Wellington tree weta (*Hemideina crassidens*) diet and the effect of some of their dietary choices

A thesis presented in partial fulfilment of the requirements for the degree of

Masters of Science
in
Zoology
at Massey University, Palmerston North
New Zealand

Melissa Jane Griffin
2011

Acknowledgements

I wish to thank the following people for their advice and input throughout the course of my Master's research. Firstly, a huge thank you to my supervisors Mary Morgan-Richards and Steve Trewick for their guidance, assistance and advice. Thank you to Niki Minards for her help collecting weta, feeding the weta, proof reading manuscripts and support during my thesis. I'm grateful for advice from Cilla Wehi and for proof reading draft manuscripts. Thank you to all those who helped collect weta; Briar Smith, Calem Griffin, Robyn Dewhurst and Rachel Westley. Thank you to the lab technicians in the Ecology Group for all your help. Thank you to Tracy Harris for organising the chemicals for the nutrient balancing diet and the equipment needed. Thank you to any other staff in the ecology group that provided assistance. I was supported by a grant from the Entomological Society of New Zealand.

Abstract

Tree weta have often been referred to as “invertebrate mice” by New Zealand ecologists. This phrase does not help in the understanding of the ecology of tree weta, and it is likely that a lack of information or simplistic interpretation has led to its use. One important aspect that can be examined to refine our understanding of tree weta ecology is diet. This would help improve our understanding of where tree weta fit into New Zealand forest ecosystems. In the present study I examined the treatment of tree weta as “invertebrate mice” and investigated in detail aspects of the diet of one species, the Wellington tree weta, *Hemideina crassidens*. Unexpectedly tree weta seemed to prefer to consume high protein sources such as invertebrates, rather than the food they are generally assumed to eat; leaves. Tree weta that were raised on a diet high in protein were able to reach much larger size than those raised on a diet containing less protein. However, the large amount of excess fat stored by the tree weta on the high protein diet, suggested that they were not strictly regulating their nutrient intake. And the larger animals did not increase their fitness by producing more or better quality eggs. When their nutritional state was set with an artificial pre-treatment diet, experimental tree weta did not then balance their nutrients by eating a complementary food. The tree weta may instead be over-consuming protein when it is readily available. New Zealand trees are low in nitrogen so if a high quality protein source was available it may be beneficial for tree weta to consume as much as possible and store it for when protein is in short supply. This could allow tree weta to stay in their roosts for longer periods to avoid predation and desiccation. More knowledge on tree weta behaviour related to activity patterns including leaving the roosts and foraging routines could be beneficial in understanding the costs and benefits of fat and protein storage in tree weta.

Table of Contents

List of Figures

List of Tables

Chapter 1

General Introduction

Tree weta are a group of orthopteran insects, known widely among the general public in New Zealand. There are seven species of tree weta in New Zealand that belong to the endemic genus, *Hemideina*. Tree weta species are generally abundant and are widely distributed around the country (Trewick & Morgan-Richards 2005, 2004, 2009). Although both common and familiar, surprisingly little is known about basic biology of tree weta, such as how far they travel, what their stridulatory calls mean, or what they eat. In this study I focus on tree weta diet.

My study species was the Wellington tree weta (*Hemideina crassidens* Blanchard) found in the southern North Island and at higher altitudes in mountainous areas in central North Island, as well as west of the main divide in the South Island to Fiordland (Trewick and Morgan-Richards 1995). The distribution of *H. crassidens* suggests that this species is better adapted to cooler conditions than its relative the Auckland tree weta (*H. thoracica*) which has a more northern distribution (Trewick and Morgan-Richards 1995, Sinclair et al. 1999). All tree weta are wingless and nocturnal. *Hemideina crassidens* can be found in tree roosts during the day, like most other tree weta species. They commonly take refuge during the day in holes of both living and dead trees that were previously occupied by wood-boring larvae (Gibbs 2001).

1.1 Why is diet important?

Diet and the need to acquire food for growth and reproduction is one of the basic drivers of animal behaviour. When foraging for food, whether plant or animal, an individual will interact with other species by competing for resources and access to food and through predator-prey interactions. These factors may play a role in the growth and fecundity of individuals, where increased risk of predation, for example, may decrease the chance of an animal getting the optimal amount of food or the particular type of food needed for the adequate nutrition of eggs and will impact on their potential fecundity (Awmack & Leather 2002).

Herbivory has its attendant problems. These include the presence of secondary metabolites produced by plants to inhibit the consumption of their leaves by insects and other herbivores (Hinks et al. 1993). Plant cell walls are made up of cellulose which is indigestible to many folivorous insects (Hochuli 1996) and many leaves are fortified with lignin (Raupp 1985). One solution is to eat more, and digestive inefficiencies in herbivorous locusts (*Chortoicetes terminifera* and *Locusta migratoria*) are ameliorated by the consumption of the large amount of food (Hochuli et al. 1993). Locusts rely on the mechanical disruption of cell walls, using heavy mandibles, to extract nutrients (Hochuli et al. 1993). Invertebrate mandibles are adapted to assist disruption, and in grasshoppers they are asymmetrical so that the left mandible closes over the right bringing them together like the grinding molars of mammals (Bernays et al. 1991).

Tree weta have generally been thought of as herbivores and this is supported by isotope analysis of *Hemideina thoracica* (Wehi & Hicks 2010). Consuming a diet largely made up of leaf material means that these insects have large droppings that persist in the environment. It is this observation and others relating to their general ecology (nocturnal, daytime roosts, polygamous reproduction) that led to tree weta being referred to as "invertebrate mice" by some New Zealand ecologists (e.g. Fleming 1973, 1977; King 1974; Ramsay 1978). Herbivory is an unusual trait in the orthopteran family that includes the tree weta, Anostostomatidae, which comprises mostly predatory or scavenging species (e.g. New Zealand ground weta (*Hemiandrus* spp.) and tusked weta (*Motuweta, Anisora*) (Cary 1983; McIntyre 1998)).

1.2 Diet in the wider group

In the superfamily Stenopelmatoidea, to which Anostostomatidae belong, various feeding habits are expressed. The instances of leaf eating in tree weta (and giant weta, *Deinacrida*) are not unusual when orthopterans are considered more generally. For instance, members of the family Gryllacrididae encompass all feeding guilds, including herbivory, carnivory, omnivory, florivory, and granivory (Rentz 1996). Jerusalem crickets in the family Stenopelmatidae will eat roots of their host plants as they burrow through the soil and other plant products, but the consumption of invertebrates could also be of value to them (Stoffolano and Wright 2005; Weissman 2001). Australian king crickets (Anostostomatidae), however, have not been observed feeding on leafy plant material, as is seen in tree and giant weta in New Zealand (Rentz 1996; Monteith and Field 2001). These crickets tend to be generalised scavengers taking a variety of invertebrates, both dead and alive, berries and fungi (Monteith and Field 2001). More specialised diets are also seen among this family. *Exogryllacris* spp., for example, consumes fungi that grow on the bark of tree trunks (Monteith and Field 2001). There are also observations of Australian anostostomatids eating algae, animal droppings, other animals and members of their own species (Monteith and Field 2001). Members of the burrowing family Cooloolidae show obligate carnivory, eating a variety of insect larvae (Rentz 1986).

Tree weta have been thought of as generalist herbivores, eating a large variety of leaf species (Wyman 2009). Diet mixing of this kind may be helpful in overcoming toxins in leaves and acquiring particular quantities of nutrients; in other words optimising nutrient intake. Polyphagous grasshoppers (*Taeniopoda eques*) were found to have a greatly increased survivorship in captivity when fed a diet of mixed plant species rather than food that remained the same over time (Bernays et al. 1992). Individuals were observed to regularly switch food in the wild and would feed for longer on novel food than on the plant species they had previously been eating (Bernays et al. 1992).

1.3 Recent research into weta diet – seed dispersal

Recently there has been increased interest in the diet of tree weta, especially with regard to their potential as seed dispersers. Tree weta (*H. crassidens*) were shown to slightly increase germination of two New Zealand plant species when they ate their seeds (Duthie et al. 2006). However, the ability of seeds to pass through the weta and have increased germination is not all that needs to be taken into account. Seed predation very likely results in a net loss to the plant (Wyman et al. 2010, King et al. 2010). If tree weta were effective seed dispersers it might be predicted that when given a choice they would choose fruits with seeds they are able to disperse over other food types present, such as leaves. However, tree weta showed no preference for the fruits of *Fuchsia excorticata* over the leaves of mahoe (*Melicytus ramiflorus*) (Wyman et al. 2010).

1.4 Thesis overview

I aim to gain a wider understanding of the place of tree weta in New Zealand forest ecology, focussing on their diet and some implications of the dietary choices that they make. I have used three methods to examine tree weta diet; a dietary choice experiment, controlled growth experiments and feeding trials using artificial foods.

Chapter 2: First I review the use of the "invertebrate mice" metaphor which led me to look at one aspect of this comparison – the diet of tree weta.

Chapter 3: Describes the use of choice experiments to investigate the breadth of their diet, and seek an answer to the question “Are tree weta obligate herbivores?”

Chapter 4: Using an experimental approach I asked “Are all food choices equal?” Juvenile tree weta were raised in captivity on two contrasting diets to observe the effect of protein on their growth rate and fecundity.

Chapter 5: Adult tree weta were given highly manipulated synthetic foods to investigate whether or not weta are able to distinguish between nutrients in their foods, and whether they are able to balance these nutrients over time.

Chapter 2

Exploring the concept of niche convergence in a land without rodents:

the case of weta as small mammals.

A version of this chapter has been accepted for publication in the New Zealand Journal of Ecology as:

Griffin MJ, Trewick SA, Wehi PM, Morgan-Richards M. 2011. Exploring the concept of niche convergence in a land without rodents: the case of weta as small mammals. New Zealand Journal of Ecology 35(3): 302-307

http://www.nzes.org.nz/nzje/new_issues/NZJEcol35_3_302.pdf

2.1 Introduction

The fauna of New Zealand is widely recognised as distinctive and unusual in terms of composition and ecology (Daugherty et al. 1993; Trewick & Morgan-Richards 2009; Wallis & Trewick 2009, and refs. therein). An example of this distinctiveness is the prominent place in New Zealand's culture of certain Orthoptera and in particular members of the family Anostostomatidae, known as weta[1] (Johns 1997; Trewick & Morgan-Richards 2009). Four groups of weta are present in the New Zealand anostostomatid fauna; all are flightless and nocturnal, and comprise 11 species of giant weta (*Deinacrida*), seven tree weta (*Hemideina*), three tusked weta species (*Anisoura, Motuweta*) and approximately 40 species of ground weta (*Hemiandrus*). The prominence of these large crickets in New Zealand contrasts with a natural absence of small mammals, which in other parts of the world are a major component of terrestrial ecosystems. This perhaps explains why a comparison of these very different animals has been made. In this paper we review the uses of the weta/rodent or weta/small mammal comparison and consider its relevance and value in understanding the evolutionary ecology of New Zealand.

Immediately prior to the arrival of humans (c. 13th century, Wilmshurst & Higham 2004) New Zealand had few native mammals. Although at least one, probably flightless, small mammal was present in the mid-Miocene (Worthy et al. 2006), abundant Holocene and late Pleistocene bone deposits collected in caves, swamps and dunes provide strong evidence that terrestrial mammals were absent in more recent times (Worthy & Holdaway 2002). Thus, the recent evolutionary history of New Zealand's biota has proceeded without a well-developed mammalian fauna. Inferred outcomes of this situation include a relatively high diversity of flightless birds and the occupation by non-mammalian taxa of ecological niche space utilised by mammals elsewhere in the world (Diamond 1990). For example, some small birds, such as the now extinct Stephens Island wren, *Traversia lyalli,* are said to have had a niche parallel to that of small mammals such as mice and rats (Diamond 1990). At the other size

---

[1] The Maori name weta is applied to Orthoptera of two species-rich cricket families Anostostomatidae and Rhaphidophoridae, but the latter are usually called "cave weta". Cave weta have not been compared to small mammals.

extreme, New Zealand moa (Dinornithiformes) have been described as occupying the niche of ungulates (Ramsay 1978), and the unique characteristics of the kiwi (*Apteryx* spp.) have seen it given the status of honorary mammal (Calder 1978). There are, however, few data that explicitly explore or test the accuracy or relevance of such descriptions.

Probably the most frequently cited example of putative niche convergence involves the comparison of weta with rats (Ramsay 1978; Southern 1979; Daugherty et al. 1993), mice (Fleming 1973, 1977; King 1974, 1991; Ramsay 1978; Southern 1979; Daugherty et al. 1993), rodents (Ramsay 1978; Stevens 1980; Daugherty et al 1993; Guignon 2005), and small mammals generally (Fleming 1973; Southern 1979; Duthie et al. 2006; King et al. 2010) including voles (Fleming 1977; King 1974). In the more recent literature, most authors simply acknowledge these comparisons without necessarily supporting such a treatment (Trewick & Morgan-Richards 2005; Watts et al. 2008a, b; Gibbs 2010), whilst at least one author marginalised the proposition, stating that when Pacific rats (*Rattus exulans*) invaded New Zealand, the "rodent niche was empty" (Gibbs 2009). We believe that comparisons between weta and various small mammals might be useful if they lead to a better understanding of niche convergence, or the ecology and potential ecosystem services of weta within the New Zealand forest ecosystem, including diet and seed dispersal studies, as seeds are an important part of rodent diet (Trewick & Morgan-Richards 2004).

2.2 Basis for the metaphor

Reference to weta as equivalent to some form of small mammal is first attributed to H.N. Southern in 1964 (Fleming 1973; Ramsay 1978). Since then various characteristics of weta have been used as putative evidence for their rodent-like nature. These include nocturnal foraging (Fleming 1977; Ramsay 1978; Stevens 1980; Daugherty et al. 1993; McIntyre 2001), occupation of diverse habitats (Fleming 1977), retreat to daytime roosts (Fleming 1977; Stevens 1980; Daugherty et al. 1993), frass similar in size to rodent droppings (Fleming 1977; Ramsay 1978; Southern 1979; Stevens 1980; Daugherty et al. 1993), combined biomass (Ramsay 1978; Daugherty et al. 1993), polygamous reproduction (Ramsay 1978; Daugherty et al. 1993), omnivory (Ramsay 1978; McIntyre 2001), relatively large individual size (McIntyre 2001), nocturnal terrestrial activity (McIntyre 2001) and seed dispersal (Duthie et al. 2006).

Each of these features characterise only partially or inconsistently the subjects being compared and are founded on few if any data.

