

Responses to direct versus indirect cues of predation and competition in naïve invasive mice: implications for management

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Abstract: Many populations of invasive mice *Mus musculus* in New Zealand have experienced the removal of mammalian predators and competitors, with the consequence of mouse population irruptions. The effects of these removals on mouse foraging are largely unknown, yet this information is essential for developing and implementing better mouse control. We investigated the effects of direct and indirect predatory cues on foraging of free-ranging mice at a site where mammalian predators were eradicated 5 years previously. We used 17 stations, each containing four trays of millet seeds mixed thoroughly in sand, with three unfamiliar mammalian (a predator, a competitor, and a herbivore) odour treatments and a control (water), during the four phases of the moon. We measured mouse selectivity for treatment/control trays, giving-up densities (GUDs, a measure of food consumption), and tray encounter rates. Foraging by mice was not affected by odour cues from any of the unfamiliar mammals. Moonlight intensity, however, affected mouse foraging, with higher GUDs being recorded on brighter moon phases (full and waxing > new and waning) during the first night of the trials. This effect was less pronounced during the second night. Resource encounter rates were also affected, with the proportion of trays foraged lower during the brighter phases of the moon on both the first and second nights. We suggest that coordinating management efforts according to the phases of the moon has the potential to improve mouse control and reduce bait wastage.

Keywords foraging; GUD; moonlight intensity; *Mus musculus*; predatory cues.

Introduction

Predators exert strong selection pressure on the foraging behaviours of prey species (Gould 1982; Lima & Dill 1990; Hawlena & Schmitz 2010). Animals generally increase their exposure and conspicuousness to predators when foraging, and may decrease their vigilance when feeding (Sih 1992; Brown & Kotler 2004). Therefore, when predators are present, prey species face a conflict between satisfying their nutritional requirements and minimising predation risk (Bernays 1998; Brown & Kotler 2004).

Cues of predation risk might be direct, for example, scent cues indicating the presence of a predator, or indirect, representing a general predation risk (e.g. illumination intensity, which might affect exposure in nocturnal foragers). The use of animal odours as deterrents has been suggested to have the potential to constrain foraging and breeding of pest animals (Sheriff et al. 2009; Hughes & Banks 2010; McPhee et al. 2010; Webb et al. 2010). However, other studies suggest that this trait is species-specific and that naïve animals may be less receptive to these cues (Dickman 1992; Orrock 2010). Since there are costs both to being too risk averse in the face of these cues (foregone foraging opportunities) and too risk prone (increased predation), there is a strong incentive for foragers to continually recalibrate the correlation between cues and predation (Lima & Dill 1990; Brown & Kotler 2004).

One situation in which this calibration might occur is when prey species have become isolated from their predators.

Potential consequences of this include loss of the ability to recognise predators, the neglect of cues indicating their presence, and the loss of anti-predator behaviours (Dickman 1992; Beauchamp 2004; Blumstein & Daniel 2005; Cox & Lima 2006; Orrock 2010). The process of losing anti-predator behaviours could be due either to individual learning (Griffin et al. 2000; Blumstein 2002; Cox & Lima 2006) or, in the longer-term, to the effect of relaxed selection on gene pools (Lahti et al. 2009).

House mice (*Mus musculus*) show responsiveness to predatory cues of mammalian predators with which they are familiar, including dogs (*Canis familiaris*) (Hughes & Banks 2010), red foxes (*Vulpes vulpes*), feral cats (*Felis catus*) (Dickman 1992; Arthur et al. 2005) and western quolls (*Dasyurus geoffroii*) (Dickman 1992). The odour of ship rats (*Rattus rattus*) was also found to affect mouse foraging (Hancock 2008). While rats are interspecific competitors of mice (Ruscoe & Murphy 2005), they can also be considered as intraguild predators (O'Boyle 1974). Mice have also been shown to reduce foraging activities during the brighter phases of the moon (Dickman 1992). However, field and laboratory studies show that wild mice can become indifferent to cues of predation in the form of predator odours or illumination intensity (Dickman 1992; Coulston et al. 1993; Bramley 1999; Powell & Banks 2004), sometimes even if avian predators are present (Dickman 1992).

Mice are among the most destructive invasive species in New Zealand (Atkinson 2006) but are seldom targeted

during pest control operations. They are opportunistic omnivores and highly successful breeders (Ruscoe & Murphy 2005). Growing evidence shows that invasive mice can damage native vegetation (Ruscoe et al. 2005) and reduce invertebrate (Tann et al. 1991) and vertebrate (Jones et al. 2003) populations. Mouse populations in New Zealand can irrupt both when food sources become abundant, e.g. after mast years in South Island beech forests (Murphy 1992), and when rat and mustelid populations are intensively controlled (Caut et al. 2007; Goldwater 2007; Ruscoe et al. 2011). The two principal strategies for ongoing pest management are the proactive (i.e. preventing establishment of pests in a pest free environment) and reactive approaches (i.e. management of existing populations of pests) (Parkes & Murphy 2003), both of which are used for mouse control in New Zealand. To date the reactive approach (usually used when complete eradication has not been achieved) has had limited success for mouse control (Ruscoe & Murphy 2005; Goldwater 2007; MacKay et al. 2007), probably because current management of bait stations is not efficient enough.

