Oecologia (2012) 168:947–957
DOI 10.1007/s00442-011-2168-9

BEHAVIORAL ECOLOGY - ORIGINAL PAPER

Population and behavioural responses of native prey to alien predation

Eszter Krasznai Kovacs · Mathew S. Crowther ·
Jonathan K. Webb · Christopher R. Dickman

Received: 25 May 2011 / Accepted: 3 October 2011 / Published online: 29 October 2011

Abstract The introduction of invasive alien predators often has catastrophic effects on populations of naïve native prey, but in situations where prey survive the initial impact a predator may act as a strong selective agent for prey that can discriminate and avoid it. Using two common species of Australian small mammals that have persisted in the presence of an alien predator, the European red fox *Vulpes vulpes*, for over a century, we hypothesised that populations of both would perform better where the activity of the predator was low than where it was high and that prey individuals would avoid signs of the predator's presence. We found no difference in prey abundance in sites with high and low fox activity, but survival of one species—the bush rat *Rattus fuscipes*—was almost twofold higher where fox activity was low. Juvenile, but not adult rats, avoided fox odour on traps, as did individuals of the second prey species, the brown antechinus, *Antechinus stuartii*. Both species also showed reduced activity at foraging trays bearing fox odour in giving-up density (GUD) experiments, although GUDs and avoidance of fox odour declined over time. Young rats avoided fox odour more strongly where fox activity was high than where it was low, but neither adult *R. fuscipes* nor *A. stuartii* responded differently to different levels of fox activity. Conservation managers often attempt to eliminate alien predators or to protect predator-naïve prey in protected reserves. Our results suggest that, if predator pressure can be reduced, otherwise susceptible prey may survive the initial impact of an alien predator, and experience selection to discriminate cues to its presence and avoid it over the longer term. Although predator reduction is often feasible, identifying the level of reduction that will conserve prey and allow selection for avoidance remains an important challenge.

Keywords *Antechinus* · Bush rat · Chemical cues · Giving-up density · Invasive predators

Introduction

The introduction of novel invasive species to islands and island continents is one of the leading threats to biodiversity (Williamson 1996; Vitousek et al. 1997; Mack et al. 2000). Invasive species can substantially modify natural ecosystems in several ways, but the most severe impacts often occur following the introduction of novel predators (Fritts and Rodda 1998; Doody et al. 2009). This is because invasive predators represent novel predator archetypes and native prey lack appropriate behavioural responses to counter them (Cox and Lima 2006; Banks and Dickman 2007). The ability of naïve prey to assess risk and adopt appropriate behavioural responses depends on their evolutionary history and ecology (Blumstein 2006), and on the learning ability and experience that animals accumulate through their lifetimes (Lima and Dill 1990; Dickman 1992; Hayes et al. 2006). Prey naïveté may be reduced if similar predator archetypes, or ecological analogues, of the novel predator have existed previously in the ecosystem on an evolutionary timescale (Blumstein 2006; Cox and Lima 2006).

Meta-analyses confirm that the effects of introduced predators generally are stronger than those of native

---

Communicated by Chris Whelan.

E. K. Kovacs · M. S. Crowther (✉) · J. K. Webb ·
C. R. Dickman
Institute of Wildlife Research, School of Biological Sciences,
Heydon-Laurence Building (A08), The University of Sydney,
Sydney, NSW 2006, Australia
e-mail: mathew.crowther@sydney.edu.au

predators on prey populations, and show further that the effects of such aliens are more severe in Australia than in any other part of the world (Salo et al. 2007, 2010). In Australia, the European red fox *Vulpes vulpes* has been particularly destructive and has probably contributed to the decline, local or continent-wide extinction of over a dozen species of small and medium-sized mammals since its establishment in 1871 (Dickman 1996b; Risbey et al. 1997; Saunders et al. 2010). Australia's mammalian fauna is predominantly marsupial (Van Dyck and Strahan 2008) and, with the exception of the dingo *Canis lupus dingo* that arrived 3,500 years ago, placental predators were absent until European arrival in the late eighteenth century. Hence, prey naïveté may help to explain why several species of small mammals suffered extinctions or population declines as foxes spread across southern Australia (Saunders et al. 1995; Dickman 1996a; Salo et al. 2007).

Despite these extinctions, many species of small native mammals still persist in some parts of Australia in the presence of introduced predators. Some occur commonly and even abundantly, suggesting either that they are inaccessible to foxes (e.g., arboreal possums) or that they may respond appropriately to signs of the predator's presence. Many animals use chemical cues from predators to assess the risk of predation (Kats and Dill 1998). In mammals, typical responses to predator odours include reducing activity or foraging, and shifting habitat use to areas where predator odours are absent (Brown 1999; Lima and Bednekoff 1999; Apfelbach et al. 2005). Foxes are territorial animals that communicate with each other via urinary or faecal scent marks (Macdonald 1980, 1987), and these scents can also inform prey about where foxes are active (Calder and Gorman 1991). There is conflicting evidence as to whether native Australian mammals can discriminate chemical cues from foxes as sources of predation risk (Banks 1998; Mella et al. 2010). Here, we predict that common native species should be sensitive to fox presence if they are small enough to be hunted and occupy terrestrial habitats where the probability of encounter with the predator is high.

We can make a number of further predictions, based on theories of predator–prey relationships, on how the prey will respond to predators. Firstly, many predators regulate, or at least limit, the numbers of their prey (Korpimäki and Krebs 1996; Côté and Sutherland 1997; Sinclair et al. 1998; Gurevitch et al. 2000; Korpimäki et al. 2004; Salo et al. 2007, 2010), and prey survival has been shown to depend directly on predator functional and numerical responses (Miller et al. 2006). Hence, a higher density of predators is expected to result in a lower density and survival of prey. Secondly, selection should favour individuals that avoid cues, such as odours, of predators when foraging (Dickman and Doncaster 1984; Boonstra and Craine 1985; Jones and Dayan 2000). Thirdly, if there is a learning component to predator avoidance and the recognition of such cues, this should develop over the lifetimes of any individuals that are exposed to the cues (Shettleworth 1998; Griffin et al. 2001; Blumstein et al. 2002).