2.3 Validity of the metaphor: weta as small mammals

An initial and important difficulty with the comparison of weta with small mammals is that it is vague. Reference to small mammals (e.g. Duthie et al. 2006) is misleading because there are many species in this diffuse group (Pough et al. 2005). Even reference to rodents potentially encompasses an ecologically diverse range of species. Among approximately 5000 species of mammals (Delany 1974; Stoddart 1979) there are some 1814 rodents, ranging in size from 4 g to 50 kg (Ellenbroek 1980; Pough et al. 2005), and most are described as small mammals. Similarly, the species of weta used in the metaphor vary; tree (*Hemideina* sp.) and giant weta (*Deinacrida* sp.) are often cited in comparisons (e.g. Southern 1979; Daugherty et al. 1993; Morgan-Richards 1997), but generalisation as “weta” is also commonplace (e.g. Fleming 1973; King 1991; Burns 2006). Failure to qualify what species are being discussed means that interesting diversity in weta habits is not addressed. For instance diet, which is a commonly used parameter in ecological niche construction, cannot be addressed using this loose terminology. Ground weta (*Hemiandrus* sp.) and tusked weta (*Anisoura, Motuweta*) are primarily predators or scavengers of animal foods (Cary 1983; Winks et al. 2002), whereas tree and giant weta are unusual among their family in eating leaves (Green 2005; Trewick & Morgan-Richards 2005; Wilson & Jamieson 2005; Wehi & Hicks 2010). The diets of small mammals are similarly diverse; 7g common shrews (*Sorex araenus*) consume terrestrial arthropods and earthworms (Malmguist 1985), whereas 15g house mice (*Mus domesticus*) are omnivores with a large proportion of their diet consisting of seeds when available (Badan 1986; Tann et al. 1991). The various species of weta range in size from less than one gram to more than 50g. Small mammals that also span this range include the common shrew, *Sorex araneus*, and pygmy shrew, *S. minutus*, (7g and 4g respectively; Dickman 1988) *Mus musculus* (15g; Hamilton & Bronson 1985) and the bank vole, *Myodes glareolus* (23g; Verhagen et al. 1986).The largest weta are about one third the size of the smallest rat (*Rattus exclulans)* in New Zealand (130g; McCallum 1986) (Figure 2.1).

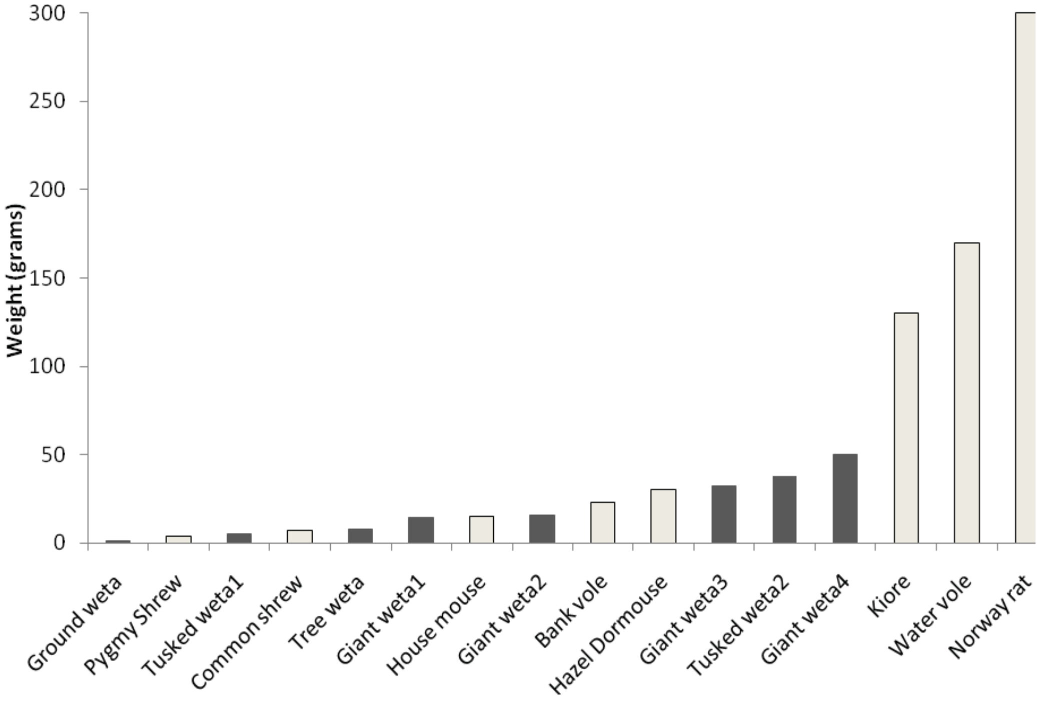

Figure 2.1: Comparison of weights between various small mammal and weta species. Taxa in this figure; ground weta, *Hemiandrus pallitarsis* (M. Griffin unpubl. data 2010); tree weta, *Hemideina* spp. (Gibbs 1998); Giant weta, *Deinacrida parva*[1], *D. elegans*[2] (Gibbs 1998), *D. rugosa*[3], *D. heteracantha*[4] (Gibbs 2001); Tusked weta, *Motuweta raparia*[1] (Gibbs 1998; McIntyre 1998) and *Motoweta isolata*[2] (Gibbs 1998); pygmy shrew, *Sorex minutus*; common shrew, *Sorex araneus*, (Dickman 1988); house mouse, *Mus musculus* (Hamilton & Bronson 1985); bank vole, *Myodes glareolus*, (Verhagen et al. 1986); hazel dormouse, *Muscardinus avellanarius* (Malatesta et al. 1999); kiore, *Rattus exulans* (McCallum 1986); water vole, *Arvicola terrertris* (Carter & Bright 2003); Norway rat, *Rattus norvegicus* (Calhoun 1962).

2.4 Does the phrase “invertebrate mice” help our science or our understanding?

Although the comparison of weta to a particular mammal is not consistent, the phrase “invertebrate mice” has become a popular cliché (e.g. King 1974; Fleming 1977; Ramsay 1978) and many authors have applied it even when making non-mouse comparisons (e.g. King 1974; Fleming 1977, referred to voles). Despite this inconsistency, we shall focus here on mice (*Mus*) and tree weta (*Hemideina*). Tree weta species have allopatric or parapatric distributions (their ranges do not overlap) and this suggests the biology of each species is very similar and thus subject to competitive exclusion where they meet (Trewick & Morgan-Richards 1995; 2004; 2005). In contrast, the co-occurrence of tree weta and introduced mice in New Zealand, suggests they are not in competition for resources. Major differences between tree weta and mice limit the usefulness of this comparison and may also allow them to exist in sympatry. The fecundity, energetics, and abundance of tree weta and mice are very different and putative similarity of some other traits provides only partial insight because the scale of influence within an ecosystem may be very different (Table 2.1). For instance, while mice and tree weta have some similarity in their predation of seeds (e.g. in New Zealand, tree weta *H. thoracica* and mice *Mus* spp. both eat seeds of kauri and rimu; Mirams 1957; Beveridge 1964; Badan 1986; Ruscoe et al. 2004), the effect that each has upon the tree species is likely to differ.

2.5 Fecundity

Although body mass of Orthoptera and rodents converge at about the size of small mice, the attributes of large insects and small mammals are nevertheless very different. Tree weta and mice are at different ends of their respective size distributions, and this highlights a difference that is expressed in their reproductive capacity. Small Orthoptera (such as *Gryllidae* crickets) often exhibit a “boom or bust lifestyle” like many smalls mammals; whereas larger Orthoptera, such as weta, tend to have slower growth and lower replacement rates (Whitman 2008).

The potential reproductive rate of mice far exceeds that of weta (Figure 2.2). Wild female mice (*Mus musculus*) become sexually mature at about 60-70 days old (Bronson 1984), have a three week gestation period, a litter size averaging six offspring and the ability to become pregnant soon after giving birth (Pelikan 1981). The reproductive characteristics of mice compared to other mammals can be characterised as r-selected, with a high intrinsic rate of increase (MacArthur & Wilson 1967). In contrast, tree and giant weta take about one year to reach sexual maturity and once adult, probably experience just one breeding season and are thus, compared to many smaller Orthoptera, K-selected (MacArthur & Wilson 1967). Although details of weta reproduction are scarce, for two tree weta species held in captivity (*H. thoracica*, *H. crassidens*) between 34 and 120 eggs per female were laid over approximately six weeks and hatching rates were between zero and 70% (Morgan-Richards, unpubl. data). Two-wild caught adult female tusked weta (*Motuweta isolata*) laid 153 eggs in captivity before death, although only 21 juveniles were recovered and 15 reared to adults (Stringer 1998). Using the tusked weta example, assuming 76 eggs per female and 100% fertility and survival, and an equal sex ratio, we calculated that a pair of tusked weta could in theory increase to 109,000 in three years. During the same time period a pair of mice (*Mus musculus*) could generate a population of over 30 million. The mouse intrinsic rate of increase is thus around 275 times greater than the weta.

The reproductive capacity of mice (and many other rodents) is highly responsive to short term changes in resource availability (also a characteristic of r-selected species; MacArthur & Wilson 1967). As mice are not limited to seasonal breeding they can respond to food abundance at any time of the year (Brockie 1992). For example, in New Zealand, seed masting of *Nothofagus* beech stimulates a rapid increase of mice (King 1983; Choquenot & Ruscoe 2000; Ruscoe et al. 2005). There is no evidence that any weta do or could respond to such resource fluctuations in this way.

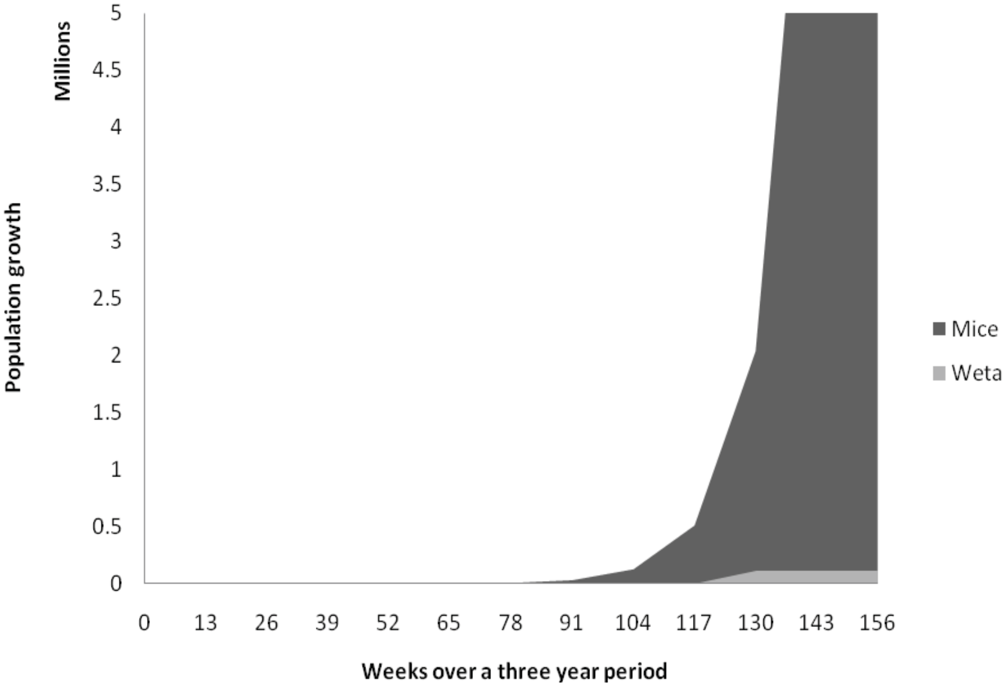

Figure 2.2: Population increase of *Mus musculus* and *Motuweta isolata* over a three year period

2.6 Metabolism

One reason that mice have such a high growth rate and responsive reproductive rate is that they are endothermic. Mammals expend a large proportion of the energy they consume maintaining their high body temperature (Bennett & Ruben 1979; Pough et al. 2005). Small mammals, such as mice, are at the physiological limits for vertebrate endotherms (cf. reptiles and amphibians) because their relatively large surface area to volume ratio results in inefficiency, compared to larger endotherms, and requires consumption of disproportionately large amounts of food to maintain their metabolic rate (Pough 1980; Pough et al. 2005). While some large mammals are leaf eaters, leaves do not appear to be sufficiently high quality food sources for small mammals. In this respect elephants could be considered a more appropriate mammalian equivalent of giant weta (*Deinacrida* spp.), in contrast to mice that consume a range of energy rich foods including insects and seeds. Ectotherms use solar energy as a heat source, so most of the energy they ingest goes to growth and reproduction (Pough 1980; Pough et al. 2005). This greater energy conversion efficiency means that insects such as tree weta and giant weta can exist even in thermodynamically demanding temperate and alpine environments even when consuming just leaves (e.g. Trewick & Morgan-Richards 1995; Sinclair et al. 1999; Joyce et al. 2004). However, the ability to survive in these circumstances is accompanied by relatively slow growth of individuals and populations. Even if tree weta and mice consumed the same types of food (which does not appear to be the case) their respective effects on the environment would be different.

The different energy requirements of these animals are reflected in their metabolic rates. Wild house mice have an average resting metabolic rate of 2.27 ml g^{-1} hr^{-1} O_2 (Miller 1999), and to sustain this mice in New Zealand need to consume about 91 kJ day^{-1} (Miller 1999). On a diet of seeds alone, this equates to 3g dry weight per day of rimu (*Dacrydium capressinum*) seeds (30kJ g^{-1} rimu seed; Ruscoe et al. 2004) or approximately 970 seeds (Ruscoe et al. 2004). An invertebrate only diet requires 4.3g day^{-1} (dry mass; Miller 1999). One investigation of mice in New Zealand found that they ate a mixed diet of adult arthropods, larva of Lepidoptera and seeds in exotic pine (*Pinus radiata*) plantations and native kauri (*Agathis australis*) forests (Badan 1986). Diets of mice and ship rats on Rangitoto Island were shown to consist primarily of invertebrates, with tree weta (*H. thoracica*) being the most common species consumed (Miller & Miller 1995).

Equivalent information on weta is scarce. However, comparable data for *Romalea guttata*, a large, herbivorous, North American grasshopper, where females weigh up to 6g (similar to the weight of adult tree weta and *Mus musculus*), are available (Hadley 1993). In this case, resting metabolic rate measured at 25^oC was found to be 0.125 mL g^{-1} hr^{-1} O_2 (Hadley 1993). Recent investigation into the metabolism of tree weta (*Hemideina crassidens, H. thoracica*) yielded a similar estimate of 0.114 mL g^{-1} hr^{-1} O_2 at 16^oC (Rowe 2009). This is about 0.05 the rate in mice. Individual tree weta (*H. crassidens, H. thoracica*) in captivity consume approximately 30 times less food than a mouse (average of 0.1g (wet weight) of leaf material per weta per night at 14^oC; Wyman 2009).

2.7 Environmental impacts

There are clearly major reproductive and thermodynamic differences between mice and tree weta and we expect these to be reflected in the impact of these animals on the ecosystem they occupy. However, there are currently few data for comparison even in terms of population densities of mice and weta. The data that do exist indicate considerable variation in space and time. For example, mouse densities range from 8 – 28 per hectare in Waitutu forest, South Island, New Zealand (Ruscoe et al. 2004). In contrast, estimates of tree weta densities range from 180 weta/ha on Banks Peninsula, South Island (Townsend et al. 1997) to over 5000 weta/ha on an island lacking native and introduced predators (Moller 1985). Thus we infer that each night mice may be consuming 8000 – 28,000 tree-seeds or 60-220g (wet weight, assuming 80% water) of arthropods per hectare, while at the same time tree weta may be eating between 20g and 500g of leaf material.

Although tree and giant weta appear to disperse and also predate seeds like some mammals (Duthie et al 2006, Wyman et al. 2010), their influence depends on the number of seeds consumed and destroyed and the distance travelled. In tree weta the number of seeds eaten is probably low, the proportion destroyed high and the distance travelled minimal (Wyman et al. 2010), so their importance as seed dispersers is likely to be low compared to other animals including mice and native birds. However, data for comparison of the actual amount consumed by various animals or even home range size are few. For example estimates of mouse home ranges of between 250m^2 and 470m^2 (Maly et al. 1985; Mikesic & Drickamer 1992), are not directly equivalent to data showing nightly movements of tree weta of <12m (Kelly 2006).