The feasibility of using the odours of predators and competitors to deter mice as part of a reactive strategy remains unclear from behavioural studies (Dickman 1992; Coulston et al. 1993; Bramley 1999; Powell & Banks 2004; Arthur et al. 2005; Hancock 2008; Hughes & Banks 2010). Key questions to such a strategy are largely unanswered and concern whether mice in New Zealand retain the ability to recognise predatory/competitive cues, and whether such cues might affect their foraging, when their predators/competitors have been removed. Also unknown is the possible connection between mouse control and a potential indirect cue, the illumination associated with the moon cycle.

Here we test the possible impacts of mammalian odours, a specific direct cue of predation or competition, and illumination intensity, a general indirect cue of predation, on the foraging of invasive mice in a mainland site free from mammalian predators and competitors. We aimed to measure the behavioural responses of these mice to predatory and competitive cues and assess the relative importance of these two factors to mouse foraging. We predicted that mouse foraging would be negatively affected by predator/competitor odours and the brighter phases of the moon. We also predicted that the effects of these cues would decrease over time as mice would get familiar with the food sources and habituate to the unreinforced cues. Based on our results, we identify implications for the management of invasive mice unfamiliar with heterospecific mammals.

Methods

Study species and site

We investigated foraging decisions in a population of feral mice within the coastal sand dunes (36°22'N, 174°49'E) of the Tawharanui Open Sanctuary, 65 km north of Auckland City. The dune site is dominated by *Muehlenbeckia complexa* shrubs, which provide an effective dense cover for the mice (Arthur et al. 2005). In 2004, a 2.5-km-long predator-deterrent fence was erected at the western end of the peninsula with the aim of creating a 588-ha pest-free park. An aerial poison drop and ground-based control followed the fence completion and resulted in the eradication of ship rats, Norway rats (*Rattus norvegicus*), cats and mustelids (*Mustela erminea*, *M. nivalis* and *M. furo*), but mice survived the poisoning. Although mice can penetrate the fence (Goldwater 2007), the existence of a

buffer zone outside the fence, which includes grazed paddocks with limited cover and bait stations targeting pest mammals, restricts immigration. Unconstrained by other mammals, mouse populations at Tawharanui irrupted and spread throughout the sanctuary. Goldwater (2007) found that while mice within the park maintained high population densities in all available micro-habitats, outside the park, where there are mammalian predators and competitors, there were fewer mice. Moreover, he found that mice inside the park were significantly larger and heavier than mice outside the park.

At the time of our study, the mouse population at Tawharanui had been free from predation by mammals for 5 years (M. Maitland, Open Sanctuary Coordinator, pers. comm.), and presumably naïve to mammalian predators. Occasional incidents of rat and mustelid reinvasions have been reported (M. Maitland, pers. comm.), but these are rare and the rats have been rapidly detected and controlled. The only other potential mouse predators at present in the park are two species of birds (Robertson et al. 2007), the strictly diurnal Australian harrier (*Circus approximans*) (Baker-Gabb 1981) and the nocturnal morepork owl (*Ninox novaeseelandiae*) (Haw & Clout 1999). Mice are generally nocturnal, although they occasionally forage during the day (Ruscoe & Murphy 2005).

Experimental procedure

We used trays of millet seeds mixed thoroughly in 0.5 L of sand, with scent treatments during four phases of the moon (waxing, full, waning and new) to study the effect of the presence of predator olfactory cues and light intensity on mouse foraging. The study was conducted in 2009 during the austral winter (June and August) when food is scarce and thus mice would potentially be more responsive to supplementary food. Sixty-eight trays were placed at 17 stations that consisted of four trays each. Trays were set up as sealed boxes (3-L clear plastic boxes with lids, Sistema, New Zealand) to protect the seeds and sand from the weather and to prevent birds from taking seeds. We used clear plastic to keep trays exposed to illumination from the moon. The mice could enter the trays via two grey plastic pipes (40 mm in diameter and 50 mm long) mounted on opposite sides of each box. Seeds were sterilised in an autoclave for 50 min at 121°C to prevent germination (Hancock et al. 2004) and then dried in an oven at 70°C for 1 h before weighing to standardised weights (see below).

We used the odours of the house cat (a predator previously present in the park), the Norway rat (a competitor (Ruscoe & Murphy 2005) and potential intraguild predator (O'Boyle 1974) also previously present), and goat (*Capra hircus*; an unfamiliar herbivore) as treatments and distilled water as the control. Goat scent was used to ensure that any effects of cat and rat scents were not due to general responses, such as neophilia or neophobia. Rat faeces were collected separately from male and female laboratory animals at Massey University, Auckland. Cat faeces were collected from a cattery in Auckland (no discrimination between male and female cats was possible). Goat faeces were collected separately from male and female goats at a private farm near Auckland. All samples were frozen at < -18°C immediately after collection. To standardise the volume of the scent samples, faeces were defrosted overnight at 4°C then mixed with distilled water at a ratio of 1:2.14 by volume and blended into a solution. The solutions were separated into 1-g samples and distributed into 10-ml plastic vials. Vials were frozen again at < -18°C, and defrosted on the night before use in the experiment. Vials containing 2 ml of distilled water were used as controls.

