

# What weta want: colour preferences of a frugivorous insect

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**Abstract** Plants use colours as signals to attract mutualists and repel antagonists. Fleshy-fruits are often conspicuously coloured to signal different types of information including fruit maturity and spatial location. Previous work on fruit colour selection focus on large diurnal vertebrates, yet fruit colours are perceived differently by frugivores with different types of visual systems. Here, we tested whether a nocturnal, frugivorous, seed-dispersing insect selects fruits based on their pigmentation and whether different lighting conditions affect fruit colour selection. We captured 20 Wellington tree weta (*Hemideina crassidens*) from a forest reserve on the North Island of New Zealand and brought them into laboratory conditions to test their fruit colour preferences. The fruits of *Coprosma acerosa*, a native shrub species that naturally produces translucent, blue-streaked fruits, were dyed either red or blue. Fruits were then offered to weta in a binary (y-maze) choice test in two light conditions, either at night during a full moon or under artificial light conditions in the lab. Weta preferred unmanipulated, naturally blue-streaked fruits and artificially-blue coloured fruits over those dyed red. Furthermore, their colour preferences were unaffected by light environment. Our results therefore suggest that weta can discriminate between colours (using colour vision) in both light and dark light environments. Their

consistent preferences for colours other than red indicate that weta might be responsible for the unusual colours of fleshy-fruits in New Zealand.

**Keywords** Colour · Fleshy-fruits · New Zealand · Weta

## Introduction

Most plants are sessile and often rely on animals for the movement of seeds and pollen. In order to attract animal mutualists, plants often use colour signals. Fruits and flowers are often brightly coloured to attract frugivores and pollinators (see van der Pijl 1972; Janson 1983; Willson et al. 1990; Kelber 1996; Burns and Dalen 2002; Raine and Chittka 2007; Pohl et al. 2008). Different lineages of animal mutualists often have unique eye structures with different photosensitive receptor cells and spectral sensitivities (Osorio and Vorobyev 2008). Therefore, a fruit colour that is highly conspicuous to birds, might not be as conspicuous to other frugivores, such as mammals, lizards and insects (Osorio and Vorobyev 2005, 2008).

Previous work on fruit colour preferences has focused on birds (e.g. Schaefer et al. 2003, 2006; Lomascolo and Schaefer 2010) and mammals (e.g. Endler 1978; Dominy and Lucas 2001; Endler and Mappes 2004; Lomascolo et al. 2008). Comparatively little work has been conducted on lizards (Whitaker 1987; Lord and Marshall 2001; Lord et al. 2002; Roth and Kelber 2004; Kelber and Roth 2006). Although insect colour vision has been discovered over 100 years ago (Lubbock 1881), most studies focus on plant-pollinator interactions or folivorous insects, without any specific consideration of frugivores (Lunau and Maier 1995; Chittka and Wells 2004; Raine et al. 2006; Raine and

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Chittka 2007). Insect frugivores contain diverse taxa from Orders such as Lepidoptera, Hemiptera, Coleoptera and Diptera (Sallabanks and Courtney 1992). However, current understanding of insect frugivore interactions is mostly simplified because knowledge of insect frugivores outside of pollination biology or an agricultural context remains largely untested (Wilson 2008). Little is known about fruit colour selection by frugivorous insects.

Weta are an entirely unique type of seed disperser that are endemic to New Zealand. Weta are massive, nocturnal orthopterans. Giant Weta (*Deinacridia* sp.) are known to grow up to nearly ten centimetres in length and weighting 20–70 g (Gibbs 2001). They are the only insect known to consume entire fleshy-fruits and pass seeds in viable condition after ingestion (Duthie et al. 2006). However, their importance to plants as seed dispersers is largely unknown and their capacity to select for particular fruit characteristics such as colour has been debated (Burns 2006, 2008; Morgan-Richards et al. 2008; King et al. 2010). Very little is known about their photoreceptor spectral sensitivities. However, based on electroretinogram analyses, weta appear to be blind at the red end of the visible spectrum, similar to many other insects (Field 2001). Orthopteran insects such as weta have rarely been studied with respect to wavelength selective behaviorals, spectral preferences, colour vision or colour learning (Zufall et al. 1988; Behmer et al. 2005, but see Wasserman and Kong 1982; Bernays and Wrubel 1985). Therefore specific information on weta vision capabilities and colour selection are lacking.

