2, Holohil Systems Ltd, Canada) were attached to six adult wetapunga (3 females and 3 males) in May 2008 and to 16 (8 females and 8 males) in May 2009 (Fig. 2). A small aluminium saddle (similar in size and shape to the pronotum) was attached to the pronotum of each wetapunga, using a thin layer of quick-setting glue (Selleys® Supa Glue gel). A transmitter was attached to the saddle using a silicone sealant that was allowed to dry for 4 hours while the weta was held captive. The transmitter antenna, a very flexible 16-cm wire coated with a thin layer of plastic, extended beyond the rear of the weta (Fig. 2). Female giant weta are larger than males, so the transmitters fitted to female weta weighed 1.08 g, with an expected battery life of 56 days, while the transmitters of males weighed 0.87 g with an expected battery life of 42 days.

Radiotagged wetapunga were released at the site of capture within 12 hours, and tracking began that night, using a Telonics TR-4 receiver and 3-element Yagi antenna. All locations of weta were recorded with a GPS and the location of daytime refuges for every weta – such as associated plant species, location on the tree, height above ground, distance to associated food plants and presence of other weta – were recorded daily. Each night (between 2130 and 0130 hours) every radiotagged wetapunga was observed for 10 to 15 min, using a head torch to determine their location on the tree, associated plant species, height above ground, distance to associated food plants and the presence of other weta. Care was taken to minimize disturbance to the weta during the study, so weta were not necessarily seen on each occasion. When radiotagged individuals were not seen it was because they were higher than 2.5 m in the vegetation. The number of nights wetapunga were tracked varied, ranging from 4 to 18 nights. Transmitters were removed by cutting through the layer of silicone sealant between the aluminium saddle and the transmitter. Therefore, weta retained the aluminium saddle until they died, probably within the following 6 months.

In May 2009, mean daily temperature and relative humidity were calculated over a 24-hour period from measurements recorded every 2 h at the weather station on Little Barrier Island.

Data analysis.—Radiotracking data were used to calculate, for each individual weta, the maximum, minimum and average distance travelled between consecutive daytime refuges, total path distance, and straight-line distance from the release point determined at the end of the study. We emphasize that our reported distances are minimum estimates of distances travelled between points, because it was not possible to follow indirect movements, some of which would have been vertical. The average minimum distance travelled by each weta was calculated for the first part of the night (between the daytime fix and the night-time fix at between 2130 and 0130 hours) and for the latter part of the night (between the night-time fix and the following daytime fix).

An analysis of variance tested the effect of year of study and sex on the average distance travelled between consecutive daytime ref-

