

Seed dispersal effectiveness increases with body size in New Zealand alpine scree weta (*Deinacrida connectens*)

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Abstract Weta are giant, flightless orthopterans that are endemic to New Zealand. Although they are known to consume fleshy fruits and disperse seeds after gut passage, which is unusual among insects, their effectiveness as seed dispersal mutualists is debated. We conducted a series of laboratory experiments on alpine scree weta (*Deinacrida connectens*) and mountain snowberries (*Gaultheria depressa*) to investigate how fruit consumption rates, the proportion of ingested seeds dispersed intact and weta movement patterns vary with weta body sizes. On average weta dispersed 252 snowberry seeds nightly and travelled at a rate of 4 m min⁻¹. However, seed dispersal effectiveness varied over three orders of magnitude and was strongly associated with body sizes. Smaller weta consumed few snowberry seeds and acted primarily as seed predators. On the other hand, the largest weta consumed and dispersed thousands of seeds each night and appear to be capable of transporting seeds over large distances. Overall results indicate that scree weta shift from being weakly interacting seed predators to strongly interacting, effective seed dispersers as they increase in size.

Key words: frugivore, fruit, mutualism, predation, dispersal.

INTRODUCTION

Many types of animals act as seed dispersal mutualists. Birds, bats, primates and reptiles commonly consume fleshy fruits and disperse seeds after gut passage (see Herrera 2002; Thorsen *et al.* 2009). However, New Zealand weta (Anostostomatidae) are arguably the world's most unusual seed disperser. Weta are giant, flightless orthopterans that inhabit a wide variety of habitats in New Zealand (Field 1980). Although endozoochory is rare among insects (de Vega *et al.* 2011), several species of weta are known to consume fleshy fruits and disperse seeds therein (Burns 2006a; Duthie *et al.* 2006; King *et al.* 2011). However, very little is yet known about how weta function as seed dispersers and no previous study has investigated how giant weta (*Deinacrida* spp.) might function as seed dispersers (see Griffin *et al.* 2011).

Although weta are known to function as legitimate seed dispersers, they also depredate seeds in fleshy fruits (King *et al.* 2011). This dichotomy in how weta interact with fleshy-fruited plants has sparked debate over the relative roles weta play as seed predators and seed dispersal 'mutualists' (Burns 2008; Morgan-Richards *et al.* 2008; Wyman *et al.* 2011). All mutualisms incur costs. Mutualistic interactions are rarely (if ever) purely beneficial to both players in the interaction (see Bronstein 2001). Therefore, mortality of some seeds during ingestion does not necessarily

imply the interaction cannot be mutualistic. To begin to address this issue, future work needs to measure relative quantities of dispersal and predation, in addition to how they might vary among individuals.

We conducted a series of laboratory experiments and field observations to investigate intraspecific functional variation in interactions between alpine scree weta (*Deinacrida connectens*) and mountain snowberry (*Gaultheria depressa* Ericaceae). Fifteen animals were captured in the field and housed in laboratory enclosures where they were subject to three experiments. In the first experiment, captive weta were presented with snowberries over several consecutive nights to estimate nightly rates of fruit consumption. In the second experiment, a known number of snowberry seeds were fed to each weta in an artificial food source to quantify relative amounts of seed dispersal and predation. Lastly, each animal was placed in a large arena and allowed to roam freely to quantify their movement rates and estimate potential seed dispersal distances. Results were then used to determine whether alpine scree weta are best classified as seed predators or seed dispersers and to document how the sign and strength of interactions with snowberries vary with weta body size.

MATERIALS AND METHODS

Study site and species

Weta are a group of flightless, nocturnal orthopterans that are among the largest insects in the world. There are four

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phylogenetic lineages of weta in the family Anostomatidae in New Zealand, including tussock, giant, tree and ground weta (Trewick 2001; Pratt *et al.* 2008). Alpine scree weta (*D. connectens*, 'scree weta' from here on, see Appendix S1) belong to the giant weta clade and live exclusively at high altitudes above the tree line on the South Island of New Zealand (Gibbs 2001). Scree weta are adapted to cope with subfreezing temperatures (Sinclair 1999), which they are exposed to regularly. They are sexually dimorphic, with females being larger in size than males at maturity, inhabit sparsely vegetated scree slopes and roost diurnally in hollows under rocks or in shallow crevices (Field 1980). Although few studies have investigated the diets of giant weta directly, they appear to be primarily vegetarian (McIntyre 2001).