New Zealand's fruit colours are unusual from a human perspective. There are no green fruits at maturity and white fruits, which are comparatively rare elsewhere in the world, make up 21.2% of the 246 fleshy-fruited floras (Lee et al. 1988, 1990, 1994; Willson et al. 1989; Lord et al. 2002). In comparison to the other various regions in the world, most fruits are either typically black (34–41% in Costa Rica, Peru and Florida) and/or red (21–27% in Galapagos Islands and Gabon). South African trees with mammal dispersal commonly have yellow (31%), green (20%) or orange (16%) fruits (full list of fruit colour comparison available from Willson et al. 1989). New Zealand is home to an unusual and diverse array of seed dispersers, including bats, birds, lizards and weta. Because each of these taxa have different visual systems and activity periods, the unusual fruit colours present in the New Zealand flora may be a reflection of differential selection by different types of frugivores (Lord and Marshall 2001; Lord et al. 2002; Wotton 2002; Burns 2006; Duthie et al. 2006). However, this explanation for the evolution of fruit colour diversity has received little evidence to date (Willson and Whelan 1990; Herrera 2002).

Past studies on the fruit colour preferences of frugivores have focused on diurnal seed dispersers and previous

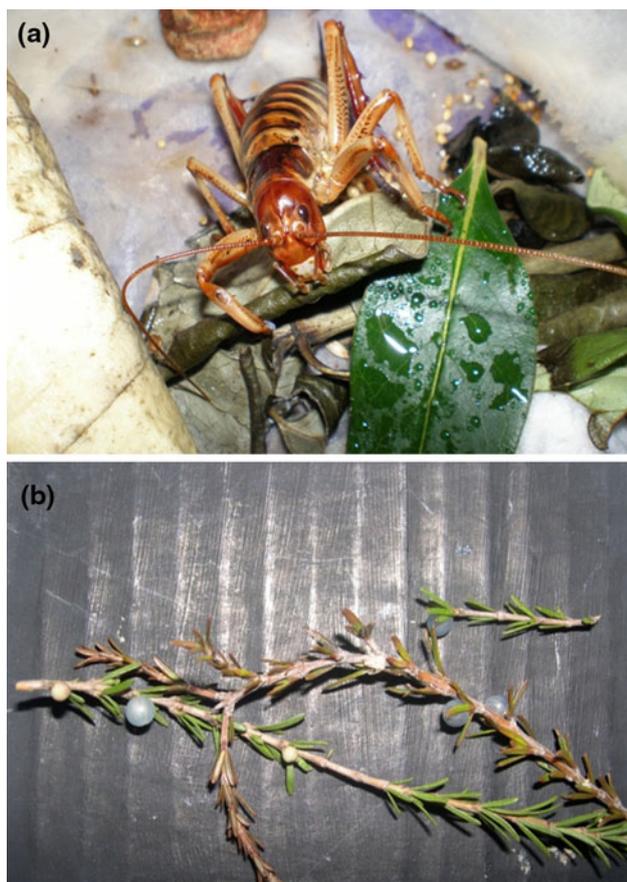
experiments have been conducted in daytime light conditions. The effect of varying light environments on fruit colour selection is therefore poorly understood. Light conditions are known to have a pronounced effect on the foraging behaviour of animals (Willmer and Stone 2004; Kelber et al. 2005; Somanathan et al. 2008a, b, 2009a, b; Caine et al. 2009). Daytime environments are illuminated by either direct or diffuse sunlight. While most available light remains constant at specific solar inclinations, other factors such as cloud cover, canopy cover and humidity are known to affect the lighting environment. In contrast, crepuscular and nocturnal light environments are influenced by multiple sources with different spectra, such as airglow emissions, scattered, low-inclination sunlight and moonlight (Leinert et al. 1998). Each of these potential influences varies in intensity and spatial extent resulting in fluctuating light environments that can change rapidly (Johnsen et al. 2006). Different light conditions can have a substantial effect on the appearance and visibility of objects and organisms (Endler 1993; Johnsen et al. 2006). Little is known about how light environments affect colour preferences in frugivorous animals and in particular how crepuscular and nocturnal seed dispersers use colour signals to make fruit choices.

Here, we investigate how light conditions affect fruit colour selection by New Zealand weta. We conducted an experiment where we dyed the fruits of *Coprosma acerosa*, an endemic plant species that we show is dispersed by weta after gut passage, either red or blue. Different coloured fruits were then presented to weta in paired choice tests under two light conditions, full moonlight and under artificial lights. Results were then used to determine whether weta make consistent fruit choices based on their colour and whether these choices are affected by the ambient light environment.