2.8 Conclusion

The usefulness of the comparison between the ecological niche of weta and mice (and other small mammals) is constrained by unspecific terminology and the superficial nature of initial comparisons which obscure much of the ecological and evolutionary distinctiveness of weta. The very different metabolic and reproductive rates and diets of these animals (e.g. mice versus tree weta) likely mean they have significantly different impacts on ecosystems (summarised in Table 1). Persistence of the invertebrate-mouse cliché, despite a lack of supporting evidence for similarity can best be attributed to lack of knowledge of weta. Thus studies of weta reproductive strategies and mate choice, population size and dynamics, fecundity, dietary repertoire, nutrient optimisation, and resource partitioning among weta taxa deserve close attention. Suitable data on these would also enable comparisons with taxa related to weta in other parts of the world, which coexist with native mammals (e.g. Australia).

Quantification of the effects that different weta species have on seed predation and dispersal, pollination, predation, and nutrient/ energy cycling is critical and would enable comparison with other animals in New Zealand ecosystems). The co-occurrence of weta and introduced rodent species in New Zealand today provides the experimental framework for comparative analyses of the ecological niches occupied by weta species, and energetics of New Zealand ecosystems. This will in turn contribute to better interpretation of the evolutionary history of the New Zealand biota and provide an empirical basis for testing what are in many cases to date, *ad hoc* interpretations.

Table 2.1: Summary of the differences between tree weta (*Hemideina*) and the mouse (*Mus*). (Data from: [a]Miller 1999; [b] Rowe 2009; [c] Ruscoe *et al*. 2004; [d] Townsend et al. 1997, Moller 1985; [e] Wyman 2009).

	Mouse (*Mus*)	Tree weta (*Hemideina*)
Weight	15g	8g
Rate of population growth	r-selected	k-selected
Metabolic rate (O_2/g/hr)	2.27 [a]	0.114 [b]
Density (per hectare)	8-28 [c]	180-5000 [d]
Diet (per night/per hectare)	8000-28,000 seeds [c] 34 - 120g arthropods [a]	20-500g leaves [e]

Chapter 3

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

A version of this chapter has been accepted for publication in New Zealand Natural Sciences journal as:

Griffin MJ, Morgan-Richards M, Trewick SA. 2011. Is the tree weta *Hemideina crassidens* an obligate herbivore? New Zealand Natural Sciences 36: 11-19.

http://www.science.canterbury.ac.nz/nzns/issues/vol36-2011/griffin.pdf

3.1 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. Most notably, Duthie *et al.* (2006) found seeds of *Fuchsia excorticata* in the faeces of wild *H. crassidens* and also identified a large variety of native fruits that they would consume in captivity, while investigating the possibility of seed dispersal by tree weta.

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 3.1). 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 3.1). 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 including 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 can only provide limited information 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 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.

3.2 Methods

Do tree weta demonstrate any partiality when offered a range of food types they might encounter in nature; leaves, insects, fruits and seeds? To test this, 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 3.1, Pers. Obs.). The leaves of *Coprosma robusta* were about 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 freshly caught wild 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

3.3 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 3.1). 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 (Figure 3.2). 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 3.1). Although there appears to be a subtle difference in the food of choice of adults compared with juveniles (Figure 3.1), 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.

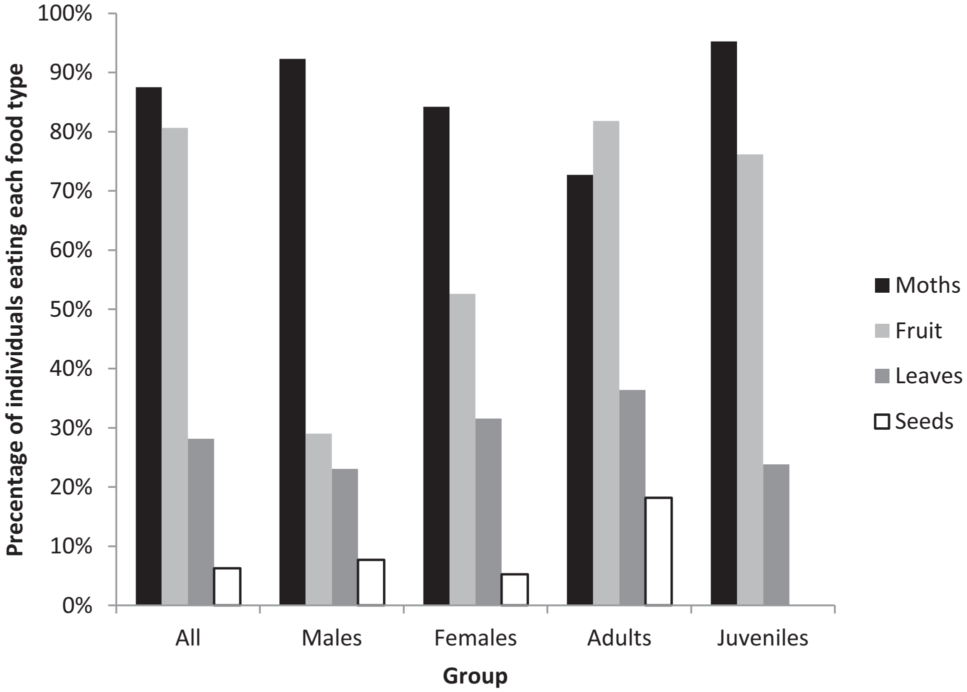

Figure 3.1: The percentage of the individual weta that ate each of the food types, grouped into males and females, adults and juveniles and overall the weta.

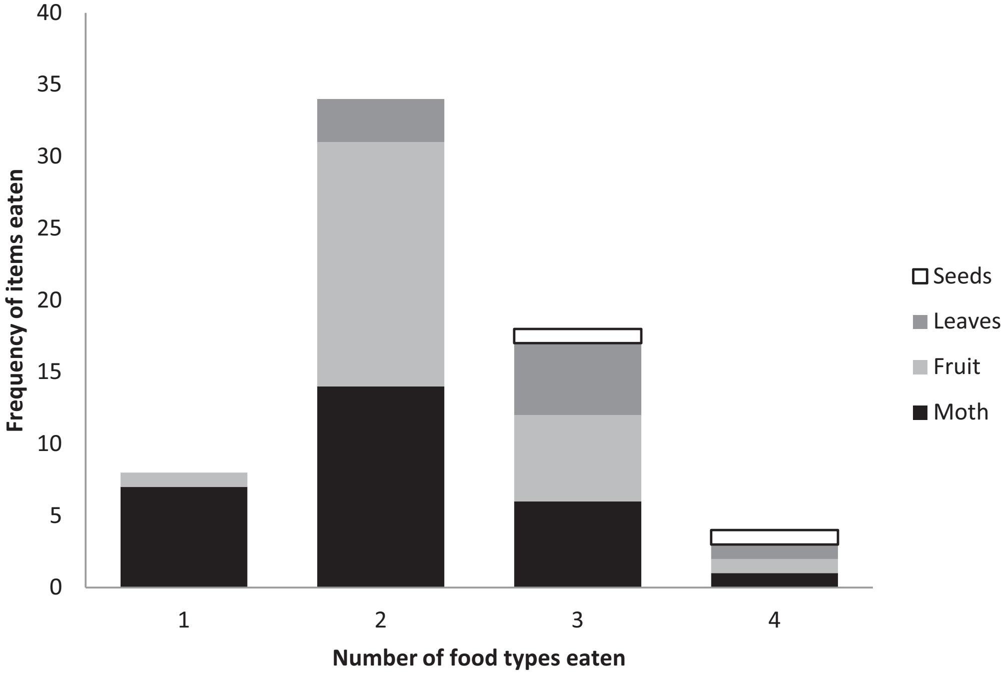

Figure 3.2: Frequency at which each food type was eaten for each of the number of food types eaten.

3.4 Discussion

Tree weta are commonly known to eat vegetation (Table 3.1). 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 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 3.1). In our experiment, tree weta that ate moths usually also ate 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 expected that further, more detailed studies of these weta will reveal a capacity for targeting nutrient optima by utilising a wide range of food types (Raubenheimer &Simpson 1993).

Table 3.1: References to tree weta diet in captivity and in the field

Food type		**Captivity†**	**Field†**
Plant Family	**Plant Species**		
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*	*crassidens*[1,2], *thoracica*[1]	*crassidens*[2]

	excorticata		
	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]

Species of weta are: *Hemideina crassidens, H. thoracica, H. femorata, Hemideina maori, H. ricta*.

[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] Personal observation, Morgan-Richards & Trewick; [9] Townsend 1995; [10] Little 1980; [11] Rufaut 1995; [12] Moller 1985.

†Captive 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.

*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 (Per. Obs., Morgan-Richards & Trewick).

Chapter 4

Dietary protein supplementation and its effect on growth and reproduction in tree weta (*Hemideina crassidens*)

4.1 Introduction

The consumption of moths and other invertebrates by tree weta (*Hemideina crassidens*; as shown in Chapter 3) in the wild may be opportunistic but there may be benefits from the occasional invertebrate in the diet. Eating invertebrates would be a much more efficient way for tree weta to add protein to their diet, compared to the consumption of large amounts of nitrogen-poor leaves. Consuming large quantities of leaves to gain adequate protein could have detrimental effects in terms of the accumulation of other compounds, possibly toxic, that plants contain in much higher concentrations than invertebrate tissue. There also may be constraints to the amount the individual is able on consume, such as the amount of food the gut is able to hold and digestive constraints (Hainsworth 1978).

Although there are many differences in the nutritional qualities of leaves and invertebrates, here I have chosen to focus on the much larger and more available protein content in other insects (moths) versus leaves. Nitrogen is essential for growth processes and reproduction of all plants and animals (Mattson 1980). Nitrogen is often the limiting nutrient for insect herbivores (Joern & Behmer 1997, 1998; White 1978). Although abundant in the world, nitrogen is often in a form which animals cannot make use of (White 1978). Grasshoppers and related species have a high demand for protein, where up to 50% of their cuticle is composed of protein (Hinks et al. 1993). Plants, however, contain a low proportion of nitrogen and to compensate for this, herbivorous insects such as grasshoppers, may have to eat large volumes of leaves to gain adequate nitrogen (Joern & Behmer 1998; White 1978). Experimental manipulation of the diet of the North American generalist grasshopper, *Melanoplus sanguinipes,* showed that protein had more of an impact on survival and reproduction than carbohydrate levels (Joern & Behmer 1998). Of the five diets tested on the grasshoppers, the diet with the intermediate (4%) nitrogen concentration gave the greatest rate of egg production (Joern & Behmer 1998). Similarly, fitness benefits to tree weta may result from gaining nitrogen from invertebrates rather than consuming large volumes of leaves to meet their needs.

Even in omnivorous insects, such as cockroaches, the limiting factor in their diet is thought to be nitrogen. One way the insects may compensate for this limitation is the consumption of their exuviae after moulting (Mira 2000). Nymphs and female cockroaches showed the highest instances of consumption of their exuviae and cockroaches fed on a high protein diet showed lower levels of exuviae eating (Mira 2000). These observations suggest nitrogen has a role in insect growth and female reproductive investment (Mira 2000). Tree weta also eat their old cuticle after moulting.

However, more than just the nutritional value of a food source may determine whether or not an organism will choose to consume it. Optimal foraging theory suggests an activity should be enlarged as long as the benefits of this activity outweigh the costs (MacArthur & Pianka 1966). Costs include the time it takes to procure the food, handling time and the likelihood of predation, as well as the digestive processes of the organism (Whelan & Brown 2005). Benefits gained from obtaining the best food possible, include increased chance of survival through proper nutrition and increased growth, also increased reproduction and therefore increased fitness. Optimal foraging theory predicts that tree weta will try to acquire the diet which will give them the best growth and reproduction. In the captive environment (choice experiment Chapter 3), more tree weta ate the high protein moths than the low protein leaves. In captivity many of the factors that may limit access to invertebrates by tree weta in the wild are absent.

4.1.1 Diet and reproduction

The effect of nitrogen and carbohydrates in the diet has been studied in many insects. Nutrition is the main environmental factor limiting reproduction where insects time their activity to coincide with the availability of high quality food (Wheeler 1996). The lack of adequate nutrients can inhibit the production of eggs (Wheeler 1996). In an herbivorous North American grasshopper species (*Ageneotettix deorum*), an elevated proportion of protein in the diet had a significant effect on the survival and reproductive potential of individuals, including weight gain and number of eggs laid (Joern & Behmer 1997). A decrease in food intake in a North American grasshopper (*Romalea guttata*) had a negative effect on egg production in females (Moehrlin & Juliano 1998). Similarly, development is fastest for locusts fed a large excess of protein (Raubenheimer & Simpson 1997).

The development of eggs and the maturation and survival of young can be dependent on the diet of the adult female, which can affect the production of the yolk protein, vitellin (Hinks et al. 1993). The yolk of an insect egg contains a high proportion of yolk proteins (Izumi et al. 1994). The fat body of insects produces vitellogenin which is the precursor for these yolk proteins (Arrese & Soulage 2010; Izumi et al. 1994). The quality of the egg, in terms of the nutrients available to the developing young, will influence their potential fitness. Dietary protein was a good predictor for the survival of gypsy moth (*Lymantria dispar*) larvae; those with a higher proportion of protein were able to survive longer though food was peridoically in short supply (Diss et al. 1996). Protein content of the eggs was also the best predictor for survival in the wasp parasitoid, *Eupelmus vuilletti,* and along with carbohydrates and lipid were correlated with egg size (Giron & Casas 2003).

If tree weta actively select moths over leaves to eat, what effect would a constant abundant protein source in their diet have on their growth and reproduction? When nitrogen is not limited we would expect tree weta to choose the optimal quantity of protein necessary to maximise survival and reproduction. To test this prediction I compared growth and fecundity of captive female tree weta (*Hemideina crassidens*) with and without protein in their diet.

4.2 Methods

Juvenile female Wellington tree weta (*Hemideina crassidens*) were caught from the wild in the Kahuterawa valley, Palmerston North. Juveniles ranged from the 6th to 8th instar when collected from the wild and most were in their 7th instar. The weta were housed individually in plastic 2L containers. The lids of the containers had mesh fitted in them for air circulation and light, and each container had a roost made from hollowed flax (*Phormium tenax)* flower stalks for the weta to hide in during the day (Wyman 2009). Each roost was split in half and held together with rubber band, so that the weta could be easily removed from the roost during the day for measurements to be made.

4.2.1 Growth

The weta were randomly assigned to one of two groups. One group received only an assortment of leaves from native plants (19 tree weta), while the second group received the same combination of leaves plus a soy protein supplement (18 tree weta), in pellet form (Red 8 protein plus nuggets). Native plants fed to the weta were mahoe (*Melicytus ramiflorus*), miro (*Prumnopitys ferruginea*), karamu (*Coprosma robusta*) and tuapata (*Coprosma repens*). Each week, individual weta were given a combination of two of these plants, these were alternated weekly, in the expectation that the weta would obtain a range of nutrients required for growth and survival, from these plants. A wet paper towel was wrapped around the bottom of the stems of leaf clusters to keep them fresh and to stop the container from drying out and their containers were misted with water regularly. The soy based protein source comprised of 80% protein provides a standard and controlled delivery of protein to the tree weta. Fifteen soy protein pellets were put into a Petri dish in the each container wit high-protein group weta with a small amount of water to soften them. This pellet was changed three times a week in clean Petri dishes to prevent mould build up.