Our study species were two native Australian mammals, the brown antechinus *Antechinus stuartii* and the bush rat *Rattus fuscipes*. We manipulated cues of predation risk directly to these species by applying fox odours (faeces) to foraging trays and traps, and compared the species' responses in areas where fox activity was high and low. We applied these treatments repeatedly for 4 months over a period (November–February) when young animals of both species are becoming established in their respective populations. We used the results to test the following predictions:

1. both study species will have higher population sizes and rates of survival in areas of low compared with high fox activity;
2. the study species will avoid fox-scented traps and reduce their activity at foraging trays bearing fox odour compared to those with no odour or non-predator odour;
3. there is a learning component to animals' behaviour if there is a strengthening of their fox-aversive responses as they mature over time; and
4. any fox-aversive responses seen in hypotheses in (2) and (3) will be more evident in areas of high compared with low fox activity.

Materials and methods

Study species

Antechinus stuartii is a terrestrial to semi-arboreal dasyurid marsupial that inhabits forest and heathland in eastern Australia (Crowther and Braithwaite 2008). It is insectivorous, feeding mainly on beetles, spiders and cockroaches. Adult body mass is 29–71 g, with males being 1.2- to 2-fold heavier than females (Crowther and Braithwaite 2008). *Rattus fuscipes* is a native rodent that inhabits forest and heathland in eastern and south-western Australia (Lunney 2008). It is omnivorous, consuming fungi, fibrous stems and leaves, insects, fruits and seeds, and has an adult body mass of 40–225 g (Lunney 2008). Both species are nocturnal and are depredated by foxes in the forests of eastern Australia (Banks 1999; Stokes et al. 2004; Glen et al. 2011), including in our study areas, where 15–25% of fox diet by frequency of occurrence comprises the two study species (Sutherland 1998). *Antechinus* spp. and bush rats rely heavily on scent cues while foraging (Toftegaard and Bradley 1999; Lunney 2008), and may use them to detect predation threats.

Study sites

We investigated the demography and behaviour of the study species at eight sites with high and low fox activity to provide data for hypotheses 1–4. Study sites were located in forested habitats in Ku-ring-gai Chase National Park (33°36′S, 151°12′E), Garigal National Park (33°42′S, 151°15′E) and Muogamarra Nature Reserve (33°34′S, 151°11′E) in eastern New South Wales, Australia. Estimates of fox activity were available through the New South Wales (NSW) Fox Threat Abatement Plan (FoxTAP; see Mahon 2009). Four spatially separate low fox activity sites were located at West Head (2) and Bobbin Head (2) in Ku-ring-gai Chase National Park, and four spatially separate high fox activity sites in Garigal National Park (2) and Muogamarra Nature Reserve (2). Low activity sites were located <100 m from fox-baiting stations, and high fox activity sites in unbaited areas several kilometres distant. Fox baiting, using 1080 poison, has been conducted in Ku-ring-gai Chase National Park since 2000 (NPWS 2001), with baiting carried out bimonthly over a 14-day period. Park rangers regularly monitor fox activity using sand plots located around baiting stations and in non-baited areas. To estimate fox activity, rangers record fox tracks (presence/absence) on 40 sand plots (500 m apart) that traverse tracks and trails. The plots are monitored over three consecutive nights in autumn (March–May) and spring (September–November), when young foxes enter the population. During our study, fox activity on plots in the baited (low fox activity) sites averaged 8.7%, while on plots in the unbaited (high fox activity) sites, fox activity averaged 28.6% (P. Mahon, NSW Office of Environment & Heritage, unpublished data).

Experimental design

To test the responses of the study species at traps and foraging trays (hypotheses 2–4), it was necessary to expose animals to different odours to quantify the extent of their avoidance to fox odour. We used fox faeces as the cue for fox presence as predator faecal odours can effect strong anti-predator behaviour in organisms, including rodents (Apfelbach et al. 2005). We used faeces of the brushtail possum *Trichosurus vulpecula*, a folivore, as a pungency control, and water as a procedural control. Fresh fox faeces were obtained from wild-caught individuals that had been kept in captivity for 3 days (W. Mason, Department of Environment and Conservation, Perth, personal communication), and fresh possum faeces came from a captive population maintained under natural conditions at the University of New South Wales field station at Cowan, very close to the study sites. Possum and fox faecal odours were made by diluting 30 g of locally provenanced fresh, crushed faeces in 250 mL of water. Solutions from identical batches were used consistently across all sites.

To evaluate trapping responses at each of the 8 sites (4 high fox, 4 low fox activity) we established 10 trapping stations (each 10 m apart) with three Elliott traps (33 × 10 × 10 cm) spaced 30 cm apart. We sprayed the open doors of the traps at each station with either brushtail possum odour, fox odour, or water. Traps were baited with rolled oats, honey and peanut butter, with non-absorbent cotton wool provided for bedding, and trapped over four nights between November 2006 and February 2007. Traps were set in the late afternoon, and checked early next morning. Odours were re-applied every 24 h when traps were checked. Traps with captured animals were replaced with new traps bearing the same experimental odour to eliminate the possibility of prey odours influencing subsequent captures in the same trap. All captured animals were measured, assessed for sex and reproductive status, and ear-nicked with a unique identification number prior to release. We cleaned traps with detergent and dried them before each session to avoid cross-contamination of scents.

To evaluate responses at foraging trays, we used the giving-up density (GUD) approach of Brown (1988). This allows investigation of the trade-offs that individual foragers make when balancing the benefits of gaining food against the costs of encountering predators (Brown 1988). The giving-up density value is a measure of the harvest rate, or density, at which foraging in a patch is no longer worthwhile and ceases. The harvest rate is equal to the metabolic cost of foraging, predation risk and missed opportunity costs arising from missed foraging opportunities elsewhere. GUD theory predicts that a forager should leave a patch when the harvest rate no longer exceeds the sum of metabolic cost, predation risk, and missed opportunity costs of engaging in foraging elsewhere (Brown 1988). The consistency of a forager's behaviour may be examined through the manipulation of a single variable of interest. Assuming that metabolic and missed opportunity costs are stable, we predicted that the application of predator cues to foraging trays should increase GUD values.

We established artificial food patches (‘trays’) with different levels of predation risk at the 8 study sites, with 16 stations set at each site. Each tray consisted of a rectangular plastic container (17 × 12 cm), covered with aluminium flyscreen mesh (45 × 45 cm) to prevent birds and other non-target animals from feeding at the stations. Two diagonal corners were cut into the mesh to allow entry of smaller animals (<6 cm high at the shoulders). Coopex® powder (Bayer, Sydney) was dusted around the trays to repel ants and other insects that might otherwise have visited the trays.