The stations were set out in two east–west transects, one comprising 14 stations and the other three. Stations were set up 25 m apart (average home range length for mice at another dune site in New Zealand was > 50 m; Miller 1999). Trays placed at each station were spaced 1–1.5 m apart. To habituate the mice to the presence of the trays, trays were placed in the field 7 days prior to the start of the experiment with 1 g of seeds mixed thoroughly into 0.5 L of sand in the trays.

After the habituation period, we ran the experiment during three consecutive nights for each moon phase (with the empty trays left in place between moon phases). In the afternoon before the first night of each phase, we mixed 3 g of seeds thoroughly into the 0.5 L of sand in the trays and placed the three scent and control vials in the four trays of each station. Upright vials were attached to the inside of the tray with gaffer tape. The treatments were distributed randomly among the trays within each station before each phase to prevent possible orientation effects. The vials were removed at the end of each phase, with new samples entered at the beginning of the next phase. During the phases, trays were checked each morning and, if foraged upon, the seeds were sifted from the sand and placed in a labelled container. New seeds (3 g) were then thoroughly mixed into the sand in the tray. On the third morning of each moon phase, all seeds were removed from the trays. The seeds collected from each foraged tray were dried (as above) and reweighed.

Analysis

Because of inclement weather, it was not possible to collect the seeds from the trays during and after the third night of the waning moon. Data from the third night could therefore only be included in analyses comparing the full- and new-moon phases. We used non-parametric tests whenever the data violated the assumption of normality and for comparisons of proportions.

Preference of mice for each of the treatments was evaluated by calculating the Manly–Chesson Selectivity Index (Chesson 1983). The mean proportion of seeds harvested from a treatment tray was divided by the sum of the means of proportions of seeds harvested from all four treatment trays. We used a one-sample *t*-test (normally distributed data) or a one-sample Wilcoxon signed rank test (data not normally distributed) to determine whether selectivity values differed from an expected random proportion of 0.25. Selectivity values >0.25 would indicate preference for the treatment, while values <0.25 would indicate preference against the treatment. Stations where none of four treatment trays was foraged upon by mice were excluded from this analysis.

We used giving-up densities (GUD) and the proportion of trays foraged to compare levels of foraging by mice. GUD refers to the amount of food a forager leaves behind in a food patch (Brown 1988) and hence gives an indication of the balance reached by the forager between foraging benefits (food gain) and costs, including the perceived risk of predation while feeding. GUD is therefore taken to reflect the density at which it is no longer worth the risk (or the effort) of continuing to exploit the resource. In contrast, the proportion of foraged trays will provide information on the probability that a mouse locates the food and initiates feeding. GUD thus reflects the decision of when to terminate a feeding bout, while the number of food stations that are exploited provides a measure of the probability that a given seed tray was encountered and exploited at least once.

GUDs were indicated by the final mass of seeds remaining in the trays. We used Kruskal–Wallis tests to compare GUDs

(foraged trays only, treatments pooled) between moon phases for each of the first two foraging nights. To evaluate interactions between moon phases and foraging nights and differences between foraging nights for each moon phase, we subtracted the second night from the first (for all 68 trays) and performed Kolmogorov–Smirnov and one-sample *t*-tests, respectively. A Kruskal–Wallis test was used to compare GUDs (treatments pooled) among the first, second and third foraging nights during full- and new-moon phases. We used Mann–Whitney tests to compare GUDs (treatments pooled) between full- and new-moon phases for each foraging night separately. To evaluate moon phases and foraging night interactions, we subtracted results for the new moon from those for the full moon for each of the foraging nights and performed a Kruskal–Wallis test on the difference.

Maximum likelihood analysis of variance (MLAV) was used to compare the effect of treatments and moon phases on the proportions of trays foraged by mice during the first and second nights separately. MLAV was also used to test the effects of the first two foraging nights during full- and new-moon phases on the proportion of foraged trays (the third night was excluded from the analysis since all trays were foraged during both these moon phases).

Results

Only during the first night of waxing and waning moon phases did odour treatments have a significant effect on mouse selectivity. Interestingly, however, the mice showed preference against control trays (one-sample *t*-test; $t_{14} = -3.45$, $P = 0.004$ and Wilcoxon signed rank test; $P = 0.001$; Fig. 1a). There were no significant preferences for any of the trays on the second night (Fig. 1b).

Moon phase had a significant effect on mouse foraging during the first night, with significantly lower GUDs during waning and new moons on the first night (Kruskal–Wallis; $H_3 = 10.038$, $P = 0.018$; Fig. 2a) and near significant differences during the second night (Kruskal–Wallis; $H_3 = 7.811$, $P = 0.050$; Fig. 2b). Interactions between the first and second nights were significant for full (Kolmogorov–Smirnov; $\chi^2 = 2.308$, $P = 0.001$) and waning moons (*t*-test, $t_{67} = 2.879$, $P = 0.005$), and not significant for waxing and new moons (Fig. 2c).