Once a week each weta was weighed using digital scales measuring to the nearest microgram and their rear tibia lengths were measured with digital callipers, in millimetres to two decimal places. Measuring the tibia lengths provided and indicator of moult status, since these lengths only change significantly when moulting occurs. As all female tree weta have 10 moults to maturity, it was possible to back calculate from adult the tibia lengths associated with each instar.

4.2.2 Reproduction

Female tree weta were distinguished as adults when their ovipositor became curved, sharply pointed and darker at the tip. Once the female weta reached maturity, an adult male *H. crassidens* was put into the female’s container for three nights. After three nights the male was removed and a plastic container of soil (sterile, Oderings nursery potting mix) was put inside the female’s box for oviposition. The oviposition box was deep enough for the female to insert her ovipositor and the soil was kept damp over the month that it was left in the weta box. After one month, the soil was sorted and the number of eggs laid counted.

However, after one month few of the female weta had laid eggs. To induce the weta to lay, the females were maintained at a slightly elevated temperature, some were given a larger container to live in, some had moss put on top of the soil to get them something to lay through and to keep the soil moist, and some weta were given the choice of laying in perlite, vermiculite or the potting mix. None of these changes increased the number of individuals laying eggs.

After a minimum of 30 days after being mated, adult weta were euthanized and their eggs collected. Weta are best dissected when fresh, so they were killed using ethyl acetate. Some weta died while adult and were immediately frozen and later dissected to remove their eggs. A longitudinal incision was made on the ventral surface of the abdomen; this was lengthened along one side of the weta then over the abdomen and down the other side of the animal so that a flap could be folded out. Care was taken to avoid any damage to the oviduct where the eggs are held. The cuticle was pinned out and this allowed for an estimate of the condition of each individual. Each weta was given a condition score based on the amount of fat present inside the animal (Table 4.1). The oviducts were then removed intact from the weta. The total numbers of eggs were counted for each weta and added to the number of eggs that the weta had laid if they did so. The weta and the eggs were then frozen in air-tight containers.

Table 4.1: Scale used for condition score of dissected adult female tree weta

Condition score	**Amount of fat**
0	No fat
1	Very small amount
2	Medium amount, patchy
3	Thin layer, covering most of cuticle, maybe some small accumulations
4	Abundant, thick, fat layer over all organs

The lengths of 20 randomly selected eggs from each female were obtained using a graticule in the eye piece of a dissecting microscope.

4.2.3 Nutrient analysis of eggs

Nutrient analysis of the eggs was conducted by the nutrition laboratory at Massey University (AHA level 2), Palmerston North. A sample of 10 eggs, from 6 weta in each feeding group (12 individuals in total) were selected at random. Nitrogen content of eggs was important for the survival of the young once hatched (Diss et al. 1996; Giron & Casas 2003). The proportion of nitrogen in the eggs of weta in each group was obtained for comparison.

4.3 Results

4.3.1 Growth

Data from weta that died during the course of the experiment were included in the growth experiment as long as they were alive for at least one full instar. The average weight, of the tree weta in each group, (18 in high protein and 19 in low protein) at each instar were compared using a one-way ANOVA (Table 4.2). There was no difference in the weights of the weta in the high protein group and low protein group at the 6th instar (F = 0.06, p = 0.847) or the 7th instar (F = 0.10, p = 0.761). In the 8th (F = 6.51, p = 0.018), 9th (F = 19.75, p = 0.000) and adult (F = 15.51, p = 0.001) instars the weta in the high protein group were heavier than those at the same instar in the low protein group (Table 4.2).

Table 4.2: Comparison of tree weta weights between the high protein diet and the low protein diet, at five group stages. (P<0.05 deemed significant)

Instar	**High protein mean weight (g)**	**Low protein mean weight (g)**	**F stat**	***P***
6th	0.6460	0.6747	0.06	0.847
7th	1.0762	1.0982	0.10	0.761
8th	1.8052	1.5596	6.51	0.018
9th	3.0737	2.3617	19.75	0.000
Adult	4.6206	3.3912	15.51	0.001

Differences were evident in the rate of weight gain per day (g/day) between the high protein diet and low protein diet adults (one-way ANOVA, F = 24.79, p = 0.000) and 9th instar individuals (F = 16.65, p = 0.001) but not in the 8th instar individuals (F = 4.63, p = 0.053) (Figure 4.1). Weta started at approximately the same weight when collected from the wild. They were maintained on these different dietary regimes and achieved different growth trajectories (Figure 4.1).

There was no difference between the two group in the length of time that was spent in the 9th instars (one-way ANOVA, F=2.29; p=0.151). One individual in the low protein group took 26 weeks to moult to adult while the shortest time for a weta in this experiment to moult to adult was 10 weeks for an individual in the high protein group.

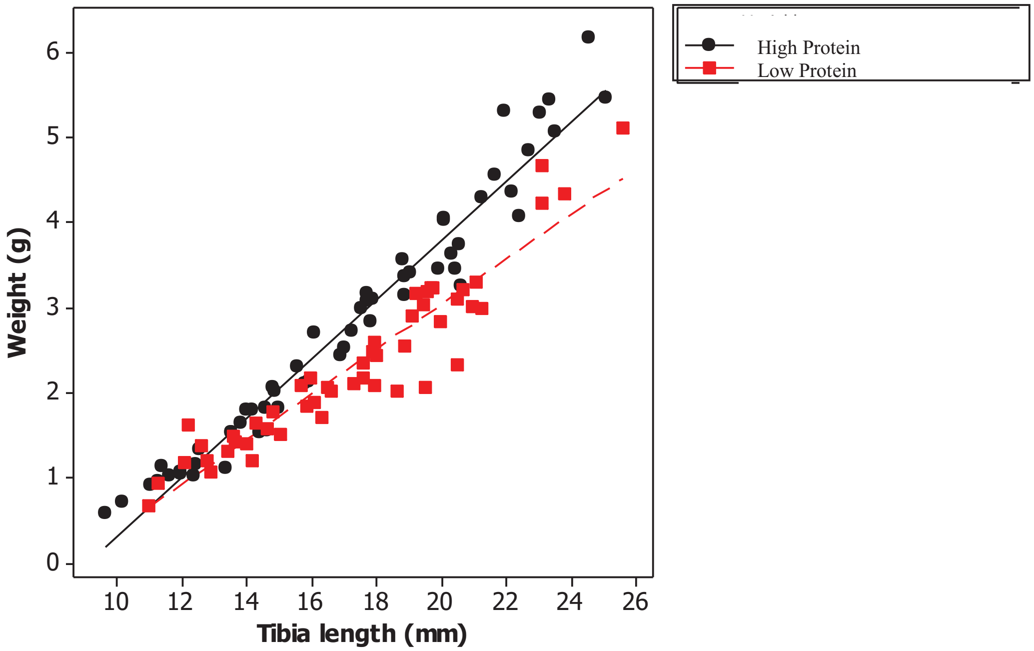

Figure 4.1: Tibia length (mm) and weight (g) of weta in the high protein and low protein groups, at all instars. Each point on the graph is an individual weta tibia length and average weight at a particular instar.

4.3.2 Condition Scores

All the weta on the high protein diet were categorised by dissection as condition score four, having high levels of fat (Figure 4.2). They all had ample fat that formed a thick covering throughout the inside of their body cavity on the as well as surrounding their organs, including the ovaries. The weta in the low protein feeding group fell into condition scores one and two. They had small to moderate amounts of fat, those in category two were distinguished from those in category one because the fat deposits seemed to be more evident inside of the cuticle. One weta had a condition score of zero and had died and it was possible that this is not an accurate estimate of this individuals condition score.

4.3.3 Egg number and size

From the 37 female weta in the growth experiment 18 reached maturity and produced eggs in the time available to them (8 from the protein group and 10 from the low protein group). A further two females in the high protein group were adult and had been put with a male but failed to produce eggs it is likely that these two individuals may not have been adult for long enough to produce eggs. The total number of eggs produced (laid + dissected) in the time that was available ranged from 55 to 140 eggs per individual. The mean number of eggs produced by weta in the high protein group was 104, while the mean of the low protein group was 80. However, there was no significant difference in the number of eggs produced between the two groups (one-way ANVOA, F=4.32, p=0.054). A larger sample size would be advantageous in finding any differences that may be between these two groups. There was also no difference in the length of the eggs between the two feeding groups (one-way ANOVA, F=1.21, p=0.287). When considering both the number of eggs and the length of these eggs there is a much greater variance seen in the data from individuals in the high protein group than in the low protein group. Variance in the high protein group for egg length is about 8 times greater than in the low protein group. The variance in egg numbers in the high protein group is twice that of the variance in the low protein group.

There was no relationship between the number of eggs that a female produced and the number of days that she had been an adult for either of the feeding groups (Figure 4.3). The graph does however; show that the average number of eggs produced by the weta in the high protein group was greater than the number of eggs produced by those in the low protein group.

4.3.4 Nutrient analysis of eggs

The mean percentage of nitrogen in the eggs from the weta on the high protein diet was 7.5% while the mean nitrogen percentage of those weta on the low protein diet was 7.2% (Figure 4.4). However it is evident that the individual with the highest nitrogen content had the smallest eggs. With the small sample size this individual is unable to be excluded from the data as an outlier. Using an ANOVA there was shown to be no difference in the percentage of protein in these two groups (F=2.31, p = 0.176). This lack of difference could be related to the small sample size. However, this is valuable baseline information on the egg nitrogen content in tree weta.

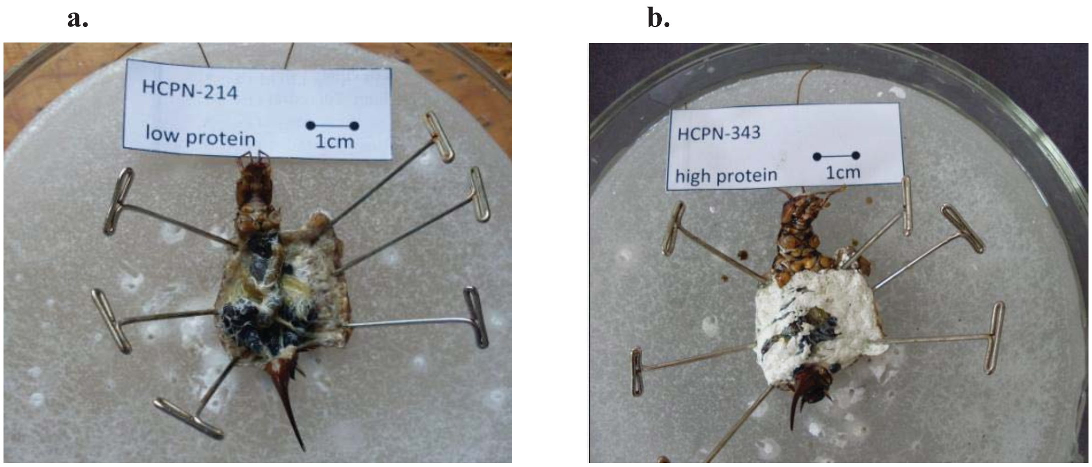

Figure 4.2: Examples of condition of female adult tree weta **a.** Condition score 2, moderate amount of fat, definite coverage of inside of cuticle, low protein diet; **b**. Condition score 4, very thick layer of fat covering organs, high protein diet.

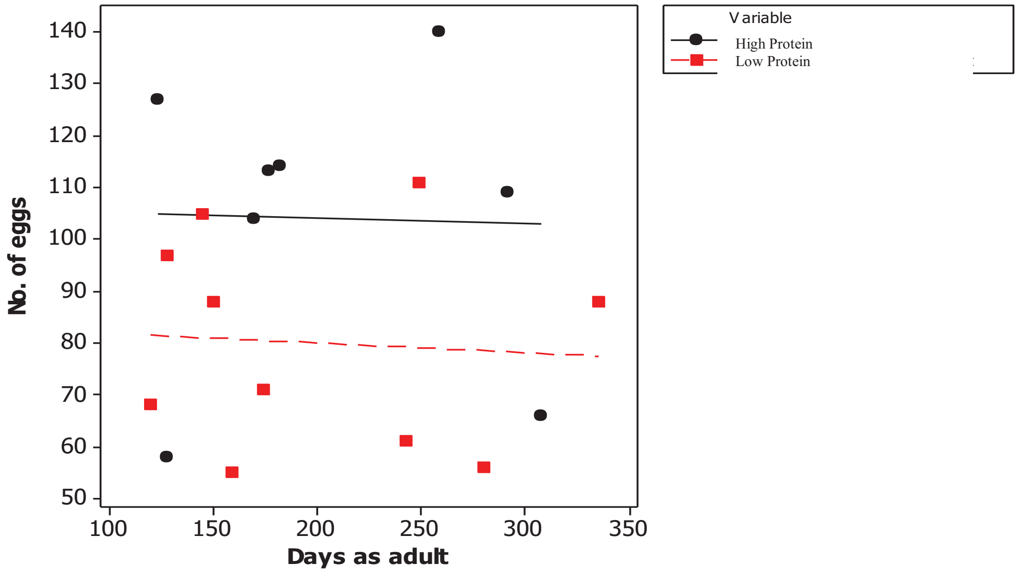

Figure 4.3: Relationship between the number of days that a female tree weta was an adult and the number of eggs it produced, for each feeding group.

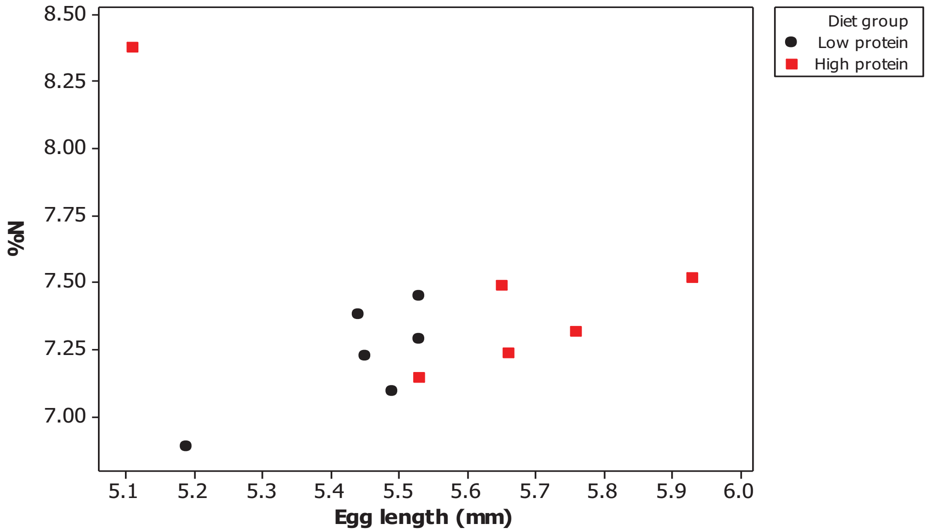

Figure 4.4: Relationship between the average lengths of eggs produced by each female and the proportion of nitrogen in the eggs, across the low (black circles) and high (red squares) protein groups.

4.4 Discussion

Diet is important for the growth and reproductive potential of an individual. The diet of an individual can determine number or quality of offspring produced. Better quality offspring will have an increased chance of survival and therefore a better chance of reproducing themselves. Tree weta are able to survive on a diet largely made up of leaves and one advantage of this in a forest ecosystem lacking herbivorous mammals is there is ample resource of foliage. I predicted that the addition of a more readily available protein source to their diet would have positive effects on the reproduction and growth of the Wellington tree weta.

