FORUM ARTICLE

When is it coevolution? The case of ground wētā and fleshy fruits in New Zealand

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Abstract: Both tree and ground wētā have been proposed as potential seed dispersers of some New Zealand fruit. We examine evidence for coevolution of ground wētā and fleshy fruits as suggested by Burns (2006). We found that although ground wētā consume fruits from *Gaultheria depressa* and *G. antipoda*, they do not do so in a way that would suggest they had coevolved as dispersers with these or other New Zealand plants (*Coprosma, Muehlenbeckia, Leucopogon*). In our experiments, ground wētā ate fruits piecemeal and avoided most seeds even when these were very small (<1 mm) as in *Gaultheria*. We also found a positive preference for eating fruits of plants with seeds that were too big for ground wētā to ingest. Several lines of reasoning we explore lend no support to the proposal that ground wētā have coevolved with New Zealand plants resulting in the unusual characteristics displayed by many species (pale fruit presented within a divaricating canopy).

Keywords: fruit colour; *Gaultheria*; *Hemiandrus*; seed dispersal

Wētā hold a near-iconic status for New Zealanders. Many biologists have promulgated a thesis that members of the group play critical ecological roles occupying, in many instances, the niches more usually associated with small mammals in other parts of the world (Ramsay 1978; Daugherty et al. 1993). This view has been advanced specifically for tree (*Hemideina*) and giant (*Deinacrida*) wētā and is largely speculative. However, two recent papers report the ingestion of seeds of *Fuchsia* and *Pratia* by a species of tree wētā, *Hemideina crassidens* (Duthie et al. 2006), and snowberry *Gaultheria depressa* by a species of ground wētā, *Zealandosandrus maculifrons* (Burns 2006; note *Zealandosandrus* is a synonym of *Hemiandrus*; Johns 1997). Evidence of consumption and defecation of intact seeds of native plants might constitute the first direct evidence of close adaptive associations between wētā (of one sort or another) and native plants. Burns (2006) hypothesised that the unusual characteristics of fleshy fruits of many New Zealand shrubs (pale fruit borne on inner branches) may be the product of coevolution with wētā. These same features of New Zealand fruits have previously been ascribed to coevolution with lizards (Whitaker 1987).

Burns (2006) identified 39 intact seeds of *Gaultheria depressa* from three faeces produced by a single ground wētā individual (*Hemiandrus maculifrons*), and concluded that this was the first evidence of seed dispersal by ground wētā. If it were also shown that the seeds had not originated from the gut contents of the prey of the ground wētā, and that the seeds remained viable following passage through the wētā gut, and were moved a significant distance from the parent plant, these meagre data could indeed be taken as evidence that ground wētā are seed dispersers as suggested by Burns (2006). However, even this extrapolation is far from demonstrating coevolution (Janzen 1980) as a general selective force driving the evolution of fleshy fruits of plant species in New Zealand. As noted by Duthie et al. (2006), without measures of overall fitness gains from seed dispersal versus seed predation, even the eating of fruits by tree wētā has not been shown to be mutualistic.