All data were collected in Nelson Lakes National Park, South Island, New Zealand in April 2010. Field samples were collected from shallow, mobile rock surfaces (i.e. scree slopes) just above of the tree line on Mt Robert (41°49'S 172°48'E) at an elevation of approximately 1450 m. Fifteen alpine scree weta (*D. connectens*, Appendix S1) were captured, placed in small plastic containers and transported down-slope into laboratory conditions located at the base of the mountain (41°48'S 172°50'E). All animals were located under large, isolated rocks (typically 20–40 cm in diameter) sitting on top of sparsely vegetated scree slopes or fine-grained soils. Upon arrival in the laboratory, weta were transferred individually into larger plastic enclosures (18 × 18 × 9 cm) that were lined with moist cloth. Subjects were offered fresh carrots to eat daily and leafy, fruitless branches of *Gaultheria antipoda* for cover.

After capture, each weta was sexed and its body size was characterized by measuring both its length (the distance between the apex of the pronotum to the posterior of the last abdominal segment to the nearest millimetre) and body mass (weight to the nearest milligram with an electronic scale). Eight weta were females, six were males, and one was too young to be sexed accurately. All were housed in laboratory conditions for no longer than a month and they were returned to the exact position that they were found at the completion of the experiments. No animals died in captivity and most gained weight during their period of captivity.

Mountain snowberry (*G. depressa*) is a common prostrate shrub that is distributed throughout New Zealand in montane regions (500 m–1500 m elevation). It attains a maximum height of 10 cm and produces fleshy fruits that are 1–2 cm in diameter and have a somewhat unusual morphology. At maturity, the sepals of snowberry flowers enlarge to function as fruit pulp and are coloured white, red or sometimes pink. Swollen sepals engulf the ovary, which is dry, occasionally dehiscent and contains hundreds of seeds that measure 0.40–0.65 mm. Snowberries are usually produced underneath the leaf canopy within the leaf litter below, severely hampering their detection from above. At our site, snowberry plants typically grow around the fringes of large rocks surrounding scree slopes. Several hundred snowberries were collected haphazardly from the general vicinity of where scree weta were collected for laboratory experiments.

Seed dispersal 'effectiveness' refers simultaneously to both the 'quantity' and 'quality' of seed dispersal services provided by frugivores (see Schupp *et al.* 2010 for a recent discussion). Seed dispersal 'quantity' refers to the number of seeds dispersed from parent plants. Seed dispersal 'quality' refers to

the probability seeds will successfully recruit into adult plant populations. The 'quality' component of seed dispersal is rarely quantified fully and instead one or a few aspects of this component are quantified. In this study we investigate a key component of seed dispersal quality – the movement patterns of seed consumers – which is a primary determinant of the distances over which seeds are deposited.

Field observations

Two analyses were conducted to determine whether wild populations of scree weta consume snowberries and act as legitimate seed dispersers. First, all excrement ('scat' from hereafter) produced by weta captured for experiments was thoroughly searched for intact snowberry seeds, which are easily identifiable by their size, shape and colour. After 3 days on a laboratory diet of carrot, all evidence of snowberries in scat had disappeared.

Second, during field searches for scree weta to participate in laboratory experiments, all weta scats that were encountered fortuitously were collected. All were found along the margins of larger rocks sitting on top of scree slopes, which were turned over to find roosting weta. Whitaker (1987) suggested that these sites might be especially suitable for seedling establishment in arid or exposed environments (see also Wotton 2002). Weta scats are easily identifiable by their distinctive cylindrical shape with blunted ends and white lateral serrations. All scats that could not be confidently attributed to weta were ignored. Burns (2006a) documented that a species of ground weta (*Zealandosandrus maculifrons*) also disperses snowberry seeds on Mt Robert. However, this species is far rarer and is found in different types of habitat (e.g. tussock grasslands). We have yet to encounter any other species of weta at this study site. The contents of all scats were carefully inspected under a dissection microscope and the total number of *G. depressa* seeds in each was counted.