The prediction was met in a limited way. The female Wellington tree weta, *Hemideina crassidens*, on the high protein diet gained much more weight and gained weight faster than those on the low protein diet. These weta also all had large amounts of fat accumulated around their organs and covering the whole of the inside of the cuticle. The increased rate of growth of the weta on the high protein diet means that they would reach adult size before those individuals that were on the low protein diet. This is likely to allow weta to reproduce earlier than those on a low protein diet. High nitrogen diets in the larvae of gypsy moths (*Lymantria dispar*) lead to faster growth rates but during food shortage these individuals had decrease longevity (Stockhoff 1991). Larvae on a high nitrogen diet may have an advantage when food reserves were ample but had lower fitness when food was scarce. Consumption of a high nitrogen diet means less storage of carbohydrates which are a more readily available energy source during starvation (Stockhoff 1991). A lack of lipid reserves after consuming a diet high in nitrogen in the tree weta in this study was not seen. The high protein diet resulted in weta storing abundant lipids in their body cavity, suggesting that they would be able to survive for periods without food. Tree weta readily eat leaves and can survive and reach adult instars on a diet of leaves alone. So there is potential for tree weta to survive periods, when other sources of protein are not plentiful, on a diet of leaves alone and still be able to grow and reproduce. The length of time that an individual could survive and grow successfully may depend on the amount of protein that was previously eaten in their diet. The nymphs of the omnivorous big eyed bug, *Geocoris punctipes,* were more likely to survive periods without prey when they had previously been feed high protein corn-ear worm (*Helicoverpa zea*) eggs than when they had been fed on relatively low protein pea aphids (*Acyrthosiphum pisum*) (Eubanks & Denno 1999). Conversely, when the nymphs were fed on lima bean pods alone the lack of a suitable amount of protein meant that they were not able to complete development past the third instar (Eubanks & Denno 1999). Big eyed bugs benefit from mixing a diet of plants and animals, and the consumption of higher quality prey can offset the cost of long periods without sufficient prey (Eubanks & Denno 1999).

The added fat reserves in the high protein group of tree weta may be advantageous in resisting starvation. Starvation is the depletion of reserves that an individual requires for energy metabolism (Stockhoff 1991). Individuals with low fat reserves may not suffer high mortality when feeding opportunities are fewer such as during the winter when temperatures are lower, or when the risk of predation is higher. Increased condition (fat stores) could mean that individuals do not need to leave protective their roosts as often. The diet which an individual has been previously consuming may affect the length of time that it is able to survive without adequate nutrition as individuals with larger body size will have increased resistance to starvation through decreased energy requirements from lower relative metabolic rate (Stockhoff 1991).

This extra fat in the tree weta in this experiment however, did not correspond to an advantage that was seen in their reproduction. There were no extra eggs produced from the high protein weta. The eggs produced were not bigger and there was not an increased amount of nitrogen in the eggs to increase the survival of the offspring. This experiment though, was relatively short term. There is a possibility that the increased fat that accumulated in the tree weta on the high protein diet may have more of an impact in the longer term. If conditions are right for laying the weta with larger amounts of fat reserves may have been able to lay many more batches of eggs. From limited observations of tree weta laying in the wild (Moller 1985) it is thought that females will insert their ovipositor into the ground multiple times and may only lay one or two eggs each time it is inserted into the ground. This suggests it might be beneficial to be able to survive for longer periods of time without food so that they can spend more of the night laying eggs.

Increased fat reserves may also mean the weta do not have to leave their roost as often to search for food. The fat deposits inside the weta were white in colour. In the American cockroach, *Periplaneta americana,* it is presumed that the white deposits in the fat body are uric acid (Mullins & Cochran 1975). Nitrogen is an important compound in American cockroaches, and when there is excess nitrogen in the diet of the American cockroach preferential storage is as uric acid (Mullins & Cochran 1975). Uric acid may be used as a nitrogen reserve that is able to be mobilised when they are low in nitrogen, supplementing the post moult process (Mullins & Cochran 1975). Similar patterns may be seen in the tree weta if they are storing nitrogen reserves for provisioning the body when nitrogen in the diet is not as plentiful. The risk of predation will determine if an animal goes out to forage for food or how long the animal will forage for. When predators are present foraging may be inhibited (Hassell & Southwood 1978). Gravid females become large and conspicuous and may lose some of their mobility and this can lead to an increased risk of predation if these females have to venture out each night to search for food (Magnhagen 1991). Female tree weta with large fat reserves could stay in their roosts for longer and avoid this predation risk.

However, the large amount of fat that had accumulated in the body cavity and around the organs of the tree weta on the protein diet tentatively suggests that the weta were not tightly regulating their intake of protein. The weta seemed to not have been able to regulate the amount of fat that was being accumulated from the diet. Leaves are low in nitrogen and foliage of New Zealand trees are particularly low when compared to the nitrogen content of tree leaves in other countries. Some New Zealand trees (e.g. *Agathis australis*) can even have a nitrogen content of below 1% (Wehi & Hicks 2010). Of 23 tree species grown in North America sampled for their nutrient content the nitrogen content was highest at the beginning of the growing season, generally above 2% and some as high as 5% of the dry weight of the leaf and while nitrogen content decreased as the season advances it did not got below 1% for any of the plants tested (McHargue & Roy 1932). In the wild it is possible that because of this low nitrogen content in food they will eat high protein foods whenever they come in to contact with them. The tree weta in this captive experiment with a constant supply of protein may not have been able to regulate their desire to consume the protein and did so continually causing a large build-up of excess fat.

There is a possibility that even though there has been no difference in the effect of the high protein to the diet of female tree weta in the short term there could be long term benefits. The increased availability of protein to some of the weta increased their rate of growth and these weta grew to larger sizes as adults. This could be beneficial for longer term survival when food is scarce or the risk of predation is higher. More observations and information about the frequency of predation or scavenging of invertebrates by Wellington tree weta, *H. crassidens*, in the wild are needed and how this relates to their reproduction and longevity in the wild. Also long term studies on the frequency that tree weta leave the roost to eat could help understand the relationship with this large amount of fat storage seen here.

Chapter 5

Carbohydrate and protein feeding patterns in Wellington tree weta (*Hemideina crassidens*)

5.1 Introduction

The balance of nutrients ingested by insects may influence the growth and survival of individuals in the population. Nutrients are those chemicals, such as protein and carbohydrate considered here, used in growth and development of an organism. Insect nutrition is concerned with the conversion of food into insect performance such as growth, survival and reproduction (House 1969). Some nutrients are essential in the diet and without these, development will not be completed. Nutritional requirements are the specific types and amounts essential to adequately provide for the body functions (House 1969), and the general nutritional requirements of most insect orders are known (House 1962). Nutrients must be ingested in specific quantities for the optimal level of nutrition and excess amounts of some, which may be overeaten to gain enough of others, can be toxic (House 1959; Raubenheimer et al. 2009). If nitrogen is the limiting factor in their food, it is assumed that all other nutrient needs are met by consuming enough nitrogen (Joern and Behmer 1998).

Nutrients are used more efficiently when the specific intake is self-selected by the individual than if the diet has a set nutrient level, as the nutrients can be best used for survival (Waldbauer & Friedman 1991). A food that is nutritionally balanced will allow an animal to reach a balance of nutritional requirements fastest without the consequences of overindulgence that are results with unbalanced foods (Raubenheimer and Simpson 1993). At different stages in an individual's life history there may be changes in these nutritional requirements (Raubenheimer and Simpson 1993); growth in juveniles may require a different set of nutrients than those required by adults. Males and females may also have different needs for nutrients, for example female requirements may change depending on the stage of their egg development.

Insects have different mechanisms by which they recognise what nutrients are needed to help balance their nutritional requirements (House 1969). In some cases this is through selection of prey depending on their nutrient content, or by variation in the amount eaten (in the case of single prey types) depending on their nutrition state (Maytnz et al. 2005). Some insects are able to extract only the specific nutrients they need from their prey (Maytnz et al. 2005), and some are able to regulate their nutrient balance once foods have been ingested. Locust nymphs retained proportionally more nitrogen when consuming less than 30mg of nitrogen than when their protein consumption was higher due to higher nitrogen content in their frass (Zanotto et al. 1993). The haemolymph can provide information on an individual's nutritional state to assist with the intake of nutrients in a balanced manner (Simpson & Raubenheimer 1993). Sugars and amino acids in the diet are also important phagostimulants and may be central in regulating the intake of foods (Simpson & Raubenheimer 1993). The proportion of digestible material in some plants is much greater than others (House 1969), and an ability to distinguish between high and low digestibility plants could have important implications for the time spent foraging and being exposed to predation. The rate at which insects consume a food varies depending on the balance of nutrients presented in the food source, such as the amount of indigestible cellulose (House 1969).

Dietary self-selection by insects has important implications for our understanding of the way insects interact with plants and other organisms and allows the exploration of behavioural and physiological approaches of insects to feeding (Waldbauer and Friedman 1991). Generalist herbivores tend to tolerate nutritionally imbalanced food than insects that are monophaguous; this is likely because they have higher probabilities than specialists of encountering a nutritionally equivalent food (Raubenheimer and Jones 2006). Wellington tree weta exhibit polyphagy and will also eat dead invertebrates suggesting that they would be able to cope with nutritionally imbalanced foods. Locusts (*Locusta migratoria*) are able to regulate both their protein and carbohydrate intake through phagostimulants such as amino acids and sugar and the regulation of nutrients in the blood (Raubenheimer and Simpson 1993). Larvae of *Agria affinis* (Diptera) selected diets according to the balance of nutrients which was also the same as the order of importance for optimal growth and development (House 1969). Ground beetles (*Agonum dorsale*) were given a pre-treatment food of a high lipid or a high protein food then given the test diet where they were given the pre-treatment food plus a complementary food choice (Mayntz et al. 2005). The ground beetles showed that they were able to detect the content of their food and were then able to balance their nutrients in the test. Those beetles consuming a pre-treatment diet high in lipids went on to eat more of the high protein diet in the test circumstances (Mayntz et al. 2005). In some insects, short pre-feeding periods were sufficient to generate nutrient specific feeding responses (Mayntz et al. 2005).

Tree weta are fairly mobile with movements up to 12 metres in one night (Kelly 2006), suggesting that they have ample opportunity to encounter diverse of food types with differing nutrition values. They would have to make decisions about the kinds of food they consume and the amount of a particular food type they consume, based on their developmental needs or even daily needs.

The overall aim of the present study was to determine whether tree weta *H. crassidens* balance nutrients (protein and carbohydrates) in their diet by selective foraging. I investigated this in a laboratory setup, with artificial foods to control nutrient composition. If the tree weta were able to balance their food; once fed the pre-treatment, setting the nutritional state, they should then elicit a compensatory nutrient feeding response.

5.2 Methods

Thirty-six adult wild caught Wellington tree weta (*H. crassidens*) (14 males and 22 females) were kept in captivity in 2 litre plastic containers, as described in the previous chapters (Wyman 2009). These tree weta were reared from wild caught juveniles to adults in captivity on an *ad lib* diet of a variety of native leaves and soy protein pellets. They had been previously used in non-invasive metabolism experiments but not in dietary analysis. Adult tree weta were chosen so that a single life stage was assessed, none of these weta would be nearing moulting which may have an effect on nutritional needs. Juveniles at early instars may also have different nutritional needs than those at later instars.

The diet used was cellulose based dry food. The high protein diet contained 28% protein and 7% carbohydrates, while the concentrations in the high carbohydrate diet were 28% carbohydrates and 7% protein. The diet was based on those described in Simpson and Abisgold (1985) and Simpson and Raubenheimer (2001) and was prepared with instruction from D. Raubenheimer, Massey University (pers. comm.). Protein was in a 3:1:1 ratio of casein, peptone and albumin. The carbohydrates used were sucrose and dextrin (1:1). The diet was balanced so that only the quantities of protein and carbohydrates changes between the two diets. Linoleic acid, cholesterol, Wesson's salt and the vitamin mix was at the same concentrations in both diets. Once mixed the diets were dried at 30^{o}C for 48 hours; then stored by freezing until use.

The tree weta were allocated randomly into one of four groups, with nine individuals in each group and two sexes approximately evenly distributed among the groups. Each group had their food removed for three nights before the start of the experiment. They were then given a pre-treatment diet of either high protein component or a high carbohydrate component. They were fed this diet for four nights with the objective of setting the nutritional state of each individual tree weta. After this time they were given a test diet where individuals in each group had the choice of their pre-treatment food and a complementary food, or the pre-treatment food again (Table 1).

Table 5.1: The four diet groups in the nutrient balancing test.

	Pre-treatment	Test foods
Group 1 (PPP)	High protein	High protein + High protein
Group 2 (PPC)	High protein	High protein + High carb.
Group 3 (CCC)	High carbohydrate	High carb. + High carb.
Group 4 (CCP)	High carbohydrate	High carb. + High protein

Each tree weta was weighed individually using digital scales to four decimal places at the start of the pre-treatment diet and at the end of the test diets. The diets were provided in small Petri dishes. Each Petri dish was weighed, and the weight recorded, the scales were then zeroed and approximately one gram of the appropriate diet was measured out into the dish. After each of the four nights, the pre-treatment diet was re-weighed to obtain a measure of the amount that individual tree weta were eating. At the end of the pre-treatment period this food was removed and the test diet provided. New, clean Petri dishes were used and labelled clearly as to which diet was in each dish. Each dish was weighed and again approximately one gram of the appropriate diet was put into them. The test diet was left with the tree weta for seven nights (initially the plan was to provide the test diet for four nights also but most of the weta did not eat at all for the first three or four nights). Each Petri dish was weighed every day for the duration of the trial. At the end of the trial each tree weta was re-weighed.

Identical containers, for each group, were set up minus the weta to obtain a measure of the amount of moisture that was absorbed/ lost by the diet in order to correct for experimental effects. There was an average of 1.2% increase in the weight of the protein diet through water absorption. The carbohydrate diet increased on average by 2.24% due to water absorption.

5.3 Results

The general trend shown by individual weta during the pre-treatment period was to eat progressively less over the four days (Figure 5.1). The greatest amount was eaten on the first night of the pre-treatment. The tree weta in this experiment ate much more food in the pre-treatment (mean = 0.7012 g/ weta) than in the test diet phase of the experiment (mean = 0.0370 g /weta; one-way ANOVA, F = 15.64, p = 0.000). There was no difference in the average amount of food eaten between males and females in the pre-treatment phase of the experiment (one-way ANOVA F = 0.01; p = 0.922) (Table 5.2). The actual amount of protein and carbohydrate eaten was related to the total volume of food eaten (Table 5.3).

Table 5.2: Amount of diet eaten by males and females during the pre-treatment phase of the experiment

	Average (g)	Lowest individual (g)	Highest individual (g)
Males (n=14)	0.7149	0.2359	1.0192
Females (n=22)	0.7012	0.1276	1.0988

Table 5.3: The average amount (g) of carbohydrate and protein eaten in each diet during the pre-treatment for each of the pre-treatment groups (high carbohydrate versus high protein).

