

Behavioural, morphological and dietary response of rabbits to predation risk from foxes

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We report on the responses of wild European rabbits (*Oryctolagus cuniculus*) to a reduction in predation risk from red foxes (*Vulpes vulpes*) in a predator removal experiment in montane Australia. Specifically we tested whether rabbits in two sites with reduced fox numbers moved further from refuge than rabbits in two sites with abundant foxes. We then compared diet quality by analysing stomach contents, gut morphology and age-specific body mass to determine if release from predation risk enables rabbits to access higher quality food and hence attain higher body mass and condition.

During spotlighting on three quarterly surveys in 1994–1995, rabbits in fox removal sites were observed, on average, three times further from refuge compared to rabbits at sites with foxes. However, this freedom to forage far from cover did not translate into a higher quality diet. Analysis of the nitrogen and neutral-detergent fibre content of stomach samples taken from a shot sample of rabbits at their peak densities after fox removal showed no differences in short-term diet quality of male or female rabbits due to fox removal. In contrast, analyses of gut morphologies, which reflect long-term fibre intake, suggested that rabbits in removal sites fed on a diet higher in fibre and hence of lower quality. This was possibly due to the large increases in rabbit density associated with fox removal. Despite this, male rabbits in fox removal sites were heavier for their age, had longer intestines, and heavier stomach and gut contents. We suggest that rabbits in fox removal sites compensated for the lower quality diet by increasing intake which enabled them to maintain higher age-specific body mass but only because predation risk was reduced. This result highlights the untenable link between resource limitation and predation risk.

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The net result of predator impact is usually measured as population growth following predator removal (Norrdahl and Korpimäki 1996, Banks et al. 1998). Predator impact is likely to be a function of both direct (lethal) effects of predation, and indirect (sub-lethal) effects of avoiding or reducing predation risk (McNamara and Houston 1987, Sinclair and Arcese 1995). Most often, it is access to food that is restricted by the risk of being eaten, and the implications of predator avoidance behaviour on individuals and populations have been extensively reviewed (Lima and Dill 1990, Ylönen 1994). The most significant impacts for mammalian prey are decreased body mass (Saarikko 1992, Hik 1994) and

condition, and as a consequence, decreased fecundity (Korpimäki et al. 1994) and survivorship (Rohner and Krebs 1996). The immediacy of mortality by predation may outweigh the problems of energy gain so that prey overestimates the risk of being eaten at the expense of accessing food (Abrams 1994). Ultimately though, animals are expected to balance their level of energy intake with the risk of being eaten in order to maximise individual fitness (McNamara and Houston 1987).

Sub-lethal effects of predation on population dynamics have a strong theoretical basis (e.g. Ives and Dobson 1987, Abrams 1989, 1990a, b, 1992, 1993), but are supported by limited empirical evidence, particularly

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for terrestrial vertebrates. Moreover, the relative contributions of lethal and sub-lethal impacts of predation to population dynamics are difficult to measure (Hik 1995). Numerous studies have demonstrated shifts in habitat use by prey species in response to predation risk (Desy et al. 1990, Lima and Dill 1990, Dickman 1992, Bowers and Dooley 1994). However, only recently has the link to population dynamics been demonstrated (Hik 1995, Sinclair and Arcese 1995).

In this paper we investigate the potential for risk-sensitive food limitation on the European rabbit (*Oryctolagus cuniculus*) in Australia. The population dynamics of rabbits may be influenced strongly by predation (Wood 1980, Jaksic and Soriguer 1981, Andrewartha and Birch 1984, Newsome et al. 1989, Trout and Tittensor 1989). Once released from predation pressure, rabbit populations increase rapidly (Newsome et al. 1989, Banks et al. 1998) and survival of young increases as mortality due to predation declines (Richardson and Wood 1982, Newsome et al. 1989). However, the indirect effect of predator avoidance behaviour on the suppression of rabbit populations has not been considered.

Individual rabbits appear to respond to predation risk by restricting their foraging activities to the neighbourhood of protective cover (Wheeler and King 1985a), and once disturbed, rabbits retreat rapidly to refuge (Kolb 1994, P. Banks pers. obs.). Where predation pressure is low, rabbits make greater use of open habitats (Jaksic et al. 1979, Jaksic and Soriguer 1981) and forage during daylight when risks would ordinarily be highest (Fraser 1992). Simonetti and Fuentes (1982) suggested that, as juveniles, rabbits stay close to cover, making greater use of open habitats as they grow older, but only when there is little exposure to predators (see also Vitale 1989). Importantly, adults may show seasonal shifts in habitat use depending upon predation risk and energy requirements (Kolb 1991a, b).