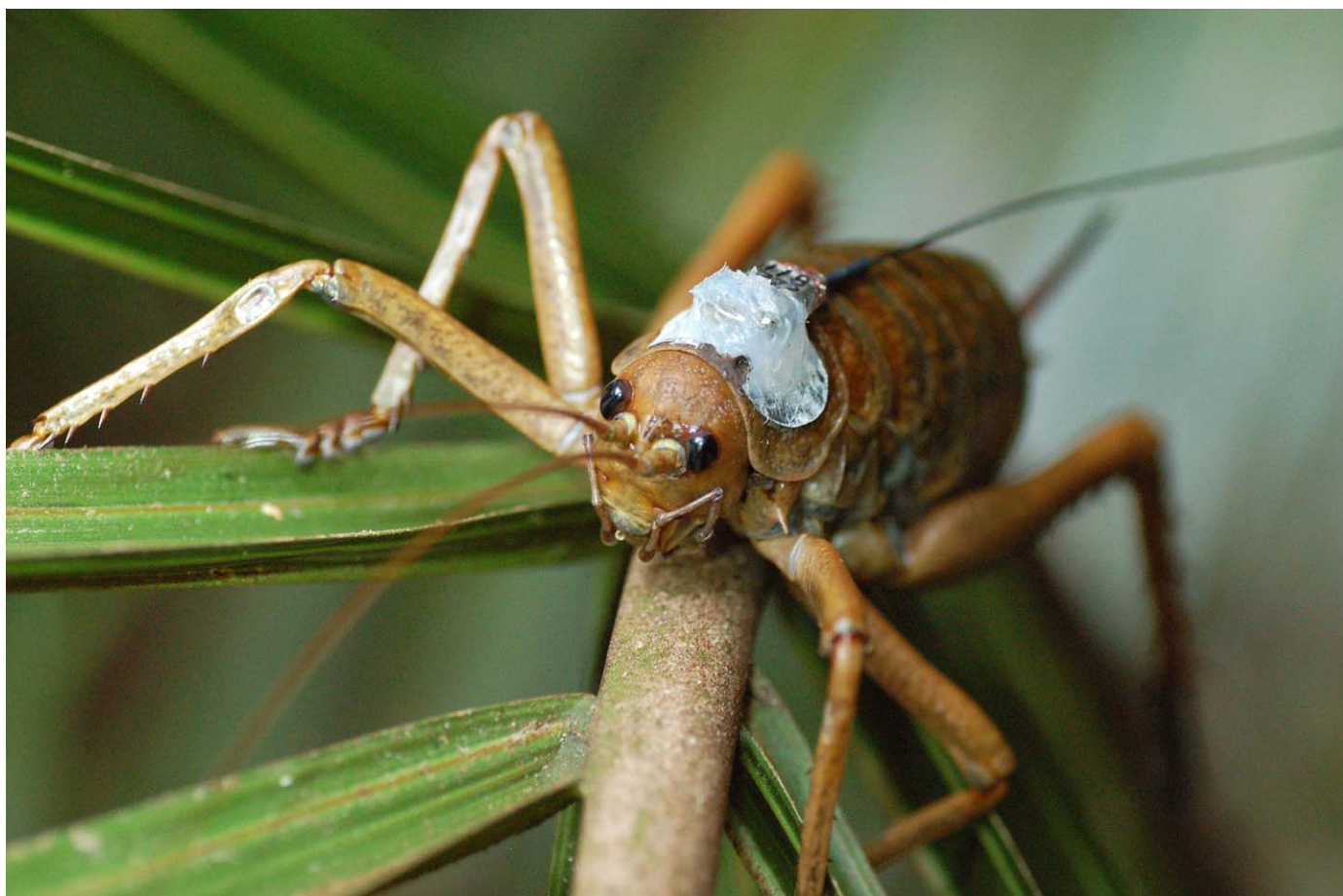


Fig. 2. Female wetapunga with BD-2 transmitter (Holohil Systems Ltd., Canada) attached. For color version, see Plate VIII.

uges. We also compared the interactions between these factors. An independent *t*-test was used to compare the average distance travelled by each weta during the first part of the night with that during the latter part of the night. To test whether the proportion of transmitter weight to weta body weight affected distance travelled between daytime refuges, data were analysed using correlation analyses (*r*). The data were log-transformed and all analyses performed using GenStat version 8.0 (VSN International 2007). Means are presented as untransformed values \pm 95% confidence intervals.

The effect of mean daily temperature and relative humidity on the average distance travelled between daytime refuges for female and male wetapunga were analysed using a simple linear regression in GenStat version 8.0 (VSN International 2007).

Results

The use of transmitters for tracking wetapunga.—All transmitters were working when recovered at the end of the study. In 2008 and 2009, wetapunga were visually confirmed in their day refuges for 201 of 317 observations (63%), while they were seen during 119 of 297 (40%) of the night time observations. During the daytime, female weta were seen more often (75%) than male weta (48%). In contrast, both male and female wetapunga were seen equally often at night. There was no relationship between average distance travelled between daytime refuges and the percentage of the transmitter weight to weta body weight ($r=0.263$, $n=22$, $P>0.05$).

Movement behavior.—The results of the telemetry study, including

time tracked, total distance travelled, average distance between consecutive daytime refuges, maximum and minimum distance between consecutive refuges, and distance from release site at the end of the study for each wetapunga, are summarized in Table 1. On average in 2008 and 2009, male wetapunga travelled 16 m between consecutive daytime refuges, twice the distance that females travelled ($F_{1,21}=30.33$, $P<0.001$; Fig. 3). There was no difference in the average distance travelled between refuges of wetapunga tracked in 2008 and 2009 ($F_{1,21}=1.66$, $P=0.213$; Fig. 3) and no interaction between year and the sex of the weta ($F_{1,21}=0.23$, $P=0.638$).

Of the 297 radiotracking nights, female and male wetapunga did not move from their daytime refuges on 23 (21%) and 11 nights (12%) respectively. Overall, both female and male wetapunga (73% and 51%, respectively) moved less than 5 m between daytime refuges, and when they moved greater distances than this, males consistently went greater distances than females (Fig. 4). Males, in particular, moved more frequently than females (Fig. 4). When female wetapunga moved greater than 20 m overnight this activity was usually followed by a few nights of no or little movement. In contrast, male wetapunga frequently moved more than 20 m over consecutive nights.