## Materials and methods

### Weta

New Zealand weta are a group of insects in the order Orthoptera and are related to grasshoppers, locusts, katydids and crickets (Gibbs 2001; Gorochov 2001). All of the experiments were conducted using a single species, the Wellington tree weta (*Hemideina crassidens*, Blanchard) (Fig. 1a), a common species of weta, in New Zealand. Wellington tree weta are nocturnal and spend most of their time foraging arboreally. They are primarily herbivorous, feeding on the leaves, flowers and fruit of a wide range of trees and shrubs, but they will also take living or recently dead invertebrates when they get the opportunity (Gibbs 2001). Twenty adult animals (10 male and 10 female) were



**Fig. 1** **a** A close up of a female Wellington Tree Weta (*Hemideina crassidens*). **b** *Coprosma acerosa* fruit natural colouration

collected from Otari-Wilton Bush, which is located on the Southern tip of the North Island of New Zealand ( $41^{\circ}15'S$ ,  $174^{\circ}45'E$ ), for use in the experiment. Each weta was housed in its own (180 mm  $\times$  180 mm  $\times$  90 mm) plastic container (containing air holes) that was lined with damp paper towel. The containers were kept in the laboratory illuminated by fluorescent lights (Philips TL R5 64 15L, 230 V, 60 Hz). The illumination was kept consistent with the natural light–dark cycle to prevent disruption to the animals' normal circadian cycle. All animals were fed daily with commercially bought fruit (sliced apples, white coloured) and carrots (dull orange colour), as well as leaves from native plant species. The food colours were carefully chosen to prevent pre-exposure to the test colours.

#### *Coprosma acerosa*

We used a common, naturally occurring fruit species *Coprosma acerosa* (A Cunn), in all of our experiments on fruit colour preferences. *Coprosma acerosa* is a small-statured, divaricate shrub with branches and branchlets often forming a cushion like mass up to two meters in diameter and height. Commonly known as Tatarakehe,

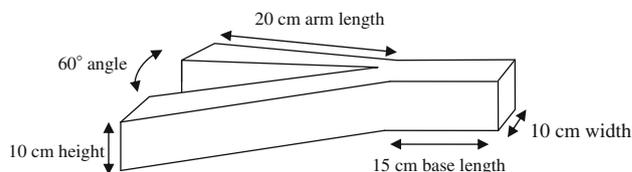
*C. acerosa* belongs to the Rubiaceae family. *Coprosma acerosa* produces fleshy-fruits that are globose, 7 mm in diameter (Fig. 1b) and each contain two flattened seeds. *Coprosma acerosa* fruits are translucently white coloured and are sometimes streaked with blue.

#### Spectrographic analyses

To test whether weta respond consistently to the reflectance properties of fleshy-fruits, we dyed fruits either red or blue. To reduce odour effect, all the fruits were carefully washed with cold water. To completely alter fruit colours, fruits were left to soak in a strong concentration of food dye (Star Brand, Bright Blue and Red) for 2 h. Spectrographic analyses were then conducted with a USB Ocean Optics 2000 spectroradiometer and Xenon Pulse X2 lamp (Ocean Optics) light source to establish precisely how the dyeing procedure affected the reflectance properties of fruits. An object's reflectance properties were measured as the proportion of a diffuse, Teflon—based, white reflectance standard. The fiber optics probe was mounted inside a matte black plastic tube to exclude ambient light. The distance between each object and the probe was fixed at 1 cm. The angle of illumination and reflection was fixed at  $45^{\circ}$  to minimize glare. Spectra were calculated at 5 nm intervals from 300 to 700 nm with SpectraSuite software. The light reflected from an object can give rise to a variety of perceptual phenomena.

#### Y maze test

We tested weta fruit colour preferences using a Y-maze, which are a common experimental design that forces an animal to make a choice between two objects (Wehner 1971; Chen et al. 2003; Behmer et al. 2005; Kapustjansky et al. 2010). We constructed three sets of Y-mazes using white polyurethane plastic measuring 10 cm (width)  $\times$  10 cm (height)  $\times$  20 cm (arm length), with the arms set at a  $60^{\circ}$  angle from each other. The base length is 15 cm (Fig. 2). The top was covered with clear plastic to allow sufficient illumination while preventing weta from climbing out. Weta fruit colour preferences were evaluated by offering animal a choice between each paired combination of colours (natural vs. dyed red; natural vs. dyed blue; dyed blue vs. dyed red). We first tested weta colour preference



**Fig. 2** Y-maze diagram used in the binary test

using artificial targets (coloured plasticine and small plastic beads). However, preliminary testing shows that weta did not react to artificial targets. The animals tested simply remained still and refused to choose. Therefore we decided to use real fruits rather than artificial targets. Furthermore it is impossible to replicate the natural *C. acerosa* reflectance onto artificial targets.

