

Body size determines rates of seed dispersal by giant king crickets

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Abstract New Zealand is home to giant king crickets called weta, which are the only insects known to consume fleshy-fruits and disperse seeds after gut passage. Although they disperse seeds in viable condition after consumption, their importance as seed dispersers is unknown. We conducted a series of field observations and laboratory experiments to investigate intraspecific variation in the capacity of Wellington tree weta (*Hemidenina crassidens*) to disperse seeds of tree fuchsia (*Fuchsia excorticata*). We asked three questions. How frequently do weta disperse fuchsia seeds? Do seed passage rates differ between sexes and different-sized weta? Might weta select for particular seed sizes via differential seed mortality after ingestion? A total of 2,272 *F. excorticata* seedlings germinated from 241 scats (i.e., faecal pellets) that were collected from the field. Experimental results showed that, on average, 15% of seeds ingested by weta successfully germinated, whereas 75% germinated in control trials. Larger weta dispersed greater numbers of seeds in experimental trials, while no differences in dispersal rates were observed between sexes. Regardless of sex and size, weta preferentially dispersed larger seeds. When interpreted collectively, results indicate that (1) weta are frequent seed dispersers of *F. excorticata*, although many seeds are destroyed during ingestion, (2) larger-bodied weta consistently disperse greater quantities of seeds, which is unusual in seed dispersal mutualisms, and (3) weta preferentially disperse larger seeds, suggesting that they might interact evolutionarily with New Zealand plants.

Keywords Coevolution · Fleshy-fruits · Frugivore · Mutualism · New Zealand · Weta

Introduction

Seed dispersal mutualisms are markedly unspecialised (Herrera 1985, 2002a; Jordano 1987; Fuentes 1995). Individual species of fleshy-fruited plants rarely possess attributes that elicit special treatment by particular species of frugivorous animals (Herrera 1998; Levey and Benkman 1999; Herrera 2002b; Burns et al. 2009; but see Moran et al. 2004). Frugivorous animals rarely show consistent preferences for particular fruit traits and often consume fruit indiscriminately (e.g., Whelan and Willson 1994; Traveset et al. 2001; Burns 2006a; Burns et al. 2009; but see Carlo et al. 2003). Therefore, the ecological precursors of more specialised coevolutionary relationships between species pairs of fruits and frugivores, such as those displayed by some pollination mutualisms (e.g., figs and fig wasps; see Cook and Rasplus 2003), are rarely observed.

Specialised relationships between fruits and frugivores can arise on coarser taxonomic scales, between broad ‘guilds’ of fruits and frugivores (Gautier-Hion et al. 1985; Lord 2004; Hollander and Vander Wall 2009; but see Fischer and Chapman 1993). For example, birds and bats interact with fleshy-fruits in very different ways, due to differences in how they locate fruits and treat seeds during ingestion (Korine et al. 2000). Bats forage at night and use olfactory and echolocation cues to locate fruits, while birds are diurnal and use visual cues. Birds also swallow fruits whole, while bats chew fruit prior to ingestion. Correspondingly, broad guilds of fruits can be distinguished that correspond with bird and bat consumption. For example, bird-dispersed figs (*Ficus* spp.) tend to be small, odourless

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and coloured red or black, while bat-dispersed figs are larger, scented and are either green or yellow (Lomáscolo et al. 2008). Yet within these coarse taxonomic guilds, species may often be functionally equivalent and interact interchangeably (Zamora 2000; Burns 2006a).

Birds and mammals (e.g., bats, bears and primates) are common frugivores. However, other frugivores, most notably reptiles, are often important seed dispersers on isolated islands (Wotton 2002; Traveset and Riera 2005). Comparatively little is known about seed dispersal by reptiles, but they may be responsible for a range of unusual fruit traits possessed by plant species that are endemic to isolated islands (see Olesen and Valido 2003). For example, in New Zealand, many plant species produce translucently-coloured fruits within the interior of ‘wire-plants’, which display a distinctive, right-angled branching habit that results in an overall matted appearance (Christian et al. 2006; Bond and Silander 2007). Fruits that are produced within the inner recesses of wire-plants are not easily accessible to birds, which are the primary seed dispersers in New Zealand (Burns 2009; Emeny et al. 2009; Kelly et al. 2010). So this unusual suite of fruit traits may have evolved in response to reptile dispersers (Lord and Marshall 2001). However, recent research has identified another group of small, flightless frugivores that may also be responsible for the unusual characteristics of fleshy-fruits in New Zealand.

