

Mutualism or opportunism? Tree fuchsia (*Fuchsia excorticata*) and tree weta (*Hemideina*) interactions

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Abstract Mutualisms or interspecific interactions involving net mutual benefits, are an important component of ecological theory, although effectively demonstrating mutualism is notoriously difficult. Among two New Zealand endemics, a slightly elevated germination rate of *Fuchsia excorticata* (Onagraceae) seeds after passage through tree weta (Orthoptera: Anostomatidae) compared with seeds manually extracted from fruit, led to the proposal that a mutualistic relationship exists between this plant and animal. An improved germination rate, or any other single trait, however, does not alone constitute evidence for mutualism; the relative costs and benefits of numerous components of the interaction need to be accounted for. We considered the costs and benefits to *F. excorticata* of the putative seed dispersal mutualism with tree weta. Tree weta provided with *F. excorticata* fruits destroyed 78% of the seeds they consumed, did not move fruit; and faeces containing seeds were deposited near their roost holes (which are naturally in trees). The seeds remaining after fruit consumption and those that are ingested but survive gut passage are unlikely to be deposited in suitable habitat for seedling survival. Plant food preferences of captive tree weta assessed using pairwise leaf choice tests showed that the leaves of *F. excorticata* were the least preferred of six commonly encountered plants. In addition, we found that tree weta did not show a preference for *F. excorticata* fruit over a standard leafy diet, indicating they are unlikely to be actively seeking fruit in preference to other sources of food. These observations indicate that any interaction between tree weta and *F. excorticata* is likely to be opportunistic rather than mutualistic, and highlight the difficulty of characterizing such interactions.

Key words: Anostomatidae, frugivory, *Fuchsia excorticata*, *Hemideina*, mutualism, seed dispersal, seed predation.

INTRODUCTION

Mutualisms are thought to be important and even ubiquitous components of ecology and evolutionary biology (Bronstein *et al.* 2006). Mutualism has been defined as ‘an interspecific interaction involving net mutual benefits: members of two species experience higher fitness when they occur together than when they occur alone’ (Bronstein 1998). Typically, mutualisms are characterized as involving ‘service’ providers that receive a ‘payment’ in return (Bronstein 1994). In plant–insect interactions, insects are well-known for providing services such as pollination and defence, whereas plants are often sources of food, shelter or oviposition sites. Such systems are well characterized, but many studies of mutualism fail to demonstrate that both participants gain significant benefits. As a result,

interactions have been labelled as mutualistic without detailed evidence (Cushman & Beattie 1991). When evaluating potential mutualistic interactions, it is necessary to determine the net benefits gained by putative mutualists. Although putative mutualists may receive a benefit, if the net effect of the interaction is negative then it cannot be deemed mutualistic. It is, however, often difficult to determine the net benefits gained.

Seed dispersal is an interaction which, if effective, could in many circumstances be considered mutualistic, and is the focus of many studies of plant–animal interactions, although relatively few involving insects. Effective dispersal of seed has strong fitness implications for plants, but animals are often interested in seeds as food. Plants use nutritious fruits or similar structures to engage seed dispersal services from animals (usually vertebrates), and selection on fruit and seed characteristics is presumably exerted primarily by the dominant animal type involved. For example, many trees produce fruits of size and colour that attract birds, and with seeds that are resistant to damage by bird feeding (e.g. Wheelwright & Janson 1985; Traveset 1998; Stanley *et al.* 2002). Other

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organisms may opportunistically take advantage of these fruits and seeds, but exert relatively little selective pressure on the plant. Seed-related mutualisms involving invertebrates are dominated by ants; and many plants have evolved seeds with elaiosomes, which are the edible parts consumed by ants after they have transported seeds to their nests (Christian 2001; Giladi 2006; Lengyel *et al.* 2009). Understanding the relative contribution to seed dispersal/predation made by different animal groups is a valuable part of biome research (Saba & Toyos 2003).

The vast majority (84%) of fleshy fruits of New Zealand plant species are consumed by four native avian frugivores (silveryeye *Zosterops lateralis*, bellbird *Anthornis melanura*, New Zealand pigeon *Hemiphaga novaeseelandiae* and tui *Prosthemadera novaeseelandiae*) and their seeds deposited in faeces (Lord 2004; Kelly *et al.* 2006). Nevertheless, the lack of native terrestrial mammals (Trewick & Morgan-Richards 2009) and ill-balanced avifauna (Trewick & Gibb 2010), are circumstances that allow for the possibility that large endemic invertebrates have evolved specialized interactions with plants (e.g. Micheneau *et al.* 2010). It has recently been proposed that native crickets, known locally as weta (Orthoptera: Anostomatidae), have a mutualistic relationship with fleshy-fruited New Zealand plants, and that they are seed dispersers (Burns 2006; Duthie *et al.* 2006). In particular, it has been documented that Wellington tree weta, *Hemideina crassidens* Blanchard, consume fruits of *Fuchsia*, *Pratia* and *Gaultheria*, and ingest their seeds (Duthie *et al.* 2006). The germination rate of intact seeds after passage through tree weta guts was found to be slightly but significantly greater for two species (*Fuchsia excorticata* J.R. et G. Forst and *Pratia physaloides* (A. Cunn) Hemsl.) compared with seeds manually extracted from fruit (Duthie *et al.* 2006). Germination of *P. physaloides* was 85% for hand-cleaned seeds and 95% for weta-ingested seeds; means for *F. excorticata* were not given. Also, seeds of the subalpine shrub, *Gaultheria depressa* D.A. Franklin, have been recovered from faeces of a single individual ground weta (*Hemiandrus maculifrons* Walker; Burns 2006).

