Austral Ecology (2002) **27**, 353–359

Selective predation on the broad-toothed rat, *Mastacomys fuscus* (Rodentia: Muridae), by the introduced red fox, *Vulpes vulpes* (Carnivora: Canidae), in the Snowy Mountains, Australia

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Abstract Since 1981 there has been debate over whether foxes (*Vulpes vulpes* Linnaeus) selectively prey on the broad-toothed rat (*Mastacomys fuscus* Thomas) relative to the bush rat (*Rattus fuscipes* (Waterhouse)). In the present study, three areas of the argument are examined. (i) In a study of fox diet over 3 years at both alpine and subalpine altitudes, *M. fuscus* outnumbered *R. fuscipes* in faecal remains in all seasons, in all years, and at both altitudes. Overall, *M. fuscus* occurred in scats five times as frequently as did *R. fuscipes* in the alpine zone and twice as often in the subalpine zone. (ii) Data from population studies of *M. fuscus* and *R. fuscipes* showed no evidence that *M. fuscus* is trap shy; neither the pattern of captures of individuals caught once, twice and so on, nor the proportion of the estimated population of each species captured during trapping sessions was significantly different. (iii) The suitable habitat for *M. fuscus* within the potential home ranges of foxes contributing to the subalpine fox scat collection constituted approximately 50% of the total area. However, there was no significant difference between the numbers of fox trails encountered in habitat suitable or unsuitable for *M. fuscus* in 19 paired transects skied in winter, indicating no preferential foraging in either habitat. Selective feeding on *M. fuscus* was therefore established, but how that choice is exercised was not determined.

Key words: alpine, diet, preferential predation, snow, subalpine, trap shy.

INTRODUCTION

Selective predation has been documented for a variety of organisms based on the size of prey (Blomberg & Shine 2000; Kloskowski 2000; Ruggerone *et al.* 2000), differences in sex and reproductive condition in a single prey species (Ruggerone *et al.* 2000), and the behaviour of different prey species (Feldman & Savitz 1999). Selective predation has been documented for a number of mammals, including foxes. For example, red foxes (*Vulpes vulpes* Linnaeus) show a clear preference for voles over murine rodents (Macdonald 1977; Jensen & Seqira 1978), and arctic foxes (*Alopex lagopus*) either prefer lemmings (*Lemmus lemmus*) over other small mammals, or forage disproportionately in good lemming habitat (Elmhagen *et al.* 2000). However, since the publication of a paper examining the diet of introduced red foxes and the concurrent local food availability in Australia (Green & Osborne 1981), there has been intermittent criticism of one of the key suggestions of that paper: that foxes exhibited disproportionately higher predation on the less common broad-toothed rat (*Mastacomys fuscus*) than on the more common bush rat (*Rattus fuscipes*).

Support for the findings of Green and Osborne (1981) has come from more recent research within the distribution of *M. fuscus* in New South Wales (Broome 1992; Bubela 1995; Bubela *et al.* 1998), whereas criticism has come mainly from studies conducted in Victoria (Wallis *et al.* 1982; Brunner & Wallis 1986; Menkhorst 1995) but see also Wallis (1992). These criticisms were based on the proposition that *M. fuscus* is more common than trapping suggests. If foxes do not selectively prey on *M fuscus*, then one of two conditions must be met for remains of *M. fuscus* to outnumber those of *R. fuscipes* in fox scats. Either *M. fuscus* is trap shy (Wallis *et al.* 1982) and in fact outnumbers *R. fuscipes* in the wild, or the two prey species differ in habitat use, and foxes prey non-randomly in the habitat preferred by *M. fuscus*. Menkhorst (1995) discounted the suggestion by Green and Osborne (1981) of selective predation on *M. fuscus* on two bases, one of which will be dealt with here. Menkhorst assumed that because 21 of 52 new localities recorded for *M. fuscus* in Victoria between 1972 and 1981 by Wallis *et al.* (1982) were from predator scats, then this indicated that *M. fuscus* was more common than trapping

Accepted for publication November 2001.

suggested. However, the same results could be used to argue a case for selective predation on a prey species in extremely low abundance.

