

TOWARDS A MORE DETAILED UNDERSTANDING OF HABITAT: THE RESPONSES OF BUSH RATS TO MANIPULATION OF FOOD AND PREDATION AFTER FIRE

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Abstract

Prescribed fire is widely used as a management tool in Australian protected areas, yet the ecological effects of its use are not well understood. The responses of small mammals to fire demonstrate considerable variation between localities and fires. To better comprehend small mammal fire responses it is necessary to understand the underlying ecological processes. Close associations between the regeneration of habitat and the responses of small mammals to fire have been recognised. However habitat regeneration after fire may represent temporal gradients in several resources capable of affecting small mammal responses to fire. This study reports two mark-recapture experiments undertaken in Eucalypt forests of Fraser Island to test the role of food availability and predation in determining population responses of the Australian bush rat (*Rattus fuscipes*) to prescribed fire. In the first experiment supplementary food was added to treatment sites. In the second dingoes were excluded from treatment sites. Both food availability and effective reduction of predators showed a trend towards increased *R. fuscipes* densities in the treatment sites. In both experiments the increases in densities were the result of immigration rather than increased survival or reproduction. Thus while food and predation may affect utilisation of a site by *R. fuscipes* after fire, demographic changes in populations are likely to be affected by additional components of habitat and interactions between components. The results of this study stress that habitat incorporates multiple ecological factors.

Introduction

An understanding of the effects of prescribed fires on wildlife populations and the ecological processes driving those responses is essential to the development of ecologically sound fire management (Whelan *et al.* 2002). Patterns of population and community responses of small mammals to fire events have been well documented (e.g. Fox 1982, 1990, Friend 1993). The responses of small mammal communities to fires have been demonstrated to be driven by the interaction between species life histories and the regeneration of vegetation structure in the post-fire environment (Fox 1982, Friend 1993, Monamy and Fox 2000). Regeneration of vegetation structure after a fire event may potentially provide a temporal gradient of resources for small mammals including nest sites (Friend 1993), microclimate (Sutherland and Dickman 1999), food availability (Fox 1982, Friend 1993), shelter from predators (Spencer *et al.* 2005), and mediation of inter- and intra-specific competition (Monamy and Fox 2000). Despite the physical structure of vegetation being confirmed as influencing small mammal responses to fire, the role of the various resources that regenerating vegetation provides are unclear and largely untested (Sutherland and Dickman 1999).

This paper reports the results of two experiments examining the responses of Australian bush rats (*Rattus fuscipes*) to a) supplementation of food and b) exclusion of dingoes after prescribed fire on Fraser Island. These experiments were established to test the hypotheses that a) food availability is a resource capable of influencing *R. fuscipes* population responses to fire and b) that dingo (*Canis lupus dingo*) predation affects responses of *R. fuscipes* populations to fire.

Materials and Methods

Study area and site selection

The study was conducted in open, mixed Eucalypt forest in the southeast of Fraser Island (25°30'S 153°07'E), a large quartz sand island which lies off the coast of southeast Queensland approximately 185km north of Brisbane. The open, mixed Eucalypt forests have a canopy dominated by Scribbly gum (*Eucalyptus racemosa*) with occasional Blackbutt (*E. pilularis*) emergents and a dense, mixed understorey. In April and June 2002 two areas of non-contiguous forest (both <1000ha), which were assigned to be burnt with prescription fires in August 2002, were selected, one for the food supplementation experiment and the other for the dingo exclusion experiment. Within these two areas replicated one hectare sites were selected using a GIS database. Sites all had similar vegetation, a southeast aspect, a low incline, were greater than 100m from the nearest road and 400m from neighbouring sites, characteristics which were then verified on the ground. Prescription fires were set by Queensland Parks and Wildlife staff in August 2002 in both areas of forest including each site.

Food supplementation experiment

The food supplementation experiment consisted of three treatment sites and three control sites. Within each treatment site forty kilograms of commercial, pelleted rat feed ('Rat and Mouse Nuts', Norco Stockfeeds, Lismore, Australia) were added at six weekly intervals commencing in September 2002, two weeks after the fire event and continued for 15 months until November 2003. Food was supplied at 15 feeding stations, placed in a grid of three parallel rows each containing five stations. Rows were separated by 25m, and stations were placed 20m apart on each row. Each feeding station consisted of a pair of two litre milk containers wired to a tree, suspended two centimetres off the ground. A four centimetre diameter hole at the base of each container allowed access to the food.

