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The foraging behaviour of the Black rat (*Rattus rattus*) within Australian macadamia orchards

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Abstract

The black rat (*Rattus rattus*) has been shown to be the primary species responsible for causing significant crop losses within the Australian macadamia industry. This species success within macadamia orchards is directly related to the flexibility expressed in its foraging behaviour. In this paper a conceptual foraging model is presented which proposes that the utilisation of resources by rodents within various components of the system is related not only to their relative abundance, but also to predator avoidance behaviour. Nut removal from high predation risk habitats during periods of low resource abundance in low risk compartments of the system is considered an essential behaviour that allows high rodent densities to be maintained throughout the year.

Keywords: rodent; foraging; nut removal; macadamia; habitat utilisation; *Rattus rattus*

Introduction

Most species possess numerous behavioural strategies that attempt to maximise their survival and reproductive success *ie.*, fitness (Stearns 1992). In order to optimise fitness it is sometimes necessary for organisms to “trade-off” efficiencies in various behavioural activities. For example, foraging efficiency may vary in relation to predator avoidance behaviour resulting in habitats rich in food resources being utilised sub-optimally if sufficient predator protection is not provided (Strickberger 1990; Stearns 1992). These trade-offs will have an influence on how an organism utilises various components of a habitat spatially and temporally. Small mammals are often at high risk of predation from birds, reptiles and larger mammalian predators (Eilam *et al.* 1999, Powell and Banks 2003). In order to reduce the risk of predation, small mammals have been shown to utilise multiple habitat components in relation to predator numbers, habitat structure, and resource abundance (Powell and banks 2003, Apfelbach *et al.* 2005). This is demonstrated in desert habitats where gerbils alter their foraging behaviour and utilise areas of high cover when owl numbers are high (Kottler *et al.*, 1991, Hughes *et al.* 1994).

Foraging behaviours of species inhabiting agricultural systems are often significantly different to the behaviours expressed within their native habitats. For a species to successfully colonise and establish within an agricultural environment, it must be able to utilise multiple resources and have plastic reproductive behaviours, as food and cover resources associated with most agricultural systems vary greatly throughout the crop cycle. Elements of a life history strategy that may enhance the success of a species include: (a) high dispersal capabilities to allow movement between spatially distinct components of the agricultural system, (b) a reproductive capacity that allows it to closely track rapidly changing resource levels and (c) the ability to utilise varied food and shelter resources. Many large agricultural systems include non-crop habitats of exotic weeds and native shrubs that are patchily distributed throughout and adjacent to the crop. These habitats often supply organisms with alternative food and shelter resources that cycle out of phase with the crop habitat. In many instances this results in a relatively constant supply of food resources within the agricultural system throughout the year (White *et al.* 1997).

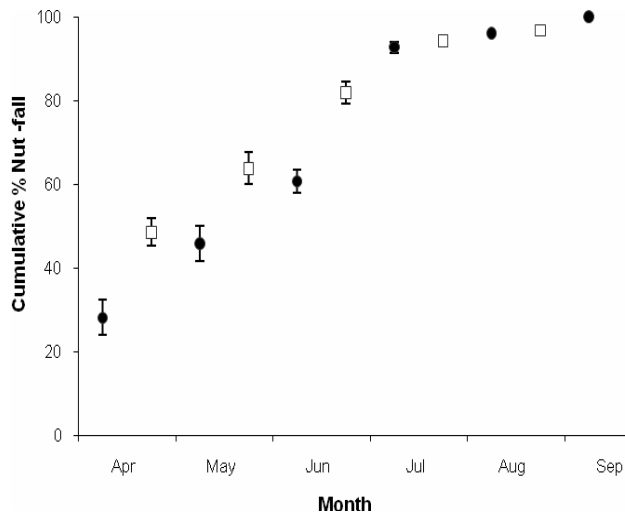


Fig 1. Cumulative percentage nut-fall for the 2000 season (mean \pm SE) (\bullet = orchard 1, \square = orchard 2).