Species-specific visitations to the trays were monitored using tracking plates, which consisted of a single 8.5 × 6 cm sheet of stiff plastic placed at the two available entrances to the feeding trays. The sheets were sprayed with a 95:5 solution of methylated spirits:paraffin oil, into which 50 g of coloured chalk had been dissolved. The methylated spirits evaporated after application, leaving a fine residue of chalk powder that clearly showed any footprints on the plastic sheets.

Ten mealworms (*Tenebrio molitor* larvae) were placed in a sawdust matrix in each foraging tray. The surrounding 30 cm of ground was sprayed with fox faecal odour, possum faecal odour (pungency control), or water (odourless control). Trays were randomly allocated an odour. Foraging trays were checked and reset in the early morning for four consecutive nights over three consecutive months (November and December 2006, January 2007). The number of mealworms remaining after a single night of foraging was recorded as the giving-up density (GUD) value. Values used in analyses were from stations where the same species had visited over all four nights; all other data were discarded.

Data manipulation and analyses

To test our first hypothesis, we sought to compare abundances and survival of the study species in the high and low fox activity sites. We could not reliably estimate survival of *A. stuartii* as too few were recaptured, and used the minimum numbers of animals known to be alive (MNKTBA) as an index of abundance. Two-way ANOVA, with MNKTBA as the dependent variable, and time (month) and fox activity (high/low) as factors, was used to assess temporal and fox-effects on abundance.

Higher numbers of recaptures of *R. fuscipes* meant that mark–recapture analyses could be used. The Cormack–Jolly–Seber (CJS) method (Cormack 1989) was used to estimate survival rates from the mark–recapture data using MARK v.4.1 (White and Burnham 1999). The bush rat data were separated into four groups: adults and juveniles from sites with low fox activity, and adults and juveniles from sites with high fox activity. A bootstrap goodness of fit procedure in MARK was used to test the fit of the 'saturated' (most highly parameterised) Cormack–Jolly–Seber model Φ $(g \times t)$ p $(g \times t)$ in which the probabilities of survival (Φ) and recapture (p) were dependent on group (g) and time (t), respectively (Cooch and White 2006). Based on 1,000 bootstrap replicates, there was no significant deviation from the mark–recapture assumptions ($P = 0.276$).

The Akaike Information Criterion (AIC) was used as an objective means of model selection (Burnham and Anderson 2002); this identifies the most parsimonious model from a set of candidates given the bias corrected, maximised log-likelihood of the fitted model and a penalty for the number of parameters used. AIC values were adjusted for over-dispersion by calculating a variance inflation factor, $\hat{c}$ (here $\hat{c} = 1.25$) from the goodness of fit statistics (Cooch and White 2006). The $\Delta\mathrm{AIC_c}$ was calculated for each model; those with $\Delta\mathrm{AIC_c} < 2$ were interpreted as being well supported by the data, and those with $\Delta\mathrm{AIC_c} > 2$ as being poorly supported (Burnham and Anderson 2002). Once the most parsimonious model was identified, it was used to estimate survival rates of rats in the study sites.

Final population size estimates for *R. fuscipes* were obtained using Pollock's robust design assuming that the population was closed over the 4-day sampling period, and open between the monthly sessions (Kendall et al. 1997). Estimates of survival and recapture probabilities were calculated for the time periods in which the populations were considered open using the CJS method. Population size was estimated with a closed-capture full-likelihood model.

Tests of hypotheses 2–4 on the trapping data used a 3-factor ANOVA design, with site as the unit of replication, number of animals trapped as the dependent variable, and fox activity, month and odour as factors. Significant differences were investigated with Tukey's Honestly Significant Difference (HSD) test. Captures of the two study species were analysed separately, as they differ greatly in life-history, habitat and phylogenetic position. Data for recaptured animals were omitted to maintain independence. A 2-factor ANOVA was performed on the data for juvenile *R. fuscipes*, with baiting treatment and odour treatment as factors; month was not included as juveniles were trapped during January and February only. The separation of data on *A. stuartii* into adult and young age classes was not possible due to the low trapping success of young.

Equivalent tests were performed on the GUD data after summing GUD values per foraging tray over the four nights of foraging. The results for *A. stuartii* and *R. fuscipes* were analysed separately. A 3-factor ANOVA was performed with the GUD value as the dependent variable, and fox activity, odour, and month as factors. Tukey's HSD was used to distinguish significantly different means. Data were checked for normality and homogeneity of variances prior to analysis, with all computations made using SPSS Version 15.0.

Although joint use of both the AIC and hypothesis testing approaches is unusual because of their different philosophical bases (Burnham and Anderson 2002; Symonds and Moussalli 2011), it is appropriate here because we are interested both in model evaluation and in formal testing of identified hypotheses using controlled and replicated experimental manipulations.

Results

Hypothesis 1: abundance and survival

Sixty *A. stuartii* were trapped from November to February, with eight individuals recaptured. There was no significant difference in antechinus abundance, expressed as MNKTBA, between baiting treatments ($F_{1,24} = 0.626$, $P = 0.437$), month ($F_{3,24} = 1.102$, $P = 0.368$), or any interaction between the factors ($F_{3,24} = 1.34$, $P = 0.285$).

For *R. fuscipes*, 155 individuals were trapped over the course of the study, including 34 juveniles (<60 g), with 17 adults recaptured once or more. The results of the CJS analysis identified two models with ΔQAICc values <2.0 that were well supported by the data (Table 1). The best-supported model was ϕ (fox activity), $p(t)$, in which survival was dependent on the level of fox activity, and the probability of recapture was time-dependent. In this model, survival was higher in sites where fox activity was low ($\phi = 0.79$, SE = 0.20) than in sites where it was high ($\phi = 0.43$, SE = 0.18) and recapture rates decreased over time ($p_1 = 0.78$, SE = 0.20, $p_2 = 0.22$, SE = 0.11, $p_3 = 0.11$, SE = 0.07). The next best supported model was ϕ(c), $p(t)$, in which survival was constant and equal across groups ($\phi = 0.67$, SE = 0.19), and the probability of recapture was time-dependent ($p_1 = 0.74$, SE = 0.21, $p_2 = 0.21$, SE = 0.11, $p_3 = 0.10$, SE = 0.07).

