Is the tree weta *Hemideina crassidens* an obligate herbivore?

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Abstract

Tree weta are well known insects of New Zealand's forest ecosystems; however, there is limited research into their general ecology. A literature review suggests they are mainly herbivores. Wellington tree weta, *Hemideina crassidens*, were given the choice of possible foods that they may come into contact with in the wild. Unexpectedly, leaves of *Coprosma robusta* were consumed the least by the weta, which suggests a more accurate label for the diet of *H. crassidens* may be omnivory. There are possible implications for the mixing of foods in the diet that need further investigating.

Key words: diet – herbivory – *Hemideina crassidens* – omnivory – polyphagy.

Introduction

Weta of the family Anostostomatidae are large bodied, flightless, orthopterans that are well known insects in New Zealand. Nevertheless, detailed knowledge of their ecology in the wild is limited, even to the extent that information of their diet is fragmentary. One general observation is that tree weta (*Hemideina* spp.) are, unusually for their family, predominantly herbivores (Meads 1990; Green 2005; Trewick & Morgan–Richards 2005; Gibbs 2009; Wehi & Hicks 2010; but see Barrett 1991). More precisely, *Hemideina* appear to thrive on a diet of leaves. Although this inference has often been repeated in the literature its basis has not been extensively tested. Wilson and Jamieson (2005) examined the diet of one species, the mountain stone weta *H. maori*, using faecal analysis and found plant and invertebrate fragments. But for the other six *Hemideina* species, studies have primarily been directed at other questions. For example, while investigating the possibility of seed dispersal by tree weta, Duthie *et al.* (2006) found seeds of *Fuchsia excorticata* in the faeces of wild *H. crassidens* and identified a large variety of native fruits that they would consume in captivity.

In the orthopteran suborder Ensifera, which includes the Anostostomatidae, there is a variety of insect dietary traits seen. Some taxa show extreme specialisation, such as the stick katydids (subfamily Phasmodinae) which feed exclusively on flowers (Rentz 1996; pp. 105). Others show generalisation in their diets, as seen in the family Tettigoniidae (Rentz 1996; pp. 105).

We collated records on the diet of tree weta observed in captivity and in the wild (Table 1). From this, it is apparent that plants are indeed an important component of tree weta diet. Leaves generally dominate the food types eaten by individuals of four species of weta (*H. crassidens*, *H. femorata*, *H. maori* and *H. ricta*; Table 1). However, availability of information is variable and almost certainly incomplete. For instance, published records for one of the most well known species, the Auckland tree weta *H. thoracica*, consists of seed predation, cannibalism in captivity, two instances of leaf eating and one instance of fruit eating. The majority of published observations are of captive weta and include the foods eaten under experimental conditions (e.g. food choice trials). As tree weta are generally treated as herbivorous and thus usually provided only with leaves, captive studies may not be informative about food preference. Field observations of natural diet include nocturnal observations of weta eating and identification of food particles in the faeces collected in the wild.

Direct field observations provide valuable information but their significance is difficult to quantify when there are so few data. Similarly, determining diet from the remains of food components in faeces also has intrinsic problems as digestion differs among food types (Fitzgerald 1976; Trewick 1996). Soft tissues from fruit flesh may not be obvious in weta droppings so quantification of fruit eating may come only from the presence of seeds in the faeces and then only when seeds are small enough to be ingested whole. Invertebrate remains in faeces are often difficult to distinguish and identify, even to a family level (Little 1980). Large droppings that persist in the environment have a high plant content, whereas faeces containing tissues from an animal diet are softer and may more readily break down in the environment. This difference is evident when large, firm plant-based droppings of tree and giant weta are compared to the soft liquid droppings of carnivorous ground weta and tusked weta (Gibbs 1998; pers. obs. SAT). Method bias could easily result in only the plant cuticles being identified and other particles from faeces being effectively ignored, so the full diet is not observed. In particular, foods that are rare but perhaps nutritionally important will tend to be overlooked.