The demonstration of seed consumption in these insects is interesting and novel, and might constitute the first evidence of a mutualistic association between fleshy fruits and an insect fruit consumer. However, as emphasized by Morgan-Richards *et al.* (2008), the eating of fruit can only be considered part of a mutualistic relationship if the overall fitness gains from seed dispersal outweigh losses due to seed predation. In the plant–weta interaction there is, as yet, no evidence of a net benefit to either partner. Many studies of putative mutualisms, including Duthie *et al.* (2006), fail to show that both partners acquire benefits and are commonly regarded as mutualistic when only the host species (a plant in this case) is shown to gain some benefit (but not

necessarily a net benefit) from the services of the visitor (e.g. tree weta; Cushman & Beattie 1991). Balancing the relatively modest benefit of improving germination by approximately 10% (Duthie *et al.* 2006), even small negative effects of weta on the plant could result in a net fitness reduction for the plant. That would mean the relationship is not mutualistic, but antagonistic. Tree weta could have a negative effect on the plant by destroying a large proportion of seeds, depositing seeds closer to the parent plant than if they had fallen to the ground and rolled or floated away, and/or dispersing seeds less efficiently than alternative seed dispersers such as frugivorous birds.

Disperser effectiveness (*sensu* Schupp 1993) has both qualitative and quantitative components. A high-quality disperser consumes fruit without destroying a high proportion of seeds, and deposits viable seeds in suitable habitat, a significant distance from the parent plant. A high-quantity disperser removes a large number of seeds. Diet and food preferences of the dispersing animal affect the number of seeds removed.

We investigated the *F. excorticata* – tree weta interaction by testing four components:

1. Seed survival: when *F. excorticata* fruit is eaten by tree weta, what proportion of seeds survive gut passage? If *F. excorticata* and tree weta are involved in a mutualism, we would expect a high proportion of seeds to pass through the tree weta undamaged.
2. Seed dispersal: do tree weta move *F. excorticata* seeds away from the tree by avoiding defecation near roost holes? If *F. excorticata* and tree weta are involved in a mutualism, we would expect that tree weta move seeds a significant distance from the parent plant to habitat suitable for plant germination and growth.
3. Leaf preference: do tree weta prefer *F. excorticata* leaves over other forest species? Available information suggests that tree weta use leaves as a major part of their diet so if weta prefer leaves of *F. excorticata* they are more likely to forage in the trees and will encounter and disperse a larger number of fruit, increasing disperser quantity.
4. Fruit attraction: do tree weta prefer to eat *F. excorticata* fruit over palatable leaves? If *F. excorticata* and tree weta are involved in a seed dispersal mutualism, we would expect tree weta to have a preference for *F. excorticata* fruit so that a sufficient number of seeds are dispersed for plant regeneration.

METHODS

Study species

The New Zealand tree fuchsia, *F. excorticata* (Onagraceae), is a small (up to 12 m tall) endemic tree; the largest in the

genus *Fuchsia*. *Fuchsia excorticata* is the most common of New Zealand's three species, found throughout the country from North Cape to Auckland Island, and is associated with disturbed habitats (Robertson *et al.* 2008). It has small (approx. 10 mm) pendulous purple-black fleshy fruit typical of the genus (Burrows 1995). Fruits have four peripheral groups of small, embedded seeds, typically with 500–600 seeds per fruit (Godley & Berry 1995). Mature seeds are slightly curved and ellipsoid, measuring approximately 0.8 mm by 0.4 mm (Godley & Berry 1995). Birds known to take *F. excorticata* fruit include New Zealand pigeon (*H. novaeseelandiae*), tui (*Pr. novaeseelandiae*), bellbird (*A. melanura*), silvereye (*Z. lateralis*), fantail (*Rhipidura fuliginosa*), European blackbird (*Turdus merula*) and European starling (*Sturnus vulgaris*; Craig *et al.* 1981; O'Donnell & Dilks 1994; Burrows 1995). Robertson *et al.* (2008) found that there was a higher proportion of ripe and overripe fruit on *F. excorticata* trees growing on mainland New Zealand compared with those on offshore Kapiti Island, which is densely populated by birds. One inference from the observation of more rapid removal of fruit where bird densities are higher is that birds are likely to have a substantial influence on seed dispersal. *Fuchsia excorticata* requires disturbed ground for recruitment, and because such habitat tends to be patchily distributed, selection on transportation of fruit away from parent plants may be intense (Robertson *et al.* 2008). For these reasons, the dispersal of viable seed is likely to be important for the persistence of this species.