GUDs were higher during full compared with new moons on the first night (Mann–Whitney; $U = 239.5$, $P = 0.024$) but not the second and third nights (Fig. 2d). During full compared with new-moon phases, the foraging night (first, second and third) had a significant effect on mouse GUDs (Kruskal–Wallis; $H_2 = 12.806$, $P = 0.001$; Fig. 2d). There was a significant interaction between foraging nights and moon phases when foraging during full compared with new moons (Kruskal–Wallis; $H_2 = 15.122$, $P = 0.001$; Fig. 2e).

Scent had no effect on the number of trays foraged by mice on either the first or second nights (MLAV; $P > 0.1$). Moon phase had an effect on the number of trays foraged by mice, with fewer trays foraged upon during the full moon on the first and second nights (MLAV; $\chi^2_3 = 22.6$, $P < 0.001$; $\chi^2_3 = 13.24$, $P = 0.004$, respectively; Fig. 3a–b). There were no interactions between treatment and moon phase on either night (MLAV; $\chi^2_9 = 6.39$, $P = 0.700$; $\chi^2_9 = 2.37$, $P = 0.984$, respectively).

Proportions of foraged trays were higher during new compared with full moons on both the first and second nights (MLAV; $\chi^2_1 = 15.13$, $P < 0.001$; Fig. 4). The proportion of foraged trays was higher on the second night than on the first

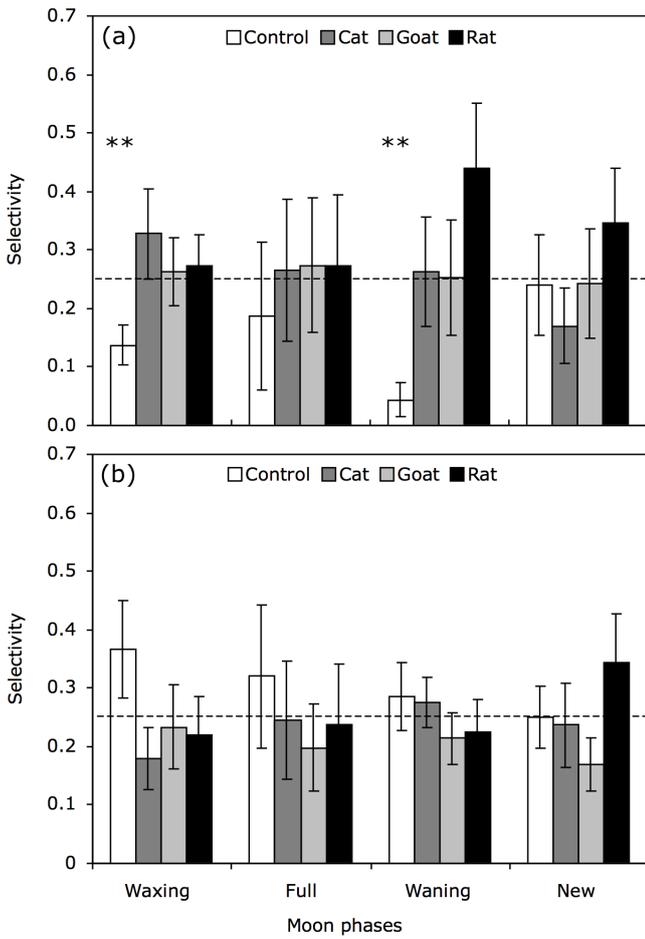


Figure 1. Effect of odour treatments on mouse selectivity (mean \pm SE) on the first (a) and second nights (b) and during all moon phases. Selectivity values >0.25 (represented by dashed line) indicate preference for the treatment while values <0.25 indicate preference against the treatment. Only control trays during waxing and waning moons significantly differ (negatively) from 0.25. ** indicates $P < 0.01$.