The question of selective predation on *M. fuscus* is important because in Victoria the species is classified as 'rare' (CNR 1993) and in New South Wales as 'vulnerable'. The population at Barrington Tops (NSW) is now classified as 'endangered' and is under severe threat from foxes, which may well have assisted in the reduction in numbers of *M. fuscus* and its replacement by *Rattus lutreolus* (Gray) (Green 2000). However, Seebeck (1995) regarded *R. fuscipes* as 'widespread and common in suitable habitat' and stated that it 'may, in fact, be the most abundant native small mammal in south-eastern Australia.' The present study addresses three areas of the argument. Is greater predation on *M. fuscus* than *R. fuscipes* more general than in the study by Green and Osborne (1981)? Is *M. fuscus* trap shy? Within the foraging area of foxes, is the occurrence of *M. fuscus* habitat significantly higher than that of *R. fuscipes* or do foxes concentrate their foraging within this habitat?

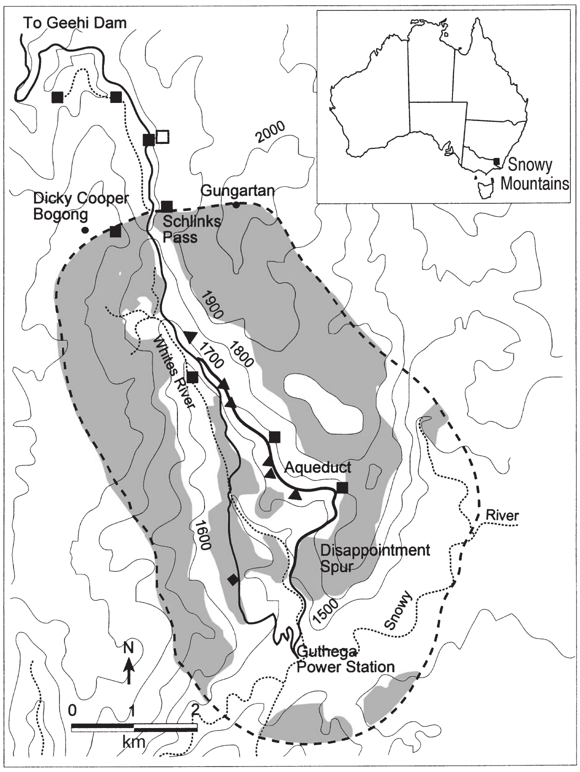

Fig. 1. Subalpine fox transect and surrounding study area. Trapping sites are from: (▼) Calaby and Wimbush (1964); (■) Green and Osborne (1979); (□) Green and Osborne (1981); (◆) Carron (1985); (▲) Sanecki (1999). The dashed line is situated one fox home range length (based on Bubela 1995) from the scat collection transect (solid line on Disappointment Spur and Aqueduct). Broad vegetation classifications within this line are heathland and grassland (shaded) and woodland (unshaded).

METHODS

Scats

The study area was located in the Snowy Mountains of New South Wales, Australia (Fig. 1). One subalpine transect for collection of fox scats ran mainly through woodland along a four-wheel-drive track from approximately the 1500-m contour on Disappointment Spur, then followed a Snowy Mountains Hydro-electric Authority aqueduct at 1600–1650 m to the junction with the Guthega Power Station–Geehi Dam gravel road (Fig. 1). This constituted a part of the study transect used by Green and Osborne (1981). A second, alpine, transect was on the gravel road between Charlottes Pass and the summit of Mount Kosciuszko (2228 m), with the scat collection area running from the summit, through alpine vegetation, to the treeline (1840 m) approximately 1 km from Charlottes Pass. Scats were collected at the end of each month. Foxes still used the subalpine transect when it was covered by winter snow because it provided an easy route through the trees, so winter scat collection was possible. However, with snow cover in the alpine zone, there was little benefit to foxes in travelling on the sites of summer tracks; the dispersed nature of the foxes' movements, combined with greater frequency of drifting snow than on the subalpine transect, made regular scat collection difficult either on or off the alpine transect. Consequently, few winter scats were collected in the alpine zone. Data for the occurrence of *R. fuscipes* and *M. fuscus* in scats were derived from these transects (K. Green, unpubl. data) and published sources (see Table 1) and were compared using a paired Student's *t*-test. The seasonal occurrences of *R. fuscipes* and *M. fuscus* in scats were arcsine transformed and compared for both the alpine and subalpine transects using a paired Student's *t*-test.

