# Adult free zones in small mammal populations: Habitat Preferences and Response of Australian native rodents to reduced cover.

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**Abstract** Cover provides shelter, food, nesting opportunities, and protection from predators. The behavioural response of small mammals to reduced cover has been well documented. However, very little is known about the effect of cover on community and population dynamics. Australian small mammals generally inhabit extremely dynamic ecosystems, where cover and food supplies are greatly affected by fire. Species are described as early or late seral specialists, generally returning to a disturbed area once their habitat requirements are met. Habitat requirements have loosely been interpreted as cover and food supply, however, these factors are not mutually exclusive and few studies have attempted to determine the driving factors behind small mammal succession. In this study, we manipulated specific aspects of cover in the eucalypt forests of Fraser Island and show that the behaviour and population dynamics of small mammals were greatly affected. A reduction of cover from grass-trees (*Xanthorrhoea johnsonii*) did not affect small mammal species composition, however, the abundance and size structure distribution of the dominant species (*Rattus fuscipes*) decreased. Patch use by rodents also decreased after cover was reduced. *Rattus fuscipes* must trade-off remaining in an environment with increased risk of predation or disperse to an area with greater cover but increased competition. Juveniles dominated (>60%) populations of *R. fuscipes* after cover was reduced, however, size distributions of control sites were relatively more even (<25% juvenile). While adult *R. fuscipes* are either killed by predators or disperse to other areas, juveniles that remained or immigrated to an area of reduced cover gained a selective advantage over control sites, because reduced competition with adults increased body condition of juvenile *R. fuscipes*.

## Introduction

Vegetation cover has long been known to affect the abundance and composition of ground-dwelling fauna in Australia (Braithwaite & Gullen 1978, Suckling & Heisler 1978, Newsome & Catling 1979, Catling & Burt 1995, Cork & Catling 1996). Cover provides shelter, food, nesting opportunities and protection from predators (Fox & McKay 1981, Fox 1982, 1990, Sutherland & Dickman 1999, Monamy & Fox 2000). Small mammals respond to a change in food resources (Dickman 1989, Boutin 1990, Banks & Dickman 2000, Predevac 2000), but it is generally assumed that they respond to total habitat complexity rather than specific habitat characteristics (Newsome & Catling 1979). Habitat structure can indicate relative risk of predation, because an individual's vulnerability to a predator may depend on the density of vegetation. For example, Snowshoe hares (Rohner & Krebs, 1996) and rabbits (Banks et al. 1999) avoid open spaces because the chances of successful attack from owls and foxes respectively is higher than in closed, more structurally complex habitats. Studies describing small mammal succession after fire have mainly focused on general aspects of habitat structure (e.g., habitat complexity scores, Newsome & Catling (1979). Yet specific characteristics or vegetation associated with an increase in habitat complexity may drive mammal succession.

Many grass-trees (*Xanthorrhoea* spp.) respond to fire by producing strongly scented flowers within 7-8 weeks after a fire; attracting insects, birds and mammals (Gill 1981). *Xanthorrhoea* spp. also produces a distinctive 'grass skirt' around the base of the plant, which may provide medium to long-term shelter for small mammals. *Xanthorrhoea* spp. produce a large trunk that is composed of a mass of old leaf bases held together by a natural resin (Staff & Waterhouse 1981). The trunk can take up to a decade to form and over 20 years before their linear leaves rise above the ground. Thus the dense 'grass skirt' may form an important long-term source of shelter for ground-dwelling small mammals. Two species of *Xanthorrhoea* are common on Fraser Island (*X. johnsonii* and *X. australis*). *Xanthorrhoea johnsonii* are especially distinctive prior to the formation of a trunk, because they produce a circular mass of dense leaves, providing a large area for shelter. Several studies have

suggested that small mammal composition and abundance in Australian forests may relate to *Xanthorrhoea* spp. as a source of food (Dettmann et al. 1995, Whelan et al. 1996); however only one study has considered grass-trees as an important source of shelter (Tulloch 2001).