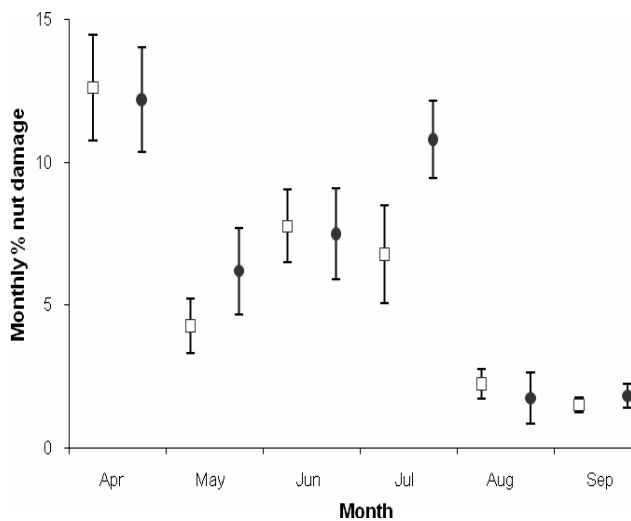


Fig 2. Monthly percent nut damage for the 2000 nut-fall season (mean \pm SE) (\bullet = orchard 1, \square = orchard 2).

Therefore switching between resources in different habitats is a mechanism that may allow generalist species to maintain elevated populations throughout the year when crops are seasonal.

A substantial amount of research has been undertaken on the ecology of the rodent *Rattus rattus* in both Hawaiian and Australian macadamia orchards. *R.rattus* within Hawaiian systems was found to have limited dispersal ranges with minimal movement occurring between crop and non-crop habitats (Tobin *et al.* 1996). The continuous habitation of the orchard was considered to be a consequence of the extended flowering season in these orchards (Tobin 1994). Due to the type of

cultivars and the climatic conditions within Hawaiian orchards, macadamia nuts are available as a food resource for the majority of the year, with various cultivars fruiting and flowering at different times throughout the season. Therefore in-crop food resources remain at a level that is sufficient to support rodent populations within the crop and rodents do not depend on alternative, non-crop resources. Thus, there is no great need for rodents to forage outside the crop and utilise non-crop food resources. In contrast, in-crop food resource levels in Australian macadamia orchards exhibit a greater degree of temporal variability due to a pronounced fruiting and flowering season, with the bulk of the resource being present only between late January and early September. In Australian systems, rodent damage to macadamia nuts has been directly correlated with the size and temporal stability of adjacent non-crop habitats (Horskins *et al.* 1998; White *et al.* 1998), with considerable bi-directional movement occurring between the crop and non-crop habitats (Horskins *et al.* 1998). Horskins *et al.* (1998) and Elmouttie and Wilson (2005) determined that in-crop damage was restricted to the canopy of macadamia trees with no nuts being eaten from the ground layer of the system. However, Elmouttie and Wilson (2005) showed that nut removal, a previously unidentified component of the damage process, was responsible for between 37-53% of damage associated with the front row of the orchard system. Rodents removed nuts from the ground layer of the orchard to adjacent non-crop habitats and consumed nuts in areas which had high levels of aerial cover (Elmouttie and Wilson 2005). Furthermore, no nuts found within the adjacent habitat were undamaged, suggesting that nuts were not being stored or cached (Elmouttie and Wilson 2005). It was also suggested that this behaviour may be a predator avoidance response. This paper extends the findings of Elmouttie and Wilson (2005), by investigating the temporal variation in nut removal and food resource levels within adjacent non-crop habitats. In doing so, we develop a foraging model for *R.rattus* in Australian macadamia orchards that incorporates food resource availability in all four compartments of the system namely; in-tree resources, on-ground resources, nut removal from on-ground resources and resources within the adjacent habitat.

Materials and methods

Studies were conducted in two 30 year old macadamia orchards at Maleny, south-east Queensland, Australia, that historically received high rodent damage (White *et al.* (1997), Horskins *et al.* (1998), White *et al.* (1998) and Elmouttie and Wilson (2005).

Each orchard block was adjacent to a large temporally stable non-crop habitat characterised by thick ground layer and canopy vegetation dominated by Lantana (*Lantana camara*), wild tobacco (*Solanum mauritianum*), native raspberry (*Rubus rosifolius*) and ink weed (*Phytulacca spp.*). Maintained grasslands (headlands) of 10-20m separated orchards blocks from adjacent non-crop vegetation. Rodent populations at the two orchards were considered independent as they were approximately 2km apart and separated by other orchard blocks, grazing paddocks, grasslands and dirt roads. Damage and removal estimates were measured using the same methodology as outlined in Elmoultie and Wilson (2005). Eleven mature front row trees were selected at the first orchard and fifteen trees at the second with all replants excluded from analysis. The study focused on front row trees as White *et al.* (1997) demonstrated this to be the region of highest nut damage due to rodent foraging from the adjacent non-crop habitats. Horskins *et al.* (1998) also established a relationship between nut damage and distance from adjacent non-crop habitats.