No juvenile rats were recaptured during the study, so analyses were rerun in MARK using only the mark–recapture data from adults in the sites with high and low fox activity. As before, the best-supported model was $\phi(g)$, $p(t)$, in which survival was dependent on fox activity, and the probability of recapture was time dependent (Table 2). From this model, bush rat survival was higher in sites where fox activity was low ($\phi = 0.76$, SE = 0.18) than in those where it was high ($\phi = 0.41$, SE = 0.19), and recapture rates decreased over time ($p_1 = 0.78$, SE = 0.19, $p_2 = 0.23$, SE = 0.11, $p_3 = 0.13$, SE = 0.09). Population estimates provided through the robust design model in MARK indicated that abundance did not vary between baited and unbaited areas.

Hypotheses 2-4: behavioural responses to foxes, odours and time

The capture data on *A. stuartii* met the assumptions for parametric analysis, and were therefore not transformed prior to ANOVA. Baiting treatment and month had no effect on trap entry, nor were there any interactions between factors (Table 3). However, trap odour strongly affected captures (Table 3), with significantly fewer antechinuses captured in traps treated with fox odour than in those with control (Tukey's HSD, $P < 0.01$) and possum odours ($P < 0.01$) (Fig. 1). The numbers of *A. stuartii*

Table 1 Candidate models used to determine whether fox activity influences the survival (ϕ) and recapture (p) probability of the bush rat *Rattus fuscipes*

Model	QAICc	ΔQAICc	QAICc weight	Model likelihood	*n*	QDeviance
ϕ(fox activity), $p(t)$	112.11	0.00	0.4200	1.0000	5	9.77
$\phi(c)$, $p(t)$	113.56	1.44	0.2041	0.4859	4	13.39
ϕ(ad, juv), $p(t)$	114.63	2.51	0.1193	0.2842	5	12.29
$\phi(g)$, $p(t)$	115.43	3.32	0.0798	0.1900	7	8.65
$\phi(t)$, $p(c)$	115.72	3.60	0.0693	0.1649	4	15.55
$\phi(c)$, $p(t)$	115.72	3.60	0.0693	0.1649	5	13.38
$\phi(t)$, $p(g \times t)$	122.75	10.63	0.0021	0.0049	10	9.01

The letters *g* and *t* refer to group (bush rats were divided into four groups, consisting of adults in sites with high and low fox activity and juveniles in sites with high and low fox activity) and time, respectively, the letter *c* denotes constant survival, and *n* indicates the number of parameters in each model. Models are ordered according to the adjusted Akaike information criterion (QAICc)

Table 2 Candidate models used to determine whether fox activity influences the survival (ϕ) and recapture (p) probability of adult bush rats *Rattus fuscipes* in sites with high and low fox activity

Model	QAICc	ΔQAICc	QAICc weight	Model likelihood	*n*	QDeviance
$\phi(g)$, $p(t)$	111.03	0.00	0.4129	1.0000	5	8.65
$\phi(c)$, $p(t)$	112.49	1.46	0.1991	0.4822	4	12.29
$\phi(t)$, $p(c)$	113.90	2.87	0.0981	0.2374	5	11.53
$\phi(t)$, $p(t)$	114.15	3.12	0.0865	0.2095	4	13.95

The letters *g* and *t* refer to group (high versus low fox activity) and time, respectively, the letter *c* denotes constant survival, and *n* refers to the number of parameters in each model

Table 3 Three-factor analysis of variance on the numbers of trapped brown antechinus *Antechinus stuartii* and bush rat *Rattus fuscipes* in areas of high and low fox activity over 4 months

Source	Brown antechinus				Bush rat			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
Fox activity	1	0.375	0.651	0.42	1	0.375	0.318	0.58
Month	3	0.861	1.494	0.22	3	1.750	1.482	0.23
Odour	2	8.844	15.343	<0.01	2	2.698	2.285	0.11
Fox activity × month	3	1.125	1.952	0.13	3	0.569	0.482	0.70
Fox activity × odour	2	0.219	0.380	0.69	2	0.281	0.238	0.80
Month × odour	6	0.330	0.572	0.75	6	1.990	1.685	0.14
Fox activity × month × odour	6	0.427	0.741	0.62	6	0.934	0.791	0.58
Error	72	0.576			72	1.181		
Total	96				96			

Traps were alternately treated with fox, possum, and odourless scents for the odour factor

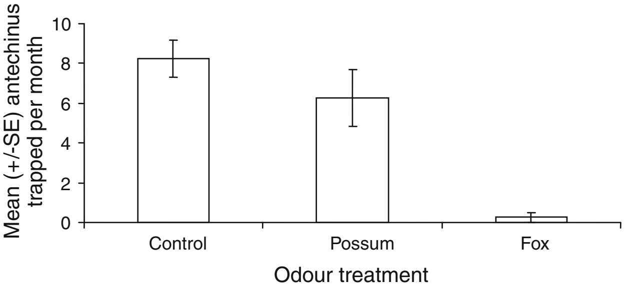

Fig. 1 Mean numbers (±SE) of brown antechinus *Antechinus stuartii* captured in traps bearing the odour of fox, possum or no odour. Captures were pooled over months and sites with high and low fox activity

Table 4 Two-way ANOVA on trapped juvenile bush rat *Rattus fuscipes* in sites with high and low fox activity in traps containing control, fox and possum odours

Source	*df*	MS	*F*	*P*
Fox activity	1	6.000	9.818	0.006
Odour	2	10.792	17.659	<0.001
Fox activity × odour	2	2.625	4.295	0.030
Error	18	0.611		
Total	24			

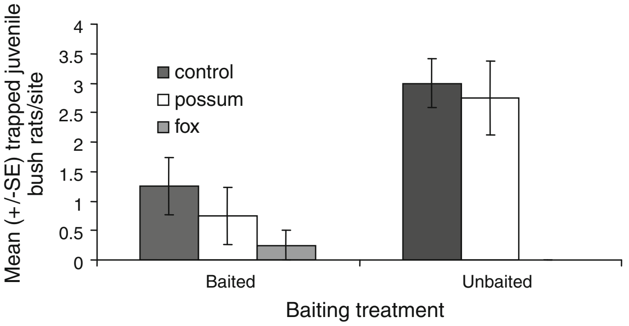

Fig. 2 Mean numbers (±SE) of juvenile bush rat *Rattus fuscipes* captured in sites with low fox activity (baited) and high fox activity (unbaited) in traps bearing the odour of fox, possum or no odour, pooled across eight sites during January and February 2007

captured in traps with control and possum odours did not differ (Tukey's HSD, $P = 0.48$).