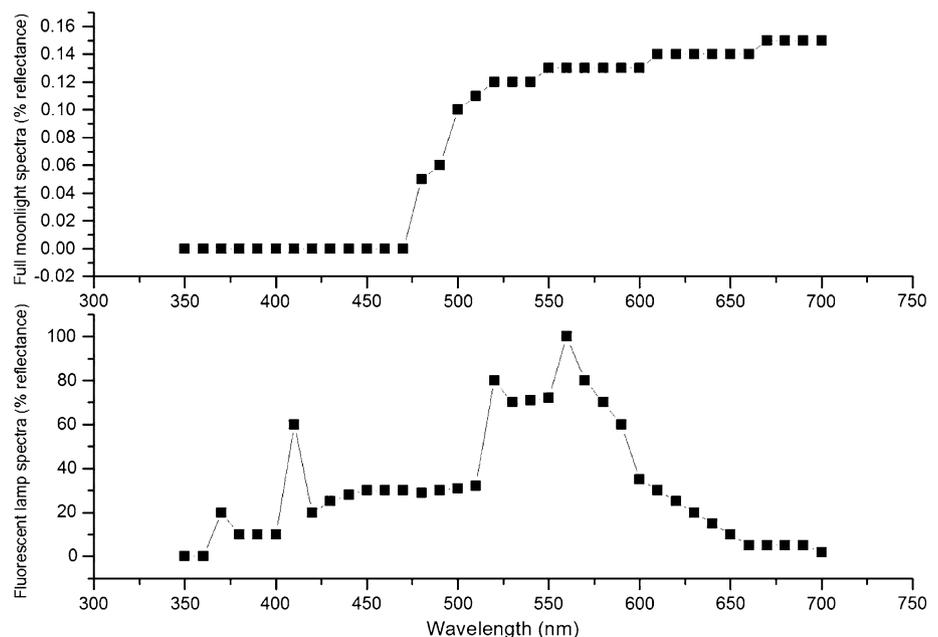
Three fruits were placed at the end of each maze along with their leaves as background. The leaves of *C. acerosa* are quite small in size (6–16 mm in length). However, the matted branching pattern of adult plants typically display the fleshy fruits against a solid mass of leaves and branches. In an effort to reduce the artificial nature of experimental fruit displays, we stacked multiple branchlets (approximately 10 branchlets that were 60 mm long) at the end of each maze arm immediately behind fruit displays.

For each colour combination, all weta were placed in the maze individually and once they moved beyond the intersection of the two arms of the y-maze (i.e. they chose to move down a single arm towards the fruit located at the end) the trial was halted. If no movement was detected after 20 min (i.e. weta remained still), the trial was stopped and the trial was not included in statistical analyses. Weta were deprived of food for 24 h before each experiment to increase the likelihood they would participate. Tests were conducted an hour after sunset and before sunrise to coincide with the natural circadian rhythm of weta (Lewis and York 2001). The identity of fruit colours placed at each arm of the Y maze was randomly allocated for each trial to remove the potentially confounding effect of directional preferences.

To test whether weta made different fruit colour choices under different lighting conditions, we conducted trials for each fruit colour combination in two light environments. The first was in “artificial” light, where the y-maze was illuminated by fluorescent, light (4100 K, Philips TL R5 64 15L, 230 V, 60 Hz). The second was natural “moonlight”, which was conducted in the dark during full moons, with the Y-mazes positioned near a window in the laboratory to provide natural illumination. All trials for each colour combination and light condition were conducted on separate nights. We allowed a rest period of 3–4 days between the artificial trials. For the “moonlight” trials, if the night sky was heavily clouded, the experiment was rescheduled to the next full moon cycle. Figure 3 shows the spectra properties of the fluorescent lamp and full moonlight conditions. There are essentially three sets of binary tests. Each binary test under different light conditions (two light conditions) was replicated twice (total number of binary test = 12).