Determining underlying processes driving small mammal communities can only be achieved by experimental manipulation (Sutherland & Dickman 1999, Krebs 2002). Few studies have experimentally tested causal relationships between small mammal abundance and habitat characteristics; primarily because some factors are not mutually exclusive e.g. vegetation is used as food and shelter. Reducing ground cover of *Xanthorrhoea* spp. by cutting leaves, reduces food availability (e.g. reduce ground invertebrate densities). Hence, in this study we reduced total ground cover of *Xanthorrhoea johnsonii* by tying leaves together to determine the impact of reduced cover on the population dynamics and behaviour of small mammals in eucalypt forests of Fraser Island. Reducing total ground cover impacts on the arthropod community (Whelan et al. 2002), but reducing cover by tying leaves is likely to interrupt potential food supplies far less than total removal. Nicol (1994) reduced cover by 50% by tying vegetation into clumps on a single site in coastal heath in southern Australia. The clumping of vegetation had limited impact on food availability and *Rattus lutreolus* declined because of reduced cover. However, it is not clear whether rodents were responding to specific habitat characteristics or an overall decrease in habitat complexity and cover.

Reduced cover can influence patch use and population dynamics of small mammals by increasing perceived risk of predation (Rosenzweig 1973, Norrdahl & Korpimaki 1995, Boonstra et al. 1998) or actual predation rates (Kotler et al. 1991). Prey generally decreases activity with increased risk of predation (Lima 1998). This predator-induced microhabitat shift can reduce fecundity by limiting access to resources, hastening declines and lengthening the recovery phase (Hik 1995). The eucalypt forests of Fraser Island off the east coast of Australia may contain over 15 native rodents and marsupials. Hence a reduction of cover may alter species behaviour, which affects population dynamics and may ultimately affect species composition. In this study, we reduced cover provided by grass-trees (*X. johnsonii*) to determine the affect on small mammal community structure. We also determined the mode of any increase or decrease in abundances by determining changes in species population

dynamics (recruitment, reproductive status, size structure and sex ratio) and behaviour
(patch-use).

**Methods**

*Study animals and sites*

Fraser Island is the world's largest sand island and was inscribed as a world heritage
area in 1992 (UNESCO WHC 1992). The island supports more than six types of vegetation
communities, but we concentrated our study in the mixed eucalypt forests, which are
extremely low in accessible nutrients and often have stunted canopy trees (Thomas 2002).
Scribbly gum (*Eucalyptus racemosa*) and Brushbox (*Lophostemon confertus*) dominate the
canopy trees (>15m). Banksias (*Banksia serrata*) and Casuarinas (*Allocasuarina littoralis*) are
common middle canopy layer (5-15m) species. Bracken fern (*Pteridium esculentum*), grass
trees (*Xanthorrhoea johnsonii*), burrawangs (*Macrozamia douglasii*), midyim (*Austromyrtus
dulcis*), spiny-headed mat rush (*Lomandra longifolia*) and grasses (*Themda triandra* and
*Imperata cylindrica*) are common lower canopy and ground cover species. The ground-
dwelling small mammal communities in eucalypt forests of Fraser Island are similar to most
east coast communities, which are dominated by native rodents (*Rattus fuscipes*, *R. lutreolus*,
*R. tunneyi*, *Melomys cervinipes*) and marsupials (*Antechinus flavipes*, *Acrobates pygmaeus*,
*Sminthopsis murina*).

*Habitat preferences*

To determine habitat preferences of small mammals, we trapped in 15 sites of 1ha
each throughout the southeastern section of Fraser Island. Detailed fire histories of each site
were known (QPWS) and sites of different fire histories were used to evaluate habitat
preferences. Sites were located randomly within a 30 000ha area (30kmx10km), conditioned
on them being at least 1km apart and 100m from any road. In each hectare plot, fifteen traps
(Elliot scientific equipment 33X10X19cm) were set in three transects for three consecutive
nights in June 2002. Each transect consisted of five traps set 20-25m apart and each transect

was 25m apart. Traps were baited with a peanut butter/honey/oats mixture and were checked and emptied each morning (06:00-09:00). Cotton wool was placed in each trap to provide insulation for captured animals. We determined the species and sex of each animal (Strahan 1998). Head length (HL) was measured by placing callipers from the base of the skull to the tip of the nose and body length (BL) was measured with a 30cm rule from the tip of the nose to the base of the tail. Each animal was weighed using a spring balance (Salter®) with an error of either ± 0.1g or ± 2g depending on the size of the animal. Animals were individually marked by a unique series of ear notches. We used head length to estimate size structure and an estimate of body condition was calculated by the formula:

$$\text{Body condition index (BCI)} = \frac{\text{Mass (kg)}}{\text{Head length(m)}^2}$$