Fruit consumption experiment

To quantify the strength of interactions between scree weta and mountain snowberries, we conducted a simple fruit consumption experiment. Three snowberries were randomly selected from the pool of snowberries collected from the field and offered to captive weta simultaneously over a 48-h period. Individual enclosures were manually inspected every 4 h for evidence of fruit consumption. Each fruit was placed into one of three categories based on levels of seed consumption. Fruits were categorized as unconsumed if no seeds were ingested. They were classified as completely consumed if >90% of the seed capsule was ingested. Fruits were classified as half-consumed when 50–90% of the seed capsule was consumed. All seed capsules used in the experiment were either completely unconsumed, 50–90% consumed or >90% consumed. None could be classified as 1–50% consumed. These categories were based solely on seed consumption; if the fleshy sepals were completely consumed, but the seed capsule remained untouched, it was classified as unconsumed. Once a fruit was categorized as completely consumed, any remaining pieces of fruit were

removed, and the consumed fruit was replaced by another randomly selected fruit. To test whether fruit consumption rates varied with weta body length, we conducted a simple linear regression (SPSS Inc. 2008) using the total number of fruits consumed by each captive weta as the dependent variable and weta body length as the independent variable. The dependent variable was natural logarithm-transformed to conform to test assumptions.

Seed passage experiment

To quantify amounts of seed dispersal and predation after seed consumption, we fed a known number of snowberry seeds to each captive scree weta in an artificial food source. Twenty intact snowberry seeds were extracted from ripe fruits and fed to each captive weta in a small portion of cheese (approximately 3 mm in diameter). Once consumed, enclosures were thoroughly checked for dislodged (unconsumed) seeds by wiping a clean, damp paper towel over the bottom and sides of the enclosures, which was then examined under a dissection microscope. All objects aside from the artificial food source were removed prior to the start of the trials and weta were given carrots *ad libitum* for consumption and fruitless *G. antipoda* branches for shelter afterwards. All scat produced after the artificial food source was consumed was collected, examined under a dissection microscope, and all intact snowberry seeds were counted. Four days after the resumption of carrot diets, all traces of cheese disappeared from their excrement and trials were considered complete. Consumption rates varied among weta. Some took only a few seconds to find and consume the cheese, while others took up to 30 h. Four weta did not consume all 20 seeds during the trial (10, 10, 14 and 12 seeds respectively). For these subjects, proportions of intact seeds dispersed were taken from the number of seeds that were consumed. Because seeds used in this experiment were extracted from pulp and placed in an artificial food source, the effects of fruit pulp on seed passage and survival were not investigated.

To test whether the proportion of seeds dispersed intact varied with weta body length, we conducted a simple linear regression. The proportion of consumed seeds that were voided intact by each captive weta was used as the dependent variable and weta body length was used as the independent variable. The dependent variable conformed to test assumptions without transformation.

Seeds were judged to be dispersed successfully if their seed coats were completely intact and they showed no signs of damage. Damage to seeds during consumption is often conspicuous (see King *et al.* 2011) and seeds with any signs of potential damage were considered depredated. To test whether our estimates of seed viability were accurate, we collected 20 seeds that were judged to be intact after being consumed by weta and subjected them to a staining procedure using 2,3,5-triphenyl tetrazolium chloride (de Souza *et al.* 2010, see also de Vega *et al.* 2011 for a detailed description of the technique). Nineteen showed clear evidence for enzymatic activity following gut passage, so our judgements of seed viability after gut passage appeared to be reasonably accurate.

To estimate total amounts of seed dispersal for each captive animal, we amalgamated results from the fruit con-

sumption and seed passage experiments. First, we multiplied average nightly fruit consumption rates by the average number of seeds contained in each snowberry. These values were then multiplied by the proportion of ingested seeds that were excreted intact. Estimates of seed numbers were obtained by dissecting 15 randomly selected fruits from the total pool collected for the experiment. Simple linear regression was then used to determine whether the total numbers of seeds dispersed varied among weta according to their body size. The total number of seeds dispersed by each captive weta was used as the dependent variable and weta body length was used as the independent variable. The dependent variable was natural logarithm-transformed to conform to test assumptions.