To test the effect of light conditions on fruit colour selection statistically, we performed a contingency table analysis. Each light environment was treated as a separate row and each fruit colour was treated as a separate column, to form a  $2 \times 2$  table with counts of animals in each cell. If the results from these tests were not statistically significant, the results for both light conditions were pooled for each colour combination and a binomial test was used to compare overall fruit colour preference regardless of light environment. Binomial tests calculate the probability of obtaining a certain number of ‘successes’ in a sequence of  $n$  trials and in this context tests whether an observed

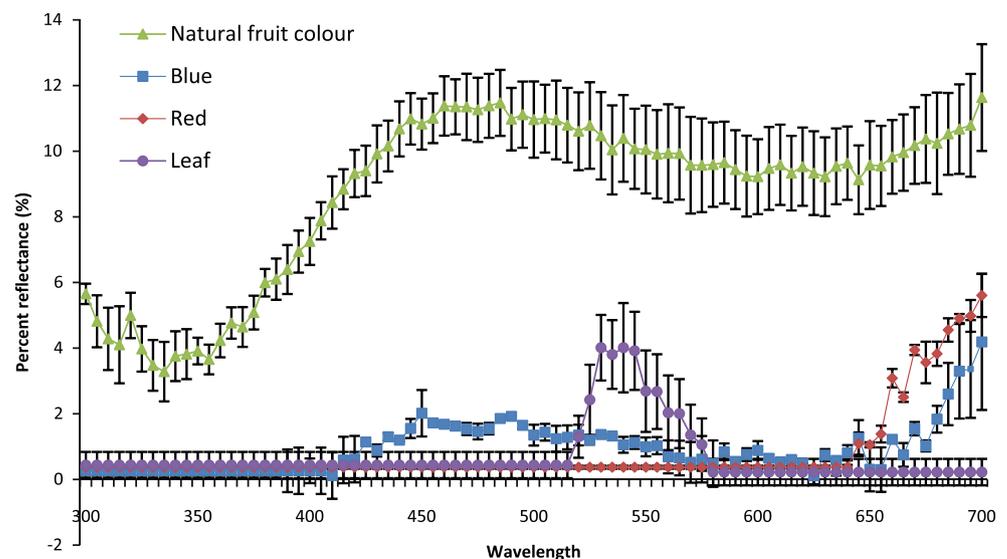
**Fig. 3** Spectra properties of full moonlight (*top*) and fluorescent light (*bottom*) condition. The intensity level for moonlight is very low; full moon is about 2,50,000–5,00,000 times fainter than the sun



number of choices for a particular fruit colour deviates from randomised expectations.

A benefit of running contingency tables tests followed by binomial tests for fruit colour preferences is that both are standard procedures that will be familiar to most readers. A disadvantage is that contingency tables only test for an interactive effect of fruit colour and light environment; it does not assess whether weta prefer certain fruit colours, regardless of light environment. Further the binomial test for fruit colour preferences suffers from independence problems associated with light environments. Therefore, we conducted a simple computer simulation to determine how frequently observed results could be replicated by simulated weta making random fruit colour decisions. We simulated the experiment using the observed number of successful trials (excluding those where weta neglected to make a choice) for each light environment 1,000 times in R 2.10.1 (R Development Core Team 2010). For example, in comparison of weta selection between natural colour fruits and red coloured fruits in artificial daylight, weta chose 13 natural colour fruits against one red fruit. This total up to 14 successful trials. We then calculated the probability of weta choosing a set number of fruits (zero, one, two, three and so forth until 14). This is repeated 1,000 times by a randomization code in R software. Based on the probability values, we then calculated the probabilities of weta choosing all the possible number combination selection between the two colours. Therefore, if weta were to choose 13 natural fruit and one red fruit, the result would be from the total probability of weta selecting 13 out of 14 fruits added with the probability of weta selecting one out of 14 fruits. During each simulation replicate, simulated weta made a random choice between each fruit colour and the fraction of trials that were equal to or less probable than that observed was taken as the type-one error rate for non-random fruit colour preferences.

**Fig. 4** Reflectance spectra of natural *C. acerosa* fruits (triangle), fruits dyed blue (square), fruits dyed red (diamond) and the leaves (circle). Each spectral results were obtained from the average reading of 10 samples ( $N = 10$ ). Error lines represent standard error



To evaluate whether weta pass seeds intact after consumption, three *C. acerosa* fruits were offered to five randomly selected weta over the course of 3 consecutive nights. All fruits were completely consumed, leading to a total sample size of 30 ingested seeds (all species of *Coprosma* consistently produce two seeds per fruit). All scat produced by weta during the ingestion trials and for 3 days afterward were collected all seed material was examined under a light microscope. Seeds were then tested for viability by staining them with 2,3,5-triphenyltetrazolium chloride (1%). A small longitudinal cut was made alongside each seed to allow the stain to seep in through the seed coat. Imbibed seeds were placed in a petri dish inside an incubator with a temperature of 40° Celsius for 24 h and then examined under a light microscope. Viable seeds turned a distinctive reddish hue (Marrero et al. 2007).