Weta are a group of large-bodied Orthopterans that occupy a range of environments throughout New Zealand (Field 2001). Many species of weta are nocturnal and live in tree canopies where they feed on a wide range of food items, including other invertebrates, plant matter (e.g., leaves, flowers and fruits) and carrion (Gibbs 2001). Given the ecological similarities between weta and small mammals inhabiting other parts of the world, and that New Zealand lacks native mammals (except for two species of bat), weta are sometimes referred to as New Zealand’s ‘invertebrate mice’ (see Duthie et al. 2006).

Fruits and seeds are commonly consumed by small mammals. Although they often destroy seeds, small mammals can also form mutualistic associations with plants as seed dispersers (Amico and Aizen 2000; Williams et al. 2000). Therefore, if weta are truly ecological replacements for small mammals in New Zealand, they should consume fleshy-fruits and interact with plants as both seed dispersers and seed predators. Duthie et al. (2006) tested this hypothesis and found that weta do indeed interact with fleshy-fruits in a similar way to small mammals. Weta consume a wide range of fleshy-fruited plant species, and although seeds of many species were either avoided or destroyed, some species were dispersed in viable condition after gut passage. Consequently, the unusual characteristics of many New Zealand fruits could be coevolutionary adaptations to weta in addition to reptiles (Burns 2006b).

However, very little is known about seed dispersal by weta (Burns 2008; Morgan-Richards et al. 2008). Previous work has focused on laboratory fruit choice experiments, so frequencies of seed dispersal by wild populations of weta are largely unknown. Weta are also strongly sexually dimorphic and they change enormously in size during ontogeny, but how seed dispersal processes vary between sexes and among different-sized individuals remains explored.

We conducted a series of field observations and laboratory experiments to investigate intraspecific variation in the capacity of New Zealand weta to disperse seeds contained in fleshy fruits. First, we collected hundreds of scats produced by wild Wellington tree weta (*Hemideina crassidens*) in a protected forest reserve on New Zealand’s North Island and quantified how frequently they disperse the seeds of tree fuchsia (*Fuchsia excorticata*). Next, we housed 32 Wellington tree weta in laboratory enclosures and fed 25 *F. excorticata* seeds of known size to each of them in feeding trails. Subsequent germination experiments were conducted to quantify how frequently weta dispersed seeds in a viable condition and to determine whether they preferentially disperse different-sized seeds. Results were used to test four hypotheses: (1) weta frequently disperse *F. excorticata* seeds under natural field conditions, (2) males and larger weta disperse more seeds than females and smaller weta, (3) smaller seeds are more likely to survive gut passage and later germinate, and (4) seed size filters during ingestion are stronger in females and smaller weta.

Materials and methods

Field observations

All field observations were conducted in the Karori Wildlife Sanctuary (KWS), which is located on the southern tip of the North Island of New Zealand (41°18.3’S, 174°44.8’E). The area experiences a mild, temperate climate, with annual rainfall averaging 1,270 mm and an average maximum daily temperature of 16°C. The vegetation is classified as coastal broadleaf–conifer forest, which is dominated by evergreen trees, tree ferns and vines (Dawson 1988; Wardle 2002). The area was cleared for agriculture in the late nineteenth century, but then abandoned approximately 100 years ago, so is still undergoing succession (Blick et al. 2008).