In light of recent speculation about specialised interactions between weta and various plants (Duthie *et al.* 2006; Burns 2006; Morgan-Richards *et al.* 2008) we asked the more general question: does the tree weta, *Hemideina crassidens* show a pronounced choice for particular food types? If *H. crassidens* is a herbivore, we predict that under experimental conditions, individual weta will choose leaves more often than other food types available. In contrast, if *H. crassidens* is polyphagous then we expect to see each weta eating a number of different food types when given a choice.

Methods

We tested whether tree weta demonstrate any partiality when offered a range of food types they might encounter in nature: leaves, insects, fruits and seeds. 32 wild Wellington tree weta, *H. crassidens*, were collected from southern North Island. These weta included males and females, adults and juveniles. The weta were kept individually in two-litre plastic containers with lids fitted with fine mesh to allow light and air circulation (Wyman *et al.* 2010). They were kept in a quiet room with natural light and ambient temperature. Each container had a hollowed flax (*Phormium tenax*) flower stalk as a daytime roost for the weta (Wyman 2009). The weta were given seven days to acclimate to this environment during which time they were given a maintenance diet of carrot (Wyman *et al.* 2010), which was removed at the start of the choice experiment. Leaves and fruits used were collected fresh from *Coprosma robusta* in Palmerston North, a plant known to be palatable to tree weta (Table 1, Pers. Obs.). The leaves of *Coprosma robusta* were approximately 85 mm x 40 mm. The fruits of *C. robusta* are elliptical and orange, approximately 8mm x 5mm and contain two seeds of a size that are too large (4.2 - 6.5mm x 2 - 3mm; Webb & Simpson 2001) for tree weta to ingest whole. All fruit were ripe and intact when given to the weta. The relatively large seeds of the fruits of this species enabled a distinction to be made between the consumption of fruit pulp and predation on the seeds.

The choice experiment was run over two consecutive nights using wild-caught weta. Each weta was supplied with three leaves, five fruit (approximately 1g) and two freeze-killed *Wiseana* moths (approximately 0.5g) at the start of the experiment. This volume of each food type meant that weta consumption was not limited. There were no other foods in the container. Weta were checked after the first night and the total of each food type eaten was recorded on the second morning.

Results

The experiment recorded feeding of 32 *Hemideina crassidens* tree weta; 11 adults (6 females and 5 males) and 21 juveniles (13 females and 8 males). The most frequently eaten foods were moths and fruit (Figure 1). Some or all of the two moths were eaten by 87.5% of the weta. Seeds were the least preferred, with only two of the 32 weta consuming some part of the seeds. The seeds were not eaten whole, rather they were gnawed and the kernel inside eaten. No weta ate only leaves and leaves were recorded as being eaten less often (9/32) than other food types provided (moths + fruit + seeds = 55; *t* test $P = 0.016$). The proportion of instances of adults and juvenile eating a combination of these foods were 82.6% and 87.8% respectively. Most (18/32) weta ate two food items, five ate three, one ate four items and eight ate one. There was no difference in the average number of different food types eaten by males (2.055) and females (2.085) (*t* test $P = 0.43$). Moths and fruit were the food types most commonly chosen by males and females, adults and juveniles (Figure 1). Although there appears to be a subtle difference in the food choice of adults compared with juveniles (Figure 1), this did not result in a change in the ranking of leaves over other foods, or a change in the number of food types eaten per weta.

Discussion

Tree weta are commonly known to eat vegetation (Table 1). The capacity to consume leaves and develop successfully on a purely plant diet (Morgan-Richards 2000), appears to be a specialist trait of this genus and the sister genus *Deinacrida* (Pratt *et al.* 2008) and leads to the expectation that tree weta will prefer plant foods when given the choice. This expectation is born out of observations of tree weta feeding in the wild and the consistency and content of their droppings. However, in our captive experiment we found Wellington tree weta, *H. crassidens*, did not exhibit a

Table 1. Current knowledge of the diet of tree weta, *Hemideina* spp. Species of weta are: *Hemideina crassidens, H. thoracica, H. femorata, H. maori, H. ricta*. Captivity is any food the weta ate during experimentation or while in any other captive environment. Field relates to any food that the weta were seen eating in the wild or food particles found in faeces collected in the field.