## Results

Spectrographic results show that natural *C. acerosa* fruits reflect light throughout the visible spectrum range (300–700 nm) with reflectance intensity peaking around 400–490 nm. The high brightness level of the natural fruit colour is caused by the translucent white colours while the peak (400–490) is from the blue streak lines. The dying process lowered the intensity of fruits significantly but changed the shape of the reflection function, so that reflectance peaks occurred either in the blue spectral domain (400–490 nm) or the red spectral domain (630–700 nm) (Fig. 4). Therefore, the three fruit colour treatments were unmanipulated natural bright blue, dyed dull blue and dyed dull red. All colours mentioned are based on the human perception.

**Table 1** Total number of fruit colour selection by weta

	Natural versus red		Natural versus blue		Blue versus red	
	Artificial light	Moonlight	Artificial light	Moonlight	Artificial light	Moonlight
Natural	13	12	7	6		
Blue			6	6	9	7
Red	1	1			2	2

The results for both light conditions were pooled for each colour combination and a binomial test was used to compare fruit colour selection regardless of light environment

Contingency table analyses showed that fruit colour preferences did not differ between light conditions. All three colour combinations, natural versus red ( $\chi^2 = 0.29 \times 10^{-2}$ ,  $df = 1$ ,  $P = 0.96$ ), natural versus blue ( $\chi^2 = 0.37 \times 10^{-1}$ ,  $df = 1$ ,  $P = 0.85$ ) and blue versus red ( $\chi^2 = 0.51 \times 10^{-1}$ ,  $df = 1$ ,  $P = 0.83$ ), did not interact with light environment. After pooling results from both lighting conditions (Table 1), binomial tests showed that weta preferred naturally coloured blue fruits to red fruits ( $P = 0.01$ ) and artificially coloured blue fruits to red fruits ( $P = 0.01$ ). Weta chose naturally coloured blue fruits and artificially coloured blue fruits at similar rates ( $P = 1.00$ ).

Simulation analyses confirmed these results (Fig. 5) Weta selectively chose naturally coloured bright blue fruits over fruits dyed dull red ( $P < 0.01$ ) (Fig. 5a). Naturally coloured bright blue fruits and fruits dyed dull blue were chosen at equal frequencies. ( $P = 0.85$ ) (Fig. 5b). Fruits dyed dull blue were also selectively chosen more than fruits dyed dull red ( $P < 0.01$ ) (Fig. 5c). The five additional trials conducted to determine whether weta interacted mutualistically with *C. acerosa* fruit showed that they passed *C. acerosa* seeds in viable condition after gut passage. Weta consumed all fruits offered to them during these trials and 27% (eight out of 30) of seeds passed in apparently viable condition. Seedling viability tests revealed that 63% (five out of eight) of the intact seeds are viable.