The Wellington tree weta (*Hemideina crassidens*) is one of only a few large, native animal species that occurs in substantial numbers outside areas undergoing extensive control of invasive predators. They are large (approximately 40 mm long), nocturnal and feed on plants, insects and carrion. They are strongly sexually dimorphic (males are larger than females) and both sexes moult up to ten

times as they grow to maturity. This species was present in KWS at the time the fence was built, and in the absence of predatory mammals, its numbers have increased substantially. Tree fuchsia (*Fuchsia excorticata*, Onagraceae) is a common tree species in KWS. It can grow to over 10 m tall at maturity and commonly occurs along valley bottoms in close proximity to small streams. It produces purple, oblong fleshy-fruits that are 20 mm long and 10 mm wide, which typically contain hundreds of small seeds (approximately 0.6 mm), at the beginning of the Austral summer (Robertson et al. 2008). Previous feeding trials have shown that captive Wellington tree weta consume *F. excorticata* fruits and pass their seeds in germinable condition after ingestion (Duthie et al. 2006).

To evaluate how frequently wild Wellington tree weta might disperse *F. excorticata* seeds, we collected their scats along a footpath at the bottom of small stream that traverses approximately 1 km of gently sloping terrain in KWS. This footpath was chosen because it contains numerous wooden platforms and bridges that facilitate searches for weta scats, and because it is located under the canopy of mature fuchsia trees. Scat produced by *H. crassidens* has a distinctive appearance. They are approximately 10 mm long and 5 mm wide and have conspicuous lateral serrations, which enabled us to unambiguously attribute each scat to *H. crassidens*. All scats that could not be unambiguously attributed to *H. crassidens* were ignored. The wooden sections of the path were searched approximately every other day for a period of 28 days during peak fruit production in *F. excorticata*, between December 18, 2008 and January 16, 2008. All scats that could be located by eye while traversing wooden bridges along the footpath were collected.

Spencer (1995) showed that larger (later instar) weta produce larger scats. To test whether larger weta might disperse greater numbers of seeds, the length of all scats collected from the field was measured with vernier callipers. Each scat was then moistened with water and spread evenly across the bottom of a 90-mm-diameter Petri dish lined with filter paper. A light microscope was then used to search for the presence of seeds and other plant propagules. Afterwards, Petri dishes were placed under PAR wavelength fluorescent lamps ($209 \pm 11 \mu \text{ moles m}^{-2} \text{ s}^{-1}$) set to a 15:9-h diurnal light/dark cycle for a duration of 28 days at room temperature. Samples were inspected daily and all germinated seedlings, which we defined by the presence of a radical and two, fully-expanded cotyledons, were counted and then removed. To test whether larger weta disperse more seeds, we tested for a positive relationship between the number of seedlings emerging from each scat and scat size. We used a non-parametric Spearman's rank correlation test because data could not be transformed to conform to normality.

In addition to determining the total number of germinating seedlings from each scat, we also tested whether the frequency distribution of seedling numbers followed the Poisson distribution using a chi-squared goodness-of-fit test. The Poisson distribution characterises the distribution of rare, random events (see Sokal and Rohlf 1995). Therefore, if the distribution of the number of seedlings germinating from each scat follows the Poisson distribution, it would suggest that seed dispersal by weta is an infrequent, stochastic phenomenon.

Laboratory experiment

To investigate seed passage rates and to test whether weta preferentially disperse different-sized seeds, we conducted laboratory feeding trials on 32 Wellington tree weta that were collected from the field. Each individual was housed separately in small plastic enclosures ($20 \times 20 \times 10$ cm) throughout the duration of the experiment. When they were not participating in feeding trials, they were given fresh leaves of several native plant species (*Coprosma repens*, *Melicytus ramiflorus* and *Macropiper excelsum*) and pieces of carrot (*Daucus carota*) for sustenance. Enclosures were located next to a series of large glass windows that provided indirect access to natural light conditions. Enclosures were housed in laboratory conditions with an average temperature of 20°C and an average relative humidity of 10 g/m³.