Dingo exclusion experiment

The dingo exclusion experiment consisted of two treatment sites and three control sites. Two weeks after the prescribed fire, fences were constructed around the boundary (100m × 100m) of the two treatment sites to restrict dingo access. The fences were constructed of commercial dog mesh (1.4m high, graduated, link mesh) and iron posts. The base of each fence was buried to a depth of 20cm and secured to the ground using metal pegs. Fences were monitored at six weekly intervals to ensure they were free of fallen branches and holes in or under the mesh. Trapping ceased 15 months after the fire in November 2003. Within each site four sand plots of smoothed sand, two meters in diameter and baited with half a sardine were used to detect the presence of dingoes. Sand plots were used at three intervals after the fire (February, August and November 2003) and were baited in the afternoon for three consecutive days.

Small mammal trapping

A trapping grid of 15 trapping stations was established in each site. Three rows of five stations, at 20m intervals, were placed 25m apart. Two Elliott traps were set on the ground at each station for three nights during each trapping session. Traps were baited with a mixture of peanut butter, rolled oats and honey. A small amount of dry leaf litter was placed in the each trap for bedding and insulation. Traps were set in the afternoon and checked at first light in the morning. Animals captured were identified to species, weighed and body and head length measured. Each animal was marked with a unique series of ear notches before being released at the point of capture. Trapping was conducted in all sites for one sampling session prior to the August 2002 fire. After the fire event and application of experimental procedures trapping sessions were conducted at approximately three monthly intervals for 15 months in both experiments.

Analysis

In both experiments abundance of *R. fuscipes* was calculated using minimum number alive (MNA). Animals were assigned to into an age group (juvenile, sub-adult or adult) according to (Hockings 1977) and residential status according to Sutherland (1998). Animals captured only once were considered transient, animals captured multiple times in one sampling session were considered resident and animals captured in more than one sampling session (a subpopulation of the residents), were classified as permanent residents.

Analysis of the population data was performed separately for each experiment as they were conducted in different localities and under different conditions. In the supplementary feed experiment the density (MNA) and the proportion of each age group in newly captured animals were compared between treatment and control sites using repeated measures ANOVAs. The proportion of transient and permanent resident animals was compared between treatment and control sites using one-way ANOVA and the number of sampling sessions over which each permanent resident was captured was pooled between sites and compared between treatment and control sites using a chi-squared analysis.

Due to the low number of treatment replicates and the resultant low power of analysis in the dingo exclusion experiment, a conservative, non-inferential method of analysis was adopted. An index of the extent of deviation of each treatment site from the control mean at each sampling session was calculated. This was done by calculating the absolute value of the difference between the total for each treatment site at each sampling session and the control mean for that sampling session, divided by the control standard deviation. As follows

$$\text{Index of deviation} = |(\text{control mean}_t - \text{treatment total}_t) / \text{control sd}_t|$$

Where t = sampling session. For normally distributed data 95.44% of all measurements should fall within two standard deviations (s.d.) of the mean (Zar 1999). Where the treatment results exceeded an index value of two (the equivalent of two s.d.), they were considered to be different to the control populations. This technique allows for a potential negation of the effect of the fence in either treatment site and is not hampered by low power. However, it does not provide a

measure of probability and so is only indicative of trends in the data. The index of deviation from control means was used to assess difference in the density and the proportion of each age group in newly captured animals. Additionally the residential status of each animal and the number of sampling sessions permanent residents were captured in were pooled across all sampling sessions and compared using the index of deviation.

Results

R. fuscipes was the most numerous species in each site, of each experiment. Low densities ($<1.33 \text{ ha}^{-1}$) of the Pale field rat (*R. tunneyi*), Grassland melomys (*Melomys burtoni*), Fawn-footed melomys (*M. cervinepes*), Feather-tailed glider, (*Acrobates pygmaeus*) and Yellow-footed antechinus (*Antechinus flavipes*) were recorded but are not considered further.

Supplementary food experiment

Over the 3240 trap nights of the supplementary feed experiment a total of 118 and 195 *R. fuscipes* were captured in the control and treatment sites respectively. While fluctuations in abundance showed similar temporal patterns in the control and treatment sites, the density of *R. fuscipes* in the treatment sites ranged between 1.20 and 1.55 times the density of the control sites (Fig 1a). Despite this difference, the greater density in the treatment sites was not sufficient to be considered a significant difference ($F = 6.542$, $df_{1,4}$, $p = 0.064$). There was no detectable difference between the treatment and control sites in the proportion of each age group in the newly captured animals. Neither was the number of sampling sessions over which permanent residents were captured significantly greater in the treatment sites than control sites. There was no significant difference in the proportion permanent residents in the populations of treatment and control sites, although there was a greater proportion of transient animals in the treatment sites than the control sites ($F = 11.117$ $df_{1,4}$, $p = 0.029$) (Fig 1b).