On average, radiotracked wetapunga moved substantially further during the first part of the night (between the day-time fix and the last night-time fix, 7 m) than during the latter part of the night (between the night-time fix and the following day-time fix; 3 m; $t=3.27$, $df=21$, $P=0.002$).

In May 2009, the average distance travelled between daytime refuges for male and female wetapunga increased significantly with

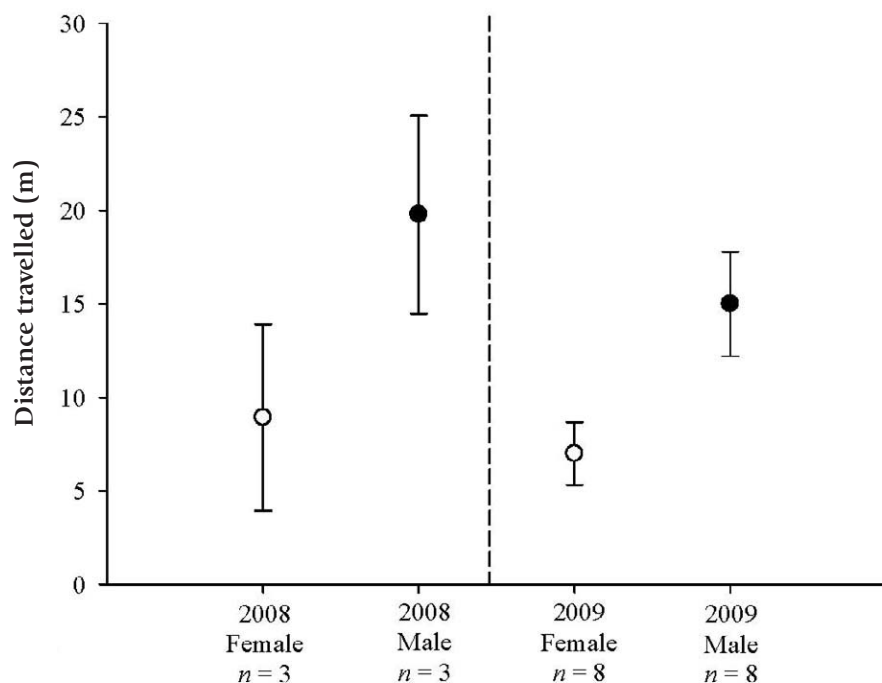


Fig. 3. Average distances ($m \pm 95\%$ CI) travelled between consecutive diurnal refuges for female and male wetapunga in May 2008 and 2009.