New Zealand tree weta (*Hemideina* spp.) are common throughout most of New Zealand in forest and suburban settings, across a range that overlaps that of *F. excorticata*. They are flightless, nocturnal orthoptera that are distinctive among their family (Anostostomatidae) in that they are primarily herbivores feeding on leaves, flowers and fruit (Trewick & Morgan-Richards 2005). Tree weta are so named because most species habitually hide in cavities (also called galleries or roosts) in trees during the day, finding safety from predators and weather. Tree weta typically return to the same cavity and do not move horizontally very far each night (Ordish 1992; Kelly 2006). We studied two tree weta species: *H. crassidens*, the Wellington tree weta, which occurs in the southern North Island and the west coast of the South Island; and *H. thoracica* White, the Auckland tree weta, which occurs throughout central and northern North Island (Trewick & Morgan-Richards 1995). Weta are thought to hold an important place in the New Zealand ecosystem, sometimes compared with that of small mammals elsewhere in the world. They have even been referred to as 'invertebrate mice' on account of their nocturnal foraging, polygamy, large droppings and importance as food for a number of vertebrate species (Ramsay 1978). There is, however, a general lack of basic information on weta biology and ecology.

Husbandry of weta

Hemideina crassidens and *H. thoracica* were collected in North Island, New Zealand. Weta were weighed using a digital scale and given unique codes that identified their species and sex. They were housed individually in plastic containers measuring 15 × 15 × 9 cm, fitted with 10 × 10 cm stainless steel insect mesh (1 mm aperture) for ventilation. The weta were

kept at a constant temperature of 14 ± 1°C, with natural day/night lighting and the boxes sprayed with water daily to maintain humidity. Faecal material and uneaten food were removed daily. Each weta had access to a 'roost' made from hollowed sections of flax flower stalks (*Phormium tenax*), which they used for concealment during the day. This design facilitated manipulation of food during the day with feeding trials taking place at night.

Fuchsia excorticata seed survival

Ripe *F. excorticata* fruit were collected in the wild and provided to captive weta. Each fruit was cut in half length wise; and each weta was provisioned with one half of a ripe fruit for each of two consecutive nights (i.e. a total of two half fruits per weta after two nights). The retained fruit halves were used for estimation of fruit seed numbers (seeds in each fruit half were counted by dissecting out). After two nights with *F. excorticata* fruit, each weta was given a carrot slice each day thereafter, which acted as a food and as a marker to help track the passage of food, due to faeces changing from a dark brown to orange colour on ejection of carrot residues. After provision of *F. excorticata* fruit, faecal pellets were collected over successive days until new faeces were bright orange (indicating mostly carrot) or after 9 days had passed (whichever came first). Any fruit and/or seeds remaining in the weta containers were also collected in order to assess the number of seeds left uneaten. To determine seed content, faeces were broken down in 10 mL of 4.4% sodium hypochlorite using a blunt probe. A Buchner funnel and filter paper were used to collect and wash the cleared solid material and distribute it onto a flat surface suitable for examination. Filter papers bearing the remaining bleached faecal material were placed in Petri dishes and the number of intact, unbroken seeds counted under a dissecting microscope. Fruit was offered to, and consumed by 27 weta.

The proportion of seeds surviving gut passage was calculated as follows. The number of seeds counted in the two fruit halves that were not given to a weta gave an estimate of the number of seeds in the corresponding two halves that were given to that weta and thus available for consumption. This number, less any uneaten seeds, gave an estimate of the number of seeds actually consumed. The number of intact seeds in all faecal pellets collected from each weta gave the number of seeds that survived gut passage. The number of intact seeds in faeces divided by the estimated number of seeds consumed gave the proportion of seeds consumed that survived gut passage. The number of seeds in the fruit halves kept for counting multiplied by two gave an estimate of seed numbers per fruit. Data were analysed using Minitab software.

Movement of *Fuchsia excorticata* seeds

This experiment used perspex enclosures (40 × 40 × 26 cm) fitted with nylon mesh lids. A 2-cm grid divided into quadrats was placed beneath each enclosure and the grid could be viewed from above through the clear perspex base. A single weta roost containing a weta was placed in one corner of each

enclosure so that the opening of the roost faced the centre of the container. One *F. excorticata* fruit was placed at the centre of the container. After one feeding night, the position of the fruit and whether it had been eaten was recorded using the grid coordinates, whereas faecal pellet position was recorded as the quadrat it was deposited in. For each weta the procedure was repeated on two successive nights. Twenty-eight weta (seven male and seven female *H. thoracica*, seven male and seven female *H. crassidens*) were used in individual trials. A chi-squared goodness-of-fit test was conducted using Minitab on the number of faecal pellets in each quadrat, to assess whether pellets were more likely to be deposited in the quadrat containing the roost.

