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Rats on the run: removal of alien terrestrial predators affects bush rat behaviour

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Abstract Predators can strongly influence the microhabitat use and foraging behaviour of prey. In a large-scale replicated field experiment in East Gippsland, Australia, we tested the effects of reduced alien red fox (*Vulpes vulpes*) and alien wild dog (*Canis lupus familiaris*) abundance (treatment) on native bush rat (*Rattus fuscipes*) behaviour. Bush rats are exposed to two main guilds of predators, namely mammalian carnivores and birds of prey. Tracking rat movements using the spool-and-line technique revealed that, in treatment sites, rats used ground cover, which provides shelter from predators, less often than at unmanipulated fox and wild dog abundance (non-treatment sites). In treatment sites, rats more frequently moved on logs where they would have been exposed to hunting foxes and dogs than in non-treatment sites. Furthermore, in treatments, rats showed a preference for understorey but not in non-treatments. Hence, bush rats adapted their behaviour to removal of alien terrestrial predators. Giving-up densities (GUDs) indicated no treatment effects on the marginal feeding rate of bush rats. Interestingly, GUDs were higher in open patches than in sheltered patches, suggesting higher perceived predation risk of bush rats during foraging at low versus high cover. The lack of treatment effects on GUDs but the clear response of bush rats to cover may be explained by the impact of predators other than foxes and wild dogs.

Keywords Predation risk · Microhabitat use · Foraging behaviour · GUD · Alien predator

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Introduction

Predators can influence the behaviour, distribution, and abundance of prey, as well as population dynamics (Rosenzweig and MacArthur 1963; Korpimäki and Krebs 1996). Non-native predators are thought to be of particular importance in a system (Salo et al. 2007), and more knowledge of their impacts is needed (Gurevitch and Padilla 2004). The influence of predators on prey can be lethal or non-lethal, the latter forcing prey to make

behavioural decisions caused by fear and avoidance of predation (Edmunds 1974; Kotler and Holt 1989; Lima and Dill 1990; Brown 1992; Lima 1998). In most studies of the behavioural responses of small mammals to predation risk, predator abundance is not directly manipulated. Instead, predation risk is represented through changes of the prey's environment such as cover (Brown et al. 1992; Jacob and Brown 2000; Stokes et al. 2004), illumination (Meyer and Valone 1999; Sutherland and Predavec 1999; Abramsky et al. 2004; Griffin et al. 2005) or escape substrate (Kotler et al. 2001). In addition, such studies have often been conducted under captive conditions (Jedrzejewski et al. 1993; Koivisto and Pusenius 2003; Stapley 2003, 2004), which may lead to overestimation of anti-predator behaviours or the intensity of predator–prey interactions (Parsons and Bondrup-Nielsen 1996; Mappes et al. 1998; Lima and Bednekoff 1999).

In general, information about species- and guild-specific predator avoidance is hard to distinguish from behavioural responses to indirect cues because the effects of different predator guilds can be additive or compensatory (Kotler et al. 1992; Bouskila 2001). Studies dealing with direct predator manipulation either use manipulations of cues of predation such as odour (summary in Apfelbach et al. 2005) or direct manipulations of predators abundance (summary in Salo et al. 2007). For example, odour experiments have been used with native and introduced predators in Australia (Hayes et al. 2006; Russell and Banks 2007). Signals left in the environment by predators come from a variety of sources such as faeces, urine, anal gland secretions or fur, but these are usually used separately in studies relying on predator odour (see Apfelbach et al. 2005). In a more realistic evaluation of a predator–prey interaction, all cues released by the predator should be applied or predator abundance should be manipulated. Also, more than one behavioural attribute of the prey should be investigated to elucidate the range of adaptations by prey to predation risk. For example, both microhabitat use and foraging behaviour have been shown to change in response to perceived predation risk. The extent of adaptations is of special interest in systems where predator–prey coevolution has been of limited duration, e.g. if alien species are involved.

Within heterogeneous habitat, small mammals prefer specific microhabitat structures. *Antechinus* spp. select dense understorey (Sutherland and Predavec 1999), logs and rock crevices (Stokes et al. 2004). Swamp rats (*Rattus lutreolus*) prefer to move in dense ground cover of up to 20 cm height (Kearney et al. 2007). If preferences for some microhabitat structures depend on perceived predation risk, they should be dependent on the current level of risk.