We used a simple experimental design to evaluate seed passage rates and seed dispersal filters during ingestion. First, 25 *F. excorticata* seeds were extracted from fleshy-fruits obtained from the field. The length of each seed (longest linear distance) was measured using a binocular microscope. After measurement, seeds were placed at the centre of a 0.15-g portion of store-bought cat food. Cat food was used as a medium to feed seeds to weta, because it is a preferred food item (G. Gibbs, personal communication). Portions of cat food containing *F. excorticata* seeds were placed in small, shallow Petri dishes within each weta enclosure, so that unconsumed food could be easily be located. Weta were fed only carrot for 2 days prior to experiments to help facilitate seed identification. All scats produced before the experiment began were removed from enclosures prior to the start of trials. Food was presented to all individuals at the same time and all enclosures were thoroughly searched for faecal material daily. Preliminary trials indicated that newly consumed food items typically passed through weta within 3 days of consumption. Therefore, we continued to collect faecal material from each individual for 5 days following cat food consumption, in an attempt to insure that all seeds were located. All subsequently produced scats were extracted from enclosures and thoroughly searched under binocular

microscope for intact seeds. Once located, seeds were re-measured and then placed individually on moist filter paper under the same PAR wavelength fluorescent lamps used in previous germination trials.

The majority of the weta consumed the entire portion of food and the associated seeds within 24 h. If the seed-containing cat food was not all consumed after three nights, it was removed and uneaten seeds were counted, measured and omitted from analysis. Individuals that failed to eat a majority of the seeds offered were excluded from analyses. To establish germination rates of undigested seeds, six replicates of 25 seeds were extracted from fruit pulp and placed in cat food for three nights. Seeds were then assigned to Petri dishes and placed under the same light conditions. All germination trials lasted for 30 days.

Of the 32 weta used in the experiment, 16 were male and 16 were female. Each sex was represented by 8 large weta and 8 small weta. Collectively, large weta (4.47 ± 0.34 g) were heavier than small weta (3.04 ± 0.44 g). The experiment therefore had two factors (sex and size), each with two levels (males vs female, large vs small). However, one large female, one small female and one small male refused to eat the cat food containing the seeds, leading to a total sample size of 29 for analyses of the seed passages. An additional large female, small female and small male failed to pass seeds intact. This further reduced the sample size of weta in the seed size selection experiment to a total of 26.

A general linear model was used to test the hypothesis that males and larger individuals passed more germinable seeds. Percent seed germination was treated as a dependent variable. Sex (male vs female) and size (small vs large) were both considered fixed-factors. The dependent variable was ln-transformed to conform to homoscedasticity assumptions prior to analyses.

A series of general linear models was used to test the hypothesis that females and smaller individuals have stronger digestive filters for smaller seeds. As with the previous analysis, sex (male vs female) and size (small vs large) were both considered fixed-factors. However, two dependent variables were assessed in separate analyses. First, differences in seed sizes following ingestion (average seed length following gut passage minus average seed length prior to consumption) was used as a coarse estimate of seed size selection following gut passage. While this metric is advantageous because of its simplicity, it does not contain information regarding variability in the size of seeds in each sample. To account for the variance of seed size distributions before and after ingestion, we calculated t values for the difference in the size of seed populations entering and leaving weta. Negative values of both metrics indicate preferential treatment of smaller seeds, while positive values indicate preferential treatment of larger

seeds. Both dependent variables were ln-transformed to conform to homoscedasticity assumptions prior to analyses.

While general linear model analyses investigate differences seed size preferences between different sexes and sizes of weta, it does not evaluate overall digestive filters for particular seed sizes, regardless of sex or size. To test the hypothesis that weta generally disperse greater numbers of smaller seeds, we tested whether the difference between final and initial average seed sizes differs from zero using a single sample t test. A second single-sample t test was conducted on t values.

Results

A total of 2,272 *Fuchsia excorticata* seeds germinated from weta scats collected from the field. Of the 241 scats obtained, 171 contained no seeds and instead contained shredded leaf material and invertebrate exoskeleton. However, the remainder often contained large numbers of seeds, leading to an average of 9.43 ± 25.05 SD seedlings per scat. The distribution of seedlings per scat did not follow the Poisson distribution ($\chi^2 = 27.552$, $P < 0.001$) because there were many more scats than expected with no seeds and many more scats than expected with large numbers of seeds (Fig. 1). The number of seeds that germinated from each scat also increased with scat size ($r_s = 0.254$, $P < 0.001$), suggesting that bigger weta disperse greater quantities of seeds than smaller weta (Fig. 2).