Equation 1
(Frankenfield et al. 2001)

Sexual condition for each animal was determined by observing the presence or absence of a scrotum (males), the condition of the vagina (perforated or unperforated), number and condition of the teats (lactating) (females). We measured scrotal width using vernier callipers of males. Marsupial pouches were checked for young and we determined if female rodents were pregnant (advanced stages only) by externally feeling for young in the uterus. We determined size (HL) at sexual maturity from the 10 smallest males and females in all sites that were displaying secondary sexual characteristics (ie. males displaying a scrotum and females that were pregnant or lactating). Recapture rates within each trapping period was over 70% at each site; hence we used minimum number alive (individuals captured per site per trapping period) in each site was used to determine temporal and spatial differences in population size.

Vegetation surveys were conducted in all sites throughout June and August 2002. Five 10x2m transects were randomly chosen in each site and all vegetation within each transect were counted and identified (Queensland Parks and Wildlife Service (QPWS) field herbarium). More than 90% of plants were identified to species level and the remaining plants (mainly seedlings) were identified to at least family. We surveyed important habitat variables from 10 randomly chosen 1x1m quadrats in each site. A single observer estimated

log cover (%), ground vegetation (%), leaf litter (%) and bare ground (%) within each

quadrat (total 100%). Estimates of understorey vegetation density were made using

coverboards (Fox & Fox 1984). Coverboards have been used primarily to estimate vegetation

density by recording the number of squares being occluded by vegetation from a fixed

distance (e.g., Monamy & Fox 2000). A single observer estimated the number of squares

intervened by vegetation from 1m. Our coverboard (0.9m x 0.5m in width) was divided into

5x5cm squares and partitioned into three sections (0-25cm, 25-50cm and 50-90cm)

facilitating the estimation of vegetation cover in each stratum. Total number of squares

intervened by vegetation was used for analysis

Percent cover of the mid-canopy and canopy layers were estimated by the observer

standing in the middle of a quadrat and estimating the proportion that each layer covered the

sky directly above. The height of three dominant mid canopy and canopy species were

measured using an inclinometer nine meters from the base of the trunk. Average height of

each canopy layer was used for analysis. Principal components analysis was used to reduce

the number of habitat characteristics. We used regression analyses to determine the

relationships between rodent abundances (MNA) and major plant species, habitat variables,

and the principal components.

*Cover reduction experiment*

We hypothesised, a priori, that *Xanthorrhoea johnsonii* would be a major influence on

small mammal communities because it is a dominant shrub in eucalypt forests of Fraser

Island and it potentially provides a thick, ground level shelter. Six sites were randomly

located on alternate sides of a firebreak trail in the southeastern section of the Island. We

maintained a minimum distance of 1.8km between sites that were on the same side of the

trail. Sites were a minimum of 100m from the trail and trapping occurred in 1ha (100m x

100m) blocks. Fire trails or roads are relative barriers to the movement of small mammals

(Burnett 1992, Goosem 2001, 2002) and *R. fuscipes* has a relatively small home range of 1ha

(Maitz and Dickman 2001). Small mammals were trapped in March 2002 and June 2002.

Fifteen Elliot traps (ELLIOT SCIENTIFIC EQUIPMENT 33X10X19cm) were evenly placed in

three 25m transects (25m apart) i.e. Five traps per transect. A mixture of oats, honey and peanut butter was used as bait and cotton wool was placed in each trap for protection of smaller animals. We randomly allocated three reduced cover and three control sites after the initial trapping period in March. We counted the number of *Xanthorrhoea johnsonii* within each hectare block and then used nylon string to tie overhanging foliage of every *Xanthorrhoea johnsonii* into tight clumps close to the stem of the plant in each hectare block (treatment sites only). Overhanging foliage on grass-trees is essentially circular and we measured the diameter of overhanging foliage of ten tied and untied plants to estimate the amount of cover reduced. Care was taken to not affect any surrounding vegetation or habitat.