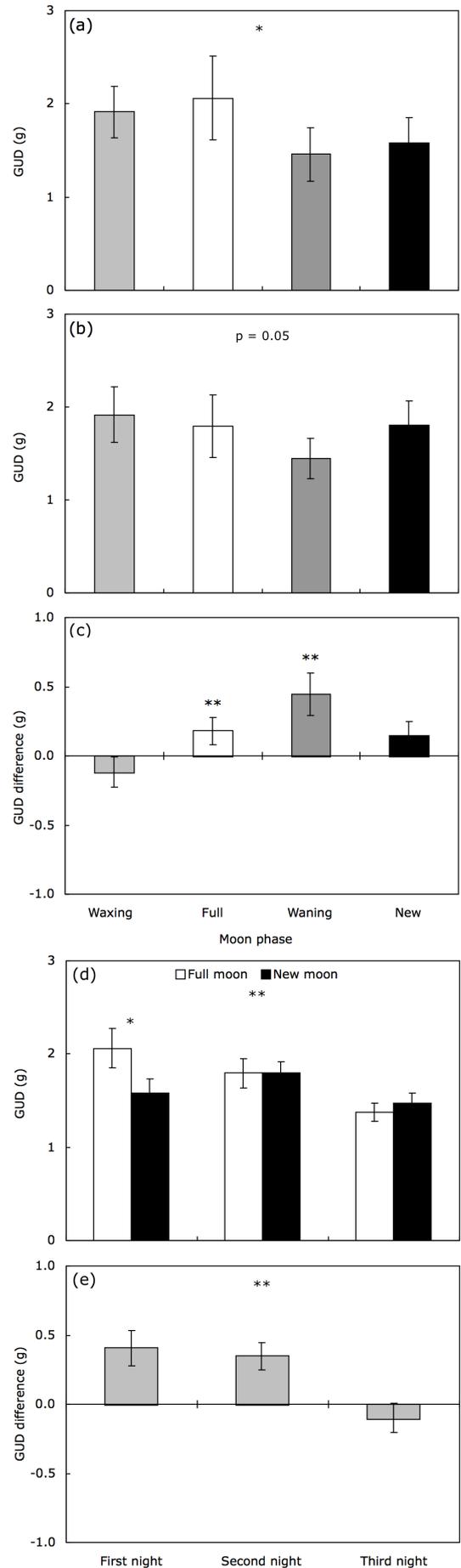


Figure 2. Effect of moon phase on mouse giving-up densities (GUDs, the density of seeds at which the forager ceases consumption; mean \pm SE, treatments pooled) from the foraged trays during the first (a) and second nights (b) and the interaction between moon phase and foraging nights as indicated by the differences in GUDs between the first and second nights (c). Effects of full- and new-moon phases on mouse GUDs (mean \pm SE, treatments pooled) from the foraged trays during the first, second and third nights (d), and the interaction between moon phase and foraging nights as demonstrated by the differences in GUDs between full and new moons during the three nights (e). GUDs were higher during bright phases of the moon and lower during the first compared with the second night. Both foraging night and the interaction between foraging night and moon phase had an effect on mouse GUDs. * $P < 0.05$ and ** $P < 0.01$.

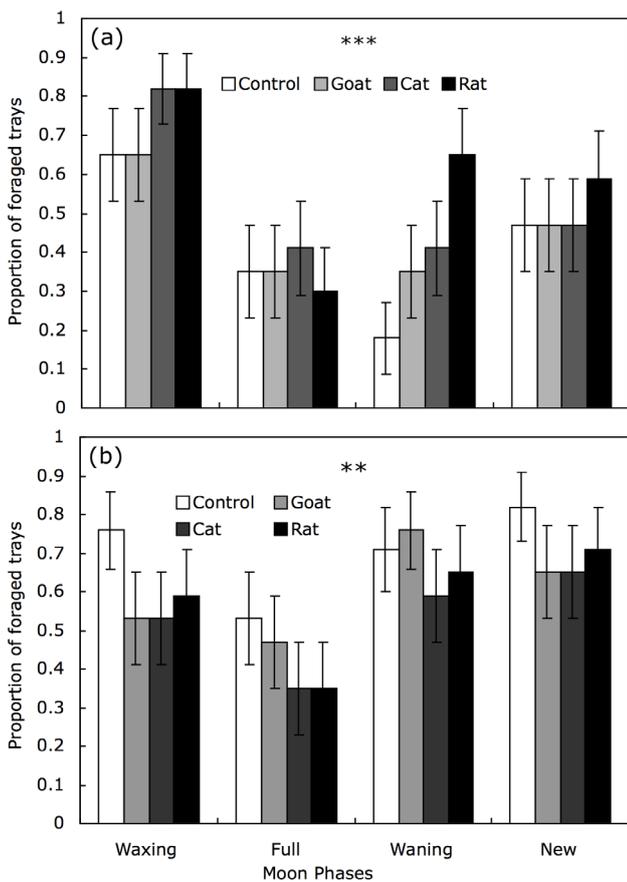


Figure 3. Effects of moon phase on the proportions of foraged trays (mean ± SE) during the first (a) and second nights (b). Moon phase had an effect on mouse foraging, proportions being the lowest during full moon. ** $P < 0.01$ and *** $P < 0.001$.

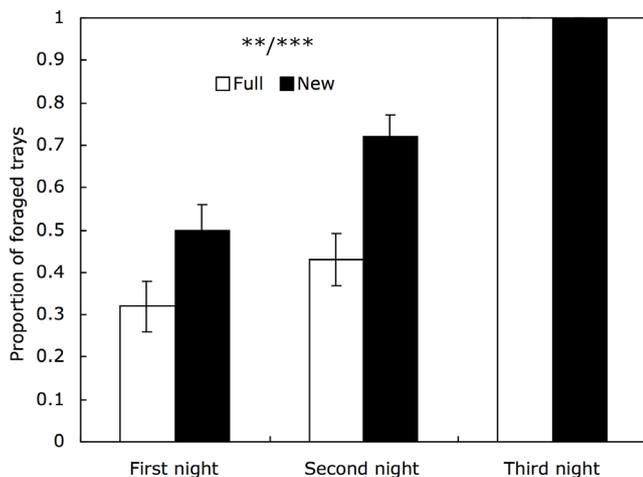


Figure 4. Effect of full and new moons on the proportions of trays with signs of foraging (mean ± SE, treatments pooled). Proportions were higher during new compared with full moons on both the first and second nights and on second compared with the first night. All trays were foraged upon on the third night during both moon phases and hence these values are excluded from the statistical analysis. ** $P < 0.01$ and *** $P < 0.001$.

night (MLAV; $\chi^2_1 = 7.45$, $P = 0.006$; Fig. 4). On the third night, all the trays showed signs of foraging during both new and full moons (Fig. 4).

