When is it coevolution? A reply to Morgan-Richards et al.

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I recently hypothesised that some characteristics of fleshy fruits in New Zealand could result from coevolution with wētā (Burns 2006a). Morgan-Richards et al. (2008) expand on the subject by offering some suggestions on how this hypothesis could be tested and by conducting several small field trials. In the process they argue emphatically against the hypothesis.

I am delighted that Morgan-Richards et al. (2008) are interested in the subject and I applaud their efforts to test the hypothesis. I would argue that the best way to gain new insight into wētā seed dispersal is through direct, experimental tests such as theirs. However, the design of their field trials suffers from several serious shortcomings. In their experiment, they presented fruits of two *Gaultheria* species to each of seven *Hemiandrus* 'evansae' ground wētā for a single night. The fruits used in the experiment are quite large relative to the body size of ground wētā. Therefore, it is not surprising that most fruits were only partially consumed during trials. Given that fleshy fruits typically persist on parent plants for weeks, longer trials are needed to test the hypothesis, objectively. Secondly, they found that the 'majority' of seeds were left intact during trials. This implies that at least some seeds were indeed consumed. Did these seeds survive gut passage or were they destroyed? Why would they not search for viable seeds and report their results? This is especially troubling given they explicitly call for these data under the enhanced germination section of their research programme: 'Germination trials following ground weta ingestion are required'.

Morgan-Richards et al. (2008) also argue that there is little evidence for the hypothesised relationship between fruit colour and wētā seed dispersal. However, there are three problems with their arguments. First, there are two components of an object's reflectance properties, the chromatic component (wavelength) and the achromatic component (intensity). They only consider the chromatic component, even though both components can independently influence an object's conspicuousness (Kelber 2005; Schaefer et al. 2006). Second, they judge a fruit's colour based on human vision. Ecologists interested in signal theory lament this approach because what appears to be 'white' to human eyes may appear quite different in the eyes of animals (see Endler & Mielke 2005). Third, an object's conspicuousness is a function of not only its own reflectance properties, but also the reflectance properties of its background environment (Schmidt et al. 2004), which they ignore entirely. Future work should avoid the circumstantial, qualitative approach adopted by Morgan-Richards et al. (2008), in favour of a more rigorous programme based on quantitative analyses of fruit conspicuousness from the perspective of the signal's receiver (i.e. wētā).

In previous papers (Burns 2006a; Duthie et al. 2006), my colleagues and I discuss the potential role of wētā as seed dispersers more broadly, without explicit consideration of wētā taxonomy. Morgan-Richards et al. (2008) object to our implicit 'treatment of all weta as a single group', based on a detailed description of how different wētā species could perform distinct ecological roles as seed dispersers, which in turn could promote more specialised coevolutionary dynamics at finer taxonomic scales. The idea that seed dispersal mutualisms are characterised by specialised adaptations between individual species enjoyed a brief period of popularity over 30 years ago, at the outset of seed dispersal ecology as a discipline (McKey 1975). However, the type of specialised coevolution Morgan-Richards et al. (2008) have in mind has never found empirical support (Herrera 2002). Most current opinion suggests that species within seed dispersal mutualisms are functionally redundant (Zamora 2000; Burns 2006b). Functional differences, when they occur, typically operate between broad species groups, for example between primates and birds (Poulsen et al. 2002), or different functional groups of birds (Moran et al. 2004). As a result, 'mutual selection pressures between plants and seed dispersers are greatly constrained (Levey & Benkman 1999)', and coevolution is most likely to occur at broad spatial, temporal and taxonomic scales (see Thompson 2005). Given current understanding of seed dispersal mutualisms, why Morgan-Richards et al. (2008) arrived at the conclusion that support for the coevolution hypothesis requires 'extreme specialisation' between weta and fleshy fruits is unclear. Such an opinion represents a dated understanding of fruit–frugivore interactions and ignores over three decades of work to better understand the evolution of seed dispersal mutualisms.

Morgan-Richards et al. (2008) have rather strong opinions concerning the validity of the hypothesis that some New Zealand fruits are adapted for wētā dispersal.

Future work might very well validate their opinion. Unfortunately, the data and logic contained in their Forum paper do not bring us any closer to the truth.

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Editorial Board member: Mike Winterbourn
Received 9 September 2007; accepted 8 October 2007