Risk-sensitive foraging behaviour by rabbits may result in indirect food limitation, as rabbit populations are frequently limited by food (Williams et al. 1995). Changes in gut morphology partly compensate for diets lower in quality (higher in fibre) (Sibly et al. 1990). However, shortages of high quality food can limit growth and body condition, restrict the length of the breeding season, and reduce the mean fecundity of females and the survival of young, both before and after weaning (Parer 1977).

In this paper, we use a predator removal experiment to investigate if rabbits respond behaviourally to the presence of foxes, and to explore the implications for individual rabbits and their population dynamics. In doing so we test three key predictions of the predation-sensitive foraging hypothesis (Hik 1995, Sinclair and Arcese 1995). If rabbit foraging is sensitive to the risks of predation, then:

Prediction 1: rabbits will forage closer to refugia where foxes are present than where they have been removed (risk-sensitive foraging behaviour);

Prediction 2: restricted foraging behaviour will result in differences in the quality or quantity of food eaten by rabbits (risk-sensitive food limitation). Where predation risk is high, the quality of food eaten will be low. This will be reflected in the short term as poor dietary quality, and in the long term in changed morphology of the gut; and,

Prediction 3: increased foraging opportunity resulting from a reduction in predation risk will result in rabbits being larger, heavier, and more fecund.

Materials and methods

Study area and removal experiment

The study was conducted in Namadgi National Park, an area of montane forest and repossessed open grassy farmland in the Brindabella Ranges, 50 km south of Canberra, Australia. We chose four valleys, each approximately 10 km² in area and separated by 7–22 km of mostly sclerophyllous forest. We assumed that these distances provided some barrier to fox movement and hence independence between sites. Rabbits were most common in the ecotone between the forest and the open grassy valley floor, and were the main mammalian prey of foxes in the area (>40% by occurrence) (Banks 1997). Foxes were prevalent throughout the area.

Details of the fox removal experiment are described by Banks et al. (1998). In summary, a persistent campaign of 1080 baiting in two sites (Boboyan and Grassy) commenced in July 1993 and reduced fox abundance from 2.8 and 3.4/km (spotlight counts) to less than 0.5/km within six months, and to almost zero for the next 12 months. Fox density in the two non-removal sites (Orroral and Glendale) remained relatively stable over this period and was typically five times higher than in fox removal sites. In response to fox control, rabbit numbers in removal sites doubled within 12 months and increased to 6.5 and 12.0 times their original densities by February 1995 when fox control ended. In non-removal sites, rabbit numbers remained suppressed over this period, at densities comparable to initial levels in fox removal sites.

Rabbit movements

For many lagomorphs, the risk of being detected and caught by a predator increases with distance from refuge (Kolb 1994, Rohner and Krebs 1996). Therefore, we used the distance that animals moved from cover to forage as the critical measure of the level of predation risk that the animal perceives (Gilliam and Fraser 1987; see also review in Lima and Dill 1990). We assumed that foraging was the main activity in these exposed areas (Gibb et al. 1978).

We conducted spotlight surveys for rabbits at each site using a 100-W spotlight from a vehicle moving at less than 5 km/h along 5-km transects. Surveys were carried out at dusk for 3–4 nights during August and November 1994, and January 1995. These dates covered the pre-, mid- and near-peak in rabbit numbers over the 1994–1995 summer (Banks et al. 1998). We estimated by eye the distance that rabbits moved from a potential refuge. Refuge from foxes was considered as warrens (Andrewartha and Birch 1984, Small and Keith 1992), the forest edge, large boulder stacks, or substantial vegetation clumps (Kolb 1991a, P. Banks pers. obs.). Flagged stakes at known warrens facilitated their detection at night, and we placed other stakes at 10-m intervals from the centre of warrens to train observers to estimate within 5 m the distances rabbits moved from refuge. When the spotlight approached, rabbits became alert and erect before retreating to refugia, making it easy to estimate the distance they fled. We recorded only the minimum distance that the observed rabbit was first seen from the nearest refuge.

Sampling the rabbit population

To determine if any anti-predator behaviours influenced the food intake of rabbits, and hence body condition, we took a shot sample of 17–25 adult rabbits from each site during February 1995. Sampling of the rabbit population in this way was considered unbiased and essentially random, as rabbits were shot when encountered, with no more than two rabbits taken from any one warren. Shooting took place in the two hours after dusk when rabbit activity is greatest (Parer and Price 1987), and the time the animal was shot was recorded. Each rabbit was sexed, measured for foot length then weighed before dissecting out the liver, spleen, kidneys, and digestive tract which were weighed separately to the nearest 10 mg.

Short-term diet quality

If, in the time before being shot, rabbits in areas with different numbers of foxes were feeding on different quality foods, stomach content samples should contain differing levels of fibre and nitrogen. The measures of dietary quality in the stomach contents used were neutral detergent fibre (NDF) and the total nitrogen content of digesta.