There are likely to be trade-offs between a prey species' foraging behaviour and its predator avoidance behaviour. While a foraging animal gains benefits from foraging (energy intake), it also suffers costs, including metabolic costs, costs of missed opportunities and costs of predation. If the benefits (the rate of energy intake) decrease to the level where they equal the costs, the animal should quit feeding (Charnov 1976). Therefore, the marginal feeding rate that can be measured directly using giving-up densities (GUDs) reflects the perceived risk of predation while foraging (Brown 1988, 1992).

Whether a prey species recognises predation risk and adapts its behaviour is of crucial importance if the predator is introduced because alien predators cause higher risk than native predators (Salo et al. 2007). This is a widespread problem in Australia, where native species are faced with the risk of several introduced predators.

In Australia, bush rats are widespread and common native small mammals, particularly in the forests of Victoria (Robinson 1987; Seebeck and Menkhorst 2000). They weigh about 200 g (Taylor and Calaby 1988) and eat plant material, fungi and invertebrates. Seeds can represent up to 44% of their diet (Cheal 1987). We tested the effects of reduced abundance of alien terrestrial predators (red fox *Vulpes vulpes* and wild dog *Canis lupis familiaris*) on microhabitat use and foraging behaviour of bush rats (*R. fuscipes*).

Red foxes are invasive alien predators in Australia and can pose a considerable danger to small- and medium-sized mammals (Dickman 1996; Banks 1999; Risbey et al. 2000; Kinnear et al. 2002). The same is the case for wild dogs (Fleming et al. 2001), which occur through much of south eastern Australia. Dingoes (*C. lupis dingo*) were introduced to mainland Australia about 8,000 years BP. Dingoes interbreed readily with wild dogs with the result that hybrids account for a high proportion of remnant dingo populations in forested regions of south eastern Australia (Newsome 1991). Bush rats are the second most important prey species for foxes in Victoria (Seebeck 1978; Hutchings 1996) and remains of bush rats were also found in wild dog faeces (Mitchell and Banks 2005). Other predators of bush rats in that area include feral cats (*Felis catus*), tiger snakes (*Notechus scutatus*), sooty owls (*Tyto tenebricosa*) and masked owls (*T. novaehollandiae*; Hutchings 1996; Green 2003; Bilney et al. 2006; R. J. Bilney, personal communication).

Studies indicate that some native prey may be naive to foxes (Banks 1998) but that others (eastern grey kangaroos, Banks 2001, and brushtail possums, Pickett et al. 2005) respond to changes in fox abundance and/or perceived predation risk. Banks (1999) found that short-term removal of foxes did not affect bush rat populations, and the impact of fox scent on bush rat behaviour is equivocal (Banks 1998; Russell and Banks 2007). The presence of dog faeces did not change the trappability of bush rats (Banks et al. 2003), although this might not always be an appropriate

measure for a response of prey to predation risk (Russell and Banks 2007).

We used bush rats' choice of microhabitat and their foraging behaviour to obtain further insights into the effect of introduced predators on a native prey species. Our study was based on a direct manipulation of fox and wild dog abundance to decrease predation risk for bush rats. We compared the behaviour of bush rats in areas where foxes and wild dogs were removed and areas with unmanipulated fox and dog densities (non treatment). In addition, we tested the effects of cover on perceived predation risk of bush rats while foraging. We expected that (1) bush rats change microhabitat use at reduced risk of predation resulting in decreased use of protective microhabitat structures in areas where foxes and dogs are removed, (2) perceived predation risk results in higher GUDs of bush rats in open versus sheltered habitat patches and (3) GUDs are lower at reduced versus unmanipulated abundance of alien terrestrial predators.

Material and methods

Study sites

The study was conducted in East Gippsland, Victoria, Australia (Fig. 1). Since 1999, Project Deliverance was run as a predator-removal experiment in large parts of East Gippsland by the Department of Sustainability and Environment (DSE; Robley and Wright 2004). For our study, we used four of the Project Deliverance sites. These were about 7,000 ha to 14,000 ha and located in pairs east (East Coast study area) and west (West Coast study area) of the coastal town, Marlo (37°48′ S, 148°30′ E; Fig. 1). On one site in each of these two pairs, there was continuous baiting with Fox-off™ baits containing *1080* poison to remove

Fig. 1 Study sites in Far East Gippsland, Victoria (after Robley and Wright 2004)

foxes, but the buried baits also removed wild dogs (A. Robley, personal communication). Each treatment site was about 18 km away from its paired non-treatment site, and the nearest distance between the pairs was 30 km.