Movement experiment

To estimate potential seed shadows produced by scree weta, we conducted a simple experiment to quantify the distances scree weta travel in 30 s. Scree weta were removed from their enclosures individually and placed in the centre of an empty, darkened room and allowed to roam freely. The experimenter followed subjects with a red light headlamp to minimize intrusion and landmarks were used to mark the path each animal travelled. After 30 s, trials were halted and subjects were returned to their enclosures. A flexible tape measure was then used to measure the total distance travelled. All weta were subject to three separate trials that were conducted on consecutive nights at 3.00–4.00 hours. Movement rates (m s^{-1}) were then calculated for each trial, which were then averaged prior to analyses.

The rate at which seeds pass through the digestive system of weta was not measured. Therefore, the number of seeds deposited over different distances could not be estimated. In addition, because animals might behave differently under laboratory conditions, results from this experiment are best viewed as coarse approximations of nightly movement patterns.

To test whether movement rates varied with weta body length, we conducted a simple linear regression. The average movement rate of each captive weta was used as the dependent variable and weta body length was used as the independent variable. The dependent variable conformed to test assumptions without transformation.

RESULTS

Captured scree weta varied strongly in body size. Subjects measured between 1.20 and 5.06 cm in length and weighed between 0.13 and 9.97 g. Mass and length measurements were strongly correlated ($R = 0.949$, $P < 0.001$), which resulted in virtually identical statistical results using body mass and body length. We therefore present results of analyses using body length only for brevity.

Field observations indicated that scree weta frequently interact with snowberries. The 15 field-caught weta excreted a total of 1945 intact seeds after being

captured. Although all 15 weta showed evidence of snowberry consumption (e.g. seed fragments and pieces of fruit epidermal tissue), the proportions of seeds dispersed intact varied markedly among individuals. Three weta did not pass any intact seeds, while a single individual passed 686 intact seeds. Additional analyses of the 40 scats collected directly from the field also showed widespread evidence for seed consumption and dispersal (Fig. 1). A total of 4587 intact mountain snowberry seeds were found, but seed numbers varied markedly among scats. Six contained no seeds, 14 contained less than 50 seeds, and the remainder each contained hundreds of seeds.

Results from the fruit consumption experiment showed that scree weta ate an average of two snowberries nightly. However, fruit consumption rates (i.e. interaction strengths) varied markedly among individual weta (Fig. 2A). Interaction strengths increased with the weta body lengths, which accounted for over 80% of nightly variation in fruit consumption rates ($R^2 = 0.834$, $P < 0.001$).

The seed passage experiment showed that scree weta function as both seed predators and seed dispersers. An average of $31.95\% \pm 7.73$ SE of ingested seeds were excreted in apparently viable condition over the course of the experiment. However, the fraction of seeds dispersed varied markedly among individual weta (Fig. 2B). Over 60% of the variation in successful seed passage could be explained by body length ($R^2 = 0.609$, $P < 0.001$), with large weta functioning primarily as seed dispersers and small weta functioning primarily as seed predators.

Seed counts in 15 naturally occurring snowberries showed that fruits contained an average of 279.67 seeds (± 12.64 SE). Combining seed counts with nightly fruit consumption rates and the proportion of

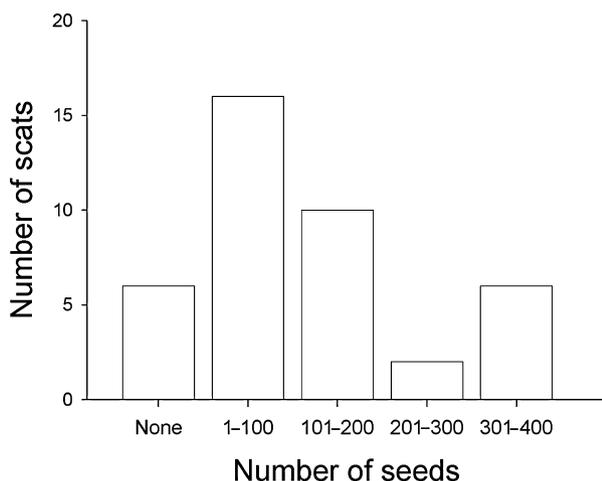


Fig. 1. Number of snowberry seeds found in 40 scree weta scats collected in Nelson Lakes National Park, South Island, New Zealand. A total of 4587 seeds were found.