During the course of our field observations, we observed several other types of plant propagules in scats collected

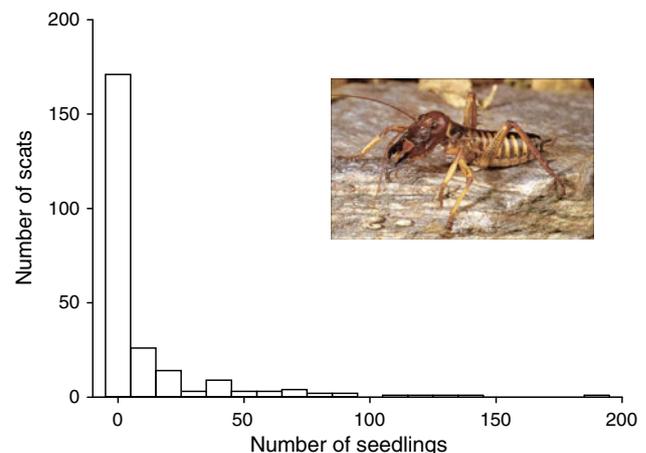


Fig. 1 Frequency distribution of the number of *Fuchsia excorticata* seeds that germinated from 241 weta scats collected from a forest reserve on New Zealand's North Island. Histogram bins illustrate the total number of scats (y-axis) with different numbers of seeds that germinated in laboratory trials (x-axis). The inset illustrates an large, male Wellington tree weta (*Hemidenina crassidens*)

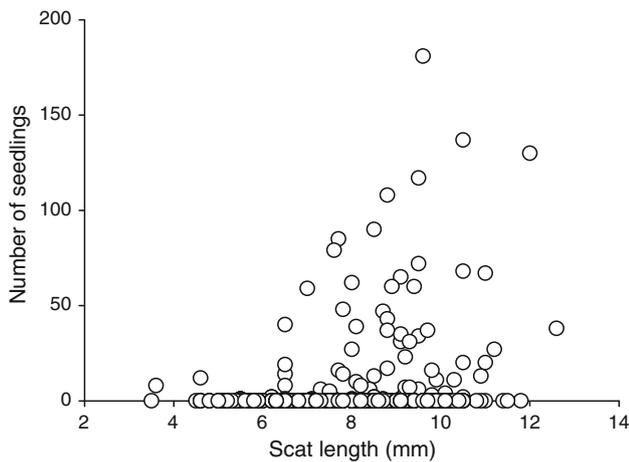


Fig. 2 Positive relationship between the size of weta scats (scat length, mm) and the number of *Fuchsia excorticata* seeds that they contained, which later germinated in laboratory trials ($r_s = 0.254$, $P < 0.001$)

from the field. Five apparently intact, unidentified seeds that were morphologically distinct from tree fuchsia were found. However, they failed to germinate and could not be identified. Interestingly, several scats also contained the remains of fern sporangia. To test whether weta might disperse fern spores in viable condition, intact sori of silver tree fern (*Cyathea dealbata*) were fed to several weta in cat food. Subsequently produced scats were dissolved in water, spread across an agar medium and placed under the same light conditions as the other scats in the laboratory. The spores ingested by weta readily germinated and hundreds of gametophytes were produced, yet none of the spores that were collected directly from sori in the field germinated.

Experimental results showed that weta successfully disperse $15.3 \pm 2.4\%$ of the *F. excorticata* seeds that they consume (Fig. 3). Larger weta ($21.8 \pm 3.8\%$) successfully dispersed greater proportions of seeds than smaller weta ($8.5 \pm 1.6\%$, $F_{1,25} = 7.315$, $P = 0.012$). Males ($18.4 \pm 3.8\%$) and females ($12.1 \pm 2.8\%$) dispersed similar proportions of seeds ($F_{1,25} = 1.633$, $P = 0.213$). Sex and size did not interact ($F_{1,25} = 0.391$, $P = 0.538$). Approximately 75% of seeds that were manually extracted from fruit pulp successfully germinated.