Study sites were matched as closely as possible by habitat type and topography. The West Coast study area is dominated by tall eucalypt forest (*Eucalyptus baueriana*, *E. botryoides* and *E. globoidea*) with some open patches and a heterogeneous shrub-rich understorey (mainly *Cassinia longifolia*, *Olearia lirata* and *Persoonia linearis*) along gullies. Ground-cover comprises ferns, grasses, sedges and leaf litter. The East Coast study area has mainly tall eucalypt (*Eucalyptus botryoides*, *E. considenana*, *E. globoidea* and *E. sieberi*) forest with some banksia (*Banksia serrata*) trees and a heterogeneous understorey of dense shrubs (mainly *Acacia terminalis* and *Ricinocarpus pinifolius*) and ferns (*Pteridium esculentum*) interrupted by patches with little cover. There is a thick layer of leaf litter especially underneath banksia trees. Study areas did not vary in the assemblage of predator or prey species (unpublished data). Beside bush rats, swamp rats were the only other rodents caught during the study and represented less than 0.5% of the rodent community (unpublished data).

The effectiveness of the control program was measured by DSE. Sand plots used to monitor terrestrial predators showed there were very few wild dogs compared to foxes in the area (A. Robley, personal communication), there was significantly less fox and wild dog activity in the treatment than in the non-treatment sites (as cited in Robley and Wright 2004), but feral cat activity did not differ between the treatment and the non-treatment sites (A. Robley, personal communication). In non-treatments, non-toxic baits were available to foxes and no culling of other predators occurred. On all sites, bait stations were established every 1 km along gravel roads, bait was replenished about every 4 weeks and bait-take was monitored by DSE (Robley and Wright 2004). Details of the fox management program will be published elsewhere. The monitoring period began in 1996 using the uptake of non-toxic baits as a pre-treatment index of fox abundance in all sites. The use of poisoned baits in treatment sites started in 1999. At the time of our study, bait-take had fallen to an average of 6% compared to a pre-treatment value of 86% in the West Coast treatment site and to 14% from 56% for the equivalent periods in the East Coast treatment site. Bait-take increased from 43% to 55% at the West Coast non-treatment site and consistently averaged 47% at the East Coast non-treatment site (A. Murray, personal communication).

Microhabitat use

We used spool-and-line tracking (Breder 1927; Stickel 1950) to examine the fine scale microhabitat use of bush rats in October 2003 and in January and March 2004. Preliminary
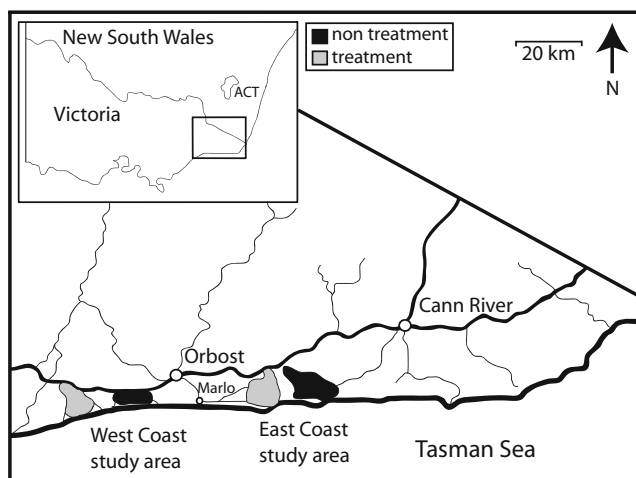
trials revealed that spool-and-line tracking was the best method to examine microhabitat use of this species. It was easier to conduct than powder tracking, particularly in wet weather, and provided more measurements than radio-tracking, which did not deliver data about microhabitat use on a sufficiently fine scale. We conducted spool-and-line tracking synchronously in the treatment and non-treatment sites of a particular area but staggered by about 2 weeks between the East and West Coast study areas. Rats were live trapped using Elliott folding traps ($325 \times 90 \times 100$ mm) between 2300 and 0300 hours. Only females of >90 g body weight were used for this study. They were individually marked with passive integrated transponder tags (Allflex, sterile injector needle with ISO FDX-B transponder, P/N 860005-001) to avoid tracking individuals twice. Each rat was released at the point of capture after attaching a spool of nylon line (Windsor, WINBOB, 140/2, size 8, enclosed in heat shrink) to its back with super glue. The end of the line was tied to a marker post before releasing the animal. As the rat continued its movements during the night, the line marked the use of microhabitat structures.