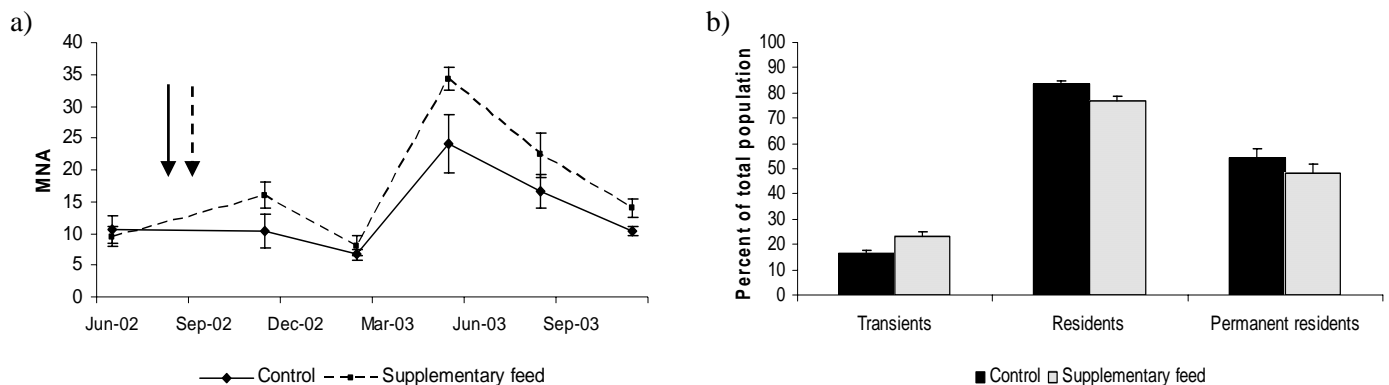


Fig 1 a) Density (mean \pm s.e.) of *R. fuscipes* in supplementary feed and control site. The arrows indicate the timing of the fire event (solid) and application of supplementary food (dashed). Fig 1 b) Mean (\pm s.e.) percent of transient, resident and permanent resident animals captured over the duration of the food supplementation experiment (Transients were captured once only, residents multiple times and permanent residents, a subset of residents, were captured over multiple sampling sessions).

Dingo exclusion experiment

A total of 182 *R. fuscipes* were captured in the dingo exclusion experiment. Of the total 83 were captured in the two treatment sites and the remaining 99 in the three control sites. Within the control sites little change in density occurred as a result of the prescription fire. Comparison of *R. fuscipes* density in the two dingo exclusion sites with the control mean reveals distinct difference in abundance in the two treatment sites (Fig 2a). The first fence site showed some change in density in comparison to the control mean, but in each case, over the period of dingo exclusion, was lower than the control mean and eventually declined to zero in the final sampling session. In comparison the abundance of *R. fuscipes* in the second treatment site was within two s.d. of the control mean prior to the fire and showed an incremental increase in density after the erection of the fences, reaching a peak abundance of 10 animals in May 2003, exceeding two s.d. from the control mean in February and May 2003 (6.5 s.d. and 6.0 s.d. respectively). A decline in abundance occurred between May and November 2003 in the second site although the MNA was two s.d. of the control mean in November 2003. There was no detectable difference in the number of sampling sessions permanent residents were captured over or in the age structure of newly captured animals between either of the treatment sites and the control mean. Both treatment sites demonstrated a greater proportion of transient animals than occurred in the control sites and there were less permanent residents in the first treatment site.

The difference in the responses of *R. fuscipes* populations in the two treatment sites may be attributable to differential dingo activity within the sites. Within the first site the exclusion of dingoes was compromised. A tree fell across the fence of the first fence site between two early sampling session and dingo prints were recorded in the final sand plot session, November 2003. The first fence site is thus referred to as the compromised site; the other is referred to as the uncompromised site.