Trapping

Data for the occurrence of *R. fuscipes* and *M. fuscus* in traps within the study area and within Victoria were derived from published and unpublished sources (see Table 2 for details), and were compared using the paired Student's *t*-test. For statistical analysis, the data from Happold (1978) were not used because figures were for percentage of total animals caught, which could not be converted to numbers of animals. For studies where a range is given in Table 2, comparison was between the highest occurrence of each species. For subalpine altitudes in New South Wales, only those trapping sites within one average home-range length (MCP) for a red fox (Bubela 1995) of the transects used by Green and Osborne (1981) and K. Green (unpubl. data) for scat collection were considered. See subsequent discussion for further details.

Trappability

An 80-trap grid over 2 ha at Smiggin Holes (6 km south of the subalpine transect used in the present study) was trapped over the period February 1978 to May 1980 (Carron 1985) and between November 1995 and March 1996 (Hill 1996). This trapping grid has been used during a number of studies of *M. fuscus* (Carron 1985; Happold 1989; Bubela *et al.* 1991; Bubela & Happold 1993; Bubela 1995; Hill 1996; K. Green, unpubl. data; D. Happold, unpubl. data). Two approaches were taken in order to determine whether *R. fuscipes* and *M. fuscus* were equally trappable. The distribution of the number of individual *R. fuscipes* and *M. fuscus* caught once, twice and so on was compared for two studies (Carron 1985; Hill 1996). Using mark–recapture data from Carron (1985), estimates were made of the population of *R. fuscipes* and *M. fuscus* (Jolly 1965; Seber 1965). The proportion of the estimated population of *R. fuscipes* and *M. fuscus* captured by Carron (1985) during trapping sessions was arcsine transformed and compared using Student's *t*-test, with 14 paired estimates.

Habitat

The home ranges (minimum convex polygon; MCP) of eight foxes, radiotracked by Bubela (1995) from October 1990 to May 1991, between the subalpine and

Table 1. Occurrences of *Mastacomys fuscus* and *Rattus fuscipes* in predator scats in the Snowy Mountains, New South Wales, and various locations in Victoria (V)

Study	Location	No. scats	*M. fuscus*	*R fuscipes*	Ratio
Green and Osborne (1981)	Snowy Mountains	1159	108	88	1.22:1
Bubela (1995)	Snowy Mountains	272	12	6	2.00:1
Broome (1992)	Snowy Mountains	197	55	33	1.67:1
K. Green, unpubl. data (alpine)	Snowy Mountains	613	195	41	4.76:1
K. Green, unpubl. data (subalpine)	Snowy Mountains	1859	395	180	2.19:1
J. Seebeck, pers. comm.	Bellell Creek (V)	59	6	7	0.86:1
Brunner and Wallis (1986)	Near Powelltown (V)	576	18	19	0.95:1
Brunner *et al.* (1977)	Sherbrooke Forest (V)	1265	51	164	0.31:1
Bertuch (1975)	Sherbrooke Forest (V)	263	8	26	0.31:1
Wallis *et al.* (1982)	Sherbrooke Forest (V)	94	4	20	0.20:1
Brunner *et al.* (1977)	600–700 m a.s.l. near Powelltown (V)	359	75	65	1.15:1

Table 2. Trap data for *Mastacomys fuscus* and *Rattus fuscipes* within the present study area (subalpine and alpine sites in New South Wales) and in Victoria