Chemical analyses

Samples of ingested food were extracted from the stomach contents of shot rabbits, avoiding caecotrophes and any material contaminated by residue from the stomach

wall tissue, which may have inflated nitrogen levels. The sample was then oven dried at 50°C to constant mass. Total nitrogen (% of dry matter) content was measured using the semi-micro Kjeldahl method of Clare and Stevenson (1964) with a selenium catalyst. The NDF content of each stomach sample was determined using the method of VanSoest and Wine (1967).

Long-term diet quality and gut morphology

For many small mammalian herbivores in the laboratory, decreases in diet quality (increase in fibre content) result in changes in gut morphology, particularly increases in the length and volume of the caecum (Smith et al. 1980, Alexander 1991, Bellier and Gidenne 1996). Similar seasonal changes in gut morphology also occur in wild rabbits (Sibly et al. 1990), voles (*Microtus ochrogaster*) (Gross et al. 1985) and snowshoe hares (Smith et al. 1980). Thus, if rabbits in areas without foxes fed on a different quality diet, over time this should be reflected in a change in gut morphology.

The entire gut of each rabbit was dissected into stomach, small intestine, caecum, proximal colon and distal colon, and then measured to the nearest half centimetre before being weighed with contents. The contents were removed and the empty segment flushed clean with water before re-weighing. Each compartment was then oven dried to constant mass at 45°C over 12 d.

Body condition

We used age-specific body mass as a measure of body condition as it directly relates to reproductive output (Gibb et al. 1978, Gibb 1981, Cooke 1982). The average mass of the left and right eye lens was used as an index of rabbit age (Wheeler and King 1980). Eyes were dissected within one hour of the animal being shot, then fixed in 10% formalin for 7 d. Lenses were then oven dried at 80°C for 5 d to constant mass, and weighed to the nearest µg as quickly as possible, as dried lenses are highly hydrophilic (Wheeler and King 1980). As an additional index of condition, we used the amount of fat surrounding both kidneys scored on a scale of 0–5 where 0 represents no kidney fat and 5 represents the kidney completely covered in fat (Koivunen et al. 1996).

Statistical analyses

Although there are likely to be some advantages of group foraging, individuals make unique foraging decisions based on their perceived risk of predation (Clark and Mangel 1984). Therefore, we used the responses of

individual rabbits as independent replicates in the experiment. For movement responses, we compared the distances that animals were observed from refuge in sites with and without foxes using a nested ANOVA with sites treated as nested variables. As rabbit density changed in two sites due to fox removal (Banks et al. 1998), we analysed results from each survey separately and chose, at random, data from only one night per survey for analysis in order to minimise confounding. To ensure that observations were independent, we considered animals further than 50 m apart as separate, and where the distance was less than 50 m, the minimum distance to cover was used. Juveniles or kittens were excluded because of their tendency to remain close to warrens at all times (Simonetti and Fuentes 1982). Bartlett's tests revealed heterogeneous variances between treatments which could not be removed by transformation (Sokal and Rohlf 1995). ANOVA is robust to moderate violations of this assumption (Underwood 1981, Day and Quinn 1989); however, the results should be interpreted with some caution.

For short-term diet quality, we used the same nested ANOVA design to analyse differences in nitrogen and NDF of gastric digesta of rabbits in sites with and without foxes. Data for % nitrogen were arcsine transformed, but most NDF values were between 30 and 70% and transformation was therefore not necessary (Sokal and Rohlf 1995). For long-term diet quality, we performed ANCOVA on the lengths, wet contents mass and dry tissue mass of each rabbit gut segment, testing for changes in the relative sizes of gut segments (Gross et al. 1985). The covariates were total gut length, body mass and total dry mass of the gut, respectively. The relationship between the variables and their covariates was confirmed as the best predictor of each measure of gut morphology using linear regression. To determine if rabbits were heavier for their age due to the removal of foxes, we performed ANCOVA on body mass using eye lens weight as the covariate. We kept sexes separate for the analyses to avoid the possibility of uninterpretable interactions complicating tests for the main effects.

Data were checked for homogeneity of variances before analysis using Bartlett's test for unbalanced data sets. We tested heterogeneity of slopes of the covariates

by incorporating an interaction term between the treatment effect and the covariate. Where this interaction term was not significant at $P = 0.05$, it was removed from the final analysis. In all analyses, if the variation due to the nested component was not significant at $P > 0.25$, the mean squares and degrees of freedom for the nested factor were pooled with those of the main effect (Sokal and Rohlf 1995). All analyses were performed using the JMP statistical package (SAS Inc. 1995).