Discussion

We found no evidence that mouse foraging was affected by the presence of scent cues of the mammalian predator, competitor or herbivore; a result that supports previous studies on *Mus musculus*, both naïve and familiar with mammalian predators (Dickman 1992; Bramley 1999; Powell & Banks 2004). Moreover, the only circumstance where selectivity was significant was against control trays, suggesting a degree of attraction to the test odours, possibly as a result of a neophilic response. At the time of our study, populations of mice at Tawharanui Open Sanctuary had been free from mammalian predators for at least 5 years. Mice do reinvade the park each year (Goldwater 2007), but these incursions are from the heavily predator controlled buffer zone outside the park’s fence, which means that invasions are rare and mouse contact with predators is limited.

In strong contrast to mammalian odours, moonlight intensity had a significant effect on mouse foraging, with GUDs being lower and visiting rates higher during darker phases. It has been shown that rodents experiencing little or no predatory pressure might not respond to light intensity as a cue for increased predation. Shapira et al. (2008) found that in sites where the presence of nocturnal mammalian predators was very low, desert-dwelling gerbils did not decrease food consumption even during full-moon nights. Dickman (1992) showed that mice inhabiting sites free of mammalian predators were less responsive to moonlight intensity than mice from sites where predators were present. In both cases, however, mammalian predators were historically either very scarce (Shapira et al. 2008) or completely absent (Dickman 2008), although owls and snakes were present. At our study site, mice have co-existed with mammalian predators for many generations, experiencing a mammal-free environment only recently. Owls are present at the site, and might affect mouse responsiveness to brighter phases of the moon.

The effect of illumination intensity on mouse foraging behaviour demonstrates a complex interplay between the vigilance of mice and their foraging strategies. During the first night, trends in mouse foraging were affected by the phases of the moon and full and waxing moon phases had higher GUDs compared with new and waning phases. Moreover, the lowest GUDs were seen during the waning rather than the new-moon phases. This suggests that after 2 weeks of relatively low food consumption (waxing and full moon) mice compensated by increasing consumption, resulting in higher GUDs during the new-moon phase. During the second night, however, differences in GUDs between the moon phases were less obvious. These differences can be attributed to an increase in food consumption during the full moon and a decrease in food consumption during the waning-moon phase. The shift in GUDs during the different moon phases from the first night to the second suggests that mice treated the trays as reliable and secure food sources. The effect was significant enough to decrease the importance of the intensity of moonlight as a cue of risk.

Proportions of foraged trays were the lowest during the full-moon phase on both the first and second nights. This suggests that light intensity affected encounters by mice with

the food stations more than the time they took to extract a given amount of food from the source upon encounter. Comparison of the full- and new-moon phases supports this conclusion; GUDs were similar during the second night but proportions of foraged trays, while increasing in both moon phases, remained higher during the new moon. Cloudy skies might have been the reason for the high GUDs and tray encounter rates recorded on the third night of the full moon. This highlights the sensitivity of the mice in the study area to illumination cues, and their opportunistic nature.

Our findings suggest that the use of these scents as deterrents for naïve invasive mice is likely to be ineffective, and although we have tested the cues from only two species likely to interact with mice (*Rattus norvegicus* and *Felis catus*), we suspect that this finding will apply to a much wider range of mammalian odours. It should be noted that we used the odours of domesticated animals that had not had access to mice as prey. However, domestic cats are predators of wild rodents (Woods et al. 2003) and laboratory rats are the same species (*R. norvegicus*) as the Norway rat and it has been demonstrated that predator scent can alter prey behaviour even in a synthesised form (Boag & Mlotkiewicz 1994).

The effect of illumination on foraging by invasive mice appears to be significant and could be used to contribute to mouse control protocols. The most common method of mouse control in New Zealand is poisoning (Towns & Broome 2003; Clapperton 2006), but it is time-consuming to maintain bait stations and replenish bait. At the same time, reducing the quantity and spread of poison are strategies used to minimise harm to non-target species (Eason & Spurr 1995; Murphy et al. 1998; Eason et al. 2002). Our results indicate that moonlight intensity has a greater effect on the probability that foraging will continue after the animal has encountered a food source than on the animal's GUD; mice varied their spatial activity more than the times they spent at a food source during brighter phases of the moon. Hence, consideration should be given to the distances between bait stations. The standard grids in New Zealand for mice traps and bait stations are 50 × 50 m or 25 × 25 m (King et al. 1996; Choquenot & Ruscoe 2000; Harper 2010; MacKay et al. 2011). Our study found that even a 25 × 25 m grid is significantly less effective when illumination conditions are not favourable compared with favourable conditions (i.e. dark nights). Moreover, as the maximum home range of mice is relatively small, especially in high density populations and high productivity habitats (Ruscoe & Murphy 2005), and extraction efficiency is high (this study), long distances between stations might target the mice that are foraging close to the station, but some individuals might never encounter a bait station.