Leaf species preference

A set of plant species, both native (tree fuchsia, *F. excorticata* (Onagraceae); mahoe, *Meliclytus ramiflorus* (Violaceae) J.R. et G. Forst; northern rata, *Metrosideros robusta* (Myrtaceae) A. Cunn; broadleaf, *Griselinia littoralis* (Griselinaceae) Raoul; tutu, *Coriaria arborea* (Coriariaceae) R. Linds); and exotic (eucalyptus, *Eucalyptus ficifolia* (Myrtaceae) F. Muell) were used in pairwise food choice experiments with captive weta. The native plant species were chosen due to their prominence in most broadleaf forests in which tree weta are found. The six plant species were used to complete a matrix in which each species was tested against every other (resulting in 15 different combinations), in order to give a rank of preference for these species. Each of 30 or more weta (approximately equal numbers of *H. crassidens* and *H. thoracica*) were presented with one leaf of each of two different plant species in their enclosure, as a choice of food every second night. Provisioning was undertaken during the daytime when weta were in their roost. After one feeding night, the leaves were removed for measurement and replaced with a slice of carrot, which acted to partition each choice experiment by 'cleansing the palate' and give some nutrition if weta had chosen not to eat the night before.

Leaves were digitally scanned before and after each food choice test. The software program Compu Eye, Leaf and Symptom Area (Bakr 2005) was used to calculate the surface area of the leaves before and after being offered to weta and the difference between these values determined the area of leaf eaten. As leaves of different species are not the same thickness, an estimate of leaf mass eaten was obtained using a conversion index for each plant species. Indices were obtained by collecting 10 fresh leaves of each species, weighing them and calculating surface area. Mass was divided by surface area for each leaf and the result averaged. Data were averaged and analysed using Minitab software. The proportion of the total amount eaten for each plant species was calculated in order to correct for differences in the total amount eaten by individual weta in any given trial (due to differences in size or hunger levels). Tukey simultaneous post-hoc tests (alpha level = 0.05) were conducted with results of the 15 pairwise choice experiments to assess which differences were significant.

Fuchsia excorticata fruit attraction

It was known from previous feeding trials that the leaves of *M. ramiflorus* are readily eaten by tree weta. Therefore, in

order to establish whether tree weta have a particular preference for the fruit of *F. excorticata* over a standard leafy diet, one *M. ramiflorus* leaf and one *F. excorticata* fruit was placed in the containers of 30 weta as a choice of food for one night. The next day it was recorded which of the two had been consumed.

Data analysis

In all experiments, data from the two tree weta species were compared and found not to differ significantly from one another. Weta that did not eat during a particular food choice experiment were excluded from analysis of that test. Most leaf proportions consumed were in the range of 30–60% and sample size was relatively large (approx. 30 tree weta each night), so we used a normal approximation for the leaf proportions and analysis of residuals supported this approach.

RESULTS

Fuchsia excorticata seed survival

The average number of seeds in our *F. excorticata* fruit was estimated to be 513 ± 10 (mean \pm SEM). When weta were given the opportunity to eat one *F. excorticata* fruit (two halves of two fruit) containing approximately 500 seeds, the mean number of intact seeds recovered in faecal pellets was 81 ± 12 (approx. 16%, Fig. 1). This is the number of seeds recovered regardless of how many were consumed. The average number of seeds consumed was 339 ± 29 , or 70% of the estimated number of seeds on offer. The mean percentage of seeds consumed that survived gut passage was $22 \pm 3\%$. On average, 87% of seeds recovered were in the first two faecal pellets produced.

The sample of tree weta used in our experiment varied in mass between 0.36 g and 6.89 g (mean = 2.79, SEM = 0.36). We therefore questioned whether the size of the weta was correlated with the proportion of seeds that survived gut passage. We found, however, no significant correlation between weta mass and proportion of seeds surviving gut passage ($R^2 = 0.127$, $P = 0.095$), and inspection of the scatter plot did not show any other kind of relationship.

Movement of *Fuchsia excorticata* seeds

There was no evidence that weta avoid defecating near their roost. Faecal pellets were deposited widely within the constraints of our experiment, but they tended to be aggregated near the weta roost. We performed a chi-squared test of goodness-of-fit to assess whether faecal pellets were randomly distributed in the four