Results

Movements

Rabbits in areas without foxes were observed, on average, more than three times further from refuge than rabbits in sites with foxes (Table 1); differences were significant in all time periods. As expected, variance was greatest in sites without foxes, as rabbits were observed both on warrens and up to 210 m from cover. Nonetheless, a higher proportion (50–75%) of rabbits was found within 20 m of cover in areas with foxes. In contrast, in fox removal sites, typically > 75% of animals were observed 20–100 m from cover (Fig. 1). This general pattern did not change as rabbit density increased after fox removal.

Short-term diet quality

Diet quality, measured by NDF and nitrogen content of gastric digesta, differed between sites but not treatments (Fig. 2a, b). Neither measure of diet quality correlated with age, sex, weight, hind-foot length, gut length or gut tissue mass. However, stomach contents of males at Grassy had a higher NDF content than of males at any other site ($F_{2,45} = 3.24$; $P = 0.05$) whereas females at Grassy tended to have less nitrogen than females at any other site ($P < 0.1$). The general pattern suggests that diet quality may have varied between sites, in increasing order Grassy to Orroral, Boboyan, and Glendale.

Table 1. Mean distance (m) rabbits were observed from refuge in fox removal and non-removal sites in Namadgi National Park. Note distances were estimated to the nearest 5 m. SE = standard error; n = number of observations. F -ratios refer to treatment effects only; site differences were insignificant except in November 1994.

	August 1994			November 1994			January 1995		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
- Fox									
Boboyan	60.2	6.5	36	62.5	6.1	36	50.4	7.4	26
Grassy	58.1	6.3	30	52.4	5.4	17	48.6	5.7	14
+ Fox									
Glendale	19.3	2.1	32	29.1	3.0	48	15.5	7.2	10
Orroral	16.8	2.2	12	18.7	3.4	30	6.20	3.7	21

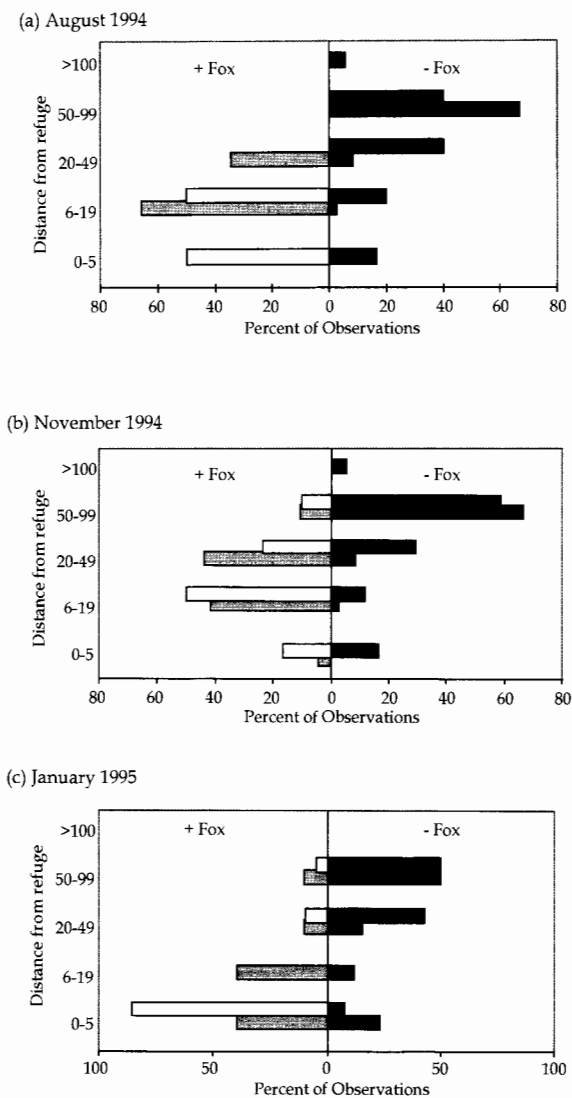


Fig. 1. Percent observations of rabbits at 5 classes of distances from refuge in sites with foxes (clear = Orroral; light grey = Glendale) and without foxes (grey = Boboyan; black = Grassy) in Namadgi National Park. Data collected during the pre- (August), mid- (November) and near- (January) peak phases in rabbit abundance associated with fox removal.