The affect of cover on mammalian community structure was determined by comparing species composition before (March) and after (June) cover was reduced (in relation to control sites). Changes in population dynamics were determined by comparing minimum number alive (MNA), body condition and size structure before and after cover was reduced (in relation to control sites). Changes in behaviour and patch use were determined using giving up densities (GUDs) (Brown 1988). Twenty-five heat sterilised sunflower seeds (*Helianthus annuus*) were mixed thoroughly into sifted sand in aluminium trays (30 x 23 x 5cm deep). Six trays were placed evenly within two 25m transects that were 25m apart within each site. Trays were placed in the open (at least 1m away from logs and shrubs) for three days, immediately prior to any trapping period. Only data from the third night were recorded for the analyses, as small mammals were familiarised with seed trays over the first two nights. Trays were only placed in each site during new or first quarter moon cycles. We recorded daily if small mammals had visited trays. Remaining seeds in each tray were counted by sifting sand through a fine mesh. Seeds remaining in trays refer to the giving-up-density. When rodents consume many seeds, then GUDs are reported as low. Higher GUDs indicate low patch use by small mammals because few seeds are consumed. Trays were refilled with 25 new seeds and returned each afternoon. We were able to identify animals (to family) consuming seeds from footprints in the seed tray (Triggs 1996). Giving up densities (GUDs) are commonly used to determine the affects of microhabitat (Brown et al. 1992,

Kotler & Blaustein 1995, Jacob & Brown 2000), distance to cover (Hughs & Ward 1993) and temporal activity (Jacob & Brown 2000) on the foraging behaviour and patch use of sma ll mammals. The number of seed trays and their location were maintained throughout the study; missed opportunity costs were considered the same among rodents on different grids because foraging activity was not considered time limited, as rodents were conditioned to the trays for two days prior any trials; and cover reduction was unlikely to impact on available food resources and affect relative energetic costs. Hence any changes in GUDs are due to increased perceived or real predation risk (Brown 1988).

Statistical analyses were performed using SPSS Student Version 11.0 for Windows (SAS Institute). A paired t-test was used to determine whether cover from *Xanthorrhoea johnsonii* was reduced significantly after tying, and whether small mammal abundances (MNA), sex ratio and body condition in control and treatment sites changed after cover was reduced. We compared size structures of each treatment before and after cover was reduced using chi-square analyses. Head lengths (males and females) were pooled within each treatment, as chi-square analyses are relatively inaccurate if 20% of each category contains less than five samples (Sokal & Rohlf 1995). The head lengths of juveniles were broken down into 0.5mm categories and adult categories were at 0.2mm intervals. Paired t-tests were used to determine if GUDs changed after cover was reduced. We only used data from trays that were visited by small mammals. All data were *In* transformed if they failed tests for normality and equal variances.

**Results**

*Habitat Preferences*

The first three principal components accounted for 80% of the variance. PC1, PC2 and PC3 accounted for 38%, 28% and 14% of the variation respectively. PC1 represents increasing leaf litter cover, depth and moisture as understorey/ground cover and bare ground reduces. PC2 represents increasing ground/understorey cover, litter depth and canopy cover as mid-story cover and logs decrease. PC3 essentially represents a decrease in bare ground

as the cover of logs and mid-story increases. Rodent numbers were not dependent on any particular habitat characteristic except for mid-story cover. Of the habitat characteristics measured, *Rattus fuscipes* were positively associated with mid-story cover ($R^2$= 0.57, $F_{1,12}$= 14.6, p=0.003) negatively associated with PC2 ($R^2$ =0.387, $F_{1,12}$= 6.94, p=0.02; Fig. 1).

Bush rats (*R. fuscipes*) comprised over 95% of the total animals captured and daily trapping rates remained less than 50% in each trapping session. We also captured *Melomys cervinipes* and *Antechinus flavipes*, however; only *R. fuscipes* were in sufficient numbers to determine habitat preferences. Rodents responded positively to only one plant species, *Xanthorrhoea johnsonii* ($R^2$= 0.29, $F_{1,14}$= 5.3, p=0.03), but negatively to the grass *Themeda triandra* ($R^2$= 0.48, $F_{1,14}$= 12.4, p=0.004) and *Pteridium esculentum* ($R^2$= 0.65, $F_{1,14}$= 24.5, p<0.001).