The next morning, we recorded microhabitat attributes along the line at 4 m intervals. We estimated the percentage of understorey and groundcover within a circle of 1 m^2, centred at the line in four categories (1, 0–25%; 2, 26–50%; 3, 51–75%; 4, 76–100% cover). Understorey consisting of shrubs and ferns higher than 40 cm was assumed to provide protection from predators but allow unhampered movement of small mammals at ground level. Low-level ground cover of leaf litter and smaller plants (at least 5 cm high) was also assumed to provide cover, although possibly restricting the movement of small mammals. We recorded the number of logs, which offer protection and "runways", and the type of log use (movement on, in, under or next to logs), as well as the number of trees. Data from the first 15 m of line were discarded to avoid bias by a possible flight reaction. These microhabitat attributes were chosen because habitat selection by small mammals often favours dense vegetation to minimise predation risk (Lima and Dill 1990). The method was based on Stokes et al. (2004) but modified after preliminary spool-and-line tracking trials.

To assess preferences of the bush rat for microhabitat structures, we estimated the habitat available to each rat with a technique similar to the estimation of microhabitat used by rats. Data for available habitat were recorded every 4 m along a path of equivalent length to the line trail of each rat, starting at the point of release and following randomly determined bearings after each measurement.

Foraging behaviour

We measured giving-up densities (GUDs) between August and November 2003, and between January and April 2004.

We conducted monthly measurement sessions synchronously in the treatment and non-treatment sites of a particular study area and back-to-back for the two study areas. We ran these sessions over four to five nights always at the crescent phase ±4 days towards new moon.

GUDs were measured using round plastic trays (depth= 4 cm, radius=12.5 cm), each containing 50 linseeds suspended in sieved beach sand. Seeds are part of the diet of bush rats and pilot trials revealed that bigger seeds, i.e. sunflower seeds, often were completely removed from trays. In each site, 12 trays were placed at 10 m spacing in alternating densely vegetated (sheltered) and open habitat patches that were cleared manually of all surface vegetation within a circle of 3 m diameter. We stocked the trays with sand and seeds in the evening, and measured GUDs in the morning by sieving the sand and counting the remaining seeds. Seeds were replaced and the procedure repeated for at least four consecutive nights per session.

To determine whether feeding trays were used by bush rats only, each tray was placed on a 70×70 cm corflute board with a 10 cm wide foam rubber ink pad along each edge. The pad was soaked with a mixture of 80% water, 10% food dye and 10% polyethylene glycol. The surface of the board was covered with brown paper (Kraft brown wrapping paper). Animals that approached the tray walked over the ink pad and left tracks on the paper. Tracks were recorded daily and paper and dye replaced when necessary.

Statistical analyses

We compared used and available microhabitat structures using repeated measurement analysis of variance (rm-ANOVA; SPSS 2001) to reveal preferences for specific microhabitat structures. We used the relative difference E (Ivlev's electivity index; Ivlev 1961) between used and available microhabitat structures to compare preferences for microhabitat structures between treatment and non-treatment sites. Correlation matrices were used to confirm that available groundcover, understorey and the Ivlev index were not correlated. Log use was compared between the treatment and the non-treatment by rm-ANOVA. In all rm-ANOVAs, treatment (treatment versus the non-treatment) and area (East Coast versus West Coast) were included as between-subject factors; session (temporal replication) was treated as a within-subject factor.

The GUD data were analysed using linear mixed-effects models in S-Plus (2002). Data were nested temporally (sessions, nights) and spatially (site, treatment, cover). The data were tested for session, treatment, and cover effects. Each model was fitted using maximum likelihood analysis to allow comparisons between models differing in their fixed-effects structures. The significance of terms in the

fixed effects part of the model was assessed using conditional F tests at the corresponding grouping level.