Our study was conducted during winter when food was relatively scarce and in a habitat that provided dense cover. Cover has been found to be an important factor in mouse activity levels and foraging (Dickman 1992; Arthur et al. 2005) and our results showing reduced activity during brighter phases of the moon are likely to be exacerbated in areas where cover is less dense. Applying baiting regimes in accordance to moon cycle should benefit management even more in productive seasons when bait consumption might be lower than in winter.

Incorporating the animal's behavioural traits into management decisions can be a powerful tool in conservation (Holway & Suarez 1999) and this is also true for the management of the house mouse (Clapperton 2006). We suggest that greater density of bait stations and shifting bait applications toward the darker phases of the moon (i.e. refilling stations at waning

moon) has the potential to target more mice that will consume greater amounts of poison bait and thus increase poison control efficacy while reducing bait waste. Further research comparing existing baiting regimes with the ones suggested here should demonstrate whether incorporating mouse foraging traits into management practices is feasible.

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References

- Arthur AD, Pech RP, Dickman CR 2005. Effects of predation and habitat structure on the population dynamics of house mice in large outdoor enclosures. *Oikos* 108: 562–572.
- Atkinson IAE 2006. Introduced mammals in a new environment. In: Allen RB, Lee WG eds *Biological invasions in New Zealand*. Ecological Studies 186. Berlin, Springer-Verlag. Pp. 49–66.
- Baker-Gabb DJ 1981. The diet of the Australasian harrier (*Circus approximans*) in Manawatu-Rangitikei sand country, New Zealand. *Notornis* 28: 241–254.
- Beauchamp G 2004. Reduced flocking by birds on islands with relaxed predation. *Proceedings of the Royal Society B – Biological Sciences* 271: 1039–1042.
- Bernays EA 1998. The value of being a resource specialist: behavioral support for a neural hypothesis. *American Naturalist* 151: 451–464.
- Blumstein DT 2002. Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *Journal of Biogeography* 29: 685–692.
- Blumstein DT, Daniel JC 2005. The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B – Biological Sciences* 272: 1663–1668.
- Boag B, Mlotkiewicz JA 1994. Effect of odor derived from lion faeces on behavior of wild rabbits. *Journal of Chemical Ecology* 20: 631–637.
- Bramley GN 1999. Habitat use and responses to odours by rodents in New Zealand. Unpublished PhD thesis, University of Waikato, Hamilton, New Zealand. 260 p.
- Brown JS 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22: 37–47.
- Brown JS, Kotler BP 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7: 999–1014.
- Caut S, Casanovas JG, Virgos E, Lozano J, Witmer GW, Courchamp F 2007. Rats dying for mice: modelling the competitor release effect. *Austral Ecology* 32: 858–868.
- Chesson J 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64: 1297–1304.
- 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.