*Cover reduction experiment*

The number of *Xanthorrhoea johnsonii* was similar between control and treatment sites ($t_4$ = 0.65, p= 0.55), however, we reduced understorey cover by over 45% ($t_9$= 8.82, P<0.001).

Capture rates of *R. fuscipes* in each site remained above 94%  (of total individuals) throughout the study, however *Melomys cervinipes* were also captured in several sites. A real decrease in *R. fuscipes* abundances (MNA) in treatment sites occurred after cover was reduced ($t_2$ = 11.0, p = 0.008) because captures remained similar in the control sites ($t_2$ = 0.19, p= 0.866) (Fig. 2). Very few rodents were recaptured (26 ± 8.3% S.D. recapture rate) after cover was reduced, whereas almost 60 ± 10.7% of *R. fuscipes* were recaptured in control sites. Average size at maturity of both males (HL = 4.5 ± 0.04 cm S.E.) and females (HL = 4.5 ± 0.08 cm S.E.) was similar. After cover was reduced very few adults were captured and juveniles dominated each population ($\chi^2_{11}$ = 33.7, p < 0.001). Each population consisted of more than 55± 7.8% juveniles after cover was reduced (before 23.3 ± 1.4%), whereas juveniles only represented 27.2 ± 3.6% of the total population in the control sites (before 23.1 ± 2.8%). Size structures remained similar between sampling periods in control sites (Fig. 3). Mean head length of both male and female bush rats did not differ between

sampling periods in control sites ($t_2$ = 0.37, p= 0.75 and $t_2$ = 0.77, p = 0.53 respectively) (Fig. 3b). In contrast, smaller females ($t_2$ = 25.43, p= 0.025) and males were captured after cover was reduced, however, the difference was not significant in the male population (Fig. 3a).

Habitat use and behaviour of *R. fuscipes* changed considerably after cover was reduced. Visitation rates to seed trays declined (Fig. 4) with a decrease in abundances of *R. fuscipes* and overall activity decreased because the number of seeds consumed per tray (of trays visited) significantly declined ($t_2$= 7.2, p= 0.018; Fig. 5). However, the number of seeds consumed per tray remained similar in control sites over both sampling periods ($t_2$ = 0.38, P = 0.74). Overall body condition decreased significantly in the control sites ($t_2$= 17.3, p= 0.003), but remained similar in cover reduction sites. Juvenile body condition also decreased in control sites ($t_2$= 11.1, p= 0.008) and remained similar in cover reduction sites.

## Discussion

Vegetation cover or structure plays a primary role in nesting (Sutherland & Dickman 1999) and protection from predators (Hughs & Ward 1993, Jacob & Brown 2000) for many small mammals. The removal of cover in eucalypt forests of Fraser Island does not affect short-term mammalian species composition, primarily because *Rattus fuscipes* is a competitively superior species (Fox 1982, Fox 1990, Fox & Pople 1984, Fox & Gullick 1989) and we only manipulated a relatively small patch of forest compared to the large size of the forest. *Rattus fuscipes* prefers areas with *Xanthorrhoea johnsonii* (Fig. 1), a dense midstorey canopy, as well as the combination of high log and midstorey cover with low densities of leaf and understorey vegetation. However, *R. fuscipes* is known as a late seral specialist (Fox 1982) and avoided areas often associated with frequent burning, such as sites with dense grass and bracken fern groundcover.

Grass trees (*X. johnsonii*) provide an important component of the understorey in many east coast forests and may also provide important nesting areas for small mammals because they are readily accessible despite their thick growth. Dense cover also provides

**Comment:** Doesn't say this

protection from adverse climatic conditions and competitors (Braithwaite & Gullen 1978, Monamy & Fox 2000). Loss of cover is often associated with increased predation risk, which can affect the behaviour of individuals by influencing their habitat use and access to resources (Lima & Dill 1990). House mice (*Mus domesticus*) favour dense vegetation when perceived risk of predation is heightened because they are far more conspicuous and easier to pursue in open vegetation (Dickman 1992). Similarly a loss of cover increases nest sharing and emigration of small mammals (Dickman 1991). A reduction in the 'grass skirt' of *X. johnsonii* greatly reduces overall cover and affects size structure and behaviour of bush rats. Control sites had a greater proportion of rodents in all size classes than reduced cover sites, despite recruitment of juveniles into all sites between sampling periods (Fig. 3). In contrast, mean age/size of both males and females were lower in areas of reduced cover.