Results

Microhabitat use

We tracked 36 different female bush rats in treatment sites (West Coast, 18; East Coast, 18) and 33 in non-treatment sites (West Coast, 16; East Coast, 17). The mean sample size per site per session was 5.5±0.4 bush rats. The mean thread length available for analysis was 103.1±25.7 m, providing a mean of 25.2±6.5 measurements per bush rat. Analyses of available habitat (rm-ANOVA, SPSS) revealed that there was no difference for any microhabitat structure between paired non-treatment and treatment sites (understorey, $F_{1,68}=0.057$, $P=0.814$; ground cover, $F_{1,68}=0.284$, $P=0.602$; logs, $F_{1,68}=4.493$, $P=0.051$; trees, $F_{1,68}=0.090$, $P=0.786$); their occurrence was also independent. However, both understorey (ANOVA, $F_{1,68}=11.323$, $P=0.004$) and groundcover (ANOVA, $F_{1,68}=9.442$, $P=0.008$) were more available at the East Coast study area than at the West Coast study area. The opposite is the case for the occurrence of logs (ANOVA, $F_{1,68}=14.930$, $P=0.002$), and trees were always present in the same frequency (ANOVA, $F_{1,68}=0.168$, $P=0.687$). Of the microhabitat attributes measured, only the availability of groundcover changed during the three spooling sessions (ANOVA, $F_{1,68}=16.056$, $P=0.001$). Consequently, the relative use of the structures represented by Ivlev's electivity index (Ivlev 1961) was used for further analyses.

There were treatment effects on the bush rats' preference for some of the microhabitat structures (Fig. 2). In treatment sites, bush rats used understorey two and a half times as often as in the non-treatment sites, but this difference was not significant (ANOVA, $F_{1,68}=3.290$, $P=0.088$). They strongly preferred understorey in treatment sites ($E=0.08±0.03$; ANOVA, $F_{1,35}=12.238$, $P=0.003$) but not in the non-treatment sites ($E=0.03±0.05$; ANOVA, $F_{1,33}=3.277$, $P=0.090$). At the East Coast study area, understorey was used by bush rats less than at the West Coast study area (ANOVA, $F_{1,68}=16.031$, $P=0.001$). Bush rats avoided moving through dense groundcover in the treatment sites ($E=-0.09±0.03$; ANOVA, $F_{1,35}=13.657$, $P=0.002$) but not in the non-treatment sites ($E=0.00±0.01$; ANOVA, $F_{1,33}=0.247$, $P=0.626$). This difference between the treatment and the non-treatment was significant (ANOVA, $F_{1,68}=10.931$, $P=0.005$).

Bush rats preferred logs in the treatment and non-treatment sites ($E=0.33±0.12$; ANOVA, $F_{1,36}=38.214$, $P<0.001$; $E=0.28±0.08$; ANOVA, $F_{1,33}=40.064$, $P<0.001$). There was no difference in the frequency logs used between the
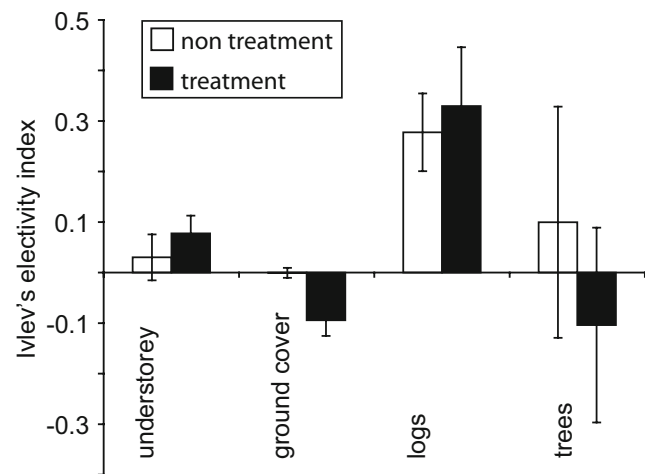
Fig. 2 Preferences (Ivlev's electivity index, Ivlev 1961) for microhabitat structures by bush rats at reduced (treatment) and unmanipulated (non-treatment) abundance of foxes and wild dogs. *Positive values* indicate that structures were used more often than they were available; *negative values* indicate they were used less often than available. Error bars are ±1 standard error