For *R. fuscipes*, overall capture data were normally distributed (Kolmogorov–Smirnov test), but variances were heterogeneous (Levene's test, $P < 0.01$). Log and square root transformations did not improve homogeneity, hence probability levels for significance were adjusted to 0.01. There was no effect of baiting treatment, odour or month on trapping success, and no significant interactions between any of these factors (Table 3). However, closer inspection of the 34 juvenile *R. fuscipes* captured in January and February showed that more juveniles were trapped where fox activity was high than where it was low (Table 4; Fig. 2). Odour also affected the entry of juvenile rats into traps, and there was a significant interaction between fox activity and odour (Table 4). Fewer juvenile rats were captured in traps with fox odour than in control (Tukey's HSD, $P < 0.001$) and possum-scented traps (Tukey's HSD, $P = 0.002$), but animals entered traps bearing control and possum odour equally (Tukey's HSD, $P = 0.272$).

The giving-up density data for *A. stuartii* showed effects of odour and month but not of fox activity at the site level, with no interaction terms significant (Table 5). GUD values at trays with fox odour were significantly higher than those at trays with control and possum odours (Tukey's HSD, $P = 0.01$). In December, control GUD values were lower than possum and fox GUD values (Fig. 3a). In November and December, fox GUD values were higher than GUD values from both possum and control trays, but this trend was not statistically significant. There was no effect of odour treatment in January. Mean GUD values decreased with time (i.e., trays were visited more often, or

Table 5 Three-factor ANOVA on giving-up density (GUD) values for brown antechinus *Antechinus stuartii* and bush rat *Rattus fuscipes* in sites with high and low fox activity and in traps bearing the odours of either fox, possum or no odour over a period of 3 months

Source	Brown antechinus				Bush rat			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
Odour treatment	2	167.915	5.893	0.004	2	155.964	6.790	0.002
Fox activity	1	9.875	0.35	0.558	1	2.419	0.105	0.746
Month	2	364.369	12.788	<0.001	2	499.596	21.750	<0.001
Odour treatment × fox activity	2	55.197	1.937	0.152	2	47.881	2.084	0.128
Odour treatment × month	4	52.879	1.856	0.128	4	50.417	2.195	0.073
Fox activity × month	2	18.360	0.644	0.528	2	5.911	0.257	0.773
Odour treatment × fox activity × month	4	19.334	0.679	0.609	4	10.551	0.459	0.765
Error	69	28.493			134	22.970		
Total	87				152			

for longer, during January than during November or December; Fig. 3a).

GUD results for *R. fuscipes* were similar to those for *A. stuartii*. There was no effect of fox activity, but strong effects of month and odour at the foraging trays (Fig. 3b); no interaction terms were significant (Table 5). Although fox-scented trays generally had the highest GUD values, there was insufficient power to confirm this in post hoc tests. Overall, GUDs were higher in November and December than in January (Fig. 3b).

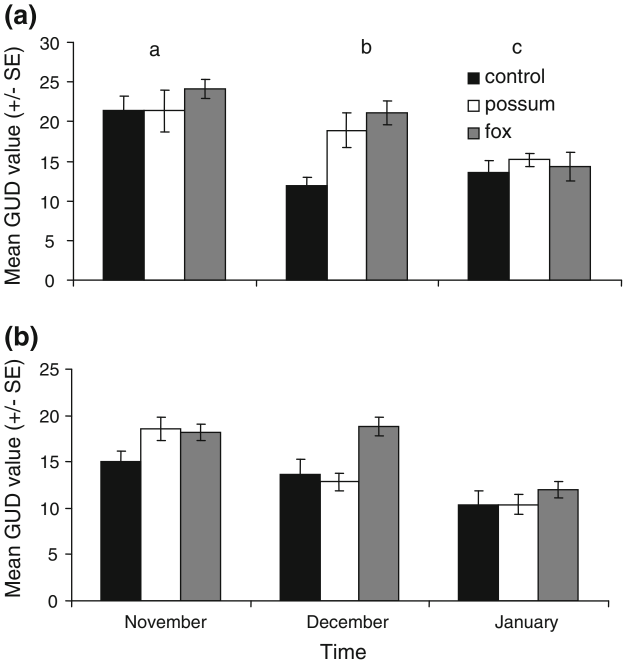

Fig. 3 Mean (±SE) giving-up density (GUD) values for **a** brown antechinus *Antechinus stuartii* ($n = 87$) and **b** the bush rat *Rattus fuscipes* ($n = 152$) after foraging at trays bearing no odour, possum or fox odour during three consecutive months. Monthly GUD values for antechinus differed significantly from each other (denoted with *a*, *b*, *c*), while January values for the bush rat differed significantly from those obtained in November and December. As there was no significant effect of fox activity on GUD values, these data were pooled

Discussion

The results provided mixed support for our initial hypotheses, especially for the expectation that the demographic performance of the study species would be greater in sites with low compared with high fox activity. However, while the species' abundances appeared to be unaffected by foxes, survival of *R. fuscipes* was reduced in sites where fox activity was high. Population modelling confirmed that recapture rates diminished as the study progressed, with all rats and adults only exhibiting roughly two-fold higher survival where fox activity was low. Data on juveniles could not be modelled; however, as more juveniles were trapped in sites with high than low fox activity but none was recaptured, it is reasonable to infer that their survival was low in the presence of foxes. It is not clear why more juveniles were trapped in sites with high fox activity. As foxes are opportunistic predators and hunt co-occurring small mammals such as other *Rattus* spp. in the study area (Sutherland 1998), *R. fuscipes* that survive to breed in sites with high fox activity paradoxically may have access to additional resources that allow them to elevate their production of young.

In other studies where foxes have been removed, small mammals have often—but not always—shown positive numerical responses. Kinnear et al. (2002) provided evidence of population increases in two species of dasyurid marsupials after fox removal, while Dexter and Murray (2009) provided similar evidence for mammals in tall forest habitats. In contrast, Risbey et al. (2000) showed that small mammal populations declined after fox removal owing to increased predation from a more specialised replacement carnivore, the feral cat *Felis catus*. We have no evidence that cats differed in activity between our study sites from either the sand plot tracking or direct observations, although cats are known predators of both rats and antechinuses in the Ku-ring-gai area (Dickman 2009). Banks (1999) found that neither *R. fuscipes* nor *Antechinus agilis* responded numerically to fox removal, and suggested that this arose because foxes removed animals that contributed little to effective population size. This explanation is also plausible here. However, the consistent inclusion of *R. fuscipes* and *A. stuartii* in the diet of the fox at all times of the year in the present study area (Augee et al. 1996; Sutherland 1998) suggests that some selective advantage should nonetheless accrue to individuals that can discriminate and avoid cues to fox presence.