	High carb. diet	High protein diet
Carbohydrates eaten during pre-treatment	0.1909	0.0504
Protein eaten during pre-treatment	0.0477	0.2018

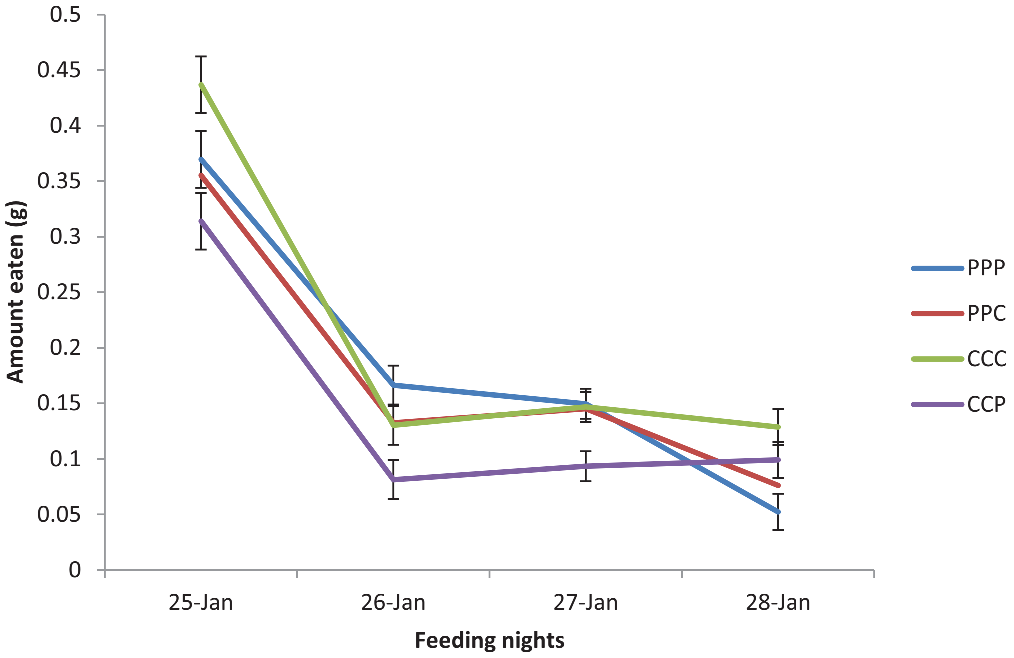

Figure 5.1: Average amount eaten by the tree weta in each of the four test groups, with standard error; on the pre-treatment over each of the four nights. Details about groups in Table 5.1.

In the test phase of the experiment, Wellington tree weta did not appear to actively balance protein and carbohydrate intake (Figure 5.2). In the PPC diet group there was no difference in the amount of the high-protein diet or high-carbohydrate diet eaten in the test after the high-protein pre-treatment (one-way ANOVA, F = 0.78; p = 0.389). The tree weta in the CCP group also showed no difference in the amount of high-protein diet eaten compared to the amount of high-carbohydrate diet eaten after the carbohydrate pre-treatment (one-way ANOVA; F=1.26; p=0.279). The control groups (one way ANOVA, PPP: F = 0.02, p=0.886 and CCC: F = 1.08, p = 0.314) also showed no difference in the amount that was eaten from each dish.

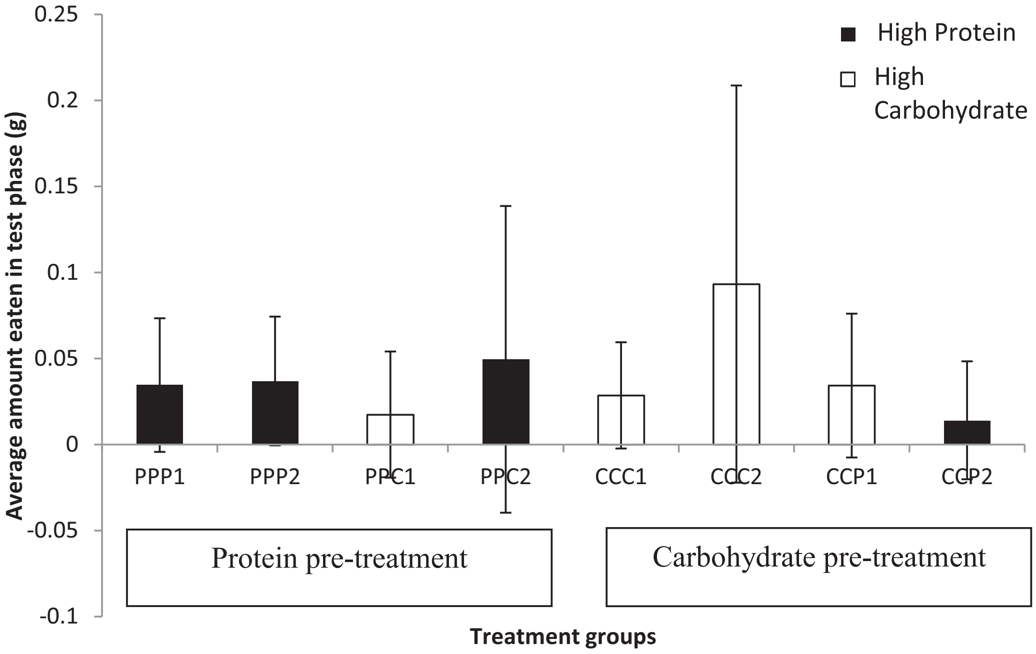

Figure 5.2: The average amount eaten by each tree weta in the test phase of the experiment from each dish presented grouped by the diet the weta were given in the pre-treatment phase, error bars show standard deviation.

Six tree weta (two males and four females) died during the test diet phase of this experiment; all of these weta had received the high-protein diet during the pre-treatment. A further three individuals were found dead four nights after the experiment was ended, one each died from the CCC, CCP and PPC diets. All the tree weta, with the exception of one individual (diet CCP) lost weight over the course of this experiment. However, the tree weta on the protein pre-treatment lost a greater amount of weight than those on the carbohydrate pre-treatment (one-way ANOVA, F=5.24; p=0.005).

5.4 Discussion

Previous studies of nutrient selection in insects have revealed an ability to track dietary composition of foods and achieve an optimum, in a range of species. Thus I expected that under experimental conditions the Wellington tree weta, *Hemideina crassidens,* would also show this ability to actively balance nutrient intake. For instance, if they had previously eaten a protein rich diet I expected the tree weta would selectively consume a relatively carbohydrate-rich food when given a choice between this and a protein-rich food. However, the tree weta did not balance their carbohydrate and protein intake over the time available. Tree weta which had received the high-protein pre-treatment did not then switch to the high-carbohydrate in the test. Similarly, tree weta on the high-carbohydrate pre-treatment did not eat significantly more of the high-protein food during the test phase. There was no difference in the amounts eaten by males versus females justifying their reference as one group. Sex of *Locusta migratoria* was also found to have no effect on nutrient balance selected by the individuals (Chambers et al. 1995).

The apparent lack in ability of these tree weta to regulate nutrient intake through selective feeding over time, contrasts with many other invertebrates. The corn earworm, *Heliothis zea*, was found to self-select an optimal diet of 80% protein and 20% carbohydrate with little variation among individuals (Waldbauer et al. 1984). Nymphs of the locust, *Locusta migratoria,* were able to detect nutrient content of their food and alternated between complimentary food types to acquire an adequate nutrient balance (Chambers et al. 1995). Predatory wolf spiders, *Pardosa prativaga,* also varied their consumption of *Drosophila* with differing lipid and protein concentrations depending on their nutrient requirements (Mayntz et al. 2005). After consuming a high-protein diet the spiders chose to consume *Drosophila* with high lipid content in the test phase (Mayntz et al. 2005). Desert spiders, *Stegodyphus lineatus*, also balanced their nutrient intake, removing more nitrogen from flies if their previous diet had been low in nitrogen (Mayntz et al. 2005). When fed food deficient in protein, ground beetles, *Agonum dorsal,* did not over-ingest lipid in the diet to reach the level of protein preferred, rather this beetle defended the level of lipid required in the body for storage (Raubenheimer et al. 2007).

The apparent absence of nutrient balancing shown by tree weta could result from disparity between two factors. The first is the nutritional requirement of the animal and the second is the availability of the nutrient in a form that is accessible to meet these requirements (Raubenheimer 1992). If a target nutrient is not available in an accessible form the insect may overeat the total diet in order to get sufficient of a target nutrient. Secondary compounds in food sources such as tannic acid in leaves may exert restrictions on compensatory feeding for proteins (Raubenheimer 1992). This could be important for tree weta and other leaf eating insects, where the small amount of available nitrogen is made less accessible by the presence of tannic acid in leaves of trees and shrubs. A lack of nutrient regulation in insects could also be caused by the mismatch between evolved regulatory mechanisms and the current (experimental) environment in which the animal is living (Simpson et al. 2004). Selection against fat storage may not occur in tree weta because there may not normally exist sufficient nutrients in the wild to cause excess fat accumulation (see Chapter 4). Tree weta are probably only opportunistic feeders of high protein sources of food such as dead insects (Chapter 3). Thus they may encounter lipid and nitrogen rich nutrients only rarely and be adapted to maximise storage of these "rare" nutrients. They appear to be specialist feeders of tree and shrub leaves, unlike most other species in Anostostomatidae, and this may mean that protein forms a relatively small proportion of their diet. Scarcity of available protein in the tree weta niche could mean that they have not evolved a mechanism for strict regulation of the diet. The limited protein available to tree weta in plants in the wild could mean that even though they may not require large amounts to sustain themselves tree weta may be unable to control their preference for this normally environmentally scarce resource. The level of protein available to insects from trees in New Zealand can be below 1% of the dry weight of the leaves (Wehi & Hicks 2010; Korner et al. 1986). In contrast, of 23 North American tree species sampled for their nutrient content, nitrogen ranged from 2 - 5% (McHargue and Roy 1932).

Tree weta could also be selectively using nutrients once they are ingested. Excess nutrients could be excreted as waste or stored for times where food is in short supply. Post-ingestive regulation of nutrients enables insects to reach their growth target when nutrient intake targets are not met by the diet (Raubenheimer & Simpson 1999). For example locust (*Locusta migratoria*) nymphs were able to grow and moult at similar rates on diets differing in their protein and carbohydrate concentrates through post-ingestive processes (Zanotto et al. 1993). It was suggested that to safely rid the body of excess dietary carbohydrates they were respired and there was an increase in lipogenesis to store fat (Zanotto et al. 1993). It is possible that excess nitrogen in the diet was synthesised into other compounds such as uric acid (Zanotto et al. 1993). In some insects protein can also be substituted for carbohydrates but the reverse cannot occur (Simpson et al. 2004).

The availability of food to an animal will be a determinant in how closely their nutrient balance will be able to be maintained (Chambers et al. 1995). Patchily distributed plants that herbivores require may decrease the ability to balance nutrients through food switching if patches cannot easily be reached (Chambers et al. 1995). However, locusts were able to use different foraging methods to compensate for the distances between foods and maintain their required nutrient balance (Behmer et al. 2003). Tree weta are mobile foragers able to move between plant species and use the differing nutrient levels that may be available in these plants. But even if food, such as leaves is not limiting, the nutrients they contain may be.

The relatively long life span of tree weta compared to the locust could be implicated in the lack of nutrient balancing seen. The migratory locust, *L. migratoria*, has five instars each lasting for eight days or less (Johnson and Hill 1973). They are then able to breed within 11 to 15 weeks of becoming adult (Lean 1931). During the dry season these locusts may live for no more than 22 weeks, and if conditions are not ideal they may die without breeding (Lean 1931). Compared to tree weta this is an extremely short time. Tree weta normally take at least one year to reach maturity, passing through up to 10 moults, and live for about one year as an adult in the wild (Kelly 2005). This very different life history strategy is likely to exert distinct evolutionary demands on the need to balance nutrients in the short term. Locusts require adequate nutrition to develop and breed within the short season of the year. Inadequate nutrients or poor nutrient balancing are likely to have strong fitness outcomes (e.g. delayed maturation, suboptimal egg laying time). Tree weta, on the other hand can take weeks or even months to moult between instars, especially in the later instars (see Chapter 4), so it is possible that they have a much longer time to balance their nutrient intake and need to manage resources over a broader range of environmental fluctuations. As adults they also have a longer time to balance the nutrients that they need for reproduction, by feeding or post-ingestively.

The long life span of tree weta may also provide the potential for them to feed in an irregular way. In the present experiment, when the tree weta were provided with the test diets after their pre-treatment most of them did not eat for the first 3 - 4 nights. This is consistent with other anecdotal information and observations of tree weta not leaving their roosts every night (Rufaut & Gibbs 2003; N. Minards unpublished data; S. Trewick pers. Obs). Avoidance of desiccation and predators may be selected for instead. In this experiment the tree weta all ate much larger amounts during the pre-treatment than in the test. They may have become sated on this diet and thus able to stay in the roost for some time. In the winter, tree weta may also remain in their roosts for several days when temperatures are low. A strategy of gorging may enable them to develop without feeding every day. Locusts on the other hand have a reputation for insatiability (Simpson et al. 2004). They eat daily to meet their requirements and can achieve high densities and plague numbers that result in extensive defoliation. The short life span of locusts requires that they eat sufficient relatively rich plant foods every day to reach their growth targets in order to moult to the next instar. Locust diet is dominated by fast growing, soft, young leaves of grasses (Chapman 1957). Tree weta on the other hand are nocturnal, live in a temperate climate, are relatively long lived with a large proportion of their food coming from of tree and shrub leaves rich in secondary compounds (Atikinson & Greenwood 1989). A capacity to develop fat reserves may be less important for locusts as it is more beneficial to put the resources towards growth. Tree weta take longer to mature and it could be beneficial for them to sequester scarce resources such as nitrogen when they become available.

A high proportion, 38%, of tree weta on the high protein pre-treatment died during the course of this experiment (compared to 11% on the carbohydrate pre-treatment). It has been suggested that high mortality of the American cockroach, *Periplaneta americana,* on a high protein diet might have been due to toxic effect of ammonia and tryptophan metabolites (Mullins and Cochran 1975). A combination of the high level of protein in the diet and lack of regulation of protein intake by the tree weta could have led to the build-up of toxic levels of nitrogen in the body. The large amount of energy needed to convert the nitrogen to a safe storage form could also be implicated in the larger weight loss seen in the protein pre-treatment group than the carbohydrate pre-treatment group (House 1969).

5.5 Conclusion

The tree weta in this experiment did not show balancing of protein versus carbohydrate in their diet. The lack of the ability to balance is rare among the animals that have been tested for nutrient balancing. It could be that the environment in which tree weta have evolved normally regulates (limits) the amount of protein they consume, and that they eat as much as is available when they encounter it, storing excess for times of nitrogen scarcity. Storing extra nutrients when they are plentiful rather than balancing them, may mean tree weta are able to survive for much longer periods of time without food or when the nutrients become scarce. The disadvantage in the lack of the ability to balance their protein intake could be the build-up of a large amount of nitrogen causing a high mortality rate. More information on nutrient intake could be gained through experiments run over a longer time frame. Nutrient balancing experiments over an entire instar could give information of what nutrients tree weta are choosing to eat, if they choose, at different stages of their growth through the instar. For instance eating more carbohydrate at the start to increase their weight and reserves and then more protein closer to moulting might allow them to have enough for the building of a new cuticle. Contrast could be made with predatory species of weta, such as *Hemiandrus* which presumably have higher protein content in their diet; it would be expected that these species would have more tightly regulated nitrogen intake. Analysis of faeces or tissues (including the fat body) would be beneficial in understanding what is happening inside the tree weta once the nutrients have been ingested.

Chapter 6

General conclusions

Tree weta are well known endemic insects of New Zealand. The Wellington tree weta, *Hemideina crassidens,* is one of the seven species of tree weta in New Zealand. It is generally common both in native forests and in more modified urban environments. This thesis has gone some way towards addressing the lack of information about tree weta diet.

