

FORUM ARTICLE

Exploring the concept of niche convergence in a land without rodents: the case of weta as small mammals

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Abstract: The distinctiveness of New Zealand's large endemic orthopterans and lack of small mammals in our forest ecosystems led to the description of weta as ecologically equivalent to rodents in other countries. We review the use of this metaphor and the characteristics, such as diet and reproductive behaviour, given to support it. We note, however, that species are rarely specified when comparisons are made, thereby neglecting the ecological diversity of both weta and rodents. We suggest that if these taxa are to be compared, the details of their ecology are important and the scale of their influence in an ecosystem must be taken into account. We consider in particular the relevance of the 'invertebrate mouse' cliché in understanding evolutionary ecology in New Zealand and find it misleading. We show that reproductive potential and scale of change in population size differ greatly between mice and tree weta. We find that endothermic mice (*Mus musculus*) have a metabolic rate almost 20 times faster than ectothermic tree weta (*Hemideina* sp.), an intrinsic rate of increase some 275 times higher, and consume a high quality diet dominated by seeds and invertebrates and devoid of leaves, in contrast to tree weta diets. Comparative quantitative analyses of the influence of different animals on ecosystem services, biomass, nutrient cycling and energy turnover of forests in New Zealand and elsewhere will contribute to interpretation of the evolutionary history of the New Zealand biota.

Keywords: Anostomatidae; ecosystem function; invertebrate mice; New Zealand; niche; omnivory

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 Anostomatidae, known as weta¹ (Johns 1997; Trewick & Morgan-Richards 2009). Four groups of weta are present in the New Zealand anostomatid fauna; all are flightless and nocturnal, and comprise 11 species of giant weta (*Deinacrida*), seven tree weta species (*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 AD; 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 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; Guignion 2005), and small mammals generally (Fleming 1973; Southern 1979; Duthie et al. 2006; King et al. 2011) including voles (Fleming 1977; King 1974). In the more recent literature, most authors simply acknowledge these comparisons without necessarily

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

supporting such a treatment (e.g. Trewick & Morgan-Richards 2005; Watts et al. 2008a, b; Gibbs 2010), whereas 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).

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.

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 which 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 (*Hemidrus* 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; 7 g common

shrews (*Sorex araneus*) consume terrestrial arthropods and earthworms (Malmquist 1985), whereas 15 g 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 50 g. Small mammals that also span this range include the common shrew, *Sorex araneus*, and pygmy shrew, *S. minutus* (7 g and 4 g respectively; Dickman 1988), *Mus musculus* (15 g; Hamilton & Bronson 1985) and the bank vole, *Myodes glareolus* (23 g; Verhagen et al. 1986). The largest weta are about one-third the size of the smallest rat (*Rattus exulans*) in New Zealand (130 g; McCallum 1986).

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 rarely 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 1). For instance, while mice and tree weta have some similarity in their predation of seeds (e.g. in New Zealand, tree weta *Hemideina thoracica* and mice *Mus* spp. both eat seeds of kauri and rimu; Mirams 1957; Beveridge 1964; Badan 1986; Ruscoe et al. 2004), the quantitative effect that each has upon the tree species is likely to differ.

Table 1. Summary of the differences between tree weta (*Hemideina* spp.) and the mouse (*Mus* spp.). (Data from: ^aMiller 1999; ^bRowe 2009; ^cRuscoe et al. 2004; ^dTownsend et al. 1997, Moller 1985; ^eWyman 2009).

| | Mouse | Tree weta |
|---|--|------------------------------|
| Weight | 15 g | 8 g |
| Rate of population growth | r-selected | k-selected |
| Metabolic rate (ml g ⁻¹ h ⁻¹ O ₂) | 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 34–120 g arthropods ^a | 20–500 g leaves ^c |

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 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 small 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. Wild female mice (*Mus musculus*) become sexually mature at about 60–70 days old (Bronson 1984), have a 3-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 with 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 with many smaller Orthoptera, K-selected (MacArthur & Wilson 1967). Although details of weta reproduction are scarce, for two tree weta species held in captivity (*Hemideina thoracica*, *H. crassidens*), between 34 and 120 eggs per female were laid over approximately 6 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 3 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.

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 with 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 in thermodynamically demanding temperate and alpine environments even when consuming mainly 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 $2.27 \text{ ml g}^{-1} \text{ h}^{-1} \text{ O}_2$, 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 $3 \text{ g dry weight per day of rimu (Dacrydium capressinum)}$ seeds (30 kJ g^{-1} rimu seed; Ruscoe et al. 2004) or approximately 970 seeds (Ruscoe et al. 2004). An invertebrate-only diet requires 4.3 g 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 (*Hemideina 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 6 g (similar to the weight of adult tree weta and *Mus musculus*), are available (Hadley & Quinlan 1993). In this case, resting metabolic rate measured at 25°C was found to be $0.125 \text{ ml g}^{-1} \text{ h}^{-1} \text{ O}_2$ (Hadley & Quinlan 1993). Recent investigation into the metabolism of tree weta (*Hemideina crassidens*, *H. thoracica*) yielded a similar estimate of $0.114 \text{ ml g}^{-1} \text{ h}^{-1} \text{ O}_2$ at 16°C (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 0.1 g (wet weight) of leaf material per weta per night at 14°C ; Wyman 2009).

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 to 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^{-1} on Banks Peninsula, South Island (Townsend et al. 1997) to over 5000 weta ha^{-1} 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 60–220 g (wet weight, assuming 80% water) of arthropods per hectare, while at the same time tree weta may be eating between 20 and 500 g 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 with other animals such as 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 250 and 470 m² (Maly et al. 1985; Mikesic & Drickamer 1992) are not directly equivalent to data showing nightly movements of tree weta of <12 m (Kelly 2006).

Conclusion

The usefulness of the comparison between the ecological niches 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 vs 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 that co-occur with native mammals in other parts of the world (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 the 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.

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