We found more evidence in support of our second hypothesis. *Antechinus stuartii* and juvenile *R. fuscipes* strongly avoided traps bearing fox odour, and both species also showed reduced foraging at trays where fox odour had been applied. Several other species of marsupials (Gresser 1996; Blumstein et al. 2003) and rodents (Dickman and Doncaster 1984; Pillay et al. 2003) are known to avoid fox faecal odour, and this response can translate into increased long-term survival (Dickman 1992). Many prey species use chemical cues from ingested conspecifics to discriminate predators as dangerous (Chivers and Mirza 2001). For example, striped mice *Rhabdomys pumilio* show stronger anti-predator behaviours in the presence of faeces from snakes fed a diet of conspecifics than from snakes fed on house mice (Pillay et al. 2003). Potentially, *A. stuartii* and young *R. fuscipes* may have discriminated conspecific cues in the fox faeces and responded to these as sources of risk. Recent work has suggested that 2,3,5-trimethyl 1-3-thiazoline (TMT) is a further fear-inducing compound in fox faeces (Fendt et al. 2005).

Previous trap-based odour research on the study species has not always produced consistent results. For example, *R. fuscipes* has been shown to enter clean and fox-scented traps equally (Banks 1998), to avoid traps with fox odour (Russell and Banks 2007), and to show no clear avoidance of the faeces of domestic dog *Canis lupus familiaris* (Banks et al. 2003). In contrast, *A. stuartii* has shown no avoidance of fox-scented traps in previous work (Russell and Banks 2007), but strong avoidance of traps with dog faeces placed near the entrance (Banks et al. 2003). Our finding that adult bush rats entered traps irrespective of their odour accords with the results of Banks (1998), whereas the results for *A. stuartii* are novel. Inconsistent results between studies may arise from differences in predation pressure between sites, differences in methodology such as the use of pungency controls, or differences in the suite of predators and prey that are present at a site (Dickman and Doncaster 1984; Jedrzejewski et al. 1993; Russell and Banks 2007). Our results for *R. fuscipes* suggest that animal age may be a further factor. Potentially, young rats are more cautious than adults as they explore new areas after leaving their natal territories. Alternatively, young *R. fuscipes* may associate fox faecal odour with potential predation threat. As they grow older, they may become less wary of fox odour due to habituation or to a lack of non-fatal encounters with the predator (Bramley et al. 2000).

Our foraging experiments supported the trapping data. Although we were unable to specify the age of foragers from prints on the tracking plates around GUD trays, adults of both study species appeared to trade-off risk with energy gain as avoidance of fox odour was detected during the first 2 months of the study when juveniles had not entered the populations. No previous work has assessed the GUD responses of *A. stuartii* or *R. fuscipes* to predator odours, although the method is likely to provide a more sensitive assay of prey responses to predation risk than the ‘all-or-nothing’ data that are obtained when an animal enters a trap (Dickman et al. 2010). Indeed, while the trapping results uncovered no temporal differences in species’ responses, the GUD data suggested that animals lost their aversion to fox odour as the study progressed. These findings provide no evidence to support our third hypothesis, and thus allow rejection of the notion that animals would learn to avoid predator cues over time.

Several explanations can be advanced to account for these results. First, as predator-naïve juveniles were recruited into the small mammal populations towards the end of the study period, they may have foraged equally in all GUD trays and equalised the numbers of remaining food items at this time. However, this seems unlikely as juvenile *R. fuscipes* showed strong aversion to fox odour at traps and relatively few young *A. stuartii* were recorded. Second, as GUDs declined generally as the study progressed, increasing energetic requirements of both species may have over-ridden their aversion to predator odours. Again, this seems unlikely. Both species are food-limited in winter (Banks and Dickman 2000); our experiments were carried out in summer when natural food resources are maximal and food shortages are least likely to occur (Dickman 1989). Third, both species may have become habituated to fox odour over time. In bank voles *Myodes glareolus*, for example, animals become habituated to the presence of a long-lasting predator scent (weasel odour) if the odour is not paired with predator attack, and increase the time they spend at predator-odour-treated stations as their wariness declines (Ylönen et al. 2006). In other species, such as some strains of domestic rat, habituation to fox odour can occur after just one exposure (Morrow et al. 2000). Habituation to predator odours has been reported in a wide range of species (Verdolin 2006; Barrio et al. 2010), and is the most likely explanation of our results.

Little support was evident for our fourth hypothesis, with only the fox activity × odour interaction for juvenile *R. fuscipes* suggesting any behavioural response to different levels of fox activity. Potentially, prey individuals simply responded to fox odour as a source of risk, irrespective of predator activity or density (Abrams 1993). Alternatively, they may have been unresponsive to, or unable to assess changes in, predation risk at the level of the landscape. Gerbils are capable of assessing variation in risk and foraging quality between open patches of habitat as large as 1–2 ha (Abramsky et al. 2002), but voles discern risk in more sheltered habitats at much smaller scales (Moenting and Morris 2006). In the present study, it is possible that the structurally complex habitats occupied by both *A. stuartii* and adult *R. fuscipes* allow them to move rapidly to secure refuges whenever a cue to fox presence is encountered, and hence that neither species derives any additional benefit from responding at a larger scale. If this is so, the response of juvenile *R. fuscipes* to fox odour can be interpreted. Young rats have less access to refuge habitats owing to their exclusion from them by the dominant adults, and therefore benefit by responding more aversively to fox odours in environments where foxes are more active. Juveniles in other species of rodents are often susceptible to predation due to their eviction from safer habitats by adults (Dickman et al. 1991), suggesting that there is a strong fitness payoff to them in distinguishing and responding to different levels of predator activity.

The red fox has been present in the study region for just over a century (Saunders et al. 2010), and can be reasonably assumed to have depredated the two species of study mammals for many generations. It depresses the survival of *R. fuscipes*; it may also reduce survival in *A. stuartii*, although the lack of recaptures meant that we were unable to demonstrate this here. As small mammals that encounter a novel predator for the first time are often unresponsive to its faecal odours (Dickman 1992; Jedrzejewski et al. 1993), our results suggest that *R. fuscipes* and especially *A. stuartii* have lost some of their naïveté and likely derive some fitness benefits from distinguishing and avoiding fox faecal odours. In consequence, perhaps, these two species remain common and locally abundant.