Burns' (2006) proposal for a coevolutionary relationship between ground wētā and fleshy fruits is confused by treatment of all wētā as a single group. Ground wētā and tree wētā belong to different genera of the orthopteran family Anostostomatidae (Johns 1997). Although all wētā tend to omnivory and scavenging, tree wētā (*Hemideina*) are larger than ground wētā and are unusual among anostostomatids in that they mostly eat leaves and infrequently eat other invertebrates. In contrast, ground wētā (*Hemiandrus*; Johns 2001) are primarily predators and scavengers (Cary 1983), although there are records of one species eating apricot fruits (Wahid 1978 cited by Cary 1983). The ground wētā species Burns studied is primarily a carnivore, and adults and juveniles eat a range of invertebrates (beetles, moths, flies) throughout the year (Cary 1983). Although 20% of the ground wētā examined contained plant material in their crops, this was interpreted as being the remains of the gut content of their moth and beetle larvae prey (Cary 1983). There are at least 40 species of New Zealand ground wētā (Johns 2001), and another eight *Hemiandrus* species in Australia, but only seven species of the endemic genus *Hemideina* (tree wētā). The other major orthopteran group also referred to as wētā in New Zealand is the Rhaphidophoridae or cave wētā (camel crickets or cave crickets in other parts of the world). The sizes, shapes and habits of these insects are diverse, although all are small-mouthed (Richards 1954, 1962). Reference to hypothesised evolutionary and ecological relationships involving wētā needs to avoid confounding inferences drawn from phylogenetically and ecologically different taxa. For instance, Burns (2006) states that 'wētā can be important seed predators' but cites observations of such behaviour made on tree wētā (*Hemideina*) not ground wētā (*Hemiandrus*) (Mirams 1957; Beveridge 1964). Similarly, although seed germination trials were performed with a tree wētā (*Hemideina*) the wētā illustrated in the publication reporting this is a giant wētā (*Deinacrida*; Duthie et al. 2006).

As noted above, wētā come in many forms. Burns (2006) suggested fruit placed at ground level will be in close proximity to ground wētā, but ground wētā (*Hemiandrus*) often hunt in trees (Brockie 1992; pers. obs.), and tree wētā frequently travel at ground level. Indeed, *Hemideina maori* spends most of its life on the ground and *H. thoracica* eats kauri seeds on the ground (Mirams 1957). Burns (2006) notes 'insects are also known to lack visual receptors for red hues' (this is indeed the case for orthopterans but not for all butterflies and dragonflies; Briscoe & Chittka 2001) and inferred that the white fruits of *Gaultheria* and other species with pale fruits in New Zealand might result from coevolution with wētā. Given that all wētā are nocturnal, visual cues are likely to be non-existent, or less relevant than tactile (via antennal contact), vibrational, or olfactory ones. We know that tree wētā and giant wētā find and eat green leaves, as well as fruit and flowers of a variety of colours, and ground wētā find and eat a range of invertebrates, few of which are white. There is therefore no direct evidence for a link between white colouration and foraging behaviour in any wētā.

Gaultheria depressa is a prostrate plant with large (8–10 mm), soft, white (or pink or red) fruits (Eagle 2006). Burns (2006) stated that these fruits are often presented in the inner recesses of the canopy and are thus 'obscured from view by aerially searching frugivores'. However, the fruits are also frequently presented on the surface of the mat and are openly visible from above (pers. obs.). Given that ground wētā are unlikely to be foraging visually, the positioning of the fruits on such a small-leaved and prostrate plant is of questionable importance. The large size of *G. depressa* fruits will similarly be of little relevance to a ground wētā, whereas large size and light colour might be important to vertebrate frugivores including birds and lizards that are more frequently cited as likely seed dispersers of New Zealand divaricating shrubs (Whitaker 1987; Lord & Marshall 2001; Oleson & Valido 2003).

Is there any pattern in the distribution of fruit colour and seed size and their availability to ground wētā? If ground wētā like the same sorts of fruit that lizards are thought to like then there are plenty of small, white fruit on divaricating shrubs in New Zealand (Lord & Marshall 2001). Although white and blue fruit in New Zealand are significantly smaller than red fruit, in a comparison of seed size within genera (using data presented in table 2 of Lord & Marshall (2001) and seed sizes given by Webb & Simpson (2001)) we did not find a similar trend towards smaller seeds in white fruit. For example, *Aristotelia* and *Leucopogon* seeds are larger in species with white fruit than in congeneric species with coloured fruit. Furthermore, although the size of seeds inside New Zealand small white fruits varies considerably, many are more than 2 mm long and so are probably too large to be ingested intact by ground wētā. The largest seeds known to survive intact inside tree wētā, although they did not subsequently germinate, were those of *Fuchsia procumbens*, which has red fruit and seeds 1.8–2.4 mm long (Webb & Simpson 2001; Duthie et al. 2006). The adults of most species of ground wētā are about half the size of the adult tree wētā studied (*Hemideina crassidens*) and may not even be able to swallow whole seeds 1.8 mm long. The diameter of the cibarium (preoral cavity) of adult ground wētā from seven species (names as in Johns (2001)) ranges from 0.7 to 1.3 mm (in order of narrowest to widest; *Hemiandrus 'timaru', H. 'okiwi', H. maculifrons, H. pallitarus, H. 'evansae', H. bilobatus*; pers. obs.). On the face of it, a general role for ground wētā in the evolution of fleshy fruits in New Zealand is not apparent.