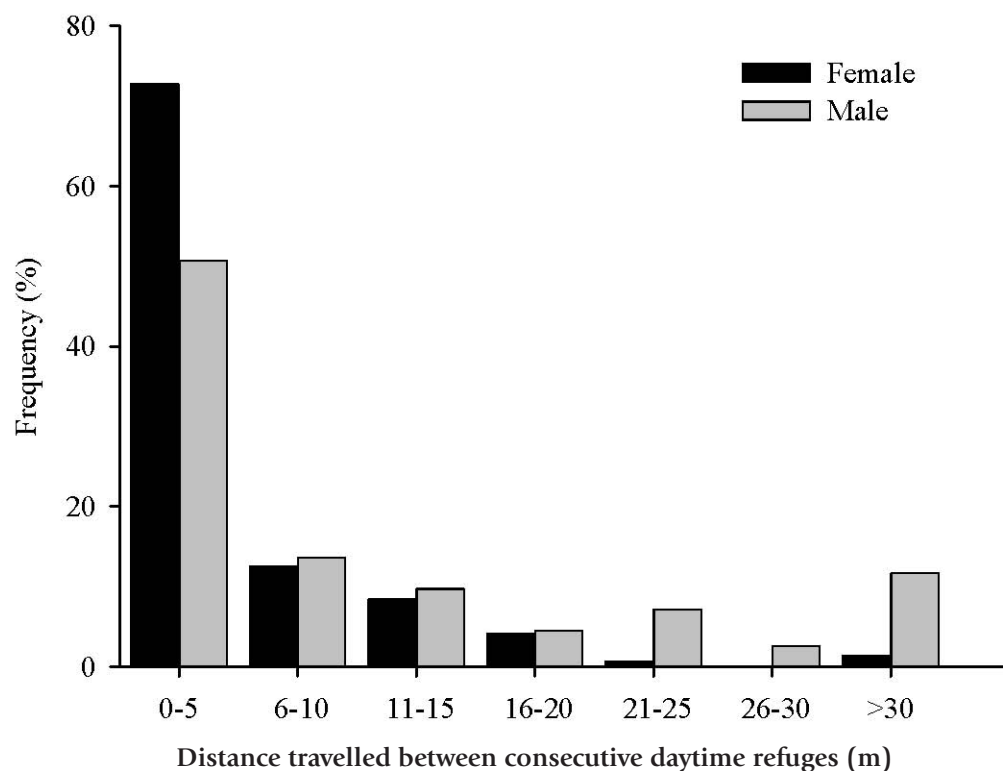


Fig. 4. Relative frequency distributions of distance between diurnal refuges of female and male wetapunga.

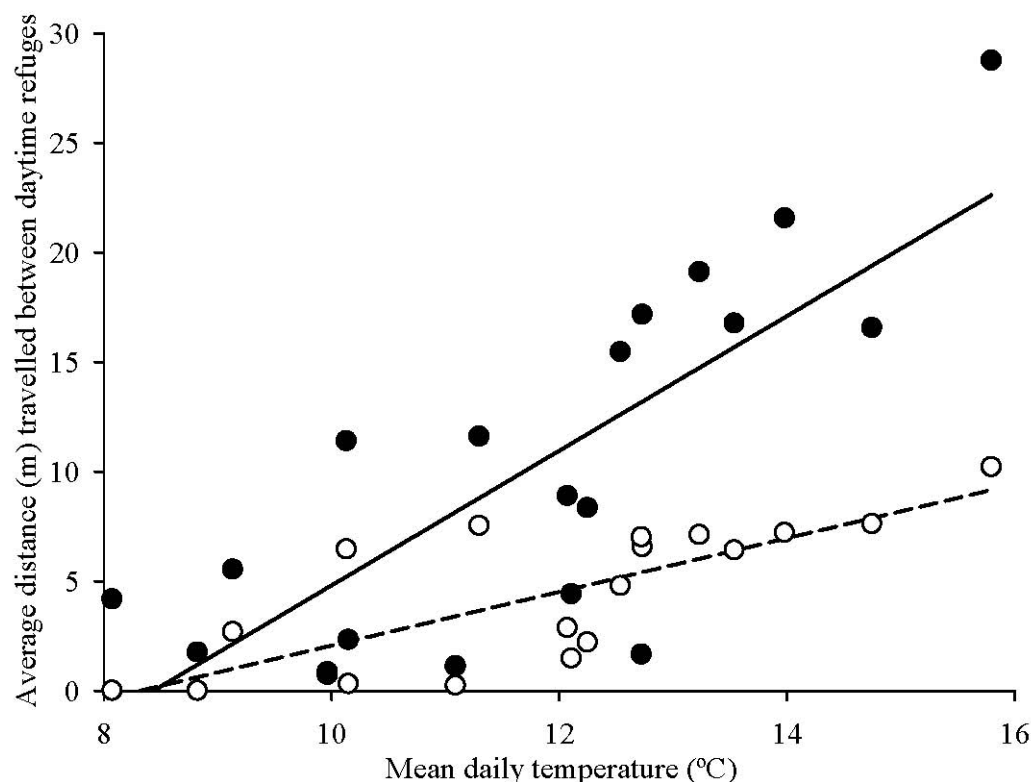


Fig. 5. Average distance (m) travelled between daytime refuges for female and male wetapunga versus mean daily temperature ($^{\circ}\text{C}$) in May 2009. Open circles and dashed line = female wetapunga ($y = -10.08 + 1.22x$), Closed circle and solid line = male wetapunga ($y = -25.87 + 3.07x$).

increasing mean daily temperature (female: $F_{1,18} = 24.26$, $P < 0.001$, Fig. 5; male: $F_{1,18} = 25.80$, $P < 0.001$, Fig. 5). When temperatures were less than 12°C (8 out of 18, 24-hour periods) female wetapunga moved from their daytime refuges on only 43% of occasions, while males moved on 63% of occasions. When the mean daily temperature was greater than 12°C , female wetapunga moved from their daytime refuges on 66% of occasions compared with 86% for males. Relative humidity had no effect on the average distance travelled by female ($F_{1,18} = 0.42$, $P = 0.525$) and male ($F_{1,18} = 1.86$, $P = 0.166$) wetapunga. We observed active wetapunga at night during thunderstorms, some storms with strong winds and heavy rain.