In many situations when an alien predator arrives in a new environment, its effects on native prey species can be rapid and catastrophic, allowing them little opportunity to respond (Mack et al. 2000). However, if a predator's impacts are slowed or ameliorated, strong directional selection on prey for predator recognition and avoidance may allow populations to escape the extinction vortex. If correct, this conclusion has important implications for in situ conservation and the reintroduction of naïve prey populations into parts of their former ranges where alien predators now occur. Firstly, predator-naïve prey species will persist if alien predators are extirpated or prey populations are maintained in predator-proof enclosures. However, such interventionist management is usually very costly and has a high chance of failure. Secondly, and more realistically, predator-naïve prey should also persist if predation pressure is reduced so that some prey individuals encounter predators, and thus have the opportunity to learn to be wary (Blumstein et al. 2002) and experience selection to discriminate and respond to predator cues. Identifying this balanced level of predator reduction remains an important challenge.

Acknowledgments This study was conducted under permission from the University of Sydney Animal Care and Ethics Committee (Licence L04/10-2006/1/4487) and National Parks and Wildlife Licence S 12 123. We are grateful to the Department of Environment and Climate Change NSW for access to fox baiting and tracking data, and particularly Mel Hall from the Pest Control Division, National Parks and Wildlife Service. We thank Alex Diment for his helpful comments on an earlier version of this manuscript, and the numerous field volunteers who made this work possible.

References

Abrams PA (1993) Why predation rate should not be proportional to predator density. Ecology 74:726–733

Abramsky Z, Rosenzweig ML, Subach A (2002) Measuring the benefit of habitat selection. Behav Ecol 13:497–502

Apfelbach R, Blanchard CD, Blanchard RJ, Hayes RA, McGregor IS (2005) The effects of predator odors in mammalian prey species: a review of field and laboratory studies. Neurosci Biobehav Rev 29:1123–1144

Augee ML, Smith B, Rose S (1996) Survival of wild and hand-reared ringtail possums (*Pseudocheirus peregrinus*) in bushland near Sydney. Wildl Res 23:99–108

Banks PB (1998) Responses of Australian bush rats, *Rattus fuscipes*, to the odor of introduced *Vulpes vulpes*. J Mammal 79:1260–1264

Banks PB (1999) Predation by introduced foxes on native bush rats in Australia: do foxes take the doomed surplus? J Appl Ecol 36:1063–1071

Banks PB, Dickman CR (2000) Effects of winter food supplementation on reproduction, body mass, and numbers of small mammals in montane Australia. Can J Zool/Rev Can Zool 78:1775–1783

Banks PB, Dickman CR (2007) Alien predation and the effects of multiple levels of prey naiveté. Trends Ecol Evol 22:229–230

Banks PB, Hughes NK, Rose TA (2003) Do Australian native small mammals avoid faeces of domestic dogs? Aust Zool 32:406–409

Barrio IC, Bueno CG, Banks PB, Tortosa FS (2010) Prey naiveté in an introduced prey species: the wild rabbit in Australia. Behav Ecol 21:986–991

Blumstein DT (2006) The multipredator hypothesis and the evolutionary persistence of antipredator behavior. Ethology 112:209–217

Blumstein DT, Mari M, Daniel JC, Ardron JG, Griffin AS, Evans CS (2002) Olfactory predator recognition: wallabies may have to learn to be wary. Anim Conserv 5:87–93

Blumstein DT, Daniel JC, Sims RA (2003) Group size but not distance to cover influences agile wallaby (*Macropus agilis*) time allocation. J Mammal 84:197–204

Boonstra R, Craine I (1985) Natal nest location and small mammal tracking with a spool and line technique. Can J Zool/Rev Can Zool 64:1034–1036

Bramley GN, Waas JR, Henderson HV (2000) Responses of wild Norway rats (*Rattus norvegicus*) to predator odors. J Chem Ecol 26:705–719

Brown JS (1988) Patch use as an indicator of habitat preference, predation risk, and competition. Behav Ecol Sociobiol 22:37–47

Brown JS (1999) Vigilance, patch use and habitat selection: foraging under predation risk. Evol Ecol Res 1:49–71

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Calder CJ, Gorman ML (1991) The effects of red fox *Vulpes vulpes* faecal odours on the feeding behaviour of Orkney voles *Microtus arvalis*. J Zool 224:599–606

Chivers DP, Mirza RS (2001) Predator diet cues and the assessment of predation risk by aquatic vertebrates: a review and prospectus. Plenum, New York

Cooch E, White G (2006) Program MARK: "a gentle Introduction", 4th edn. Available at www.phidot.org/software/mark/docs/book/

Cormack RM (1989) Loglinear models for capture-recapture. Biometrics 45:395–413

Côté IM, Sutherland WJ (1997) The effectiveness of removing predators to protect bird populations. Conserv Biol 11:395–405

Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends Ecol Evol 21:674–680

Crowther MS, Braithwaite RW (2008) Brown Antechinus *Antechinus stuartii*. In: Van Dyck SM, Strahan R (eds) The mammals of Australia, 3rd edn. Angus and Robertson, Sydney, pp 94–96

Dexter N, Murray A (2009) The impact of fox control on the relative abundance of forest mammals in East Gippsland, Victoria. Wildl Res 36:252–261

Dickman CR (1989) Demographic responses of *Antechinus stuartii* (Marsupialia) to supplementary food. Aust J Ecol 14:387–398

Dickman CR (1992) Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73:313–322

Dickman CR (1996a) Impact of exotic generalist predators on the native fauna of Australia. Wildl Biol 2:185–195

Dickman CR (1996b) Overview of the impacts of feral cats on Australian native fauna. Australian Nature Conservation Agency, Canberra, pp 1–97

Dickman CR (2009) House cats as predators in the Australian environment: impacts and management. Human Wildl Conflicts 3:41–48

Dickman CR, Doncaster CP (1984) Responses of small mammals to red fox (*Vulpes vulpes*) odour. J Zool 204:521–531

Dickman CR, Predavec M, Lynam AJ (1991) Differential predation of size and sex classes of mice by the barn owl, *Tyto alba*. Oikos 62:67–76

Dickman CR, Greenville AC, Beh CL, Tamayo B, Wardle GM (2010) Social organization and movements of desert rodents during population "booms" and "busts" in central Australia. J Mammal 91:798–810

Doody JS, Green B, Rhind D, Castellano CM, Sims R, Robinson T (2009) Population-level declines in Australian predators caused by an invasive species. Anim Conserv 12:46–53