## Discussion

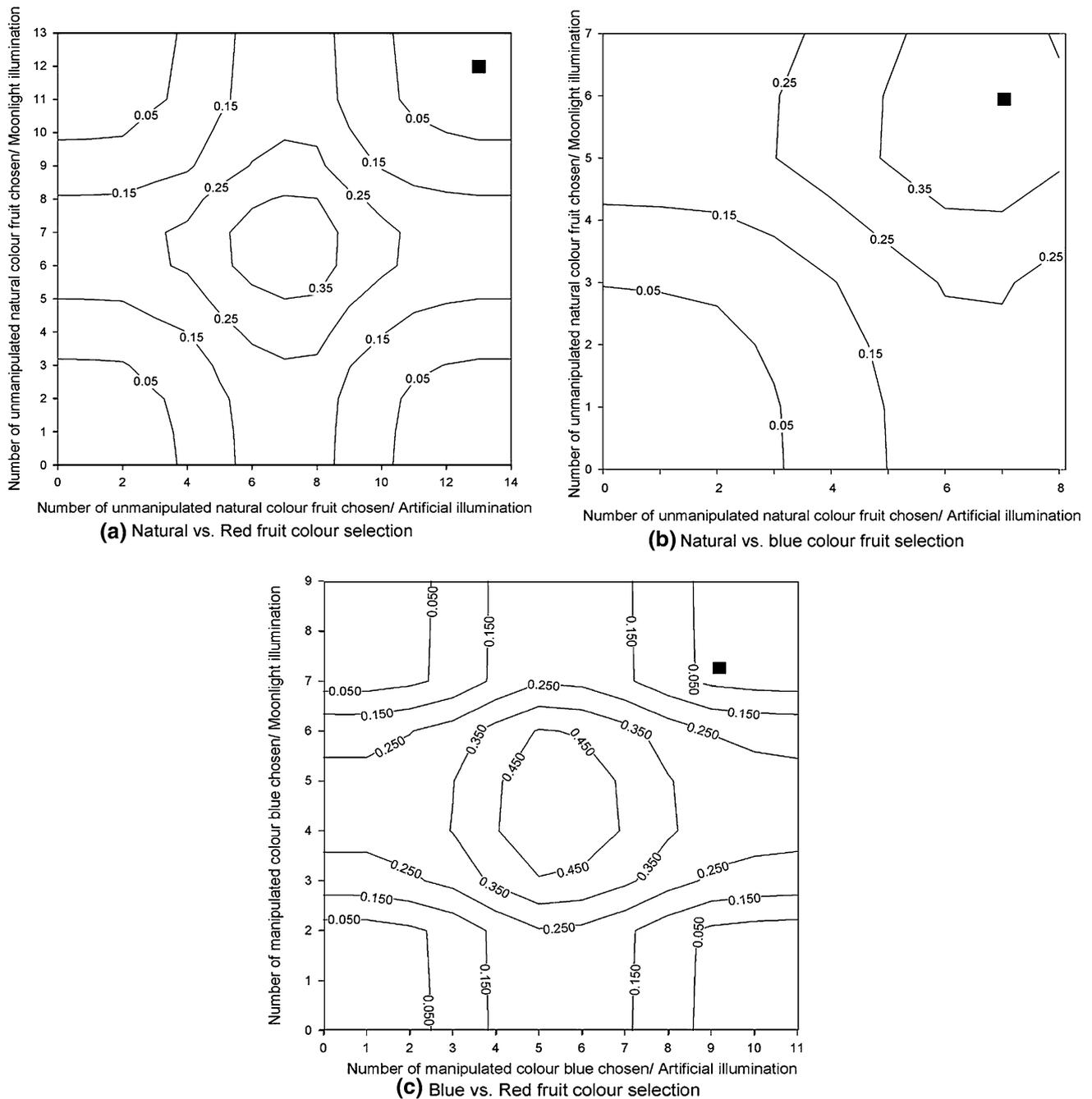
Weta showed consistent preferences for particular fruit colours. They preferentially selected unmanipulated, blue fruits and fruits dyed a blue hue over fruits dyed red (all colours described are based on human perception). Interestingly, based on the reflectance curves, the main difference in the spectral properties of unmanipulated and blue-dyed fruits was their reflectance intensity. Unmanipulated fruits showed higher intensity curve than those dyed blue. However, weta showed similar foraging preferences for both, suggesting they made foraging decisions based on colour alone.

Weta therefore appear to have colour vision at low-light conditions. They showed the same colour preferences in

moonlight and in artificial light environments. Similar results have been found in other animals. For example, dichromatic marmosets (*Callithrix geoffroyi*) excel in foraging at low light intensity conditions (Caine et al. 2009). The nocturnal helmet gecko (*Tarentola chazaliae*) also has colour vision both in starlight and dim moonlight (Roth and Kelber 2004; Kelber and Roth 2006). Certain insects have excellent colour vision in low light environments, for example grasshoppers, hawkmoths and some nocturnal bees have unique eye structures (i.e. large facet lenses and wide, very long rhabdoms) that help them distinguish between objects in dim light environments (Warrant et al. 1996, 2004; Balkenius and Kelber 2004; Johnsen et al. 2006). The Indian Carpenter Bee (*Xylocopa tranquenaarica*) is capable of flight during the night even at extremely low light intensities (Somanathan et al. 2008a, 2009a). This obligate nocturnal bee navigates through landmark colours in starlight (Somanathan et al. 2008b).

Although very little is known about the visual properties of weta, our results suggest that they have greater preference for blue colour than for red colour. Electroretinogram tests conducted on another species of Tree Weta (*Hemideina femorata*) and Giant Weta (*Deinacrida mohouenui*) showed that both species have peak sensitivities in blue (440–490 nm wavelengths) and green (520–530 nm wavelengths) (Field 2001). The spectral sensitivities are similar to the cricket (*Gryllus bimaculatus*), with spectral sensitivities at 332 nm (UV), 445 nm (blue) and 515 nm (green) (Zufall et al. 1988). Another similar orthopteran is *Locusta migratoria* with spectral sensitivities at 360 nm (UV), 430 nm (blue) and 530 nm (green) (Vishnevskaya and Shura-Bura 1990).