treatments and the non-treatments (ANOVA, $F_{1,68}=0.671$, $P=0.425$), but there was an effect of treatment on the type of log use (Fig. 3). The ratio of movements on-log/under-log was about 3:1 (47.83±1.68%/16.24±0.54%) in treatment sites, whereas this ratio was nearly 1:1 (29.10±13.00%/28.79±6.25%) in the non-treatment sites. This means that bush rats moved more often on logs in treatment sites than in the non-treatment sites (ANOVA, $F_{1,68}=4.517$, $P=0.049$), and movement under logs was reduced in treatment sites compared to the non-treatment sites (ANOVA, $F_{1,68}=7.903$, $P=0.013$). The difference in movements on logs was more pronounced at the East Coast (T/NT=50%/16%) than at the West Coast (T/NT=46%/42%; ANOVA, $F_{1,68}=5.744$, $P=0.029$), and the reduction of movements under logs due to the treatment was stronger in January (T/NT=13%/34%) than in March (T/NT=19%:23%; ANOVA, $F_{1,68}=5.448$,
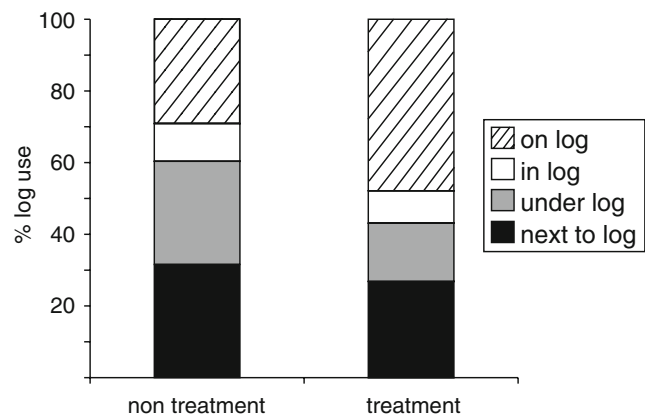
Fig. 3 Type of log use by bush rats at reduced (treatment) and unmanipulated (non-treatment) abundance of foxes and wild dogs. Movements on logs, in logs, under logs and next to logs are plotted as a percentage of total observations

P=0.033). There was no difference in movements in (ANOVA, $F_{1,68}$=0.620, P=0.443) or next to logs (ANOVA, $F_{1,68}$=0.300, P=0.591) due to the treatment. Furthermore, movements of bush rats were not affected by the presence of trees (treatment, E=−0.10±0.20; non-treatment, E=0.10± 0.23; ANOVA, $F_{1,68}$=1.287, P=0.273), and there was no treatment effect on the use of trees (ANOVA, $F_{1,68}$=0.616, P=0.230).

Foraging behaviour

The tracks left on the paper next to the feeding trays and in the sand in the trays showed that no granivorous mammals other than rats accessed the trays. All footprints of rats were assigned to bush rats. There were no tracks of birds on the paper or in the sand. Heavy rain prevented collection of data for many nights in October and November 2003. As a result, only data from August and September 2003, as well as January, March, and April 2004 remained for analyses. The mean sample size per session per plot was 40.8±7.4 GUD nights (number of feeding trays × number of nights).

There was no treatment effect on GUDs (ANOVA, $F_{1,815}$=1.1329, P=0.480; Fig. 4). The number of linseeds remaining on food trays was 29.6±2.0 in the treatment sites and 28.5±3.0 in the non-treatment sites. Interestingly, GUDs of bush rats were higher in open patches (31.7±1.4 linseeds remaining) than in sheltered patches (26.3±1.4 linseeds remaining; ANOVA, $F_{1,815}$=11.026, P=0.045). GUDs did not vary between sessions (ANOVA, $F_{1,815}$= 3.443, P=0.065).

Discussion

The reduction of the abundance of foxes and wild dogs seemed to change some aspects of bush rat behaviour,
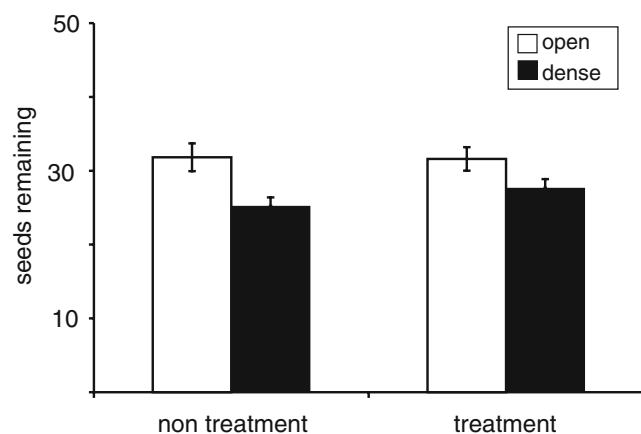

Fig. 4 Giving-up densities (GUDs, number of linseeds remaining from an initial number of 50) of bush rats in open and sheltered habitat patches both at reduced (treatment) and unmanipulated (non-treatment) abundance of foxes and wild dogs. Error bars are ±1 standard error

demonstrating that bush rats may judge these alien species as potential predators and respond accordingly. Although we identified effects on the use of microhabitat structures by bush rats, there seemed to be no effect of reduced alien predator abundance on their foraging behaviour (as estimated by GUDs).