- Clapperton BK 2006. A review of the current knowledge of rodent behaviour in relation to control devices. *Science for Conservation* 263. Wellington, Department of Conservation. 55 p.
- Coulston S, Stoddart DM, Crump DR 1993. Use of predator odors to protect chick-peas from predation by laboratory and wild mice. *Journal of Chemical Ecology* 19: 607–612.
- Cox JG, Lima SL 2006. Naiveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution* 21: 674–680.
- Dickman CR 1992. Predation and habitat shift in the house mouse, *Mus domesticus*. *Ecology* 73: 313–322.
- Dickman CR 2008. Indirect interactions and conservation in human-modified environments. *Animal Conservation* 11: 11–12.
- Eason CT, Spurr EB 1995. Review of the toxicity and impacts of brodifacoum on non-target wildlife in New Zealand. *New Zealand Journal of Zoology* 22: 371–379.
- Eason CT, Murphy EC, Wright GRG, Spurr EB 2002. Assessment of risks of brodifacoum to non-target birds and mammals in New Zealand. *Ecotoxicology* 11: 35–48.
- Goldwater N 2007. Ecology of house mice within the Tawharanui Open Sanctuary. Unpublished MSc thesis, University of Auckland, Auckland, New Zealand. 128 p.
- Gould JL 1982. *Ethology: The mechanisms and evolution of behavior*. 1st edn. New York, Norton. 544 p.
- Griffin AS, Blumstein DT, Evans CS 2000. Review: Training captive-bred or translocated animals to avoid predators. *Conservation Biology* 14: 1317–1326.
- Hancock B 2008. The influence of ship rats (*Rattus rattus*) on the habitat preferences of the house mouse (*Mus musculus*). Unpublished MSc thesis, Victoria University of Wellington, New Zealand. 117 p.
- Hancock JH, Wilkerson JB, Moody FH, Newman MA 2004. Seed-specific placement of in-furrow fungicides for control of seedling disease in cotton. *Crop Protection* 23: 789–794.
- Harper GA 2010. Habitat use by mice during winter on subantarctic Auckland Island. *New Zealand Journal of Ecology* 34: 262–264.
- Haw JM, Clout MN 1999. Diet of Morepork (*Ninox novaezealandiae*) throughout New Zealand by analysis of stomach contents. *Notornis* 46: 333–345.
- Hawlena D, Schmitz OJ 2010. Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences (USA)* 107: 15503–15507.
- Holway DA, Suarez AV 1999. Animal behavior: an essential component of invasion biology. *Trends in Ecology & Evolution* 14: 328–330.
- Hughes NK, Banks PB 2010. Interacting effects of predation risk and signal patchiness on activity and communication in house mice. *Journal of Animal Ecology* 79: 88–97.
- Jones AG, Chown SL, Gaston KJ 2003. Introduced house mice as a conservation concern on Gough Island. *Biodiversity and Conservation* 12: 2107–2119.
- King CM, Innes JG, Flux M, Kimberley MO 1996. Population biology of small mammals in Pureora Forest Park: 2. The feral house mouse (*Mus musculus*). *New Zealand Journal of Ecology* 20: 253–269.
- Lahti DC, Johnson NA, Ajie BC, Otto SP, Hendry AP, Blumstein DT, Coss RG, Donohue K, Foster SA 2009. Relaxed selection in the wild. *Trends in Ecology & Evolution* 24: 487–496.
- Lima SL, Dill LM 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619–640.
- MacKay JWB, Russell, JC, Murphy, EC 2007. Eradicating house mice from islands: successes, failures and the way forward. In: Witmer GW, Pitt WC, Fagerstone KA eds *Managing vertebrate invasive species. Proceedings of an International Symposium*. Fort Collins, CO, USDA/APHIS/WS, National Wildlife Center. Pp. 294–304.
- MacKay JWB, Murphy EC, Anderson SH, Russell JC, Hauber ME, Wilson DJ, Clout MN 2011. A successful mouse eradication explained by site-specific population data. In: Veitch CR, Clout MN, Towns DR eds *Island invasives: eradication and management*. Gland, Switzerland, IUCN. Pp. 198–203.
- McPhee ME, Segal A, Johnston RE 2010. Hamsters use predator odors as indirect cues of predation risk. *Ethology* 116: 517–523.
- Miller AP 1999. Ecological energetics of feral house mice (*Mus musculus*) inhabiting coastal sand dunes. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.
- Murphy EC 1992. The effects of a natural increase in food-supply on a wild population of house mice. *New Zealand Journal of Ecology* 16: 33–40.
- Murphy EC, Clapperton BK, Bradfield PMF, Speed HJ 1998. Brodifacoum residues in target and non-target animals following large-scale poison operations in New Zealand podocarp-hardwood forests. *New Zealand Journal of Zoology* 25: 307–314.
- O’Boyle M 1974. Rats and mice together: The predatory nature of the rat’s mouse-killing response. *Psychological Bulletin* 81: 261–269.
- Orrock JL 2010. When the ghost of predation has passed: do rodents from islands with and without fox predators exhibit aversion to fox cues? *Ethology* 116: 338–345.
- Parkes J, Murphy E 2003. Management of introduced mammals in New Zealand. *New Zealand Journal of Zoology* 30: 335–359.
- Powell F, Banks PB 2004. Do house mice modify their foraging behaviour in response to predator odours and habitat? *Animal Behaviour* 67: 753–759.
- Robertson CJR, Hyvönen P, Fraser MJ, Pickard CR 2007. *Atlas of bird distribution in New Zealand 1991–2004*. Wellington, The Ornithological Society of New Zealand. 533 p.
- Ruscoe WA, Murphy EC 2005. House mouse. In: King CM ed. *The handbook of New Zealand mammals*. 2nd edn. Melbourne, Oxford University Press. Pp. 204–221.
- 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.
- Ruscoe WA, Ramsey DSL, Pech RP, Sweetapple PJ, Yockney I, Barron MC, Perry M, Nugent G, Carran R, Warne R, Brausch C, Duncan RP 2011. Unexpected consequences of control: competitive vs. predator release in a four-species assemblage of invasive mammals. *Ecology Letters* 14: 1035–1042.
- Shapira I, Sultan H, Shanas U 2008. Agricultural farming alters predator–prey interactions in nearby natural habitats. *Animal Conservation* 11: 1–8.
- Sheriff MJ, Krebs CJ, Boonstra R 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology* 78: 1249–1258.

- Sih A 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist* 139: 1052–1069.
- 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.
- Towns DR, Broome KG 2003. From small Maria to massive Campbell: Forty years of rat eradications from New Zealand islands. *New Zealand Journal of Zoology* 30: 377–398.
- Webb JK, Pike DA, Shine R 2010. Olfactory recognition of predators by nocturnal lizards: safety outweighs thermal benefits. *Behavioral Ecology* 21: 72–77.
- Woods M, McDonald RA, Harris S 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Review* 33:174–188.

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