Many New Zealand ecologists have referred to tree and giant (*Deinacrida*) weta as "invertebrate mice" (Chapter 2). However, this view of weta is uninformative about the actual ecology of weta and the interpretation is most likely due to the paucity of information about their general biology. The comparisons made between weta and mice were based on their similar size, their shared nocturnal activity and polygamous mating behaviours. These traits are not very informative when it comes to the impact that each of these species has on the ecosystem they occupy. The population increase of mice (*Mus* sp.) is much greater than that which could be attained by weta. This means that mice are likely to consume a much larger amount of nutrients in the ecosystem than tree weta. A higher metabolic rate in mice when compared to tree weta emphasises that the food mice eat must be energy rich and abundant to sustain them. Leaf material that is eaten by tree weta would not be a sufficient food source because of the larger amount of energy needed to break down the leaf cuticle to reach the nutrients. Mice generally consume much more energy rich foods such as seeds and invertebrates.

The diet of tree weta is an important impact through which they influence their environment. It was previously thought that tree weta were generally herbivores and they are known to consume large amounts of leaves. However, when given the choice Wellington tree weta ate a mixed diet and are just as likely to consume moths and fruit as they are to eat leaves (Chapter 3). This suggests that tree weta have internal drivers that mean they will consume high quality nitrogen-rich foods when they are available.

Tree weta raised on a diet high in protein had an increased growth rate (g/day), and as adults were much larger than those that did not have added protein in their diet (Chapter 4). This however, did not appear to significantly increase the fecundity of the weta on the high protein diet. There was no difference in the size, number or the composition of the eggs between the two groups. However, total egg production (which could not be measured in this study) could be higher in weta with extra protein. There could also be more long-term effects from the storage of lipids from the consumption of excess protein. Stored fats and proteins could be used to sustain weta when food is in short supply. It could enable tree weta to remain in roost for much longer periods and thus avoid inclement climate conditions and predation.

This excess fat stored by the weta provided with a rich protein diet in the growth experiment (Chapter 4) also suggested that the weta were not regulating the amount of protein that was consumed. In the nutrient balancing experiment I investigated whether or not tree weta would balance their carbohydrate and protein intake, and found a lack of evidence for nutrient balancing (Chapter 5). Adaptation to the low nitrogen content of most New Zealand tree species that make up a large proportion of tree weta diet in the wild could mean that when high quality protein sources are available tree weta will eat all that they can and store the excess as fat reserves. Field observations and captive studies (N. Minards unpubl. data; S. Trewick pers. comm.) suggests that tree weta do not come out of their roost every night and this may be related to temperature or the risk of predation (Moller 1985).

Study of the diet of wild tree and giant weta via isotope and nutrient analysis of their crop contents and cuticle analysis of frass are all needed to fully understand the breath of their natural diet and the implications of this work (Wehi & Hicks 2010). In addition, a more accurate assessment of the foraging activity of weta would be beneficial in understanding the build-up of fat and the lack of nutrient intake regulation. The affect that previous food intake has on weta activity needs further study to assess whether or not they leave their roosts regularly, or if they feed every time they leave their roost.

Tree weta appear not to balance their intake of protein and carbohydrates. Chapter 3 however, showed that they would choose high quality protein sources such as moths over low nitrogen sources such as leaves and the drive to consume protein resulted in a much higher growth rate in those that had it available to them (Chapter 4). An important and interesting direction for this research would be to ascertain why tree weta do not balance their nutrient levels. One possibility is that the amount of nitrogen over a lifetime may be more important than the amount of nitrogen consumed each day by tree weta. The long life span of tree weta means there is greater time available to balance their nutrients, whereas the short lifespan and relatively fast development time of locusts means their needs must be met daily. The comparison of tree weta with more carnivorous species (such as ground weta, *Hemiandrus*) would provide a valuable comparison as to how nitrogen is utilised in species that will consistently be consuming much larger amounts of nitrogen.

Tree weta are long lived, slow developing species, they are nocturnal and consume a diet of leaves which are low in nitrogen. The sequestering of nitrogen when supply is greatest would be beneficial to tree weta in surviving this niche especially when consuming tough leaves, the possibility of toxins and low nitrogen levels. The opportunistic consumption of invertebrates could allow tree weta to maintain their largely herbivorous diet.

Chapter 7

References

Arrese EL, Soulage JL. 2010. Insect fat body: energy, metabolism and regulation. *Annual Review of Entomology* 55: 207-225.

Atikinson IAE, Greenwood RM. 1989. Relationships between moas and plants. *New Zealand Journal of Ecology* 12: 67 – 96.

Awmack CS, Leather SR. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47: 817-844.

Badan D. 1986. Diet of the house mouse (*Mus musculus L.*) in two pine and a kauri forest. N*ew Zealand Journal of Ecology* 9: 137-141.

Barrett P. 1991. Article 1. Keeping the Wellington tree weta, *Hemideina crassidens* (Blanchard, 1851). In: *Keeping weta in captivity* (eds GW Ramsey) pp. 10 - 17. New Zealand: Wellington Zoological Gardens.

Behmer ST, Cox E, Raubenheimer D, Simpson SJ. 2003. Food distance and its effect on nutrient balancing in a mobile insect herbivore. *Animal Behaviour* 66: 665-675.

Bennett AF, Ruben JA. 1979. Endothermy and activity in vertebrates. *Science* 206: 649 -654.

Bernays EA, Jarzembowski EA, Malcolm SB. 1991. Evolution of insect morphology in relation to plants [and Discussion]. *Philosophical Transactions: Biological Sciences* 333: 257-264.

Bernays EA, Bright K, Howard JJ, Raubenheimer D, Champagne D. 1992. Variety is the spice of life: frequent switching between foods in the polyphagous grasshopper *Taeniopoda eques burmeister* (Orthoptera: Acrididae). *Animal Behaviour* 44: 721- 731.

Bernays EA, Minkenberg OPJM. 1997. Insect herbivores: different reasons for being generalist. *Ecology* 78: 1157 - 1169.

Beveridge AE. 1964. Dispersal and destruction of seed in central North Island podocarp forests. *Proceedings of the New Zealand Ecological Society* 11: 48-56.

Brockie RE. 1992. *A living New Zealand forest*. Auckland: David Bateman 172 pp.

Bronson FH. 1984. Energy allocation and reproductive development in wild and domestic house mouse. *Biology of Reproduction* 31: 83-88.

Brown VK. 1983. *Grasshoppers*. Northampton: Belmont Press.

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

Calder WA. 1978. The kiwi. *Scientific America* 239: 102-110.

Calhoun JB. 1962. *The ecology and sociology of the Norway rat, Publication, No. 1008, U.S.* Englewood Cliffs: Public Health Service.

Carter SP, Bright PW. 2003. Reedbeds as refuges for water voles (Arvicola terrestris) from predation by introduced mink (Mustela vison). *Biological Conservation* 111: 371-376.

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

Chambers PG, Simpson SJ, Raubenheimer D. 1995. Behavioural mechanisms of nutrient balancing in *Locusta migratoria* nymphs. *Animal Behaviour* 50: 1513-1523.

Chapman RF. 1957. Observation on the feeding of adults of the red locust (*Nomadacris septemfaciata* (Serville)). *The British Journal of Animal Behaviour* 2:60 – 75.

Choquenot D, Ruscoe WA. 2000. Mouse population eruptions in New Zealand forests: the role of population density and seedfall. *Journal of Animal Ecology* 69: 1058-1070.

Crawley MJ. 1983. *Herbivory: The dynamics of animal-plant interactions*. (eds DJ Anderson, P Greig-Smith, FA Pitelka). London: Blackwell Scientific.

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

Delany MJ. 1974. *The ecology of small mammals*. London: Edward Arnold Publishers Limited.

Diamond J. 1990. New Zealand as an archipelago: An internationalperspective. In *Ecological restoration of New Zealand islands* (eds. DR Towns, CH Daugherty & IAE Atkinson) pp. 3-8. Wellington: Department of Conservation.

Dickman CR. 1988. Body size, prey size and community structure in insectivorous mammals. *Ecology* 69: 569-580.

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

Diss AL, Kunkel JG. Montgomery ME, Leonard DE. 1996. Effects of maternal nutrition and egg provisioning on parameters of larval hatch, survival and dispersal in the gypsy moth, *Lymantria dispar* L.*Oecologia* 106: 470-477.

Eades DC, Otte D, Cigliano MM, Braun H. 2010. *Orthoptera species file*. Retrieved 19 August 2010 from http://orthoptera.speciesfile.org/HomePage.aspx.

Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18: 586 - 608.

Ellenbroek FJM. 1980. Interspecific competition in the shrews *Sorex araneus* and *Sorex minutus* (Soricidae: Insectivora): a population study of the Irish pygmy shrew. *Journal of Zoology* 192: 119-136.

Eubanks MD, Denno RF. 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology* 80: 1253-1266.

Fisher P, Spur EB, Oglivie SC, Eason CT. 2007. Bait consumption and residual concentrations of diphacinone in the Wellington tree weta (*Hemideina crassidens*) (Orthoptera: Anostostomatidae). *New Zealand Journal of Ecology* 31: 104 - 110.

Fitzgerald AE. 1976. Diet of opossum *Trichosurus vulpecula* (Kerr) in the Orongorongo Valley, Wellington, New Zealand, in relation to food-plant availability. *New Zealand Journal of Zoology* 3:399 - 419.

Fleming CA. 1973. Foreword. In GR Williams (Ed.), *The natural history of New Zealand*. Wellington, Reed.

Fleming CA. 1977. Sir William Macleay memorial lecture, 1976: the biogeographic basis of national cultures. *Proceedings of the Linnean Society of New South Wales* 101: 218-236.

Gangwere SK. 1967. The feeding behaviour of *Atlanticus testaceus* (Orthoptera: Tettigoniidae). *Annuals of the Entomological Society of America* 60: 74 - 81.

Gibbs GW. 1998. *Ruakumara tusked weta: Discovery, ecology and management implications.* Conservation Advisory Science Notes. Wellington: Department of Conservation.

Gibbs GW. 2001. Habtats and biogeography of New Zealands Deinacridine and tusked weta species. In: *The Biology of Wetas, King Crickets and their Allies*, (eds. Field LH). Wallingford:CAB International.

Gibbs GW. 2009. The end of an 80-million year experiment: a review of evidence describing the impact of introduced rodents on New Zealand's 'mammal-free' invertebrate fauna. *Biological Invasions* 11: 1587-1593.

Gibbs G. 2010. Do New Zealand invertebrates reflect the dominance of birds in their evolutionary history? *New Zealand Journal of Ecology* 34:152-157.

Giron D, Casas J. 2003. Mothers reduce egg provisioning with age. *Ecology Letters* 6: 273-277.

Green C. 2005. Using artificial refuges to translocate and establish Auckland tree weta *Hemideina thoracica* on Korapuki island, New Zealand. *Conservation Evidence* 2: 94-95.

Guignon CA. 2005. *Behavioural displays, acoustic and chemosensory communication in the middle island tusked weta* Motuweta isolata *(Orthoptera: Anostostomatidae)*. Unpublished MSc thesis, University of Canterbury, Christchurch.

Hadley NF, Quinlan MC. 1993. Discontinuous carbon dioxide release in the eastern lubber grasshopper *Romalea guttata* and it effect on respiratory transpiration. *Journal of Experimental Biology* 177: 169-180.

Hainsworth FR. 1978. Feeding: models of costs and benefits in nergy regulation. *American Zoologist* 18: 701-714.

Hamilton GD, Bronson FH. 1985. Food restriction and reproductive development in wild house mice. *Biology of Reproduction* 32: 773-778.

Hassell MP, Southwood TRE. 1978. Foraging Strategies of Insects. *Annual Review of Ecology and Systematics* 9: 75-98.

Hinks CF, Hupka D, Olfert O. 1993. Nutrition and the proetin economy in grasshopper and locusts. *Comparative Biochemical Physiology* 104A: 133-142.

Hochuli DF. 1996. The ecology of plant/insect interactions: Implications of digestive strategy for feeding by phytophagus insects. *Oikos* 75: 133-141.

Hochuli D, Sanson G, Roberts B. 1993. Approximate digestibility of fibre for two locusts. *Entomologia Experimentalis et Applicata* 66(2): 187-190.

House HL. 1969. Effects of different proportions of nutrients on insects. *Entomologia Experimentalis et Applicata* 12: 651-669.

House HL. 1962. Insect Nutrition. *Annual Review of Biochemistry* 31(1): 653-672.

House HL. 1959. Nutrition of the parasitoid *Pseudosarcophaga affinis* (Fall.) and of other insects. *Annals of the New York Academy of Sciences* 77: 394-405.

Hodkinson ID, Hughes MK. 1982. *Insect herbivory*. Chapman and Hall Ltd, London.

Hunter MD. 2009. Trophic promiscuity, intraguild predation and the problem of omnivores. *Agricultural and Forest Enotmology* 11: 125 - 131.

Izumi S, Yano K, Yamamoto Y, Takahashi SY. 1994. Yolk proteins from insect eggs: Structure, biosynthesis and programmed degradation during embryogenesis. *Journal of Insect Physiology* 40: 735-746.

Joern A, Behmer ST. 1997. Importance of dietary nitrogen and carbohydrates to survival, growth, and reproduction in adults of the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia* 112: 201-208.

Joern A, Behmer ST. 1998. Impact of diet quality on demographic attributes in adult grasshoppers and the nitrogen limitation hypothesis. *Ecological Entomology* 23: 174-184.

Johns PM. 1997. The gondwanaland weta: family Anostostomatidae (formerly in Stenopelmatidae, Henicidae or Mimnermidae): nomenclatural problems, world checklist, new genera and species. *Journal of Orthoptera Research* 6: 125-138.

Johnson RA, Hill L. 1973. The activity of the corpora allata in the fourth and fifth larval instars of the migratory locust. *Journal of Insect Physiology* 19(10): 1921-1932.

Jonas JL, Joern A. 2008. Host-plant quality alters grass/forb consumption by a mixed-feeding insect herbivore, *Melanoplus bivittatus* (Orthoptera: Acrididae). *Ecological Entomology* 33: 546 - 554.

Joyce SJ, Jamieson IG, Baker R. 2004. Survival of adult mountain stone weta *Hemideina maori* (Orthoptera: Anostostomatidae) along an altitude gradient as determined by mark recapture. *New Zealand Journal of Ecology* 28: 55-61.

Kelly CD. 2005. Allometry and sexual selection of male weaponry in Wellington tree weta, *Hemideina crassidens*. *Behavioural Ecology* 16: 145 - 152.

Kelly CD. 2006. Movement patterns and gallery use by the sexually dimorphic Wellington tree weta. *New Zealand Journal of Ecology* 30: 273-278.

King CM. 1974. Stoats, weasels and ferrets. In, *New Zealand Natural Heritage* (eds. R Knox) pp. 845-853. Hong Kong: Hamlyn.

King CM. 1983. The relationship between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary response of stoats (*Mustela erminea*), in three New Zealand forests. *Journal of Animal Ecology* 52: 141-166.

King CM. 1991. Body Size - Prey Size Relationships in European Stoats *Mustela erminea*: A Test Case. *Holarctic Ecology* 14: 173-185.

King P, Milicich L, Burns KC. 2010. Body size determines rates of seed dispersal in giant king crickets. *Population Ecology* 53:73 - 80.

Korner C, Bannister P, Mark AF. 1986. Attitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. *Oecologia* 69: 577-588.

Lean OB. 1931. The effect of climate on the migrations and breeding of Locusta migratorioides in Nigeria. *Bulletin of Entomological Research* 22: 551-569.