Location and author	No. trap nights	*M. fuscus*	*R. fuscipes*
Subalpine			
Whites River, Schlinks Pass[1]	680	7%	91%
Whites River[1]	220	5%	64%
Aqueduct, three sites[2]	148	0	20
Schlinks Hut, 14 sites[2]	1312	17	264
Schlinks Hut, heath[3]	520	0–11.1	0–30.9
Schlinks Hut, woodland[3]	520	0	0–25.0
Horse Camp[4]	960	2–5	30–51
Aqueduct, 5 sites (February) [5]	1400	1	108
Aqueduct, 5 sites (April) [5]	800	0	69
Charlotte Pass[6]	300	6	50
Alpine			
Etheridge Range[6]	210	2	8
Mount Kosciuszko[6]	150	0	3
Wilkinson Valley[7]	3000	73	47
Victoria			
Bunyip Park[8]	2180	59	186
600–700 m a.s.l., near Powelltown[9]	3409	3	56

Data for study 1 (Happold 1978) are percentage abundance of each species, data for study 2 (Green & Osborne 1979) are number per 100 trap nights and for the remainder, data are number of individuals. Where a trapping grid was trapped on a number of occasions, the range of successful trapping is given. [1]Happold (1978), [2]Green and Osborne (1979), [3]Green and Osborne (1981), [4]Carron (1985), [5]Sanecki (1999) [6]L. Broome, K. Green & M. Walter (unpubl. data), [7]Caughley (1982), [8]Macreadie *et al.* (1998), [9]Brunner and Wallis (1986).

alpine transects of the present study, were examined to determine the area around the subalpine scat transect from which prey might be expected to be taken by foxes using the transect. These eight foxes were four adult females, two adult males and two juvenile males. The average maximal length of the home range (MCP) of foxes radiotracked by Bubela (1995) was 2.25 km. A line was therefore drawn at this distance on both sides of the subalpine transect and out from the upper and lower ends (Fig. 1). This allowed for the largest calculable catchment because the situation of a territory straddling the transect was not considered. The area encompassed 39.5 km^2. Based on Bubela (1995), the total area would have provided home ranges for approximately 70 foxes in winter and spring and twice that figure in summer and autumn with the addition of cubs. Aerial photographs were used to delineate woodland and non-wooded habitats. To ground-truth the resulting map, 93 sites located by stratified random sampling were examined for the type of vegetation supported. Additionally, at all sites visited, searches were made for scats of *M. fuscus* (see Wallis 1992) to determine whether the habitat was, or had been, occupied by *M. fuscus*. The search began at the most likely site within a 100-m radius of the chosen location and searches were terminated after 10 min of searching if no scats were found. Scats of *M. fuscus* are easily distinguished from those of sympatric species and, with an individual producing 200–400 scats per day and scats lasting for up to 5 years, searches for scats are a quick method of determining use of the habitat by *M. fuscus* (Happold 1989). In a study of the broader distribution of *M. fuscus,* K. Green (unpubl. data) found that of 223 sites searched, scats were found within 5 min in 185 of 189 sites where the presence of *M. fuscus* was confirmed.

Distribution of foraging effort by foxes

The distribution of foraging effort by foxes between woodland and treeless areas was investigated during winter 2000. Nineteen pairs of transects covering most of the subalpine study area were skied, with one transect of each pair in woodland and the other in adjacent treeless areas. All fox trails that crossed the

Table 3. Frequency of occurrence (%) of *Mastacomys fuscus* and *Rattus fuscipes* in scats collected seasonally in the Snowy Mountains

		Alpine		Subalpine	
Year	Season	*M. fuscus*	*R. fuscipes*	*M. fuscus*	*R. fuscipes*
1996	Summer	18.8	2.4	14.3	8.3
	Autumn	13.3	0.7	20.3	9.8
	Winter			53.3	16.7
	Spring	56.3	12.5	14.3	3.8
1997	Summer	34.7	1.4	18.2	3.7
	Autumn	20.6	2.9	14.1	9.0
	Winter			52.8	25.9
	Spring	52.6	26.3	21.5	12.4
1998	Summer	52.5	10.2	16.8	6.9
	Autumn	38.0	13.0	23.9	10.3
	Winter			46.2	15.4
	Spring	57.4	12.8	25.6	13.7