Food type		**Captivity**	**Field**
Leaves - Gymnosperms			
Pinaceae	*Pinus radiata*		*crassidens*[8]*
Podocarpaceae	*Podocarpus nivalis*	*maori*[10]	*maori*[10]
Leaves - Angiosperms			
Apiaceae	*Aniosotome imbricate*		*maori*[7]
Apocynaceae	*Parsonia heterophylla*	*ricta*[9], *femorata*[9]	
Araliaceae	*Pseudopanax arboreus*	*crassidens*[3,4, 11]	
	Pseudopanax colorata	*ricta*[9], *femorata*[9]	
	Schefflera digitata	*ricta*[9], *femorata*[9]	
Asteraceae	*Celmisia viscose*		*maori*[7]
	Helichysum selago	*maori*[10]	*maori*[10]
	Raoulia hectori		*maori*[7]
	Sonchus oleraceus	*crassidens*[3], *ricta*[9], *femorata*[9]	
	Taraxacum officinale	*ricta*[9], *femorata*[9]	
Celastraceae	*Euonymus sp.*	*crassidens*[3]	
Coriaraceae	*Coriaria arborea*	*crassidens*[1]	
Cornaceae	*Griselinia littoralis*	*crassidens*[1,4], *ricta*[9], *femorata*[9,10]	
Corynocarpaceae	*Corynocapus laevigatus*	*crassidens*[11]	
Fabaceae	*Sophora sp.*	*crassidens*[3]	
	Trifolium repens	*ricta*[9], *femorata*[9]	
	Ulex europeaus	*ricta*[9], *femorata*[9]	
Malvaceae	*Hoheria sp.*	*crassidens*[3]	
Myoporaceae	*Myoporum laetum*	*crassidens*[3,11], *thoracica*[3], *maori*[3]	
Myrtaceae	*Eucalyptus sp.*	*crassidens*[1]	
	Kunzea ericorides	*crassidens*[3], *ricta*[9], *femorata*[9,10]	*femorata*[10]
	Leptosermum scoparium	*maori*[10], *femorata*[10]	
	Metrosideros sp.	*crassidens*[1]	
Nothofagaceae	*Nothofagus solandri*	*femorata*[10]	*femorata*[10]
Onagraceae	*Fuchsia excortica*	*crassidens*[1]	
Piperaceae	*Macropiper excelsum*	*ricta*[9], *femorata*[9], *crassidens*[11]	*crassidens*[12]
Pittosporaceae	*Pittosporum eugenioides*	*ricta*[9], *femorata*[9]	
Plantaginaceae	*Plantago sp.*	*crassidens*[3], *maori*[3]	
Poaceae	*Poa colensoi*	*femorata*[10]	*maori*[7]
Polygonaceae	*Rumex obtusifolius*	*ricta*[9], *femorata*[9]	
Polytrichaceae	*Polytrichem juniperinum*		*maori*[7]
Rubiaceae	*Coprosma foetidissima*	*crassidens*[11]	
	Coprosma repens.	*crassidens*[3, 11], *maori*[3], *thoracica*[3]	
	Coprosma rhamnoides	*femorata*[10]	
	Coprosma robusta	*crassidens*[3], *maori*[3], *thoracica*[3]	
Scrophularaceae	*Hebe sp.*	*crassidens*[3], *maori*[3]	
	Buddliea sp.	*crassidens*[3]	
Salicaceae	*Salix sp.*	*crassidens*[3], *maori*[3]	
Thymelaeaceae	*Kelleria villosa*		*maori*[7]
Violaceae	*Melicytus ramiflorus*	*crassidens*[1,4, 11]	
Winteraceae	*Pseudowintera colorata*	*thoracica*[3]	
Fruit – Angiosperms			
Agavaceae	*Cordyline australis*	*crassidens*[2]	
Argophylaceae	*Corokia cotoneaster*	*crassidens*[2]	
Balanophoraceae	*Dactylanthus taylorii*	*crassidens*[8]	
Campanulaceae	*Pratia angulata*	*crassidens*[2]	
	Pratia physaloides	*crassidens*[2]	
Cornaceae	*Griselinea littoralis*	*crassidens*[2]	
Ericaceae	*Gautheria antipoda*	*crassidens*[2]	
Lauraceae	*Beilschmiedia tawa*	*crassidens*[2]	
Liliaceae	*Dianella nigra*	*crassidens*[2]	
Monimiaceae	*Hedycarya arborea*	*crassidens*[2]	
Myoporuaceae	*Myoporum laetum*	*crassidens*[2]	
Onagracae	*Fuchsia excorticata*	*crassidens*[1,2], *thoracica*[1]	*crassidens*[2]
	Fuchsia procumbens	*crassidens*[2]	
Rubiaceae	*Coprosma sp.*	*crassidens*[2]	
Violaceae	*Melicytus sp.*	*crassidens*[2]	
Seeds – Gymnosperms			
Araucariaceae	*Agathis australis*	*thoracica*[5]	*thoracica*[5]
Balanophoraceae	*Dactylanthus taylorii*	*crassidens*[8]	
Podocarpaceae	*Dacrydium cupressinum*	*thoracica*[6]	
Flowers			
Asteraceae	*Brachyglottis repanda*		*crassidens*[8]
Other weta		*crassidens*[8], *thoracica*[8]	
Invertebrates		*crassidens*[3,8], *maori*[3], *thoracica*[3,8]	*maori*[7,10], *femorata*[10]