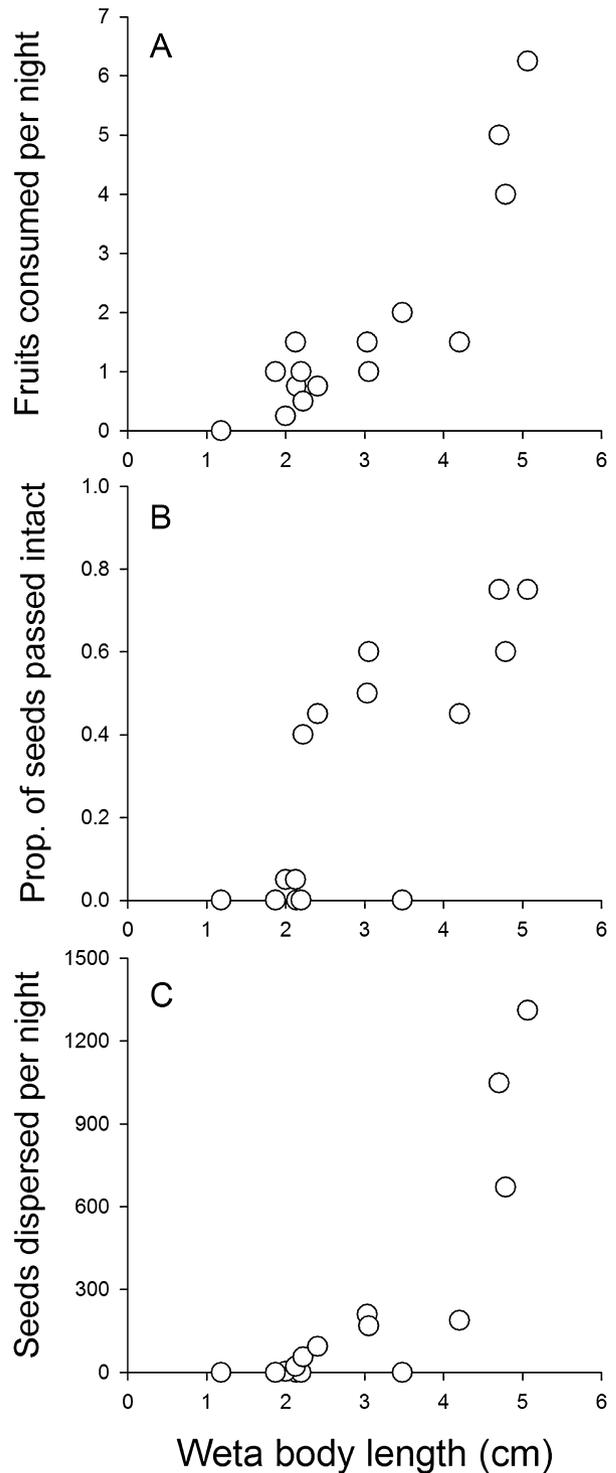


Fig. 2. Relationships between the body size of 15 scree weta and (A) the average number of snowberries consumed per night, (B) proportion of consumed seeds that were passed intact, and (C) extrapolated numbers of seeds dispersed by scree weta per night (nightly fruit consumption rates \times average number of seeds per fruit \times proportion of seeds passed intact).

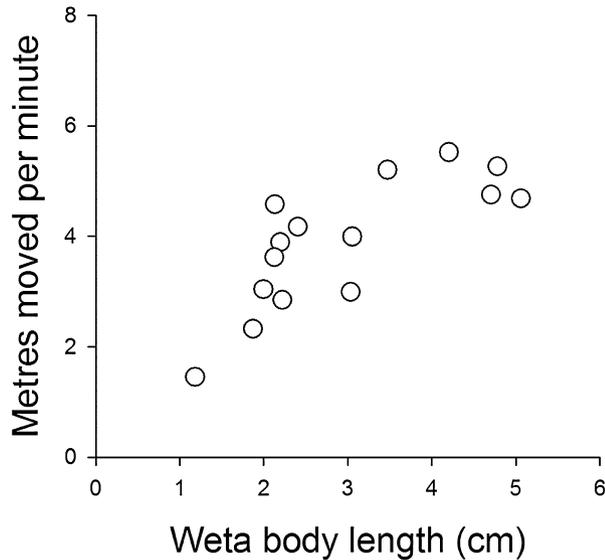


Fig. 3. Relationship between scree weta body size and the average distance (m) weta moved per minute under laboratory conditions.