What might be involved in a programme designed to determine whether ground wētā have a significant role as seed dispersers, and whether this is the result of coevolution? Coevolution is reciprocal evolutionary change in two or more interacting species (Janzen 1980). Thus, to demonstrate coevolution would require evidence of both adaptation in the wētā species (such as food choice) and adaptation in the plant species (such as reduced seed size). We suggest six approaches to test the coadaptation hypothesis, and present results from a pilot study exploring two of these.

(1) Phylogenetic test: Do fruits from unrelated plant taxa show similar (convergent) characteristics favourable

to ground wētā (potential seed dispersers) that are not shared by their phylogenetic relatives? For example, the size of the seed that a ground wētā can swallow is important and a reduction in seed size would be predicted to facilitate ground wētā seed dispersal. However, the difficulty arises that ground wētā species are found all over New Zealand, so it might be argued that a forest *Melicytus* species might suit one ground wētā species and a shrubland *Melicytus* might suit another. To avoid this problem, plant genera that have representatives outside New Zealand should be examined, while avoiding locations where ground wētā also occur (in this case, eastern Australia). Phylogeny leads to non-independence of characters, such as the traits recognised by Duthie et al. (2006) as a syndrome of fruits associated with [tree] wētā seed dispersal. The five plant species in which seeds survived intact in the gut of tree wētā represent only three genera (*Fuchsia, Pratia, Gaultheria*). The small seeds of *Fuchsia* are ancestral within the group (Berry 2004), providing no evidence for adaptive reduction of seed size unique to New Zealand. However, Anostostomatidae wētā have a distribution widely overlapping with *Fuchsia* and thus a search for evidence of mutualism may need to be much wider.

(2) Species distributions: Do distributions of potentially co-adapted species match? Coevolutionary relationships usually involve explicit species–species interactions. Reciprocal evolutionary change of plant and disperser is more likely to occur where their ranges are completely overlapping. Ground wētā species distributions are not well known but the range of altitudes at which single species are found is some indication that plant and insect distributions will not show a one-to-one relationship (Johns 2001). The distribution of *Gaultheria depressa* encompasses the ranges of more than one *Hemiandrus* species in New Zealand, and includes Tasmania where there are no ground wētā.

(3) Dispersal ability: Evidence of significant dispersal (movement) of the seeds away from the parent plant is needed. The home range of ground wētā is unknown. Dispersal of tree wētā *Hemideina thoracica* has been estimated at about 100 m per generation (Morgan-Richards et al. 2000), although *H. crassidens* is capable of walking 10 m in a single night (Ordish 1992). These distances may be similar to the normal movements of skink and gecko species (Hitchmough 1979; Shaw 1994) but a good deal smaller than those of most birds. How far is far enough from the parent plant? Information on natural home ranges of all potential seed dispersers would be useful, in concert with data on the population genetic structures of the plant species using maternally inherited (seed) markers.

(4) Enhanced germination: Is there evidence for retained and enhanced viability of seeds following ingestion by ground wētā? It has been shown that passage through the gut of tree wētā enhanced germination rates in two of the five species whose small seeds survived intact following ingestion. Germination trials following ground wētā ingestion are required. All ground wētā species are probably primarily carnivorous (Cary 1983), so it is important to distinguish between fruit and seeds the ground wētā has eaten and the fruit and seeds eaten by their prey. In addition, measures of seed predation versus seed dispersal are required to estimate overall fitness effects from ground wētā consumption of fruit.