Many aspects of decision making reflect an adaptive trade-off between the need to avoid predation and other life history traits (Lima & Dill 1990). A decrease in prey activity following an increased threat of predation is well established (Lima 1998) because reduced mobility should lead to decreased encounter frequency with predators (Lima & Dill 1990). *Rattus fuscipes* must trade-off reduced activity in higher perceived risk areas, or disperse and limit home ranges to areas with greater cover but increased competition. Dispersing animals could have aggressive encounters with other rodents in attempting to establish new territories and may also increase their risk of predation because of increased mobility (Fox & Pople 1984, Fox & Gullick 1989, Dickman et al. 1991). Adult *R. fuscipes* choose the latter option or are killed by predators, why juveniles are more common in the experimental plots despite their higher giving up densities is a little more complex. We have shown that our experimental plots are more dangerous for rodents to forage in. Differences in patch use and activity between juveniles and adult rodents (Luque-Larena et al. 2002) may result in size related differences in predation risk (Dickman et al. 1991). Since juveniles have lower reproductive values than adults, because of lower marginal values of survival, they pay a lower cost of predation for a given level of risk (Brown 1988). Juveniles may even be paying the same cost of predation or less to occupy the experimental plots compared to adults in the control plots (Olsson et al. 2002). The superior state of juveniles in the experimental plots is

a little more surprising. It probably relates to greater differences in risk between the bush and open microhabitats in the experimental plots. Since resource patches are depleted less thoroughly in the riskier patches, patches in the open microhabitat should be depleted less than patches in surrounding microhabitats on both control and experimental plots. However, this will be magnified in the experimental plots where patches in the open microhabitat are especially dangerous. Thus animals in a poor state have greater opportunity to improve their condition on riskier grids (Brown 1988, Rohner & Krebs 1996).

In conclusion, we demonstrated that specific characteristics of the habitat associated with increased habitat complexity affect the behaviour and population dynamics of a common rodent of forests in eastern Australia. While a decrease in the abundances of *R. fuscipes* after cover was reduced was not associated with a change in species composition, adult bush rats dispersed to other areas, reduced patch use to areas outside the treatment plots, or were taken by predators. There are three choices an individual faces after cover is reduced and predation risk is increased. Bush rats can remain in an area without reducing activity; they can remain in an area and reduce activity; or they can completely flee an area. The first option will maintain access to resources but increase predation risk; the second option will limit access to resources but reduce the risk of predation; and the third option may increase competitive interactions with neighbouring animals but reduce predation risk. Competitive interactions with neighbouring animals may be fatal for a small individual and juvenile *R. fuscipes* may gain a selective advantage by remaining in an area of reduced cover despite an increased risk of predation.

approved by the University of Qld's Animal Care and Ethics Committee (ACEC #NRSM/255/01/UQ).

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**Fig. 1**. Regression analyses of *R. fuscipes* numbers against Principal component two (PC2), indicating the rodents were associated with greater log and midstory cover and low abundances of leaf litter and understory cover.

**Fig. 2.** Mean minimum number of *Rattus fuscipes* known to be alive (+S.D.) in the control and treatment sites during the first (open) and second sampling period (closed).

**Fig. 3.** Cumulative distribution (HL) of *R. fuscipes* in control (closed bars) and treatment (open bars) sites in the (a) 1st and (b) 2$^{nd}$ sampling periods.

**Fig. 4.** Proportion of seed trays visited in control and treatment sites during the first (open bars) and second (filled bars) sampling periods (+S.D).

**Fig. 5.** Mean number of seeds remaining (per tray visited) in control and treatment sites during the first (open bars) and second (closed bars) sampling periods.) (+S.D).

| High Log cover | | Low Log cover |
| High Mid-story cover | ——————————— | Low Mid-story cover |
| Low Ground cover | | High Ground cover |
| Low Litter depth | | High Litter depth |
| Low Understory cover | | High Understory cover |

Head length (cm)

Proportion of rodents