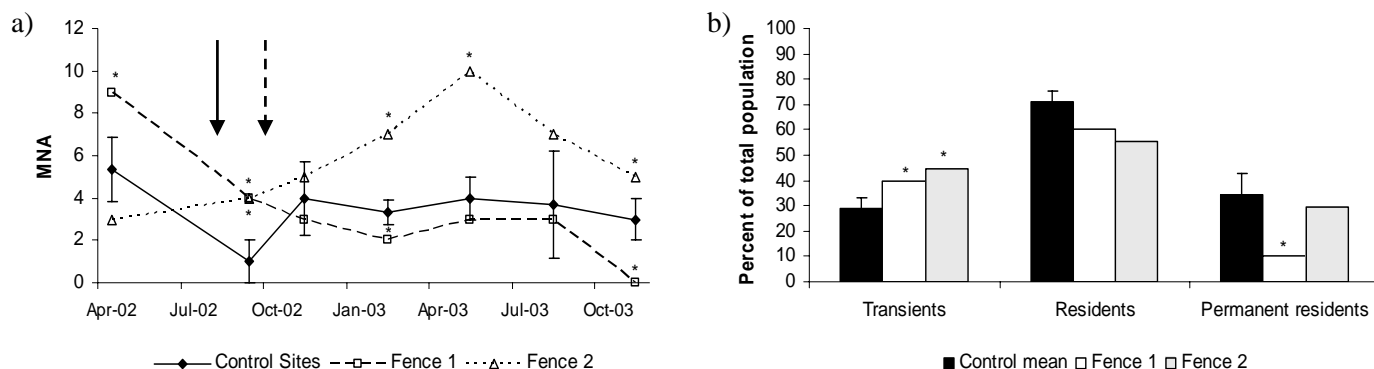


Fig. 2 a) Density of *R. fuscipes* in dingo exclusion and control sites. Arrows indicate the fire event (solid) and the erection of the fence (dashed). **Fig 2 b).** Proportion of transient, resident and permanent resident animals in captured over the duration of the dingo exclusion experiment. In each of these figures the control mean (\pm s.d. is presented) and individual treatment site values are presented. An asterisk indicates the treatment results are greater than two s.d. from the control mean.

Discussion

Food availability and predation have both been well documented as limiting factors of small mammal populations (Boutin 1990, Hubbs and Boonstra 1997) and have been proposed as affecting small mammal responses to fire events, yet have rarely been directly tested (Sutherland and Dickman 1999). This study sought to address the role of food availability and dingo predation in determining *R. fuscipes* responses to prescribed fires. Prescribed fire had a subdued effect on the control populations of *R. fuscipes* with no marked decline in density after the fire event in the control sites of either experiment. Increased food availability and possibly dingo exclusion resulted in an increase in the density of *R. fuscipes* after fire indicating a role for both factors in determining the post-fire responses of the species.

Food supplementation experiment

Responses of small mammal populations to food in undisturbed areas generally result in a doubling of treatment population densities (Boutin 1990); a trend exceeded in *R. fuscipes* populations which have demonstrated a fourfold increase in response to winter food supplementation (Banks and Dickman 2000). The limited testing that has been done on the role of food availability in affecting *R. fuscipes* response to fire provides equivocal results. Catling *et al.* (1989) found that *R. fuscipes* were not food limited in the two weeks after a prescription fire. However Sutherland (1998), in examining responses to food supplementation a year after fire, proposed that the most marked effect of food availability after fire may occur in the early regeneration stages.

This experiment showed a trend towards greater densities of *R. fuscipes* in food supplementation sites, the result was not significant and was less than 1.6 times the density of control population. The lack of significance was due in part to spatial and temporary constraints on the number of site replicates resulting in low power of the analysis ($\beta = 0.427$), a factor common to large scale manipulative ecological studies (Krebs *et al.* 2001). The change in magnitude reflects a more muted response to food supplementation than the doubling of control densities identified by Boutin (1990).

Increased food availability failed to alter the age structure of newly captured animals and did not result in greater residence times of permanent residents. Thus of the three factors responsible for increases in population densities, greater reproduction, improved survival or increased immigration (Duquette and Millar 1995), neither juvenile recruitment nor survival were responsible for the trend towards greater *R. fuscipes* densities. Rather immigration of transient animals was the primary factor causing the increase in density. Thus food availability affected the density but not the demographic structure of the post-fire populations. A pattern of food availability affecting the magnitude but not the composition of population fluctuations has been recorded previously in populations of *R. fuscipes* (Banks and

Dickman 2000). In fact changes in the demographics of small mammal populations, sufficient to cause changes in the direction of population fluctuations in response to food supplementation have only been recorded in tandem with a manipulative reduction of predation pressure (Ford and Pitelka 1984).