Long-term diet quality and gut morphology

Most differences in the gut morphology of rabbits in areas associated with fox removal were subtle; treatment effects generally differed by less than 30% of the mean and some results were not consistent between males and females (Table 2). For their mass, male rabbits in areas without foxes had 138% more dry matter in their stomach ($F_{1,41} = 3.98$; $P = 0.05$), and 119% more in their small intestine ($F_{1,39} = 22.4$; $P < 0.01$). The small intestine also had a greater dry tissue mass ($F_{1,40} = 5.72$; $P = 0.03$) in rabbits at removal sites. They also had a 6% longer caecum ($F_{1,39} = 25.5$; $P <$

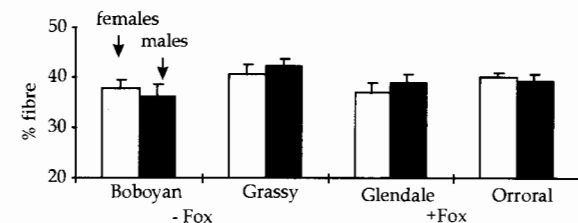
0.01), and 32% more caecal contents ($F_{1,41} = 14.7$; $P = 0.01$) than in non-removal sites. Females in areas without foxes showed the same patterns for stomach contents (56% heavier, $F_{1,32} = 15.5$; $P < 0.01$), and dry tissue mass of the small intestine ($F_{1,30} = 7.17$; $P = 0.04$) and caecum ($F_{1,30} = 5.15$; $P = 0.03$). Total gut length was also 13% and 16% greater at fox-removal sites for both males and females, respectively (males $F_{1,40} = 24.4$; $P = 0.03$; females $F_{1,32} = 36.4$; $P < 0.01$). Some site differences also occurred: Male rabbits in Orroral had heavier and longer distal colons than elsewhere ($F_{2,41} = 3.73$; $P = 0.03$; $F_{2,39} = 5.4$; $P = 0.01$), females at Grassy had the greatest caecum and proximal colon contents ($F_{2,32} = 4.21$; $P = 0.02$; $F_{2,32} = 4.23$; $P = 0.02$), and Glendale had the least.

Condition

Of the 86 rabbits shot at the four sites, 58% were males which limited the information on reproductive output relative to predation risk. However, females in the fox removal sites were significantly younger than animals from the non-removal sites ($F_{1,2} = 31.7$; $P < 0.01$). Ages of males did not differ between sites or treatments. Correlation analysis showed no relationship between the time of night that animals were sampled and age ($r = 0.011$) or body weight ($r = 0.012$).

Males were 9% heavier for their age in sites without foxes ($F_{1,41} = 8.71$; $P < 0.01$) (Fig. 3a). Females showed a similar trend, but several were pregnant or lactating when shot, which led to more variable results (Fig. 3b).

(a) Fibre (NDF)



(b) Nitrogen

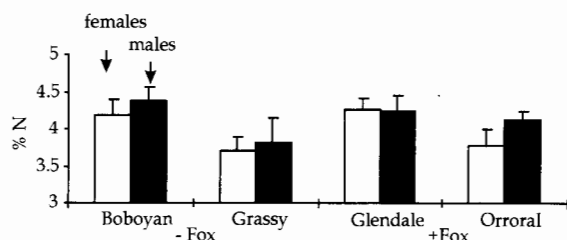


Fig. 2. Mean (± 1 SE) % neutral detergent fibre (NDF) (a), and % nitrogen (b) in stomach contents of rabbits from fox removal and non-removal sites. Shaded bars represent males; clear bars represent females.

Table 2. Mean (\pm SE) dimensions of gut segments from rabbits in fox-removal sites (Boboyan and Grassy) and non-removal sites (Glendale and Orroral) in January 1995, 19 months after fox removal began.