Daytime refugia.—Male wetapunga never returned to the same daytime refuge once they had left it and only 15% of observations of female wetapunga showed they returned to a previous daytime refuge on consecutive days. Although this was difficult to confirm for weta that were using daytime refugia in the canopy, in all cases the telemetry signal indicated that the wetapunga had moved to a new position.

The exact height and position of the weta in their daytime refuge were difficult to determine if they were higher than 2.5 m and not seen. During the day, if radiotagged wetapunga were accessible they were often easy to find and clearly visible in their refuge. They were found at < 2 m above ground on 18% of occasions, 2 to 4 m on 44% of occasions and > 4 m on 38% of occasions. Of weta that were observed, the average distance to the nearest food plant was 60 cm (range: 5–180 cm) and these plants were frequently kohekohe (42%) or mahoe (35%). They were most often (43% of observations) observed to be using silverfern (*Cyathea dealbata*) as a daytime refuge, followed by nikau palm (*Rhopalostylis sapida*, 16% of observations), kanuka (*Kunzea ericoides*, 14% of observations), haekaro (*Pittosporum umbellatum*, 13% of observations) and kohekohe (*Dysoxylum spectabile*, 7% of observations), five finger

(*Pseudopanax arboreus*, 3% of observations), mahoe (3% of observations), and hangehange (*Geniostoma rupestre*, 1% of observations). Wetapunga were often found in the canopy (26%), wedged into the stipules at the top of a silverfern trunk (22%), on the trunk of a silverfern under dead skirts (19%) or on the trunk of a tree under lichen or other vegetation (16%).

Wetapunga were found with other individuals on 27% of occasions. In all cases they were male-female pairs and in 72% of observations they were engaging in actual copulation (*i.e.*, genital contact). Wetapunga were observed mating in three positions, including, female mounting the male (78% of occasions), male mounting the female (19% of occasions), and lying on their sides (3% of occasions). Radiotagged females were most often observed with unmarked males (25 observations), but on 12 occasions they were found with radiotagged males.

Nocturnal behavior.—Wetapunga were predominantly (88% of all observations) found in the canopy above 2.5 m. They were frequently found on silverfern (47%), nikau palms (26%), and kohekohe trees (21%). Nocturnal activities included feeding (46%), resting (33%) or walking (21%, with 76% of those being male). The majority seen feeding were consuming the leaves of kohekohe (37%), mahoe (29%), and *Coprosma grandifolia* (14%). Other plants fed on were five finger (9%), hangehange (7%), and silverfern (3%). During 2008, wetapunga were also observed on the ground feeding on the leaf bases of *Gahnia setifolia* (1%).

Female and male wetapunga were observed walking quickly on the ground, with the male following the female (approximately 25 cm apart), the male's antennae being actively waved about. If the male moved too far from the female, or her trail, he appeared to lose her. Males would then stop, turn around and retrace their own trail until they were following her again.

Two females (Tx#58-1 and Tx#55) were seen ovipositing in dis-

Table 1. Summary of data collected for each radiotracked wetapunga on Little Barrier Island in May 2008 and May 2009. All distances are in meters (m). Average = average distance between consecutive daytime refuges, Max = maximum distance between daytime refuges, Min = minimum distance between daytime refuges, and Distance end = distance from release point at end of the study in a direct line. The transmitter of male Tx #20 was retrieved amongst the leaf litter after its bearer was eaten.