A circular rodent exclosures, 1m in diameter and 0.6m in height, constructed from 12 mm² bird wire was placed at the base of each tree at a distance of 1m from the trunk. The top of the exclosures sloped inwards at an angle of 20° to an opening of 100mm that was fitted with a rodent exclusion collar. A plastic lining was also fixed to the top of exclosures to assist the entrance of falling nuts. A control, of identical area to the exclosure, delineated from 20mm wide metal strapping was positioned on the opposite side of the tree. The controls were designed to allow nuts falling from the canopy to be captured, whilst enabling rodents to forage. Damaged and undamaged nuts in the exclosures and control areas were counted monthly over the entire nut-fall season. All nuts from the control areas were replaced to maintain a consistent level of resources in relation to the rest of the ground layer under the tree. When nuts or leaf litter were removed from the ground layer of the system as a result of standard farming practices (*e.g.* sweeping or ground harvesting) an equivalent treatment was applied to the control areas.

Assuming that removal of damaged or undamaged nuts does not occur from the tree to the adjacent habitat, using the following variables;

Pl = Percentage total yield loss

Dt = Damage in tree

Dg = Damage on ground

Nr = Nuts removed

Ty = Total yield

$$Pl = \frac{100(Dt + Dg + Nr)}{Ty}$$

If D_x and U_x denote the number of damaged and undamaged nuts in area x , where $x=e$ (exclosure) or $x=c$ (control), then:

$$Ty = Ue + De$$

$$Dg = Dc - De$$

$$Nr = (De + Ue) - Dc + Uc$$

$$Pl = \frac{100(De + Ue - Uc)}{(Ue + De)}$$

A relative index of food resources within the adjacent non-crop habitat at each site was determined monthly. A 5m wide belt transect that spanned the length of each adjacent non-crop habitat (Orchard 1 = 75m, Orchard 2 = 110m) was established. Within the transect, ten random trees of the three dominant plant species native Raspberry (*Rubus rosifolius*), Wild Tobacco (*Solanum mauritianum*) and Ink-weed (*Phytulacca spp.*), known to be the preferred food resources of *Rattus rattus* within the non-crop habitats (Horskins *et al.* 1998) were selected. Each month, data was collected on the presence or absence of flowers, mature and immature fruit, or whether only vegetative matter was present. The number of each of those species within the belt transect was also recorded. This data was used as an index of relative temporal variation in food resources within the adjacent non-crop habitats. Rodent densities were estimated each month at both orchard sites. Trapping as conducted as outlined White *et al.* (1997) and Horskins *et al.* (1998). Two rows of 10 snap traps were placed within the adjacent non-crop habitat. Rows were separated by a distance of 15-20m whilst traps within a row were separated by 10m. Trapping was conducted over three consecutive nights every month for 12 months.

Results

The temporal pattern of cumulative nut-fall was similar between the two orchards, with nuts available on the ground layer of the orchard from April to September, and 50% of total nut-fall had occurring by May (Figure 1). Temporal damage patterns were also similar between orchards with damage occurring throughout the season, however 50% of the total damage for the season had occurred by May (Figure 2). A strong relationship existed between the temporal patterns of nut-fall and in-crop damage at

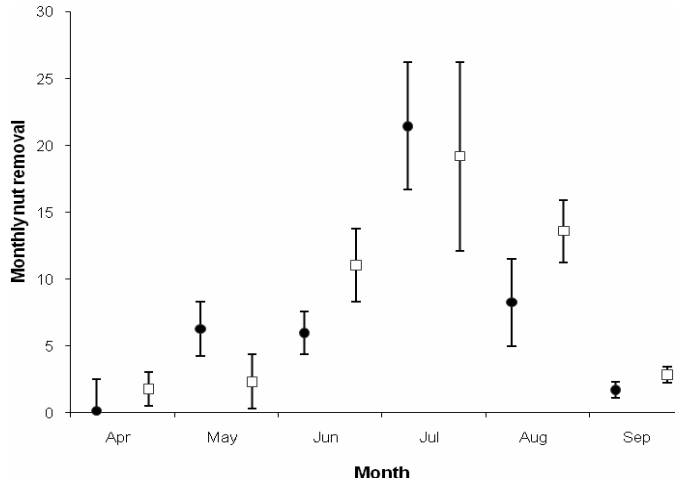


Fig 3. The number of nuts removed for during the 2000 nut-fall season (mean \pm SE) (\bullet = orchard 1, \square = orchard 2).