	<i>n</i>	Stomach	Small intestine	Caecum	Proximal colon	Distal colon	Total	
Males								
Length (cm)								
No fox	Boboyan	11	8.9 \pm 0.4	250.6 \pm 9.5	40.5 \pm 1.6	37.6 \pm 1.2	62.5 \pm 2.1	391.4 \pm 5.6
	Grassy	12	8.6 \pm 0.3	251.6 \pm 8.1	41.2 \pm 0.9	39.1 \pm 1.2	66.5 \pm 7.1	395.3 \pm 7.5
Fox	Glendale	13	8.6 \pm 0.4	250.8 \pm 9.0	38.6 \pm 1.0	37.1 \pm 0.9	60.2 \pm 2.7	383.3 \pm 11.5
	Orroral	10	7.3 \pm 0.4	244.3 \pm 7.1	38.1 \pm 1.0	36.6 \pm 0.9	63.7 \pm 1.8	382.7 \pm 6.2
Contents (g)								
No fox	Boboyan	11	50.2 \pm 3.5	14.0 \pm 1.8	62.1 \pm 3.4	30.7 \pm 1.9	5.6 \pm 0.9	163.9 \pm 7.3
	Grassy	12	56.5 \pm 3.8	22.3 \pm 2.0	68.1 \pm 5.2	35.2 \pm 2.2	7.4 \pm 1.1	189.5 \pm 10.0
Fox	Glendale	13	44.7 \pm 3.3	22.0 \pm 2.7	51.9 \pm 3.2	27.3 \pm 2.1	5.1 \pm 1.3	151.0 \pm 9.1
	Orroral	10	39.8 \pm 3.6	15.3 \pm 2.9	46.4 \pm 6.2	22.1 \pm 2.8	9.9 \pm 1.8	144.0 \pm 8.3
Dry tissue mass (g)								
No fox	Boboyan	11	1.91 \pm 0.10	4.40 \pm 1.33	2.34 \pm 0.14	1.50 \pm 0.07	0.91 \pm 0.06	14.12 \pm 1.29
	Grassy	12	2.41 \pm 0.15	3.83 \pm 1.11	2.75 \pm 0.13	1.59 \pm 0.10	1.38 \pm 0.15	16.90 \pm 1.17
Fox	Glendale	13	1.98 \pm 0.12	2.96 \pm 0.82	2.42 \pm 0.26	1.62 \pm 0.12	1.11 \pm 0.13	14.45 \pm 0.75
	Orroral	10	1.74 \pm 0.09	4.31 \pm 1.36	2.06 \pm 0.28	1.33 \pm 0.17	0.91 \pm 0.19	14.70 \pm 1.90
Females								
Length (cm)								
No fox	Boboyan	14	8.7 \pm 0.4	267.8 \pm 10.5	43.1 \pm 0.9	59.0 \pm 3.1	38.8 \pm 1.0	409.3 \pm 13.5
	Grassy	11	9.0 \pm 0.3	256.9 \pm 10.7	41.6 \pm 1.0	65.2 \pm 3.0	39.9 \pm 1.2	403.6 \pm 13.8
Fox	Glendale	7	8.9 \pm 0.3	236.8 \pm 14.2	38.8 \pm 0.9	65.6 \pm 2.4	38.1 \pm 1.1	379.3 \pm 13.9
	Orroral	8	8.2 \pm 0.2	247.6 \pm 13.2	41.6 \pm 1.5	54.0 \pm 4.5	40.0 \pm 1.9	383.3 \pm 18.3
Contents (g)								
No fox	Boboyan	14	59.3 \pm 6.6	25.9 \pm 2.8	74.5 \pm 5.6	36.4 \pm 2.8	5.9 \pm 1.2	201.9 \pm 16.5
	Grassy	11	70.2 \pm 4.8	30.4 \pm 4.5	88.0 \pm 7.7	42.6 \pm 2.8	6.6 \pm 1.1	237.3 \pm 19.1
Fox	Glendale	7	37.3 \pm 3.6	19.5 \pm 3.2	45.3 \pm 4.6	25.5 \pm 1.8	4.7 \pm 0.8	133.8 \pm 12.7
	Orroral	8	45.6 \pm 6.5	28.6 \pm 6.9	69.3 \pm 11.0	34.1 \pm 6.4	5.4 \pm 2.5	183.0 \pm 29.4
Dry tissue mass (g)								
No fox	Boboyan	14	2.31 \pm 0.16	5.75 \pm 0.21	2.64 \pm 0.15	1.80 \pm 0.13	1.46 \pm 0.13	13.98 \pm 0.55
	Grassy	11	2.46 \pm 0.23	5.26 \pm 0.45	2.77 \pm 0.15	1.89 \pm 0.16	1.43 \pm 0.20	13.83 \pm 0.54
Fox	Glendale	7	2.41 \pm 0.26	7.54 \pm 1.13	2.61 \pm 0.28	1.61 \pm 0.10	1.07 \pm 0.09	15.25 \pm 0.76
	Orroral	8	2.14 \pm 0.19	5.64 \pm 0.28	2.79 \pm 0.38	2.01 \pm 0.24	1.19 \pm 0.15	13.84 \pm 0.84

Deletion of these females left too few individuals for a meaningful analysis of the influence of predator removal on body mass. Other morphological characteristics were assumed to be less influenced by reproductive condition but few showed significant differences between treatments. Males had greater pes lengths for their mass at Grassy than at Boboyan, and at Orroral compared to Glendale ($F_{2,41} = 3.17$; $P = 0.05$). Females, however, had greater pes lengths for their mass at removal sites compared to non-removal sites ($F_{1,32} = 35.1$; $P < 0.01$).

Discussion

Prediction 1: Rabbits will move further from refuge where predation risk from foxes is reduced

Rabbits in fox removal areas were observed further from refuge (cover or warrens) than in areas with foxes, thus supporting Prediction 1 and the predation-sensitive hypothesis (Hik 1995). The response was rapid, occurred before the largest population increases and remained consistent throughout the experiment. Predation on other lagomorphs is highest in exposed habitats

(Small and Keith 1992, Hik 1994, Rohner and Krebs 1996), and a similar pattern of mortality would be expected for rabbits preyed upon by foxes, which are most successful in open areas (Small and Keith 1992).