[1]Wyman *et al*. 2010; Wyman 2009; [2]Duthie *et al*. 2006; [3]Barrett 1991; [4]Fisher *et al*. 2007; [5]Mirams 1957; [6]Beveridge 1964; [7]Wilson & Jamieson 2005; [8]pers. obs., Morgan-Richards & Trewick; [9]Townsend 1995; [10] Little 1980; [11]Rufaut 2001; [12]Moller 1985.

*Consumption of pine needles (*P. radiata*) was determined through pine cuticle found in the droppings of *H. crassidens* collected in the field.

All these species of weta have also been seen to eat carrot in captivity (pers. obs., Morgan-Richards & Trewick).

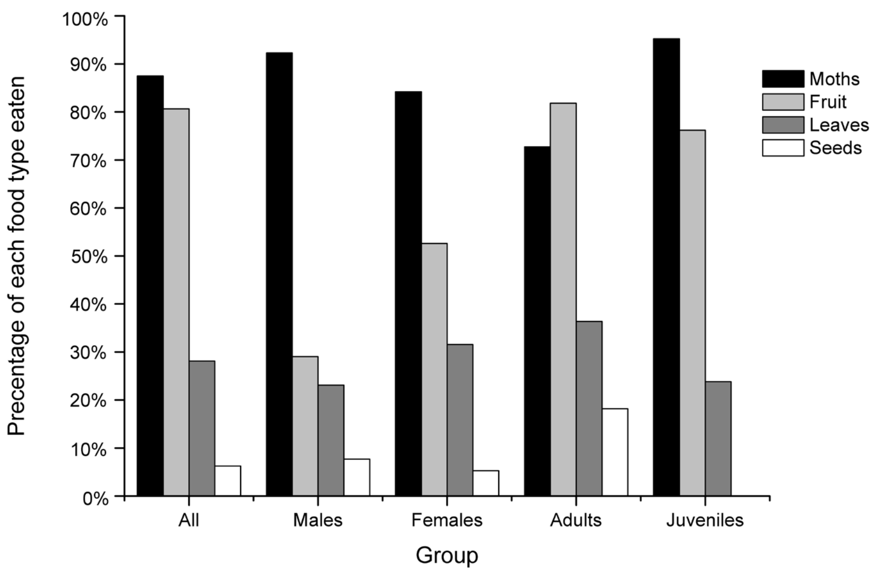

Figure 1. The percentage of the individual weta that ate each of the food types, grouped into males and females, adults and juveniles and overall the weta.