Year	Weta Tx #	Sex	Nights tracked	Total distance	Average	Max	Min	Distance end	Outcome
2008	58-1	F	6	58	10	20	0	6	Tx removed
2008	60-1	F	7	90	13	35	0	72	Tx removed
2008	55	F	4	17	4	7	1	11	Tx removed
2008	45	M	6	120	20	54	4	48	Tx removed
2008	47-1	M	6	91	15	28	1	52	Tx removed
2008	49-1	M	6	146	24	51	3	120	Tx removed
2009	58-2	F	18	9	10	5	0	5	Tx removed
2009	60-2	F	17	118	7	31	0	13	Tx removed
2009	62	F	17	76	8	16	0	11	Tx removed
2009	91	F	17	66	4	13	0	1	Tx removed
2009	93-1	F	4	24	7	11	1	4	Tx removed
2009	93-2	F	12	7	9	2	0	1	Tx removed
2009	97	F	18	52	5	8	0	6	Tx removed
2009	99	F	18	94	10	26	0	7	Tx removed
2009	10	M	15	100	17	15	0	12	Tx removed
2009	20	M	9	158	18	69	1	9	Predation
2009	44	M	18	201	11	50	0	14	Tx removed
2009	47-2	M	17	264	16	47	0	64	Tx removed
2009	49-2	M	18	181	10	59	0	117	Tx removed
2009	51	M	17	239	14	80	0	163	Tx removed
2009	53	M	18	131	16	36	0	25	Tx removed
2009	87	M	18	161	19	25	0	5	Tx removed

turbed soil near treefall sites during heavy rain on the night of 23 May 2008. Female Tx#58-1 was observed at 2145 hours ovipositing in disturbed soil on flat ground near a nikau treefall. For 45 min, she repeatedly (12 observations) lifted her ovipositor high out of the soil and then inserted it into the soil, trying a number of different sites. Once she had finished, she walked to the nearest tree (a silverfern) and climbed into the canopy. Female Tx#55 was found ovipositing in disturbed soil near a large treefall located on a steep slope at 2230 hours on 24 May 2008. The only evidence relating to oviposition in 2009 was female Tx#58-2, who was observed with soil particles on her ovipositor on 29 May 2009.

On 31 May 2009, the aluminium saddle and transmitter of male Tx#20 was found among leaf litter with the chewed remains of the wetapunga pronotum attached. The transmitter was found during the day approximately 3 m below the previous night-fix position. Male Tx#20 was seen 24 h previously mating with an unmarked female 4.3 m off the ground on a trunk of a mature haekaro tree. They were sitting among lichen but were exposed and so clearly seen from the ground. This was the only evidence of wetapunga predation we observed during the study and the avian predator and time of predation remain unknown.

Discussion

Success of the radiotelemetry technique.—This study re-affirms the usefulness of radiotelemetry for observing the ecology and behavior of wetapunga in the field. The insects did not appear to be adversely affected by the presence of the transmitter as individuals were seen feeding and mating within 24–48 h of the transmitter being attached. We were also able to retrieve all the transmitters at the end of the study by intercepting wetapunga while they were near or on the ground. There are similar technologies available for following insects to understand their movements and behavior, and these offer different capabilities for entomologists (Silcox *et al.* 2011).

Movements of wetapunga.—Adult wetapunga appeared to be quite mobile, with males moving further than females. The single adult female radiotracked by Gibbs & McIntyre (1997) in November had moved an average of 2.6 m between day-shelter sites, whereas we found the average distance travelled between consecutive daytime refuges in May ranged from 4 to 13 m. Radiotracking studies of other giant weta have reported similar distances (Richards 1994, Kelly *et al.* 2008), for example, adult Cook Strait giant weta, a ground-dwelling species, moved up to 44 m per night on Mana Island (McIntyre 1992) and a maximum of 70 m on Matiu-Somes Island (Watts *et al.* 2011a). Among other orthopteran insects, flightless bush crickets (*Pholidoptera griseoptera*) has been shown to travel an average daily distance ranging between 3.2 and 11.2 m, with a maximum of 289 m in 24 h (Diekötter *et al.* 2005). Although most recaptured Raukumara tusked weta (*Motuweta riparia*) have been observed within 10 m of their original capture point, weta have been recorded travelling 80 m in one night (McCartney *et al.* 2006). Over the duration of this study, it appeared that adult wetapunga did not have a home range, which is consistent with other giant weta studies (McIntyre 1992, Richards 1994, Kelly *et al.* 2008, Watts *et al.* 2011a).