We found no support for the hypothesis that weta preferentially disperse smaller seeds. Instead, our results suggest that weta selectively disperse larger *Fuchsia excorticata* seeds (Fig. 4). Differences between the average size of seeds consumed by weta and the average size of seeds that survived ingestion and then germinated were significantly different from zero ($T = 4.268$, $P < 0.001$). Similarly, t values relating the size distributions of seeds consumed by weta and the average size of seeds that survived and germinated also differed from zero ($t = 4.725$, $P < 0.001$). Differences between initial and final seed sizes

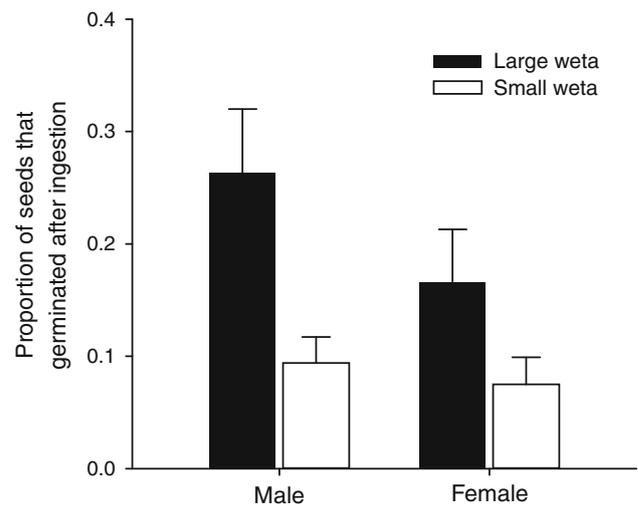


Fig. 3 Results from an experiment in which 32 weta were each fed 25 *Fuchsia excorticata* seeds. Average proportions (\pm SE) of seeds that germinated following ingestion are shown separately for large (black bars) and small (white bars) weta of both sexes (x-axis). Large individuals, regardless of sex, disperse greater numbers of seeds than small individuals

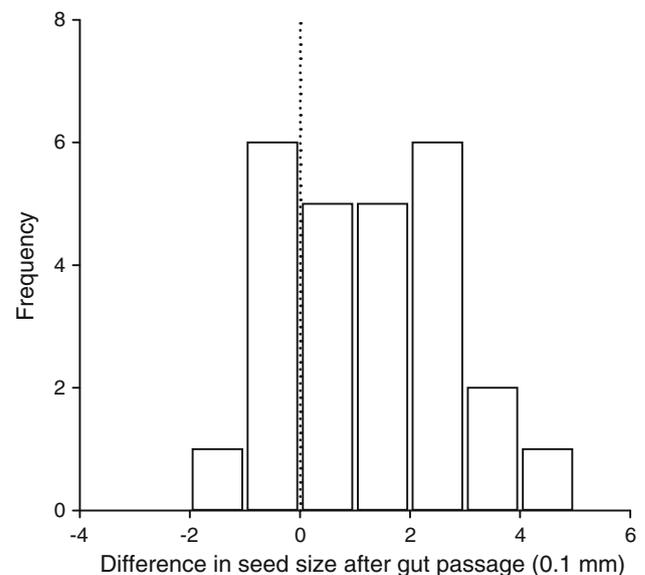


Fig. 4 Frequency distribution of differences between the average size of *Fuchsia excorticata* seeds ingested by weta and the average size of seeds that germinated following ingestion. The dashed line represents the null expectation of no difference in average seed size following ingestion. Weta preferentially dispersed larger seeds ($T = 4.268$, $P < 0.001$)

dispersed by weta did not differ between sexes ($F_{1,22} = 1.987$, $P = 0.173$) or size classes ($F_{1,22} = 0.851$, $P = 0.366$). Both factors also did not interact ($F_{1,22} = 1.987$, $P = 0.469$). Similarly, t values did not differ between sexes ($F_{1,22} = 2.092$, $P = 0.162$), sizes ($F_{1,22} = 1.400$, $P = 0.246$), and both factors also did not interact