Bush rats altered their preferences for some microhabitat structures in response to predator removal in two apparently contradictory ways. Bush rats avoided moving through dense groundcover in treatment sites, whereas they did not in the non-treatment sites. The opposite change occurred in the use of understorey. Bush rats showed a preference for understorey in treatment sites but no preference in the non-treatment sites. Both structures could provide shelter to bush rats, but this diametrically opposed change in the use of them may be explained by the different kinds of shelter and different hunting strategies of predators. Owls need open space for hunting, causing higher risk in open than shrubby microhabitat (Brown et al. 1988; Kotler et al. 1991). In general, this pattern probably applies to many mammalian predators such as canids. However, foxes can use dense shrubs as much as open areas (Meek and Saunders 2000; White et al. 2006) and do hunt in understorey (Henry 1996). Felids, such as the feral cat, generally act as ambush predators in dense vegetation (Edwards et al. 2002). Risk from snakes, which are the other potential predators of bush rats, is assumed to be not significantly influenced by microhabitat (Fitzgerald et al. 2004).

At the time of the study, the abundance of the main ground predator, the red fox, was greatly reduced (Robley and Wright 2004) and should have caused a decreased necessity for bush rats to use groundcover. Therefore, lessened risk from foxes but continuing risk from owls is a possible cause for the observed changes in habitat use. A consistent result was found by Fey et al. (2006) who suggested that a shrub (*Juniperus communis*) provides shelter for voles against avian predators rather than against an alien terrestrial predator (the American mink *Mustela vison*) in a Finnish outer archipelago. Wild dogs might be only a minor risk for bush rats (Banks et al. 2003), possibly due to a reasonably long history of exposure to predation risk from dingoes, and a stronger effect of the treatment on bush rats' use of understorey may have been suppressed by feral cats, whose abundance was low and not affected by the poison baiting program (A. Robley, personal communication).

Logs are important for bush rats for several reasons. They provide shelter for bush rats moving under, in or next to logs, and they are important for easy and fast travel for bush rats moving on logs (Olszewski 1968). In this study, the apparent lack of a treatment effect on the frequency bush rats used logs masked a more subtle change in behaviour. It appears that bush rats used logs for easy

movement in treatment sites, whereas they used logs for protection in the non-treatment sites, as indicated in differences in the type of log use: in treatment sites, bush rats moved more on logs and less under logs than in the non-treatment sites. Running on logs might expose bush rats to owls, but this may not be risky because movement on logs is likely to be quiet and the escape route to shelter (e.g. under the log) is short, indicating high probability of escape when attacked by owls. Not surprisingly, removal of terrestrial predators did not influence the use of trees by bush rats.

There was no effect of reduced fox and wild dog abundance on the foraging behaviour of bush rats as measured by GUDs. However, the effect of cover on the feeding rate indicates that GUDs are a valid index of predation risk for bush rats. The higher GUD of bush rats in open patches compared to sheltered ones was likely to be caused by perceived predation risk. This corresponds to findings from other studies where vegetation height or habitat structure was manipulated to cause habitat-specific differences in perceived predation risk (Brown 1988, 1992; Brown et al. 1992; Kotler et al. 1991; Jacob and Brown 2000; Ylönen et al. 2002; Stokes et al. 2004; Arthur et al. 2004a, b).

Conclusions

In our study, microhabitat use of bush rats was affected by reduced abundance of foxes and wild dogs, whereas foraging behaviour appeared to be not affected. The abundance of other predators, including owls, snakes and feral cats, was not manipulated. Subtle changes or lack of change in some behavioural patterns suggest that bush rats were able to estimate the current level of predation risk exerted by different guilds of predators and to respond accordingly. These results suggest that bush rats were able to recognise the alien predators as source of danger. Our results also demonstrate that more than one behavioural attribute of prey needs to be considered for an evaluation of predator–prey interactions.

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