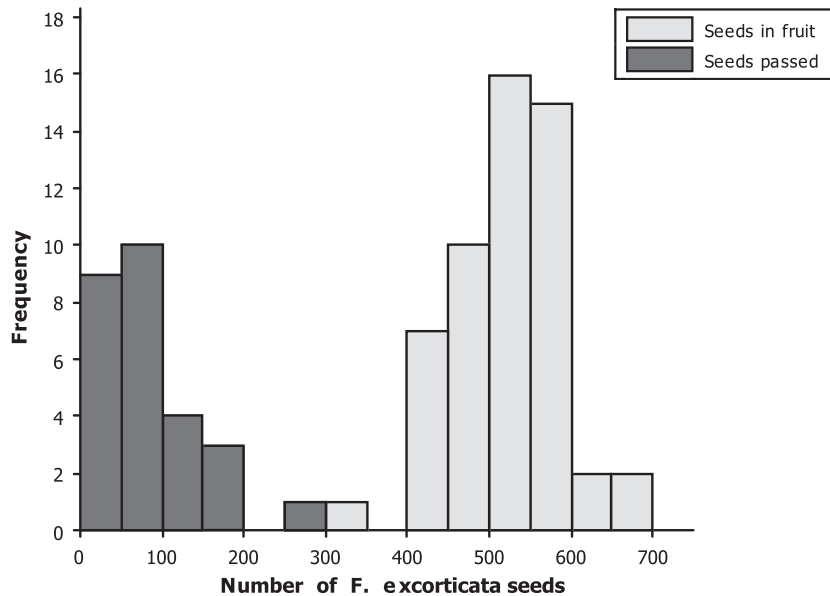


Fig. 1. The estimated number of seeds per *Fuchsia excorticata* fruit (light grey bars) compared with the number of intact seeds recovered from faecal pellets of tree weta (*Hemideina*) when they were given the opportunity to consume one *F. excorticata* fruit (dark grey bars).

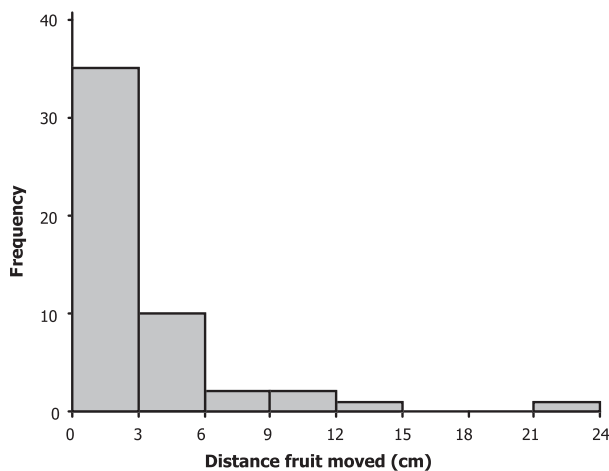


Fig. 2. Distance that captive tree weta (*Hemideina*) moved *Fuchsia excorticata* fruit over a night.

quadrats, and found they were not, $\chi^2 = 61.27$, d.f. = 3, $P < 0.001$, with considerably more than expected in the quadrat that contained the roost (47/75 observations). Weta did not move the fruit far from where it started at the centre of the enclosure; they fed on it where it was and did not take it back to their roost. In most cases (35/51), *F. excorticata* fruits were moved no more than 2 cm from their starting position (Fig. 2); and the mean distance moved was $3.4 \text{ cm} \pm 0.5 \text{ cm}$. This was less than the distance from original fruit position to roost entrance.

Leaf species preference

In the leaf choice tests, *F. excorticata* was eaten in much lower amounts (by weight) than all other species paired against it. Conversely, *C. arborea* and *E. ficifolia* were eaten in higher proportions than other species paired against them, whereas similar proportions of *M. ramiflorus*, *Me. robusta* and *G. littoralis* were eaten (Table 1). Over all 15 food choice combinations, on average, the mean leaf mass eaten for *F. excorticata* was only one-quarter of the total for *G. littoralis*, one-sixth that for *M. ramiflorus* and *Me. robusta*, and one-eighth that for *E. ficifolia* and *C. arborea* (Fig. 3).

Fuchsia excorticata fruit attraction

When given a choice of a *M. ramiflorus* leaf or a *F. excorticata* fruit, 45% ($n = 30$) of weta ate some of both, 41% ate only the leaf, but just 14% ate only the fruit. Furthermore, in no observations was the entire fruit eaten.

DISCUSSION

It has been proposed that weta have mutualistic relationships with fleshy-fruited plants (Duthie *et al.* 2006). However, the fact that a species is seen feeding upon a fruit and even dispersing the seeds is not demonstration of a mutualistic relationship between the

Table 1. Mean proportion of total weight of plant eaten per night by tree weta made up of the listed plant species (rows) when paired against a second plant species (columns)

	<i>Coriaria arborea</i>	<i>Eucalyptus ficifolia</i>	<i>Melicytus ramiflorus</i>	<i>Metrosideros robusta</i>	<i>Griselinia littoralis</i>
<i>Eucalyptus ficifolia</i>	0.36				
<i>Melicytus ramiflorus</i>	0.35	0.37			
<i>Metrosideros robusta</i>	0.30	0.46	0.52		
<i>Griselinia littoralis</i>	0.29*	0.34*	0.57	0.04	
<i>Fuchsia excorticata</i>	0.01*	0.10*	0.22*	0.09	0.16

So for example, for *Eucalyptus ficifolia* versus *Coriaria arborea*, *E. ficifolia* made up 36% and *C. arborea* 64% by weight. Results of Tukey post-hoc tests show statistically significant departures from 50:50 indicated by * (at $P < 0.05$).