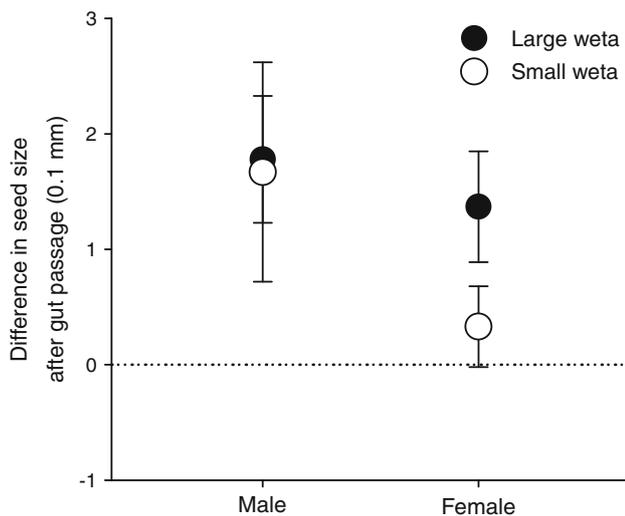


Fig. 5 Differences between the average size of *Fuchsia excorticata* seeds ingested by weta and the average size of seeds that germinated following ingestion. Averages (\pm SE) for large (black symbols) and small (white symbols) weta are shown separately for both sexes (x-axis). No statistical differences in seed size selection were observed between sexes and different-sized individuals

($F_{1,22} = 0.471$, $P = 0.500$). Therefore, regardless of sex and size, weta selectively disperse a subset of larger seeds (Fig. 5).

Discussion

Thousands of seeds germinated from scats collected in the field. More seedlings emerged from larger scats, suggesting that larger weta disperse more seeds than smaller weta. Laboratory feeding trials showed that although weta frequently destroy seeds during ingestion, many seeds survived gut passage and later germinated. Germination rates varied intraspecifically, with smaller weta dispersing fewer seeds than larger weta. Contrary to our initial hypotheses, weta appeared to disperse greater numbers of larger seeds.

The positive relationship between scat size and seedling number could result from several processes. First, larger weta, which are known to produce bigger scats (Spencer 1995), may consume greater quantities of *Fuchsia* fruit. Although we did not quantify rates of fruit consumption by different-sized individuals, laboratory results suggest that greater numbers of seedlings in larger scats results from differences in seed survivorship after seeds are ingested. While seed survivorship did not differ between the sexes, larger weta damaged fewer seeds than smaller weta.

Consistent intraspecific differences in seed dispersal services are uncommon in seed dispersal mutualisms (Herrera 2002a). Consistent differences in seed dispersal services are also uncommon among species within

broad taxonomic guilds of frugivores (Burns 2006a), suggesting that many species of frugivores are functionally redundant (Zamora 2000). On the other hand, dispersal efficiency is known to differ on broader taxonomic scales, between guilds of seed dispersers (Poulsen et al. 2002). There are several broad taxonomic groups of weta, including giant (*Deinacrida* spp.), ground (*Hemiandrus* spp.), tree (*Hemideina* spp.), and tusked weta (*Anisoura* and *Motuweta* spp.) in the family Anostomatidae and cave weta in the family Rhabdophoridae. Little is known about potential differences in the capacity of different types of weta to disperse seeds (Morgan-Richards et al. 2008). Although different types of weta could provide different types of seed dispersal services, available data indicate that at least some species of tree (Duthie et al. 2006) and ground (Burns 2006b) weta disperse the seeds of similar types of fruits. Scree weta (*Deinacrida connectens*) also disperse large quantities of *Gaultheria depressa* seeds above the tree line in the Austral autumn (H. Larson and K.C. Burns, unpublished data).

Regardless of size or sex, weta appear to disperse greater numbers of larger seeds. Preferential treatment of particular fruit and seed characteristics by a single disperser are rarely documented in seed dispersal mutualisms (Herrera 2002a). Instead, frugivores usually show variable preferences for particular fruit traits, and variable interactions are thought to preclude pair-wise coevolution between fruit and frugivore species (Herrera 1985). Coevolutionary dynamics between frugivores and fleshy-fruits are more likely to operate on broad taxonomic scales (e.g., Korine et al. 2000; Lomáscolo et al. 2008). Therefore, seed size filtering by weta is unusual.