Little GA. 1980. *Food consumption and utilisation in two speces of weta (Hemideina femorata and H. maori: Stenopelmatidae)*. Unpublished BSc (Hons) thesis. University of Canterbury, New Zealand.

MacArthur RH, Pianka ER. 1966. On Optimal Use of a Patchy Environment. *The American Naturalist* 100: 603-609.

MacArthur RH, Wilson EO. 1967. *The theory of island biogeography*. Princeton, Princeton University Press.

Magnhagen C. 1991. Predation risk as a cost of reproduction. *Trends in Ecology & Evolution,* 6: 183-186.

Malatesta M, Cardinali A, Battistelli S, Zancanaro C, Martin TE, Fakan S, Gazzanelli G. 1999. Nuclear bodies are unusual constituents in tissue of hibernating dormouse. *The Anatomical Record* 254: 389-395.

Maly MS, Knuth BA, Barnett GW. 1985. Effects of resource partitioning on dispersal behaviour of feral house mice. *Journal of Mammalogy* 66: 148-153.

Malmquist MG. 1985. Character displacement and biogeography of the pygmy shrew in Northern Europe. *Ecology* 66: 372-377.

Mattson WJ, Jr. 1980. Herbivory in Relation to Plant Nitrogen Content. *Annual Review of Ecology and Systematics* 11: 119-161.

Mayntz D, Raubenheimer D, Salomon M, Toft S, Simpson SJ. 2005. Nutrient-specific foraging in invertebrate predators. *Science* 307: 111-112.

McCallum J. 1986. Evidence of predation by kiore upon lizards from the Mokohinau Islands. *New Zealand Journal of Ecology* 9: 83-87.

McHargue JS, Roy WR. 1932. Mineral and nitrogen content of the leaves of some forest trees at different times in the growing season. *Botanical Gazette* 94: 381-393.

McIntyre M. 1998. *Raukumara tusked weta: Field and captive observations*. (Conservation Advisory Science Notes No 219). Wellington: Department of Conservation.

McIntyre M. 2001. The ecology of some large weta species in New Zealand. In *The biology of wetas, king crickets and their allies* (eds. LH Field). Wallingford: CAB International.

Meads M. 1990. *The weta book: guide to the identification of weta*. Lower Hutt: DSIR Land Resources.

Mikesic DG, Drickamer LC. 1992. Effects of radiotransmitters and fluorescent powders on activity of wild house mice (*Mus musculus). Journal of Mammalogy* 73: 663-667

Miller AP. 1999. *Ecological energetics of feral house mice (*Mus musculus*) inhabiting coastal sand dunes*. Unpublished MSc thesis, University of Otago, Dunedin.

Miller CJ, Miller TK. 1995. Population dynamics and diet of rodents on Rangitoto island, New Zealand, including the effect of a 1080 poison operation. *New Zealand Journal of Ecology* 19:19-27.

Mira A. 2000. Exuviae eating: a nitrogen meal? *Journal of Insect Physiology* 46: 605-610.

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

Moehrlin GS, Juliano SA. 1998. Plasticity of insect reproduction: testing models of flexible and fixed development in response to different growth rates. *Oecologia* 115: 492-500.

Moller H. 1985. Tree wetas (*Hemideina crassicruris*) (Orthoptera: Stenopelmatidae) of Stephans Island, Cook Strait. *New Zealand Journal of Zoology* 12: 55-69.

Monteith GB, Field LH. 2001. Australian king crickets: Ditribution, habitats and biology (Orthoptera: Anostostomatidae). In: *The biology of wetas, king crickets and their allies*, (eds. Field LH). London:CABI publishing, 79-94.

Morgan-Richards M. 1997. Intraspecific karyotype variation is not concordant with allozyme variation in the Auckland tree weta of New Zealand, *Hemideina thoracica* (Orthoptera: Stenopelmatidae). *Biological Journal of the Linnean Society* 60: 423- 442.

Morgan-Richards M. 2000. Robertsonian translocations and B chromosomes in the Wellington tree weta, *Hemideina crassidens* (Orthoptera: Anostostomatidae). *Hereditas* 132: 49 - 52.

Morgan-Richards M, Gibbs GW. 2001. A phylogenetic analysis of New Zealand giant and tree weta (Orthoptera: Anosostoatidae: *Deinacrida* and *Hemideina*) using morphological and genetics characters. *Invertebrate Taxonomy* 15: 1 - 12.

Morgan-Richards M, Trewick SA, Dunavan S. 2008. When is it coevolution? The case of ground weta and fleshy fruits in New Zealand. *New Zealand Journal of*

Ecology 32: 108 - 112.

Mullins DE, Cochran DG. 1975. Nitrogen metabolism in the american cockroach. An examination of positive nitrogen balance with respect to uric acid stores. *Comparative Biochemistry and Physiology Part A: Physiology* 50: 489-500.

Pelikan J. 1981. Patterns of reproduction in the house mouse. *Zoological Society of London Symposium* 47: 205-230.

Pough FH. 1980. The advantages of ectothermy for tetrapods. *The American Naturalist* 115: 92-112.

Pough FH, Janis CM, Heiser JB. 2005. *Vertebrate life* (7th ed.). New Jersey: Pearson Prentice Hall.

Pratt RC, Morgan-Richards M, Trewick SA. 2008. Diversification of New Zealand weta (Orthoptera: Ensifera: Anostostomatidae) and their relationships in Australasia. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 3427 - 3437.

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

Raubenheimer D. 1992. Tannic Acid, Protein, and Digestible Carbohydrate: Dietary Imbalance and Nutritional Compensation in Locusts. *Ecology* 73: 1012-1027.

Raubenheimer D, Simpson SJ. 1993. The geometry of compensatory feeding in the locust. *Animal Behaviour* 45: 953 - 964.

Raubenheimer D, Simpson SJ. 1997. Integrative models of nutrient balancing: application to insects and vertebrates. *Nutrition Research Reviews* 10: 151-179.

Raubenheimer D, Simpson SJ. 1999. Integrating nutrition: a geometrical approach. *Entomologica Experimentalis et Applicata* 91: 67-82.

Raubenheimer D, Simpson SJ. 2003. Nutrient balancing in grasshoppers: behavioural and physiological correlates of dietary breadth. *Journal of Experimental Biology* 206: 1669 -1681.

Raubenheimer D, Jones SA. 2006. Nutritional imbalances in an extreme generalist omnivore: tolerance and recovery through complementary food selection. *Animal Behaviour* 71: 1253-1262.

Raubenheimer D, Mayntz D, Simpson SJ, Tøft S. 2007. Nutrient-specific compensation following diapause in a predator: impications for intraguild predation. *Ecology* 88(10): 2598- 2608.

Raubenheimer D, Simpson SJ, Mayntz D. 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology* 23(1): 4-16.

Raupp MJ. 1985. Effects of leaf toughness on mandibular wear of the leaf toughness on mandibular wear of the leaf beetle *Plagiodera versicolora*. *Ecological Entomology* 10: 73-79.

Rentz DC. 1986. The Orthoptera family Cooloolidae, including descirption of two new species and observations on biology and food preferences. *Systematic Entomology* 11: 231-246.

Rentz DC. 1996. *Grasshopper country: the abundant orthopteroid insects of Australia*. University of New South Wales Press: Sydney.

Rowe C. 2009. *Understanding the distribution limits of tree weta (*Hemideina crassidens *and* Hemideina thoracica*) with respect to cold hardiness*. Unpublished PgDip thesis. Massey University, Palmerston North.

Rufaut CG. 1995. *A comparative study of Wellington tree weta,* Hemidiena crassidens *(Blanchard, 1851) in the presence and absence of rodents*. Unpublished MSc thesis. Victoria University of Wellington.

Rufaut CG, Gibbs GW. 2003. Response of a tree weta population (*Hemideina crassiden*s) after eradication of the Polynesian rat from a New Zealand island. *Restoration Ecology* 11: 13-19.

Ruscoe WA, Wilson D, McElrea L, McElrea G, Richardson SJ. 2004. A house mouse (*Mus musculus*) population eruption in response to rimu (*Dacrydium cupressinum*) seedfall in southern New Zealand. *New Zealand Journal of Ecology* 28: 259-265.

Ruscoe WA, Elkinton JS, Choquenot D, Allen RB. 2005. Predation of beech seed by mice: effects of numerical and functional responses. *Journal of Animal Ecology* 74: 1005-1019.

Simpson SJ, Abisgold JD.1985. Compensation by locusts for changes in dietary nutrients: behavioural mechanisms. *Physiology Entomology* 10: 422 – 439.

Simpson SJ, Raubenheimer D. 1993. The central role of the haemolymph in the regulation of nutrient intake in insects. *Physiological Entomology* 18: 395 – 403.

Simpson SJ, Raubenheimer D. 2001. The geometric analysis of nutrient-allelochemical interactions: a case study. *Ecology* 82: 422 – 439.

Simpson SJ, Sibly RM, Lee KP, Behmer ST, Raubenheimer D. 2004. Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour* 68: 1299-1311.

Sinclair BJ, Worland MR, Wharton DA. 1999. Ice nucleation and freezing tolerance in New Zealand alpine and lowland weta, *Hemideina spp*. (Orthoptera: Stenopelmatidae). *Physiological Entomology* 24: 56-63.

Southern HN. 1979. Population processes in small mammals. In *Ecology of small mammals* (eds. D. M. Stoddart). London: Chapman and Hall.

Stevens GR. 1980. *New Zealand adrift*. Auckland: AH & AW Reed Ltd.

Stockhoff BA. 1991. Starvation resistance of gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae): Tradeoffs among growth, body size, and survival. *Oecologia* 88: 422-429.

Stoddart DM (Ed.). 1979. *Ecology of small mammals*. London: Chapman and Hall Ltd.

Stoffolano JG, Wright B. 2005. Sosoopa - Jerusalem cricket: an important insect in the Hopi. *American Entomoloigst* 51: 174-179.

Stringer I. 1998. Translocation of Middle Island tusked weta *Motuweta isolata*, The Middle Island, New Zealand. *Conservation Evidence* 2: 83-85.

Tann CR, Singleton GR, Coman BJ. 1991. Diet of the house mouse, *Mus domesticus*, in the Mallee wheatlands of north-western Victoria. *Wildlife Research* 18: 1-12.

Townsend JA. 1995. *Distribution and ecology of the Banks Peninsula tree weta, Hemideina ricta*. Unpublished MSc Thesis. Massey University, Palmerston North, New Zealand.

Townsend JA, Brown B, Stringer IAN, Potter M. 1997. Distribution habitat and conservation status of *Hemideina ricta* and *H. femorata* on Banks Pennisula, New Zealand. *New Zealand Journal of Ecology* 21:43-49.

Trewick SA, Morgan-Richards M. 1995. On the distribution of tree weta in the North Island, New Zealand. *Journal of the Royal Society of New Zealand* 25: 485-493.

Trewick SA. 1996. The diet of kakapo (*Strigops habroptilus*), takahe (*Porphyrio mantelli*) and pukeko (*P. porphyrio melanotus*) studied using faecal analysis. *Notornis* 43: 79 - 84.

Trewick SA, Morgan-Richards M. 2004. Phylogenetics of New Zealand's tree, giant and tusked weta (Orthoptera: Anostostomatidae): evidence from mitochondrial DNA. *Journal of Orthoptera Research* 13: 185 - 196.

Trewick SA, Morgan-Richards M. 2005. After the deluge: mitochondrial DNA indicates Miocene radiation and Pliocene adaptation of tree and giant weta (Orthoptera: Anostostomatidae). *Journal of Biogeography* 32: 295-309.

Trewick SA, Morgan-Richards M. 2009. New Zealand Biology. In R. G. Gillespies & D. A. Clague (Eds.), *Encyclopedia of Islands* (pp. 1074). Berkeley, University of California Press.

Verhagen R, Leirs H, Tkachenko E, Van der Groen G. 1986. Ecological and epidemiological data on Hantavirus in bank vole populations in Belgium. *Archives of Virology* 91: 193-205.

Waldbauer GP, Cohen RW, Friedman S. 1984. Self-selection of an optimal nutrient mix from defined diets by larvae of the corn earworm, *Heliothis zea* (Boddie). *Physiological Zoology* 57: 590-597.

Waldbauer GP, Friedman S. 1991. Self-selection of optimal diets by insects. *Annual Review of Entomology* 36: 43-63.

Wallis GP, Trewick SA. 2009. New Zealand phylogeography: evolution on a small continent. *Molecular Ecology* 18: 3548-3580.

Watts C, Stringer I, Sherley G, Gibbs G, Green C. 2008a. History of weta (Orthoptera: Anostostomatidae) translocation in New Zealand: lessons learned, islands as sanctuaries and the future. *Journal of Insect Conservation* 12: 359-370.

Watts CH, Thornburrow D, Green CJ, Agnew WR. 2008b. Tracking tunnels: a novel method for detecting a threatened New Zealand giant weta (Orthoptera: Anostostomatidae). *New Zealand Journal of Ecology* 32: 92-97.

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

Wehi PM, Hicks BJ. (2010). Isotopic fractionation in a large herbivorous insect, the Auckland tree weta. *Journal of Insect Physiology* 56:1877-1882.

Weissman DB. 2001. North and Central America Jerusalem crickets (Orthoptera: Stenopelmatidae): Taxonomy, distribution, life cycle, ecology and related biology of the American Species. In: *The biology of wetas, king crickets and their allies*, (eds. Field LH). London: CABI Publishing.

Wheeler D. 1996. The Role of Nourishment in Oogenesis. *Annual Review of Entomology* 41: 407-431.

Whelan CJ, Brown JS. 2005. Optimal foraging and gut constraints: reconciling two schools of thought. *Oikos* 110: 481-496.

White TCR. 1978. The importance of a relative shortage of food in animal ecology. *Oecologia* 33: 71-86.

Whitman DW. 2008. The significance of body size in the Orthoptera: a review. *Journal of Orthoptera Research* 17: 117-134.

Wilmshurst JM, Higham TFG. 2004. Using rat-gnawed seeds to independently date the arrival of Pacific rats and humans in New Zealand. *The Holocene* 14: 801-806.

Wilson CG, Jamieson IG. 2005. Does melanism influence the diet of the mountain stone weta *Hemideina maori* (Orthoptera: Anostostomatidae)? *New Zealand Journal of Ecology* 29: 149-152.

Winks CJ, Fowler SV, Ramsay GW. 2002. *Captive-rearing of the Middle Island tusked wētā*. Science for Conservation, 197. Wellington: Department of Conservation.

Worthy TH, Holdaway, RN. 2002. *The lost world of the moa*. Christchurch: Canterbury University Press.

Worthy TH, Tennyson AJD, Archer M, Musser AM, Hand SJ, Jones C, Douglas BJ, McNamara JA, Beck RMD. 2006. Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. *Proceedings of the National Academy of Sciences* 103: 19419-19423.

Wyman TE 2009. *Tree weta as herbivores and seed dispersers (*Hemideina crassidens, H. thoracica*)*. Unpublished BSc (Hons) thesis. Massey University, Palmerston North.

Wyman TE, Trewick SA, Morgan-Richards M, Noble ADL. 2010. Mutualism or opportunism? Tree fuchsia (*Fuchsia excorticata*) and tree weta (*Hemideina*) interactions. *Austral Ecology*, no. doi: 10.1111/j.1442-9993.2010.02146.x.

Zanotto FP, Simpson SJ, Raubenheimer D. 1993. The regulation of growth by locusts through post-ingestive compensation for variation in the levels of dietary protein and carbohydrate. *Physiological Entomology* 18: 425-434.