In contrast, Moreno et al. (1996) suggested that rabbits in Spain use open areas at night to avoid predation from predators (including red foxes) which may launch attacks from cover. They rejected the importance of potentially higher resource availability in exposed areas because they considered risk to be lower in these areas, which is contrary to the evidence from our experiment. In Spain, however, foxes are part of a guild of nocturnal, terrestrial predators including mongoose (*Herpestes ichneumon*) and lynx (*Lynx pardanus*), both of which may use cover to approach rabbits by stealth, thus creating higher predation risk close to cover at night. At Namadgi, foxes were the most abundant nocturnal, terrestrial predator, and rabbits appeared to respond to higher predation risk in open areas.

Several factors would have influenced the observed pattern of rabbit movements. Firstly, disturbed rabbits retreat to their warrens and do not emerge for at least 30 min (Vitale 1989). Thus, in sites with foxes, rabbits

that were observed close to refuge would have included individuals that were there because of the lower risks of predation as well as others in the process of emerging after disturbance by predators. Secondly, the strong numerical response of rabbit populations to fox control would have also resulted in many predator-naïve rabbits. Naïve rabbits show little avoidance of simulated predators and emerge from refuge sooner after disturbance than more experienced animals (Vermeij 1982, Vitale 1989).

Changes in rabbit density alone are unlikely to have strongly influenced the observed behaviour. Density pressures can lead to dominant animals forcing subordinates to live and breed on the surface (e.g. Mykityowycz 1960, Cowan and Garson 1985, Kolb 1991b). However, surface dwellers may prefer to live on the surface if suitable cover is available (Kolb 1994), using exposed and closed habitats similar to rabbits inhabiting warrens and escaping to surface refuge when disturbed (Kolb 1994). More importantly though, differences in movement behaviour occurred before the major increase in rabbit numbers (early December 1994), and were consistent between the two removal sites despite their different densities.

Assuming that rabbits are foraging when observed soon after dusk (e.g. Gibb et al. 1978), it can be deduced that fox removal resulted in shifts in the foraging behaviour of rabbits. As rabbits move further

from refuge they increase vigilance behaviour and decrease the time spent feeding (Kolb 1992). For other species, foraging in exposed habitats typically enables individuals to access better quality resources in order to offset the costs of predation risk (Hik 1994, Sinclair and Arcese 1995, Rohner and Krebs 1996). Therefore, did the rabbits at Namadgi at sites without foxes feed upon a higher quality diet than rabbits at sites with foxes?

Prediction 2: Foxes and food limitation of rabbits

There were few differences in the quality of food in rabbit stomachs associated with fox removal, providing no support for Prediction 2; that the presence of foxes lowers the quality of food eaten. Large intra-site differences in the NDF and nitrogen content of gastric contents mitigated against any significant treatment effects. Power analysis indicated that with the sample sizes available, the ANOVA's could have generally detected > 15% differences due to treatment effects. Thus, any differences in short-term diet quality due to the presence of foxes, if they occurred, were subtle.

However, differences in the morphology of rabbit digestive tracts suggest that, in the longer term, rabbits in sites without foxes ate a poorer quality diet. Caecum lengths and contents were 7% and 31% greater for male rabbits in fox removal sites, while female rabbits showed a similar trend with 60% heavier caecal contents (with a site interaction showing that rabbits at Grassy had the heaviest caeca). Poor-quality diets (high in fibre) result in rapid enlargement of the caecum of small hindgut fermenting herbivores (Hoover and Heitmann 1972, Smith et al. 1980, Gross et al. 1985, Virgl and Messier 1992). While an increase in the amount of food eaten may lead to enlargement of the whole gut (Gross et al. 1985, Pond et al. 1988, Sibly et al. 1990), diets high in fibre lead to a proportional enlargement of the caecum, the main site of digest retention in small hindgut fermenters (Hume 1989), while other sections of the gut are less influenced (Sibly 1981, Sibly et al. 1990, Virgl and Messier 1992; but see Hoover and Heitmann 1972).