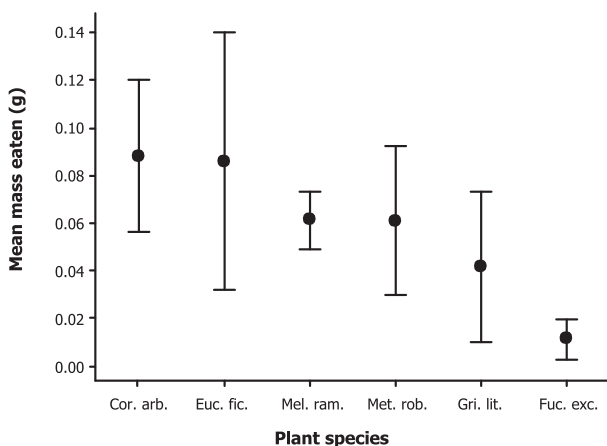


Fig. 3. The average mass of six plant species eaten by tree weta (*Hemideima*) over one night over all 15 food choice tests (95% confidence interval). Cor.arb., *Coriaria arborea*; Euc. fic., *Eucalyptus ficifolia*; Mel.ram., *Melicytus ramiflorus*; Met. rob., *Metrosideros robusta*; Gri.lit., *Griselinia littoralis*; Fuc. exc., *Fuchsia excorticata*.

plant and disperser as this requires an overall benefit to both partners arising from the interaction (Keddy 2007).

Fuchsia excorticata seed survival

For a mutualism that provides net benefits to the plants, there should be low seed mortality during consumption. In contrast, our seed survival experiment found that 78% of ingested *F. excorticata* seeds were destroyed. This survival rate is low compared with reported seed survival rates of almost 100% through some frugivorous birds (Fukui 1995; Yagihashi *et al.* 1998). Although there are no data available on the germination of *F. excorticata* seeds following bird consumption, 96–100% of seeds manually extracted directly from fruit germinated within 32 days (Burrows 1995), and Robertson *et al.* (2008) also reported high germination percentages (84%) for hand-cleaned seeds. Duthie *et al.* (2006) found that

passage through tree weta guts resulted in an approximate 10% increase in germination rate of ingested seeds compared with control seeds, but this is far smaller than the increase needed to compensate for seeds destroyed. If germination is 85% for hand-cleaned and 95% for weta-passed fruit, the proportion of germinating seeds is 0.85 for seeds not eaten by weta but only $(0.95 \times 0.22) = 0.21$ for those eaten by weta. Even fruits falling to the ground almost certainly yield more seedlings per seed than weta-ingested fruit. Burrows (1995) found that 54% of *F. excorticata* seeds germinate when simply left in the fleshy pericarp of the fruit; and Robertson *et al.* (2008) showed that trials using Petri dishes (as Burrows did) underestimate the germination from intact fruit. By destroying such a large proportion of the seeds they consume (78%), weta are probably reducing the fitness of the plant. This high percentage of destroyed seeds suggests weta are effectively seed predators, a behaviour characteristic of small mammals native to other countries (Williams *et al.* 2000).

Movement of *Fuchsia excorticata* seeds

For a mutualism to provide net benefits to the plant, weta should move seeds a significant distance from the parent tree. Frugivores that drop or pass large numbers of seeds close to parent plants are unlikely to be high-quality dispersers as seedlings of plant species tend to experience high rates of mortality beneath parents (Chapman & Chapman 1995). Although tree weta destroy many of the seeds they consume, if they deposited the remainder in habitat that was significantly better for seedling survival, at a useful distance from parents, this could potentially outweigh the cost of seed loss and constitute an acceptable trade-off for the plant. However, the results from our captive experiment indicate that tree weta do not move fruit far from where they found it. Therefore, surviving, uningested seeds remain near where fruits fall. Any viable seeds in droppings may also be deposited in unsuitable places as weta have higher defecation rates near their roosts

than further away. Seeds might be moved further in natural environments; however, our result is consistent with our own field observations of frass piles near roost holes. Here, the seeds may be in habitat that is less suitable than if the fruit were to be passively dispersed, such as by falling from branches. Because weta defecate most seeds near their roost, and roosts of weta most likely to encounter *F. excorticata* fruit are those in *F. excorticata* trees, it is likely that seeds will be deposited below the parent tree, frequently below the main trunk. If the roost is in a tree other than *F. excorticata*, the seeds will still be deposited below an alternative established tree. Neither are ideal locations as any resulting seedlings are likely to face strong competition. Given their low preference for both the fruit and leaves, it appears unlikely that tree weta would consume *F. excorticata* fruit at all if their roost were not in or near a *F. excorticata* tree. Nonetheless, because tree weta do eat fruit in addition to leaves, and may disperse some seeds away from the parent, further tests are needed of the hypothesis that weta diet is largely opportunistic, that is, a function of the location of their roost.

There may be a fitness reduction for *F. excorticata* if seeds are dispersed less efficiently by weta than alternative seed dispersers. As most *F. excorticata* fruits do get eaten by birds at a range of sites in New Zealand (Robertson *et al.* 2008), a fruit eaten by a weta would likely have been later eaten by a bird. Therefore, weta probably reduce the number of seeds dispersed by birds. Distances travelled by weta are limited by their need to return to the same roost repeatedly (Barrett 1991; Trewick & Morgan-Richards 2000; Field & Sandlant 2001), and are negligible (on average 1–3 m a night, Kelly 2006) compared with those of birds. In the absence of birds, weta might be useful as seed dispersers, but the lack of movement and low survival rate of seeds make even this questionable, and in the presence of birds, weta fruit consumption simply replaces a high-quality disperser with a low-quality one. A comparison of seed fate for plants with which weta do and do not interact is required to determine whether weta have any capacity to enhance seed dispersal.