seeds dispersed intact, a clear relationship emerged between seed dispersal and weta body length ($R^2 = 0.594$, $P < 0.001$). Although weta dispersed on average 251.5 ± 107.8 SE seeds nightly, the largest weta dispersed thousands of snowberry seeds on a nightly basis, while smaller weta dispersed few or no seeds successfully (Fig. 2C).

Results from the weta movement experiment showed that subjects moved an average of 4 m min^{-1} in laboratory conditions (Fig. 3). However, the distances travelled by weta varied strongly with their body length ($R^2 = 0.598$, $P < 0.001$), with larger weta travelling over larger distances than smaller weta. Animals that move over larger distances can potentially disperse seeds over larger distances, suggesting that larger weta may produce larger seed shadows than smaller weta.

DISCUSSION

The effectiveness of scree weta as seed dispersers varies dramatically with their body size. Smaller weta interact with snowberries only weakly and the few seeds they ingest are often depredated. On the other hand, larger weta consume hundreds of seeds nightly, the majority of which are voided intact. Larger weta also move more rapidly than smaller weta, suggesting they might disperse seeds over larger distances. Overall results therefore indicate that scree weta are legitimate seed dispersers and they become increasingly effective seed dispersers as they grow in size during ontogeny.

Although these results indicate that scree weta are effective seed dispersal mutualists, most of our data

were collected in the laboratory and scree weta might behave differently in the wild. All of the animals that we collected from the field consumed snowberries prior to their capture and most excreted hundreds of intact snowberry seeds after arrival in the laboratory. Hundreds of intact seeds were also recovered from scat collected in the field. Therefore, snowberry frugivory and seed dispersal is common in scree weta, suggesting that results from our experiments are likely to be at least broadly indicative of their behaviour in the field.

Body size in scree weta varies as a function of age (instar) and sex. They also increase substantially in size during ontogeny and exhibit reversed sexual size dimorphism, with females attaining much larger sizes than males. Because seed dispersal effectiveness increases with body size, females are likely to be more effective seed dispersers than males. However, we did not investigate the effects of sex per se on seed dispersal. The reason for this is that during exhaustive field searches we were unable to find specimens to fully cross sex and size in our experiments as in King *et al.* (2011). We therefore investigated the effects of body size and seed dispersal effectiveness more generally and additional work is needed to pinpoint how dispersal effectiveness varies with weta size and sex independently. Larger overall sample sizes (i.e. >15 individuals) were desirable, but we were unable to find additional specimens for these experiments. Strong relationships between weta body size and seed dispersal processes were nevertheless readily apparent with limited sample sizes.

Partitioning variation in dispersal effectiveness to size and sex has important implications for seed dispersal distances. Males and females of other species of weta are known to exhibit different movement patterns (see Kelly 2006; Watts *et al.* 2011 and references within). For example, Watts and Thornburrow (2011) found that a forest-dwelling species of giant weta (*Deimacrida heteracantha*) was quite mobile, with males moving across greater distances than females (16 vs. 8 m per night, respectively). Our estimates of movement patterns were collected over a short period of time in laboratory conditions and therefore provide only coarse estimates of potential seed dispersal distances. They also do not consider seasonal, ontogenetic or sex-based changes in movement patterns, in addition to gut retention times of seeds, which have an additional effect on seed dispersal distances. Future radio tracking studies could be combined with gut retention times to estimate seed dispersal kernels more precisely.