(5) Fruit and seed morphology: Is there evidence that fruits are adapted to encourage ingestion of seeds by ground wētā? We would predict such a fruit would be fleshy with small seeds distributed throughout the flesh, as ground wētā have small mouths (cibarium < 1.5 mm). In contrast, fruits with flesh enclosing seeds (many small ones or few large ones) are sufficient for reptile and bird dispersers that generally swallow fruits whole. The *Gaultheria depressa* fruit is a large (compared with a ground wētā), soft, fleshy calyx enclosing a five-chambered seed capsule. Eaten whole, the seeds would be ingested, but if the flesh is consumed piecemeal the capsule could be largely or entirely avoided.

We tested the idea that ground wētā do eat *Gaultheria depressa* and *G. antipoda* fruits, but could do so in a manner that largely avoids the seeds. Seven adult ground wētā (*Hemiandrus* 'evansae'; Johns 2001) were collected by hand on the night of 15 April 2007 from the Kurinui Creek catchment, North Otago (470 m a.s.l., NZ grid: E 2331100, N 5535528). The ground wētā were held individually in identical containers at ambient temperature with moss to retain moisture and provide cover. We offered each ground wētā a single intact, ripe fruit of *Gaultheria depressa* and *G. antipoda* (on alternate nights) and recorded consumption each morning.

None of the seven captive ground wētā consumed all the flesh of either *G. depressa* or the smaller *G. antipoda* fruit in a single night. All seven ground wētā ate part of the fruit, leaving the majority or all of the inner seed capsule intact (Fig. 1). Burns (2006) found 39 intact *Gaultheria*

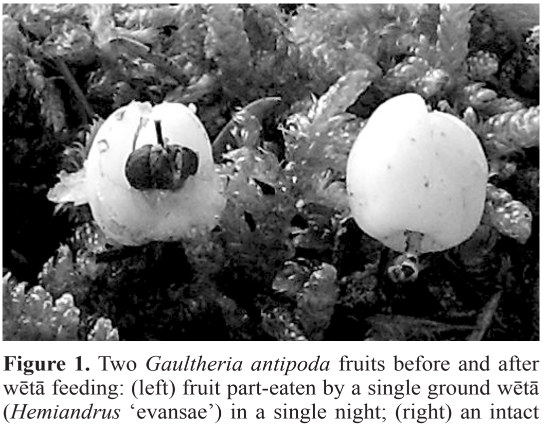

Figure 1. Two *Gaultheria antipoda* fruits before and after wētā feeding: (left) fruit part-eaten by a single ground wētā (*Hemiandrus* 'evansae') in a single night; (right) an intact fruit. Note intact seed capsule in the centre of the eaten fruit (left).

depressa seeds in three faeces from one ground wētā. As *Gaultheria depressa* fruits contain 200–240 seeds each (pers. obs.) the seeds Burns collected represent less than 20% of the seeds likely to have been present in a single fruit. This indicates that the fruit of *Gaultheria depressa* and *G. antipoda* are not well adapted to use ground wētā as seed dispersers.

(6) Wētā food choice: Is there evidence that ground wētā selectively consume fruits containing ingestible seeds (i.e. seeds small enough to swallow intact)? We predict that coevolution of ground wētā as dispersers of fleshy-fruit plant species would lead to ground wētā preferring to eat fruits with seeds small enough to ingest rather than fruits with larger seeds. Our null hypothesis is that when a wētā eats fruit it does so at random with regard to seed size.