Leaf species preference

Dispersal quantity is likely to be enhanced if the plant species is a preferred food of the disperser (for both leaf and fruit material). We describe for the first time tree weta preference for leaves of some species over others. Surprisingly, we found that *F. excorticata* leaves (targeted by possums, Pekelharing *et al.* 1998) were the least preferred by weta of the six plant species tested. Indeed, tree weta were reluctant to eat *F. excorticata* leaves at all. Of note was their preference for the native toxic *C. arborea* and the exotic well-defended eucalypt over the less obviously defended plant species.

Fuchsia excorticata fruit attraction

Dispersers differ in the importance of fruit in their diet and this affects the number of seeds removed by the dispersing animal (Schupp 1993). An animal that has a preference for fruit is likely to disperse a larger number of seeds than one that does not seek out fruit, and will be a high-quantity disperser. Tree weta show no preference for *F. excorticata* fruit over leaves of a species they are known to regularly consume (i.e. a standard leaf diet). It is likely that fruit consumption by weta is predominantly by those individuals living in or very near *F. excorticata* trees and thus individuals that encounter fruits opportunistically. In fact, weta will eat parts of many kinds of fruits if encountered, including those whose seeds they could not conceivably ingest due to their large size (Duthie *et al.* 2006).

Conclusion

At present, it appears unlikely that *F. excorticata* obtains a net benefit from tree weta eating its fruit, with weta acting primarily as seed predators, and providing low-quality dispersal to seeds that are passed intact. Hence, the relationship cannot be called a mutualism. The low preference for *F. excorticata* fruit and leaves also raises doubt that tree weta gain significant resources from *F. excorticata*, although no doubt some nutritional benefit is obtained. These and other observations (M. Griffin *et al.*, unpubl. data, 2010) indicate that tree weta feed opportunistically on nutritious food including fruit when it is found, and are not involved in specialization with fleshy-fruited plants. Similarly, other incidental accounts of invertebrates ingesting and excreting seeds (e.g. locusts Darwin 1869 p. 439; slugs Gervais *et al.* 1998) are not evidence of mutualism. Although it is worth enquiring whether large invertebrates fill the role of absent rodents in New Zealand, there is no evidence for any mutualistic role in fruit dispersal by weta. This is not surprising given that fruit dispersal worldwide is nearly always dominated by birds, which New Zealand had, and including introduced species still has, in abundance.