Our results parallel several other recent studies that investigated interactions between Wellington tree weta (*Hemideima crassidens*) and tree fuchsia (*Fuchsia excorticata*). King *et al.* (2011) found that tree weta become increasingly effective seed dispersers as they grow in size. However, they found a lower average estimate of realized dispersal (14% of ingested seeds

germinated after gut passage). They also found that seed dispersal potential differed between the sexes. King *et al.* (2011) attributed differences in the proportion of apparently viable seed passed intact to differences between the sexes and among different-sized animals to size of their mouth parts and cibarium (i.e. the space anterior to the mouth where food items are chewed). However, in *Hemideina* spp. sexual size dimorphism is reversed relative to *Deinacrida*, with males being larger than females.

In a similar study on interactions between Wellington tree weta and tree fuchsia, Wyman *et al.* (2011) documented similar results to King *et al.* (2011). However, they arrived at very different conclusions concerning the effects of weta frugivory on plant fitness. Although Wyman *et al.* (2011) did not investigate how interactions varied with weta body sizes, they argue that frugivory by weta is best viewed as opportunistic foraging. Tight coevolutionary dynamics like those displayed by some pollination mutualisms (e.g. figs and fig wasps; see Pellmyr 2002) have never been documented in seed dispersal mutualisms (Herrera 2002). Rather 'diffuse' interactions between fruits and frugivores are commonplace, and species within broad groups of frugivores often interact interchangeably (Zamora 2000). There is good evidence that species within taxonomic groups of effective seed dispersers (e.g. song birds) forage for fruit opportunistically (Herrera 1998; Burns 2006b), clearly indicating that opportunistic foraging by frugivores does not preclude the development of effective mutualistic interactions. However, because other fruit consumers (e.g. birds, lizards) do not depredate seeds frequently, it does seem reasonable to predict that weta might be less effective seed dispersers, all else being equal.

Wyman *et al.* (2011) argue that because weta destroy seeds during consumption, they are not effective mutualists (see also Morgan-Richards *et al.* 2008). However, seed predation does not necessarily preclude mutualistic interactions between frugivores and fleshy fruits. Plants often 'pay' for the dispersal of seeds with other seeds, instead of fruit pulp (Janzen 1984, see also Vander Wall 2001). Therefore, the existence of seed predation does not necessarily imply that plant-animal interactions are not mutualistic. Furthermore, Wyman *et al.* (2011) hypothesize that plant species whose seeds are dispersed by weta should have comparatively palatable leaves, implicitly assuming that plants can 'pay' for weta seed dispersal in leaves (i.e. the 'foliage is the fruit' *sensu* Janzen 1984). Why the same logic is not applied to seeds is unclear.

Wyman *et al.* (2011) also investigated seed deposition patterns. They found that weta often defecate in the vicinity of their roosts, and thereby conclude that weta are unlikely to be effective seed dispersers. However, seed dispersal in close proximity to tree weta

roost sites is not necessarily disadvantageous. Tree weta roost in cavities that commonly occur in older or dead-standing trees that are likely to be associated with tree fall gaps in both space and time, and tree fall gaps are often beneficial for plant recruitment in forested environments. Therefore, even when weta move over limited areas, they could direct seed dispersal to sites that are beneficial for plant recruitment.

Seed germination is often enhanced after ingestion by dispersers (Traveset 1998; Traveset *et al.* 2007). We did not investigate seed germination behaviour explicitly (as in Morgan-Richards *et al.* 2008; Wyman *et al.* 2011). Therefore, our estimates of seed dispersal may not accurately reflect subsequent patterns in seed germination. Few studies to date have investigated the effects of weta ingestion on seed germination (only Duthie *et al.* 2006; King *et al.* 2011), so how weta affect seed physiology and germination behaviour is worthy of greater attention. Furthermore, field exclusion experiments could be conducted to determine differences in dispersal potential of scree weta, birds and lizards, and direct observations of fruit consumption and dispersal could also be made.

de Vega *et al.* (2011) recently documented endozoochory by a European beetle, which disperses the seeds of a root parasitic tree (*Cytinus hypocistis*). They argue that the beetle is an effective seed dispersal mutualist, because it often deposits viable seeds below ground in close proximity to subtle hosts. Results reported here indicate that scree weta function similarly and likely have a net positive effect on snowberry reproductive fitness. When viewed jointly with results obtained by de Vega *et al.* (2011), results from this study suggest that insect endozoochory could be far more common than previously suspected.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Images of scree weta and mountain snowberry.