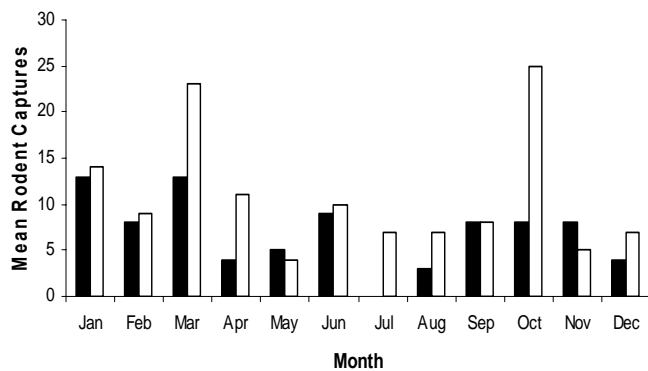


Fig 4. Mean rodent captures at both orchard sites over 12 month trapping period (\blacksquare = orchard 1, \square = orchard 2).

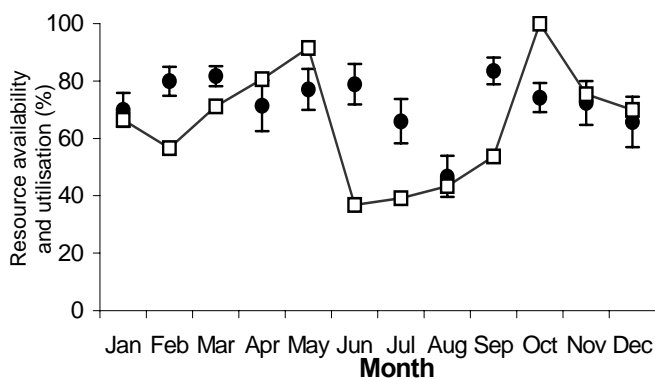


Fig 5. Temporal fluctuations in non-crop resources and utilisation of these resources over a 12 month period (\bullet = resource utilisation, \square = resource levels).

both orchards (Orchard 1: $r_{\text{arcsine transform}} = 0.975$, $n = 6$, $p = 0.001$; Orchard 2: $r_{\text{arcsine transform}} = 0.936$, $n = 6$, $p = 0.006$), suggesting that in-crop damage is directly associated with in-tree resource load. The pattern of nut removal was similar between orchards ($r = 0.872$, $n = 6$, $p = 0.024$) with the mean number of nuts removed increasing from April to a peak in July followed by a decline (Figure 3). Rodent densities varied throughout the year (Figure 4) and were not correlated to the level of nut removal, indicating that removal is not a simple function of an increase in population size ($r = 0.142$, $n = 6$, $p = 0.788$). The utilisation of non-crop resources differed through the year ($F = 2.128$, $df = 11$, $p = 0.018$), non-crop resource utilisation steadily declined from June to a low point in August, resource utilisation then sharply increased in September (Figure 5). During this period (June to August) resource levels in the adjacent non-crop habitats also reached their lowest for the season (Figure 5), whilst the level of nut removal was at its highest (Figure 3).

Discussion

Dietary switching is the change of diet from one food type to another, such that food items are consumed proportionately to their relative abundance. Consequently, dietary switching is most effective as a foraging strategy in systems where the overall food resource level remains relatively stable. It is a common behaviour when different food resources fluctuate temporally, with a food item being present in one season but not in the next (Caughley and Sinclair 1994), forcing a replacement resource to be utilised. A conceptual foraging model is proposed, that incorporates the findings of previous research and the present study. It suggests that the ability of rodents to inflict high levels of nut damage in Australian macadamia orchards is a consequence of the maintenance of relatively high and stable rodent densities throughout the year that in turn results from dietary switching between food resources in various components of the orchard system in accordance to their availability. This strategy allows rodent populations in non-crop habitats to be maintained throughout the agricultural cycle at levels higher than what would be possible if only one seasonal food source was utilised. There are four foraging options available to rodents in Australian macadamia orchards, namely: forage on nuts within the tree layer, forage for fallen nuts on ground layer of the orchard, remove nuts from the ground layer for consumption under the cover of vegetation in the adjacent habitat and forage on non-crop resources within the adjacent habitat. A comparison of Figures 6a and 6b shows that the high abundance of nut resources in both the