Duthie et al. (2006) found that fleshy-fruits dispersed by Wellington tree weta are morphologically distinct. In particular, they found that weta dispersed the seeds of fleshy fruit species with relatively low water content and smaller seeds. This suite of traits results in a distinctive type of ‘spongy’ fruit pulp, which is relatively dry. Duthie et al. (2006) also showed that this species of weta successfully dispersed the seeds of only small-seeded fruits, presumably because the small size of their mouth parts and cibarium (i.e., the space anterior to the mouth where food items are chewed) places an upper limit to the size of seeds they can consume. Therefore, there is some evidence for a syndrome of fruit traits associated with weta seed dispersal.

Results from this study suggest that weta might also have a lower limit to the sizes of seeds they can disperse successfully. Most seeds that were destroyed after ingestion by weta appeared to be cut cleanly in half. This led us to speculate that seeds are often damaged as they pass through the cibarium. Because smaller seeds appeared to be more vulnerable to damage, smaller seeds could be more susceptible to damage during mastication. However, this

seems unlikely, as the main function of the cibarium is to cut larger pieces of food into smaller pieces to prior to digestion. Alternatively, smaller seeds could be more susceptible to damage after they reach the gizzard, which is a grinding organ used to help digest coarse, hard pieces of plant and animal matter. Interpreting these two results jointly suggests that the cibarium places an upper limit on sizes of seeds that can be successfully dispersed by weta, while the gizzard might place a lower limit on seed sizes.

Although results suggest that weta may select for certain seed sizes, other plausible explanations exist for the apparent increase in seed size after ingestion. Regardless of their size when they are ingested, seeds could expand in size after gut passage. Chemical processes inside the digestive system of weta could alter seed coat characteristics or facilitate water retention leading to overall increases in seed size, without differential seed mortality. Cat food was used so that a precise number of seeds of known size could be fed to weta and this artificial medium could have influenced seed treatment during ingestion. Another explanation for the apparent increase in seed size after gut passage is that big seeds have greater overall germination potential than small seeds, regardless of whether they were ingested. We also used a coarse estimate of seed size (i.e., seed length). More accurate measurements, such as seed surface area or seed volume, could yield different results.

All of our seed germination trials were conducted in the laboratory and patterns in seed germination can be influenced by the conditions that seeds experience in the field (Robertson et al. 2006). Small-scale variation in environmental conditions, as well as the actions of fungal and microbial communities, can have strong effects on seed germination behaviour. We chose to conduct our experiments in the laboratory so that we could precisely quantify the number and sizes of seeds dispersed. Future study would benefit from investigating how intraspecific differences in seed treatment interact with field microsite conditions to determine plant recruitment. We also did not compare seed dispersal efficiency between weta and other types of dispersers, such as birds or reptiles, because it was beyond the scope of this particular study. However, comparisons of germination rates between undispersed seeds, seeds dispersed by weta, and seeds dispersed by other frugivores (e.g., birds and reptiles) would likely generate interesting and important results.

Regardless of the precise anatomical mechanism responsible for seed size selection, the fact that weta destroy some seeds during ingestion does not indicate that they are ineffective mutualists. Many small mammal species hoard large numbers of seeds on their winter territories (Vander Wall 1990). Most of these seeds are retrieved and consumed, but a small number are forgotten and effectively

dispersed (Jansen et al. 2008). Instead of producing fruit pulp to attract seed vectors, scatter-hoarded plant species ‘pay’ for the dispersal of some seeds with other seeds. In this way, individuals that are primarily seed predators ultimately form mutualistic associations with plants as seed dispersers (see Janzen 1984). A similar circumstance may be the case with weta, which destroy many seeds during ingestion, but ultimately disperse large numbers of seeds in germinable condition.

Overall results from this study showed that wild populations of Wellington tree weta frequently consume tree *Fuchsia* fruits. While the majority of seeds are often destroyed, many survive gut passage and later germinate. Larger individuals of both sexes disperse greater quantities of viable seeds, providing a rare example of consistent intraspecific variation in the capacity of an animal species to interact with plants as seed dispersers. Wellington tree weta also appear to preferentially disperse large seeds, suggesting that they could select for particular characteristics of fleshy-fruited plants.

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