preference for leaves over the other food types offered. In this experiment, seeds of *Coprosma robusta* were the least preferred food when given a choice of leaves, fruit, seeds and invertebrates. Two adult weta appeared to recognise the food potential of seeds and demonstrated an ability to access the kernel of *C. robusta* seeds, further demonstrating a capacity for seed predation by tree weta (Table 1). In our experiment, tree weta that ate moths also tended to eat the fruit, but no weta ate only leaves. This is inconsistent with the original inference that tree weta are obligate herbivores, instead indicating an omnivorous or polyphagous habit, but is in keeping with other observations of carnivory amongst anostostomatids (Little 1980; Barrett 1991; Wilson & Jamieson 2005). The majority (24/32) of weta in our experiment ate two or more food types over just two nights, which further demonstrates a polyphagous habit.

The occurrence of folivory in individual tree (*Hemideina*) and giant (*Deinacrida*) weta distinguishes them from most other members of the Anostostomatidae, which appear to be predominantly carnivorous (e.g. *Hemiandrus* Cary 1983; but see Morgan-Richards *et al*. 2008). However, even if not essential in the diet, carnivory appears to be important and might have strong implications for growth rates and fecundity of individual weta. Carnivory may be important in maximising fitness, by enabling the development of enlarged heads in males that may be important in securing mates (Kelly 2005; GW Gibbs pers. comm.), and enhancing egg number and/or quality in females.

The feeding habits of other Orthoptera are diverse, although many are herbivores; eating living plant tissues (Crawley 1983). For example, shorthorn grasshoppers (Acrididae) are obligate herbivores that specialise on grasses, while longhorn grasshoppers or katydids (Tettigoniidae)

supplement plant diet by eating other insects (Brown 1983). For instance, crop contents of individual shield-backed katydids of the genus *Atlanticus* included plant and invertebrate remains (Gangwere 1967). Although there are many examples of herbivory in orthopterans (e.g., Acrididae), polyphagy is also common and extends from eating a mixture of different plant tissues and species, to omnivory that includes plant and animal matter. This contrasts with the situation of insects in general, which tend to have narrow dietary range (Hodkinson & Hughes 1982). Close host-plant interactions and coevolution often occur with those that feed on a single plant species (Ehrlich & Raven 1964). Orthopterans, which are highly mobile as juveniles and adults, may rely on food selection to maintain homeostasis, regulate food selection to balance nutrient/toxin intake (Raubenheimer & Simpson 2003; Jonas & Joern 2008; Hunter 2009), and it has been shown than diet mixing enhances development rates (Bernays & Minkenberg 1997).

New Zealand's tree weta (*Hemideina*) and closely related giant weta (*Deinacrida*) (Morgan-Richards & Gibbs 2001; Trewick & Morgan-Richards 2004) are an ecologically prominent and diverse group (Trewick & Morgan-Richards 2005; Trewick & Morgan-Richards 2009). The success of this endemic lineage may be related to the evolution of polyphagy (folivory and carnivory), more akin to that of Tettigoniidae than other Anostostomatidae. As there is limited diversity of Tettigoniidae in New Zealand, (three native species; Eades *et al*. 2010) the *Hemideina/Deinacrida* clade may have radiated into unoccupied niche space in New Zealand's forests. We expect that further, detailed studies of these weta will reveal a capacity for targeting nutrient optima by utilising a wide range of food types (Raubenheimer & Simpson 1993).

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