Fendt M, Endres T, Lowry CA, Apfelbach R, McGregor IS (2005) TMT-induced autonomic and behavioral changes and the neural basis of its processing. Neurosci Biobehav Rev 29:1145–1156

Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case study of Guam. Annu Rev Ecol Syst 29:113–140

Glen AS, Pennay M, Dickman CR, Wintle BA, Firestone KB (2011) Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. Austral Ecol 36:290–296

Gresser S (1996) Anti-predator behaviour in the common brushtail possum (*Trichosurus vulpecula*). Honours thesis. University of Sydney, Sydney

Griffin AS, Evans CS, Blumstein DT (2001) Learning specificity in acquired predator recognition. Anim Behav 62:577–589

Gurevitch J, Morrison JA, Hedges LV (2000) The interaction between competition and predation: a meta-analysis of field experiments. Am Nat 155:435–453

Hayes RA, Nahrung HF, Wilson JC (2006) The response of native Australian rodents to predator odours varies seasonally: a by-product of life history variation? Anim Behav 71:1307–1314

Jedrzejewski W, Rychlik L, Jedrzejewska B (1993) Responses of bank voles to odors of 7 species of predators—experimental data and their relevance to natural predator-vole relationships. Oikos 68:251–257

Jones M, Dayan T (2000) Foraging behavior and microhabitat use by spiny mice, *Acomys cahirinus* and *A. russatus*, in the presence of Blanford's Fox (*Vulpes cana*) odor. J Chem Ecol 26:455–469

Kats LB, Dill LM (1998) The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5:361–394

Kendall WL, Nichols JD, Hines JE (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust sesign. Ecology 78:563–578

Kinnear JE, Sumner NR, Onus ML (2002) The red fox in Australia—an exotic predator turned biocontrol agent. Biol Conserv 108:335–359

Korpimäki E, Krebs CJ (1996) Predation and population cycles of small mammals. Bioscience 46:754–764

Korpimäki E, Brown PR, Jacob J, Pech RP (2004) The puzzles of population cycles and outbreaks of small mammals solved? Bioscience 54:1071–1079

Lima S, Bednekoff P (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am Nat 153:649–659

Lima S, Dill L (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool/Rev Can Zool 68:619–640

Lunney D (2008) Bush Rat *Rattus fuscipes*. In: Van Dyck SM, Strahan R (eds) The mammals of Australia, 3rd edn. Angus and Robertson, Sydney, pp 685–687

Macdonald DW (1980) Patterns of scent marking with urine and faeces amongst carnivore communities. Symp Zool Soc Lond 45:107–139

Macdonald DW (1987) Running with the fox. Unwin Hyman, London

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Mahon PS (2009) Targeted control of widespread exotic species for biodiversity conservation: the Red Fox (*Vulpes vulpes*) in New South Wales, Australia. Ecol Manag Restor 10:s59–s69

Mella VSA, Cooper CE, Davies SJJF (2010) Ventilatory frequency as a measure of the response of tammar wallabies (*Macropus eugenii)* to the odour of potential predators. Aust J Zool 58:16–23

Miller DA, Grand JB, Fondell TF, Anthony M (2006) Predator functional response and prey survival: direct and indirect interactions affecting a marked prey population. J Anim Ecol 75:101–110

Moenting AE, Morris DW (2006) Disturbance and habitat use: is edge more important than area? Oikos 115:23–32

Morrow BA, Redmond AJ, Roth RH, Elsworth JD (2000) The predator odor, TMT, displays a unique, stress-like pattern of dopaminergic and endocrinological activation in the rat. Brain Res 864:146–151

NPWS (2001) Threat abatement plan for predation by the red fox (*Vulpes vulpes*). New South Wales National Parks and Wildlife Service, Hurstville

Pillay N, Alexander GT, Lazenby S (2003) Responses of striped mice, *Rhabdomys pumilio*, to faeces of a predatory snake. Behaviour 140:125–135

Risbey DA, Calver MC, Short J (1997) Control of feral cats for nature conservation. I. field tests of four baiting methods. Wildl Res 24:319–326

Risbey DA, Calver MC, Short J, Bradley JS, Wright IW (2000) The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. a field experiment. Wildl Res 27:223–235

Russell BG, Banks PB (2007) Do Australian small mammals respond to native and introduced predator odours? Austral Ecol 32:277–286

Salo P, Korpimäki E, Banks PB, Nordstrom M, Dickman CR (2007) Alien predators are more dangerous than native predators to prey populations. Proc R Soc Lond B 274:1237–1243

Salo P, Banks PB, Dickman CR, Korpimäki E (2010) Predator manipulation experiments: impacts on populations of terrestrial vertebrate prey. Ecol Monogr 80:531–546

Saunders G, Coman B, Kinnear J, Braysher M (1995) Managing vertebrate pests: foxes. Australian Government Publishing Service, Canberra

Saunders GR, Gentle MN, Dickman CR (2010) The impacts and management of foxes *Vulpes vulpes* in Australia. Mamm Rev 40:181–211

Shettleworth SJ (1998) Cognition, evolution, and behavior. Oxford University Press, New York

Sinclair ARE, Pech RP, Dickman CR, Hik D, Mahon P, Newsome AE (1998) Predicting effects of predation on conservation of endangered prey. Conserv Biol 12:564–575

Stokes VL, Pech RP, Banks PB, Arthur AD (2004) Foraging behaviour and habitat use by *Antechinus flavipes* and *Sminthopsis murina* (Marsupialia: Dasyuridae) in response to predation risk in eucalypt woodland. Biol Conserv 117:331–342

Sutherland EF (1998) Fire, resource limitation and small mammal populations in coastal eucalypt forest. PhD thesis, University of Sydney, Sydney

Symonds M, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65:13–21

Toftegaard CL, Bradley AJ (1999) Structure of specialized osmetrichia in the brown antechinus *Antechinus stuartii* (Marsupialia: Dasyuridae). J Zool 248:27–30

Van Dyck SM, Strahan R (2008) The mammals of Australia. New Holland, Sydney

Verdolin J (2006) Meta-analysis of foraging and predation risk tradeoffs in terrestrial systems. Behav Ecol Sociobiol 60:457–464

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science 277:494–499

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement): 120–138

Williamson M (1996) Biological invasions. Chapman and Hall, London

Ylönen H, Eccard JA, Jokinen I, Sundell J (2006) Is the antipredatory response in behaviour reflected in stress measured in faecal corticosteroids in a small rodent? Behav Ecol Sociobiol 60:350–358