Nevertheless, the indication of a higher fibre diet in fox removal areas contradicts Prediction 2 that fox removal would allow access to a higher quality diet. This was probably due to the high numbers of rabbits in the fox removal sites (Banks et al. 1998) which may have reduced the availability of high quality forage. Pressure on feeding resources would have been relatively high when the shot sample of rabbits was taken. Grazing pressure by rabbits typically removes the softest, high quality grass first leaving a higher proportion of poorer quality food available (Myers and Bults 1977). This negative feedback from rabbit grazing has not been articulated in terms of declining resource

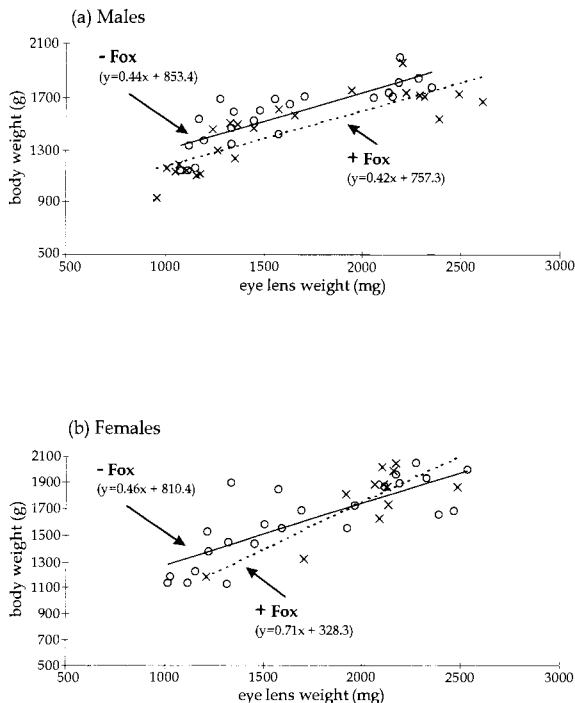


Fig. 3. Relationship between body size and eye lens weight (age) for (a) male and (b) female rabbits, shot in fox-removal sites (○) and non-removal sites (×) with respective (solid and dashed) linear regression trend lines.

quality, but is probably the underlying process in density-dependent food limitation (Wood 1980).

Although diet quality probably differed between treatments, it is not clear if this difference was sufficient to cause energy stress. Bellier and Gidenne (1996) showed that for young rabbits, a 50% increase in dietary fibre resulted in a 25% increase in intake. Similarly, a 30% increase in fibre in the diet of prairie voles (*Microtus ochrogaster*) results in 50–70% greater intake, with animals at lower ambient temperatures having a greater intake still (Gross et al. 1985). Therefore did rabbits in fox removal areas increase their intake of food to compensate for the lower diet quality, or did they simply lose condition?

Prediction 3: Predation risk and rabbit body condition

Male rabbits in fox removal sites were heavier and larger for their age than males in non-removal sites. Young female rabbits also tended to be heavier for their age in fox removal sites. Small sample size notwithstanding, the data generally support Prediction 3, that the presence of foxes reduces body condition of rabbits. Despite a lower quality diet, rabbits in removal sites were able to maintain a higher body condition than rabbits in sites where foxes remained. While it was not possible to monitor the quantity of food eaten under field conditions, rabbits in sites without foxes had significantly heavier contents of the stomach, and greater total gut length relative to body mass, suggesting that animals were indeed eating more. The increased intake probably reflects a response to the lower quality of available food, combined with greater foraging opportunities resulting from fox control. Degus (*Octodon degus*) similarly increased patch residency time in response to a decrease in predation risk (Lagos et al. 1995). While hungry animals will move further in search of feed, there is no reason to suspect that poor diet quality alone should have led to increased intake which resulted in increases in body mass. For example, Gibb et al. (1978) found rabbits spent more time feeding when population density was high, and food quality was lowest, but rabbits were not able to maintain body condition over this period.

Alternatively, rabbits in areas without foxes may have been actively choosing a diet with higher fibre content, but were maximising nutrient and energy intake nonetheless (Schmitz et al. 1992). For example, Sinclair and Smith (1984) found that snowshoe hares (*Lepus americanus*) often avoid some plants with high energy content because they contained high amounts of chemical defence compounds which limit energy assimilation. An analysis of the composition of food available to rabbits compared to that in the diet of rabbits in areas with and without predators would give considerable clarification to the influence of dietary selectivity.

Implications of risk-sensitive foraging for population dynamics

Despite lower resource quality, male (and probably female) rabbits in areas without foxes were able to maintain a higher body condition compared to rabbits in areas with foxes. However, it is not clear how this influenced their survival rates or reproductive output and hence population dynamics. As rabbits in areas without foxes were seemingly under lower food stress, it is likely they had higher reproductive success (Wheeler and King 1985b) and better survival (Wood 1980, Wheeler and King 1985a). Therefore, the data allow the suggestion that not all the increases in rabbit density (Banks et al. 1998) can be attributed to the removal of direct mortality by foxes, and that behavioural responses to predation risk may play an indirect but significant role in population limitation (Sinclair and Arcece 1995).

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