Differences in the distances travelled by male and female wetapunga between daytime refuges appear to be due to differences in reproductive behavior. We suggest that males are likely to travel further because they search for mates. Observations of Cook Strait giant weta on Mana Island showed that adult female giant weta usually remained within a small area (a radius of only a few meters) over several days and then moved (mean = 7.4 m, maximum = 56 m) overnight to a new site and repeated the pattern (McIntyre 2001). This seemed to correspond with mating, oviposition and possibly a quiescent period, followed by movement to a new area, which is likely to attract a new mate. The result is that eggs would be quite widely distributed. A similar pattern of female behavior for wetapunga was observed in this study. In contrast, male and female Wellington tree weta (*Hemideina crassidens*) did not differ in

distances travelled per night and the greatest net distance travelled by a tree weta in one night was nearly 12 m (Moller 1985, Kelly 2006). Individual mountain stone weta, *H. maori*, have been observed to move 36–672 m between rock outcrops over three years and did not exhibit sex differences in distances moved (Leisnham & Jamieson 2002). These results were to be expected as *Hemideina* species usually return to the same daytime gallery retreat (Kelly 2006). In the present study, it appeared that once adult wetapunga began moving at night, the majority did not return to the previously used day-shelter site. Although this was difficult to confirm for individuals that remained in the canopy all night, in all cases the following morning the location of the telemetry signal had changed, indicating they had moved to a new position. In contrast, several subadult weta, monitored by Gibbs & McIntyre (1997) emerged from their daytime refugia early in the evenings and sat nearby for varying periods before migrating vertically into foliage, returning to the same previously used daytime refugia.

McIntyre (2001) found that weather, particularly temperature, influenced the nocturnal activity of giant weta, particularly adult *D. rugosa*. She reported that this species is most often seen on still, warm, damp nights. In the present study, while wetapunga movement between daytime refuges was shown to increase significantly with increasing mean daily temperature above 12°C, there was no relationship with relative humidity.

Habitat use by wetapunga.—Wetapunga inhabit second-growth coastal forest dominated by silverfern, nikau palm, mahoe, and kohekohe, and no weta moved towards the edge of the forest during the study. Similarly, Gibbs & McIntyre (1997) reported that wetapunga were found in relatively low (5–7 m) forest canopy where pohutukawa (*Metrosideros excelsa*), silverfern, puriri (*Vitex lucens*), mahoe, and karaka (*Corynocarpus laevigatus*) were common. These radiotracking studies are in accord with numerous observations made during the annual wetapunga surveys over the past 5 years (Green *et al. in press*).

No quantitative data are available on the plants consumed by captive wetapunga, but they were reported as being vegetarians feeding on the leaves of a variety of trees including kohekohe, mahoe, *C. grandifolia*, silverfern, nikau palm, pohutukawa and kanuka (Richards 1973). In captivity, wetapunga have been observed eating other arthropods and were cannibalistic on other individuals that were moulting and during mating (Richards 1973), but we did not observe this during the present study and suggest that it rarely occurs in the field.

Behavioral observations of wetapunga.—Wetapunga were generally solitary and the majority of their activities, such as feeding, movements and oviposition, occurred at night. The one exception is that mating usually occurred during daylight after weta had paired during the previous night. A number of radiotagged wetapunga were observed mating during the day and individual females paired with a number of different males over the study. Richards (1973) also observed that copulation commenced in the morning and continued throughout the day and reported that wetapunga could mate in four different positions, including those seen in the present study. Observational data obtained for wetapunga and other giant weta species suggest females may produce sex pheromones to attract males (McIntyre 2001). Males have been observed following close behind females, often within antenna length, with their antenna in constant motion. Such behavior and orientation by the males was distinctive and suggestive of responding to olfactory cues.

We do not know the time period between mating and oviposition or whether weta oviposit at a particular time of year. Females #58-1

and 55 were observed ovipositing, but not copulating; copulation may have occurred before the transmitters were attached. Female #60 was observed copulating over 2 days but her transmitter was removed 3 days later at the end of the study and she was not observed laying eggs. It is possible that more copulations could have occurred but were not detected when wetapunga were in the canopy. More oviposition might also have occurred because the weta were not followed continuously at night.

Wetapunga are considered an arboreal species that spend most of their time in the forest canopy and only occasionally come down to the ground, tending to do so at the darkest time of the moon cycle (McIntyre 2001). Gibbs & McIntyre (1997) suggested that adult wetapunga remained within the forest canopy for the duration of their study (12 d) and they did not observe them on the ground. However, Watts *et al.* (2008) reported that adult wetapunga do spend time on the ground, because their footprints were often found in tracking tunnels set there. In the present study, adult wetapunga were observed walking and feeding on the ground. One possible explanation is that the present study and that by Watts *et al.* (2008) were undertaken at the time of year when the adults were sexually active and females were ovipositing on the ground, so that both sexes were spending more time on the ground. This might explain why Gibbs & McIntyre (1997) observed no wetapunga on the ground in November.