We collected ripe fleshy fruit from all available native species at the same time and place as our sample of seven ground wētā were collected (Table 1). Seed sizes were obtained from Webb & Simpson (2001). Three *Gaultheria* species bore fruit with seeds likely to be small enough to be eaten whole by ground wētā (<1 mm). Fruit from seven other species had seeds >2.4 mm long and probably could not be swallowed whole (Table 1). In our choice-experiments we gave each wētā a fruit from each of two plant species for a single night, taking care to match as far as possible fruit of similar size and colour. Each choice-experiment used one small-seeded fruit versus one large-seeded fruit as follows:

(1) White *Gaultheria antipoda* (capsule containing many seeds, each 0.5–0.65 mm long; fruit a fleshy calyx) or white *Muehlenbeckia complexa* (single large seed, 2.5–3.3 × 1.5–2.3 mm; fruit consisting of swollen fleshy tepals).
(2) Red *Gaultheria antipoda* or orange *Leucopogon fraseri* (single seed, 2.5–4.0 × 2.0–2.7 mm, in a drupe).
(3) Pink *Gaultheria macrostigma* (capsule contains many seeds, each 0.5–0.9 mm long, fruit is fleshy calyx), or white *Coprosma propinqua* (two large seeds, 4.0–6.0 × 2.5–3.5 mm, in a drupe).

All seven ground wētā ate fruits from one or more of the *Gaultheria* species while in captivity, most often (6/7) when they had no other choice of fruit to eat. Three species of large-seeded fruit were eaten (*Muehlenbeckia complexa, Leucopogon fraseri, Coprosma propinqua*) but in all cases the seed was left uneaten and intact. When given a choice of fruit, no fruit was eaten on 38% of wētā-nights (8/21). Fruits with large seeds were eaten and fruits with small seeds were untouched on 9/21 wētā-nights. During four wētā-nights both fruits were eaten, but on no occasion were small-seeded fruits the only fruit eaten by the captive ground wētā. A significant variation from random eating with respect to seed size was found with more large-seeded fruit being eaten ($\chi^2 = 13.764$, $P < 0.001$, d.f. = 1, excluding nights no fruit was eaten, or $\chi^2 = 8.005$, $P < 0.01$, d.f. = 1, all nights included). From this we infer that *Hemiandrus* 'evansae' did not prefer the fruits of species it could potentially disperse.

In conclusion, we find no evidence of a coevolutionary relationship between the ground wētā *Hemiandrus* 'evansae' and New Zealand fleshy fruit species. Ground wētā, we suggest, eat nutritious foods as and when they are found, including invertebrates, fruits and flowers, and are probably not involved in extreme specialisation with any of their food species. However, comparative studies of the diet of our ground wētā fauna are likely to be rewarding. Although New Zealand has an unusually large proportion of native plants with pale fruits borne on inner branches (Lord & Marshall 2001), it is not yet clear which if any potentially seed-dispersing animals have selected for these traits. The evolution of the unusual characteristics

Table 1. Ten New Zealand plants that bore ripe fleshy fruit in April at Kurinui (North Otago) and their range of seed sizes (Webb & Simpson 2001). *Hemiandrus* 'evansae' was collected in the vicinity of all fruits. Three species classed as 'small-seeded' are indicated *.

Species	Colour of fruit	Seed size (mm)
Leucopogon fraseri	Orange	2.5–4.0 × 2.0–2.7
Muehlenbeckia complexa	White	2.5–3.3 × 1.5–2.3
Gaultheria antipoda	White or red	0.50–0.65*
Gaultheria depressa	White	0.40–0.65*
Gaultheria macrostigma	Pink	0.50–0.90*
Melicytus alpinus	White (purple where exposed)	3.8–4.4
Coprosma crassifolia	Yellowish white	4.0–5.2 × 3.0–3.7
Coprosma rhamnoides	Red	2.4–3.7 × 1.7–2.0
Coprosma propinqua	White	4.0–6.0 × 2.5–3.5
Coprosma tailoriae	White or pink (rare form)	2.8–4.0 × 2.2–3.0

of fleshy fruits in New Zealand will provide scope for many future studies.