Several factors prevented us from using a theoretical eye model (an assessment of photon absorbance by the specific eye photoreceptors) in our analyses of fruit colour (Osorio and Vorobyev 1996; Vorobyev and Osorio 1998; Endler and Mielke 2005; Schaefer et al. 2006; Fadzly et al. 2009). It is possible to quantify how birds perceive objects visually based on our understanding of the physiology of the avian eye (e.g. Fadzly et al. 2009). Similarly, Chittka (1992) proposed the chromaticity diagram to illustrate colour opponency based on the hymenopteran species. However, vertebrate and insect visual pigments, although structurally



**Fig. 5** Observed and expected probabilities of weta fruit colour choices obtained in a computer simulation. *Contour lines* represent the expected number of fruits consumed under artificial illumination

(x-axis) and natural moonlight (y-axis) if weta foraged for fruits randomly. *Symbols* represent the observed number of fruits consumed of each colour combination

and functionally similar, generally differ in a number of important ways (Briscoe and Chittka 2001). Because the eye physiology of weta has yet to be fully documented we lack an accurate understanding of how they see the world (Field 2001). Many insects are also nocturnal or crepuscular, so there is less available environmental light/illuminant during their active browsing period to provide a single visual pigment matching analysis.

The New Zealand flora has an unusually high abundance of opaque or pale blue coloured fleshy fruits, which are often displayed in the inner recesses of the plant canopies (Lord et al. 2002). The numbers of opaque or pale blue fleshy fruits are collectively a higher proportion compared to others in the temperate floras (Iberian Peninsula, Florida and Europe) (see Lord et al. 2002; Herrera 1989). Fruit production within canopies of divaricating (the divaricate

habit is characterised by small leaves, with thin interlaced stems at wide branch angles) plants would appear to restrict access to larger frugivores, such as birds and facilitate access to smaller frugivores such as weta (Burns 2006). Strong preferences for pale blue fruits suggest that weta may interact with fleshy-fruited plant traits evolutionarily. However, weta are not the only small-sized frugivore that might select for translucent, pale blue fruits in low light environments within divaricating plants. Nocturnal geckos are capable of distinguishing blue colour at very dim light levels when humans are colour-blind (Roth and Kelber 2004; Kelber and Roth 2006). Other insects such as ants are known to disperse seeds without ingesting them (Boulay et al. 2005). However, myrmecochory is rare in New Zealand (Gibbs 2006). Results from seed viability trials indicated that weta are viable seed dispersers, although only a fraction of seeds passed through weta intact. As discussed in detail elsewhere, some seed damage during ingestion does not necessarily imply that a particular frugivore is an antagonist (Burns 2006; King et al. 2010). Janzen (1979) describes a variety of plant species that “pay in seeds for the dispersal of other seeds”, and a similar situation may occur with weta.

Our results suggest that weta are capable of colour vision and select fruits based on colour at night. Weta prefer blue colour over red colour suggesting that the preponderance of opaque-blue fruits in matted divaricate shrubs in New Zealand may be an adaptation to promote seed dispersal by weta. However, there are other explanations that could be offered. Weta equal selection between natural fruit colour and dyed blue in moonlight setting could also be attributed to behavioural mechanism based on achromatic vision and brightness threshold. It is possible that in lowlight conditions, weta perceived both colours as black. Another alternative explanation is the possibility of wavelength-dependent behaviour rather than full colour vision. For example, Whiteflies *Trialeurodes vaporariorum*, are strongly attracted to UV light, which possibly induces migratory behaviour, whereas green-yellow light promotes landing (Coombe 1981). Wavelength-dependent behaviour occurs when different behaviour patterns of an animal have markedly different spectral sensitivities (Menzel 1979). This refers to how different behavioural patterns are controlled or triggered by different spectral sensitivities but the outputs of these receptors are not integrated in the central nervous system (Coombe 1981). Certain selection responses (such as honeybees colour selection) might indicate a “primitive” hard wiring between spectral receptors and motor circuits, but it is also possible that both colour vision and wavelength-dependent behaviour are processed serially, so that stereotypic motor patterns are elicited when objects in the animal’s visual field are perceived in certain colour (Skorupski and Chittka

2011). Furthermore, wetas were not laboratory raised and might have had the opportunity to learn fruit colours in nature. It is therefore uncertain whether the colour selections were based on innate or learned behaviour.

These theories reflect how little is known about weta’s impact on New Zealand’s natural history. We believe that this study provides the initial step towards a better understanding on the evolution of fruit colours and a frugivorous insect. A more holistic research program involving comparisons of various fruit colour selection by a variety of frugivorous insect seed dispersers is needed to fully elucidate how frugivore visual systems and foraging behaviour have influenced the evolution of plant traits in New Zealand.

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