During the annual surveys of wetapunga, adults have been increasingly found in relatively exposed sites with little or no protective cover (Green *et al. in press*). Surveys in the 1990s did not record such observations, implying that adult wetapunga have changed their behavior since kiore eradication. Their disregard for protective cover may also reflect the ability of adult wetapunga to better withstand attacks from potential native avian predators such as saddleback or morepork, these being visual hunters. Comparable changes in behavior have been recorded for Wellington tree weta that roosted closer to the ground and were more active on Nukuwaiata (Chetwode Islands) 4 years after the eradication of kiore (Rufaut & Gibbs 2003). In addition, Bremner *et al.* (1989) showed that escape responses of tree weta on islands with predators were significantly more pronounced than on predator-free islands. Two years after mammal eradication from within a predator-proofed enclosure on Maungatautari there was a dramatic increase in weta pitfall captures, weta tracking rates and the incidence of weta footprinting per tracking card (Watts *et al.* 2011b). This may simply reflect increases in weta abundance following mammal eradication, but they could also reflect behavioral changes. These results could, of course, also be caused by a combination of these effects. Data presented here are indices of density and/or activity, and research giving absolute estimates of abundance (*e.g.*, through closed mark-recapture; McCartney *et al.* 2006) is required to distinguish between these effects.

Potential predators of wetapunga on Little Barrier Island include tuatara (*Sphenodon punctatus*), lizards (geckos and skinks), kingfishers (*Halcyon sanctus*), kaka (*Nestor meridionalis*), North Island brown kiwi (*Apteryx australis*), morepork (*Ninox novaeseelandiae*) and the North Island saddleback (*Philesturnus carunculatus*; Richards 1973). Direct evidence of predation is difficult to obtain – a predation event is rapid and with a rare prey item the chances of obtaining evidence are remote. Wetapunga exhibit a defensive behavior when disturbed of flicking their hind legs over their body with considerable strength (Richards 1973), which may be an effective deterrent.

Implications for the monitoring and management of wetapunga.—During the present study, 82% of radiotagged wetapunga were more than 2 m off the ground in their daytime refuges, compared with 88% of

night observations, indicating that wetapunga were higher than 2.5 m in the canopy. These results indicate that it is more efficient to search for wetapunga during the day when they remain in daytime refugia, rather than at night when they are mobile on the ground or higher in the canopy.

Footprint tracking tunnels have been used to identify the presence of wetapunga at sites on Little Barrier Island (Watts *et al.* 2008). However, further development of this monitoring tool is required. Adult wetapunga are clearly capable of moving considerable distances each night, so the question arises as to how far apart tracking tunnels should be placed to reduce the probability of individual wetapunga tracking more than one tunnel. Tracking tunnels have been spaced at 30-m intervals on Mitiu-Somes Island for monitoring the ground-dwelling giant weta, *D. rugosa* (Watts *et al.* 2011a).

Our present results only give distances between observations, but wetapunga obviously do not move in straight lines and so must travel much further than this during a night. However, when only movement is considered, then our results suggest that fewer than 7% of radiotagged wetapunga were capable of tracking two tunnels that are 30 m apart in one night. These are probably overestimates because they only apply if the wetapunga moves from one tracking tunnel to the next, whereas most weta seemed to move in random directions. However, we suggest monitoring wetapunga using the procedure for monitoring small mammals (Blackwell *et al.* 2002, Gillies & Williams 2002). This allows the tracking tunnels to be used for the dual purpose of monitoring both rodents and wetapunga. The procedure involves placing tunnels 50 m apart, which further reduces the likelihood of sequential tracking by wetapunga.

Radiotelemetry has extended our knowledge of the habits of wetapunga behavior. Given that telemetry proved useful in analysing the movements, use of diurnal shelters, nocturnal activity patterns and habitat use of wetapunga, this method could be applied to other large invertebrates. Unfortunately it is not possible to use radiotelemetry to monitor other weta genera, such as tree weta (*Hemideina* species), due to their roosting behavior in tree holes. Radiotracking adult wetapunga after translocation onto another Hauraki Gulf island should be considered, as using this monitoring tool will provide important data on survival rates and behavior of wetapunga immediately after translocation.

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