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References

Berry PE, Hahn WJ, Sytsma KJ, Hall JC, Mast A 2004. Phylogenetic relationships and biogeography of *Fuchsia* (Onagraceae) based on noncoding nuclear and chloroplast DNA data. American Journal of Botany 91: 601–614.

Beveridge AE 1964. Dispersal and destruction of seed in central North Island podocarp forests. Proceedings of the New Zealand Ecological Society 11: 48–55.

Briscoe AD, Chittka L 2001. The evolution of color vision in insects. Annual Review of Entomology 46: 471–510.

Brockie R 1992. A living New Zealand forest. Auckland, Bateman.

Burns KC 2006. Weta and the evolution of fleshy fruits in New Zealand. New Zealand Journal of Ecology 30: 405–406.

Cary PRL 1983. Diet of the ground weta *Zealandosandrus gracilis* (Orthoptera: Stenopelmatidae). New Zealand Journal of Zoology 10: 295–297.

Daugherty CH, Gibbs GW, Hitchmough RA 1993. Mega-island or micro-continent? New Zealand and its fauna. Trends in Ecology and Evolution 8: 437–442.

Duthie C, Gibbs G, Burns KC 2006. Seed dispersal by weta. Science 311: 1575.

Eagle A 2006. Eagle's complete trees and shrubs of New Zealand. Wellington, Te Papa Press.

Hitchmough RA 1979. The ecology and behaviour of two green gecko (*Naultinus*) species. MSc thesis, University of Auckland, Auckland, New Zealand.

Janzen DH. 1980. When is it coevolution? Evolution 34: 611–612.

Johns PM 1997. The Gondwanaland weta: Family Anostostomatidae (formerly in Stenopelmatidae, Henicidae or Minermidae): nomenclatural problems, world checklist, new genera and species. Journal of Orthoptera Research 6: 125–138.

Johns PM 2001. Distribution and conservation status of ground weta, *Hemiandrus* species (Orthoptera: Anostostomatidae). Science for Conservation 180. Wellington, Department of Conservation.

Lord JM, Marshall J 2001. Correlations between growth form, habitat, and fruit colour in the New Zealand flora, with reference to frugivory by lizards. New Zealand Journal of Botany 39: 567–576.

Mirams RV 1957. Aspects of the natural regeneration of the kauri (*Agathis australis* Salisb.). Transactions of the Royal Society of New Zealand 84: 661–680.

Morgan-Richards M, Trewick SA, Wallis GP 2000. Characterization of a hybrid zone between two chromosomal races of the weta *Hemideina thoracica* following a geologically recent volcanic eruption. Heredity 85: 586–592.

Olesen JM, Valido A 2003. Lizards as pollinators and seed dispersers: an island phenomenon. Trends in Ecology and Evolution 18: 177–181.

Ordish RG 1992. Aggregation and communication of the Wellington weta *Hemideina crassidens* (Blanchard) (Orthoptera: Stenopelmatidae). New Zealand Entomologist 15: 1–8.

Ramsay GW 1978. Invertebrate mice. New Zealand Entomologist 6: 400.

Richards AM 1954. Notes on food and cannibalism in *Macropathus filifer* Walker, 1869 (Rhaphidophoridae, Orthoptera). Transactions of the Royal Society of New Zealand 82: 733–737.

Richards AM 1962. Feeding behaviour and enemies of Rhaphidophoridae (Orthoptera) from Waitomo Caves, New Zealand. Transactions of the Royal Society of New Zealand (Zoology) 2: 121–129.

Shaw T 1994. Population size, distribution, home range and translocation of the jewelled gecko, *Naultinus gemmeus*, at the Every Scientific Reserve, Otago Peninsula. Unpublished Wildlife Management Report no. 56. Dunedin, University of Otago.

Webb CJ, Simpson MJA 2001. Seeds of New Zealand gymnosperms and dicotyledons. Christchurch, Manuka Press.

Whitaker AH 1987. The roles of lizards in New Zealand plant reproductive strategies. New Zealand Journal of Botany 25: 315–328.

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