The muted response to food supplementation, in comparison to the studies reviewed by Boutin (1990), may be due to several factors. Firstly the increase in temporary immigrants may be attributable in part to the application of supplementary food at six weekly intervals. While the food application was intended to act as a continual application of food over the experimental period, the relatively long interval between renewals of food may have resulted in periodic “pulses” of food which were quickly exhausted and thus contributed to the high number of transient animals. However, food was frequently present in the containers at the time of renewal suggesting this is not the case. More importantly, in the studies of food supplementation reviewed by Boutin (1990) few resulted in a greater than threefold increase in density in response to food supplementation. This upper limit of responses to food supplementation was attributed to additional ecological factors reducing the proximal importance of food availability beyond a certain level of population increase (Boutin 1990). This phenomenon may be occurring in the current context. The selective omnivorous diet of *R. fuscipes* may mean that after fire there is sufficient food resources such that food is less important as a limiting resource than other resources, such as nest sites or shelter which then act as the more proximal limiting factors.

Predator removal experiment

The response of *R. fuscipes* populations differed between the two dingo exclusion sites. It is assumed that the compromised treatment site, in which dingo prints were recorded in November 2003, was compromised for the duration of the experiment so only the uncompromised site represents effective dingo exclusion. An alternate interpretation is that there was no difference in the effectiveness of either dingo exclusion site until November 2003 when a dingo entered the compromised site. Under this interpretation the differences in the *R. fuscipes* populations between the treatment sites could be attributed untested edaphic or ecological factors. Two factors support the assumption that the uncompromised site represents an effective exclusion of dingoes. Firstly the similarity in the patterns of density between the control sites and the compromised site during the period of dingo exclusion and secondly additional trapping after the fence was removed showed the density of the uncompromised site decline to within two s.d. of the control mean. However, due to the absence of treatment replication the results should be interpreted with caution.

The role of predation in affecting fluctuations of small mammal populations has received considerable research attention. This study presents some contrast to each of them. Canid predation has been shown not to affect density or other population characteristics of *R. fuscipes* in montane conditions (Banks 1999). In comparison this study indicates that dingo predation can affect *R. fuscipes* densities. Several studies of arctic rodents have shown that predator reduction results in an increase in density through increased survival of individuals, greater reproductive output or a combination of the two processes (Karels *et al.* 2000, Norrdahl and Korpimäki 2000). In comparison to these studies the increase in density after fire in the uncompromised fence site was primarily due to immigration of animals, and a greater proportion of transient animals than the control sites.

The increase in density through temporary immigration as a result of dingo exclusion may reflect a response to reduced predation risk. Small mammal species can respond to auditory, olfactory and visual cues of predators and modify their habitat use to reduce the chance of encountering predators (Kats and Dill 1998). Reduction in predator density results in greater use of open space by small mammal species (Banks 1999, Banks *et al.* 1999), although the responses are generally recorded at the microhabitat scale. The increase in temporary immigration of *R. fuscipes* into the uncompromised fence site after fire may indicate that areas of low predator density are a resource which may be detectable by *R. fuscipes* and used for foraging or other purposes by non-resident animals.

The response to of *R. fuscipes* to dingo exclusion showed temporal variation which may reflect alteration of predation pressure or resource availability over the post-fire regeneration period. Reduction of a single predator species can result in increased predation by alternate predator species (Banks 1999). On Fraser Island both reptiles and raptors are predators of small mammals, these predators may have responded to the increased availability of *R. fuscipes* resulting from the exclusion of dingoes by increasing predation pressure in the site (e.g. Loyn *et al.* 1986). Resource availability may also act to cause temporal variation in the response to dingo exclusion. As the population increased in the absence of dingoes, the availability of other resources such as food or nest sites may have become proximal limiting factors. Interactions between predation and resources, particularly food availability are integral to the fluctuations of small

mammal species in undisturbed environments (Karels *et al.* 2000). In the post-fire environment alteration of resources may occur as a result of the regeneration of vegetation altering predator-prey relationships, in particular small mammals may be more exposed to predation in the open, regenerating vegetation (Spencer *et al.* 2005). However, the incremental increase in density to a peak at nine months after fire, followed by a gradual decline suggests that interactions between resources and predation may have been occurring. If shelter from predation alone was the only variable *R. fuscipes* was responding to a greater initial difference between the treatment and control sites, followed by the treatment site becoming more similar to the control mean as the vegetation regenerated would be expected.

Both food availability and predation appear to limit *R. fuscipes* populations after fire, however the responses of *R. fuscipes* to both manipulations suggest that neither of these factors act in isolation to determine the post fire responses and both are likely to be interacting with other variables. The findings of the two experiments stress that habitat is not a one-dimensional variable. Rather there are multiple, potentially interacting factors which constitute habitat and which warrant further investigation.

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