tree compartment of the system and adjacent non-crop compartment in the early part of the season lead to utilisation of these components. As resources within the tree decline, a parallel decline in resources is observed in non-crop habitats making the overall level of food resources available within these low predator risk compartments minimal. This leads to a reduction in utilisation, as the overall resource availability in both compartments is low. During this period, there is a subsequent increase in resources on the ground layer. Rodents do not forage directly on this resource (Elmoultie and Wilson 2005) but collect nuts from this high predator risk compartment and remove them to a low predator risk compartment for consumption, that is, high aerial cover areas within the adjacent non-crop habitats. Once food resources again increase in the non-crop habitat, the rate of nut removal is significantly reduced. Even though there are still resources available on the ground layer, rodents preferentially feed on the resources in the non-crop habitats until the commencement of the next nut-fall season, presumably to reduce the risk of predation.

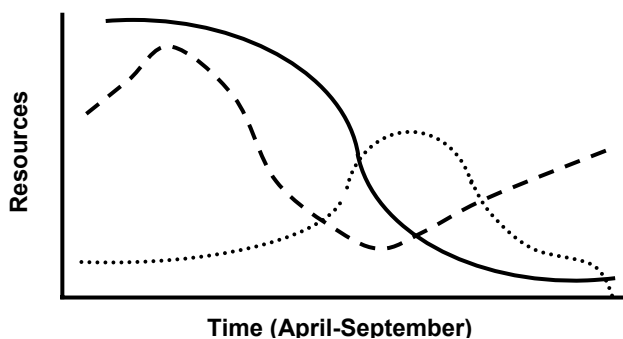


Fig 6a. Temporal fluctuations in available food resource levels in tree, ground and non-crop compartments. (— = In-tree resource, = ground resource, - - - = Adjacent non-crop resource)

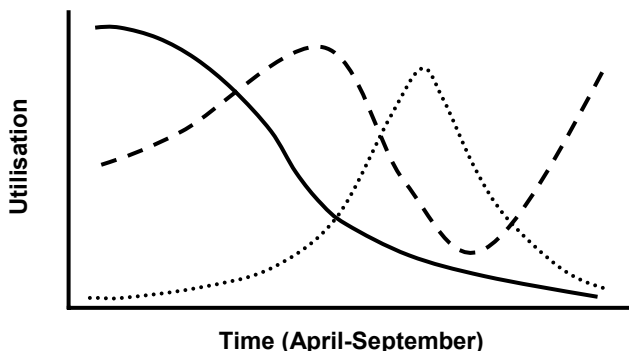


Fig 6b. Temporal fluctuations in in-crop damage, nut removal and non-crop resource utilisation

Nut removal from a compartment of the system where predation risk is high, forms an essential component of the model as it provides a food gathering mechanism that is used only when food resources in both low predation risk habitats (tree and non-crop habitats) are at a minimum. Horskins *et al.* (1998) and White *et al.* (1997) have demonstrated that the adjacent non-crop habitats support large populations of rodents which forage into the orchard habitat to feed. It is reasonable to suggest that a rodent returning to the adjacent non-crop habitat after a feeding session in the orchard may simply return with a nut and the process may be nothing more than advantageous nut removal. Alternatively rodents may forage within the tree layer of the orchard when resources in this component are abundant so as to avoid predation and only begin removing nuts from the orchard floor when resources decline in this compartment minimising any interaction with potential predators on the ground layer of the orchard. The first scenario is unlikely, as if removal was solely a function of rodents returning from the orchard to the adjacent habitat with a nut, the rate of removal would be a function of the population size. This was not the case in this study as rodent population size was not correlated with removal. The second scenario is more likely as removal only occurs when food resources in both the tree and non-crop components of the system are low and subsequently declines with the increase in adjacent non-crop resources. In addition, the strong correlation that exists between nut distribution within the adjacent non-crop habitats and aerial (canopy) cover, and the evidence of damage being exclusive to the tree component of the system suggests that *R. rattus* forage in a manner to reduce the risk of avian predation (Elmoultie and Wilson 2005). The success of *R. rattus* in Australian macadamia orchards is due to their ability to utilise a foraging strategy that incorporates food resources in all compartments of the system. This strategy incorporates both a diet and foraging location switch and a predator avoidance response. This is an effective and efficient strategy within this system and has enabled the species to maintain high population levels throughout the year. The plasticity in *R. rattus*' foraging strategy in terms of its ability to adapt to different habitat conditions both spatially and temporally (eg. Hawaii vs. Australia) has seen it become the dominant pest species in macadamia orchards.

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