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REFERENCES

- Bakr E. M. (2005) A new software for measuring leaf area, and area damaged by *Tetranychus urticae* Koch. *J. Appl. Entomol.* **129**, 173–5.
- Barrett P. (1991) *Keeping Wetas in Captivity: A Series of Nine Articles for Schools and Nature Lovers*. Wellington Zoological Gardens, Wellington.
- Bronstein J. L. (1994) Our current understanding of mutualism. *Q. Rev. Biol.* **69**, 31–51.
- Bronstein J. L. (1998) The contribution of ant plant protection studies to our understanding of mutualism. *Biotropica* **30**, 150–61.
- Bronstein J. L., Alarcon R. & Geber M. (2006) The evolution of plant–insect mutualisms. *New Phytol.* **172**, 412–28.
- Burns K. C. (2006) Weta and the evolution of fleshy fruits in New Zealand. *NZ J. Ecol.* **30**, 405–6.
- Burrows C. J. (1995) Germination behaviour of seeds of the New Zealand species *Fuchsia excorticata*, *Griselinia littoralis*, *Macropiper excelsum*, and *Melicactus ramiflorus*. *NZ J. Bot.* **33**, 131–40.
- Chapman C. A. & Chapman L. J. (1995) Survival without dispersers: seedling recruitment under parents. *Conserv. Biol.* **9**, 675–8.
- Christian C. E. (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* **413**, 635–9.
- Craig J. L., Stewart A. M. & Douglas M. E. (1981) The foraging of New Zealand honeyeaters. *NZ J. Zool.* **8**, 87–91.
- Cushman J. H. & Beattie A. J. (1991) Mutualisms: assessing the benefits to hosts and visitors. *Trends Ecol. Evol.* **6**, 193–5.
- Darwin C. (1869) *On the Origin of Species by Means of Natural Selection, Or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- Duthie C., Gibbs G. & Burns K. C. (2006) Seed dispersal by weta. *Science* **311**, 1575.
- Field L. H. & Sandlant G. R. (2001) The gallery-related ecology of New Zealand tree wetas, *Hemideina femorata* and *Hemideina crassidens* (Orthoptera, Anostomatidae). In: *The Biology of Wetas, King Crickets and Their Allies* (ed. F. L. Field) pp. 243–57. CABI Publishing, Wallingford.
- Fukui A. W. (1995) The role of the brown-eared bulbul *Hypsypetes amaurotis* as a seed dispersal agent. *Res. Popul. Ecol.* **37**, 211–18.
- Gervais J. A., Traveset A. & Willson M. F. (1998) The potential for seed dispersal by the banana slug (*Ariolimax columbianus*). *Am. Midl. Nat.* **140**, 103–10.
- Giladi I. (2006) Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos* **112**, 481–92.
- Godley E. J. & Berry P. E. (1995) The biology and systematics of *Fuchsia* in the south-pacific. *Ann. Mo. Bot. Gard.* **82**, 473–516.
- Keddy P. A. (2007) Animals and seed dispersal. In: *Plants and Vegetation: Origins, Processes, Consequences* (ed. P. A. Keddy) pp. 365–79. Cambridge University Press, New York.
- Kelly C. D. (2006) Movement patterns and gallery use by the sexually dimorphic Wellington tree weta. *NZ J. Ecol.* **30**, 273–8.
- Kelly D., Robertson A. W., Ladley J. J., Anderson S. H. & McKenzie R. J. (2006) The relative (un)importance of introduced animals as pollinators and dispersers of native plants. In: *Biological Invasions in New Zealand* (eds R. Allen & W. G. Lee) pp. 227–45. Springer, Berlin.
- Lengyel S., Gove A. D., Latimer A. M., Majer J. D. & Dunn R. R. (2009) Ants sow the seeds of global diversification in flowering plants. *PLoS ONE* **4**, e5480.
- Lord J. M. (2004) Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. *Austral Ecol.* **29**, 430–6.
- Micheneau C., Fournel J., Warren B. H. et al. (2010) Orthoptera, a new order of pollinator. *Ann. Bot.* **105**, 355–64.
- Morgan-Richards M., Treweek S. A. & Dunavan S. (2008) When is it coevolution? The case of ground weta and fleshy fruits in New Zealand. *NZ J. Ecol.* **32**, 108–12.
- O'Donnell C. F. J. & Dilks P. J. (1994) Foods and foraging of forest birds in temperate rain-forest, South Westland, New Zealand. *NZ J. Ecol.* **18**, 87–107.
- Ordish R. G. (1992) Aggregation and communication of the Wellington weta *Hemideina crassidens* (Blanchard) (Orthoptera: Stenopelmatidae). *NZ Entomol.* **15**, 1–8.
- Pekelharing C. J., Parkes J. P. & Barker R. J. (1998) Possum (*Trichosurus vulpecula*) densities and impacts on fuchsia (*Fuchsia excorticata*) in south Westland, New Zealand. *NZ J. Ecol.* **22**, 197–203.
- Ramsay G. (1978) Invertebrate mice. *NZ Entomol.* **6**, 400.
- Robertson A. W., Ladley J. J., Kelly D. et al. (2008) Assessing pollination and fruit dispersal in *Fuchsia excorticata* (Onagraceae). *NZ J. Bot.* **46**, 299–314.
- Saba S. L. & Toyos A. (2003) Seed removal by birds, rodents and ants in the Austral portion of the Monte Desert, Argentina. *J. Arid Environ.* **53**, 115–24.
- Schupp E. W. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* **108**, 15–29.
- Stanley M. C., Smallwood E. & Lill A. (2002) The response of captive silvereyes (*Zosterops lateralis*) to the colour and size of fruit. *Aust. J. Zool.* **50**, 205–13.
- Traveset A. (1998) Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspect. Plant Ecol. Evol. Syst.* **1**, 151–90.
- Treweek S. A. & Gibb G. C. (2010) Vicars, tramps and assembly of the New Zealand avifauna: a review of molecular phylogenetic evidence. *Ibis* **152**, 226–53.
- Treweek S. A. & Morgan-Richards M. (1995) On the distribution of tree weta in the North Island, New Zealand. *J. R. Soc. NZ* **25**, 485–93.
- Treweek S. A. & Morgan-Richards M. (2000) Artificial weta roosts: a technique for ecological study and population monitoring of tree weta (*Hemideina*) and other invertebrates. *NZ J. Ecol.* **24**, 201–8.
- Treweek S. A. & Morgan-Richards M. (2005) After the deluge: mitochondrial DNA indicates Miocene radiation and Pliocene adaptation of tree and giant weta (Orthoptera: Anostomatidae). *J. Biogeogr.* **32**, 295–309.
- Treweek S. A. & Morgan-Richards M. (2009) New Zealand, biology. In: *Encyclopedia of Islands* (eds R. G. Gillespie & D. A. Clague) pp. 665–73. University of California Press, Berkeley, CA.
- Wheelwright N. T. & Janson C. H. (1985) Colors of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.* **126**, 777–99.
- Williams P. A., Karl B. J., Bannister P. & Lee W. G. (2000) Small mammals as potential seed dispersers in New Zealand. *Austral Ecol.* **25**, 523–32.
- Yagihashi T., Hayashida M. & Miyamoto T. (1998) Effects of bird ingestion on seed germination of *Sorbus commixta*. *Oecologia* **114**, 209–12.