Table 4. Distribution of the capture rates of individuals of *Mastacomys fuscus* and *Rattus fuscipes* at Smiggin Holes

	Carron (1985)		Hill (1996)	
Times individuals captured	*M. fuscus*	*R. fuscipes*	*M. fuscus*	*R. fuscipes*
1	25	23	27	24
2	13	13	12	20
3	12	9	8	12
4	8	10	12	12
5	4	14	3	8
6	7	4	6	5
7	3	1	1	1
8	2	2		
9	5	1		
10+	8	8		
Total	87	84	69	82
Statistics	$G^2 = 11.383$, $P = 0.25$, d.f. = 9		$G^2 = 4.332$, $P = 0.63$, d.f. = 6	

transect and then disappeared from sight were counted. Trails that criss-crossed the transect were only counted once. The numbers of fox trails encountered for the pairs of transects were compared using Student's paired *t*-test. Fox trails encountered on the interface between woodland and treeless areas were not counted.

RESULTS

Scats

The proportion of *M. fuscus* and *R. fuscipes* in 6500 predator scats collected over nine studies ranged from 0.2:1 to 4.8:1, with the higher ratios in the Snowy Mountains and at higher altitudes (Table 1). The difference overall was not significant ($P = 0.3628$, $t = 0.9534$, d.f. = 10). In 2453 fox scats collected for 3 years on alpine and subalpine transects in the Snowy Mountains, *M. fuscus* occurred more commonly than *R. fuscipes* in all seasons (Table 3). The difference was significant for alpine ($P < 0.001$, $t = 6.6732$, d.f. = 8) and subalpine samples ($P < 0.001$, $t = 4.9853$, d.f. = 11).

Trapping

In all studies but one, *R. fuscipes* outnumbered *M. fuscus* in traps (Table 2). The difference overall was significant ($P < 0.05$, $t = 2.9025$, d.f. = 12). The site at Wilkinson Valley to the north-west of Mount Kosciuszko is generally above an altitude of 1900 m a.s.l., and both Caughley (1982) and Hill (1996) trapped more *M. fuscus* than *R. fuscipes* at this site, although numbers in the study by Hill (1996) were minimal.

Trappability

The distribution of captures for individual *R. fuscipes* and *M. fuscus* (Table 4) was not significantly different in 1978–1980 ($G^2 = 11.383$, $P = 0.25$, d.f. = 9) nor 1995–1996 ($G^2 = 4.332$, $P = 0.6318$, d.f. = 6). The proportion of the estimated population of *R. fuscipes* and *M. fuscus* captured during trapping sessions (Table 5) was not significantly different ($P = 0.102$, $t = 1.693$, d.f. = 26).

Habitat

Within the catchment area for the prey of foxes sampled on the subalpine scat transect, the area of 39.5 km^2 contained 17.6 km^2 of woodland, 21.8 km^2 of heath and grass and 0.1 km^2 of other habitat. Much of the heath and grass in the subalpine area was suitable habitat for *M. fuscus*. Although evidence of *M. fuscus* was found within 100 m of most alpine sites, large areas were unsuitable and, based on vegetation mapping by Costin *et al.* (1979), alpine habitat suitable for *M. fuscus* (heath and boulders) probably makes up as little as 27% of the alpine zone.

Distribution of foraging effort by foxes

In all, 19 paired transects totalling 28.3 km were skied in the subalpine study area during winter 2000. The numbers of fox tracks in woodland (169) and adjacent treeless areas (118) when expressed as tracks per kilometre skied were not significantly different ($P = 0.759$, $t = 0.309$, d.f. = 36).

DISCUSSION

Considering the widespread distribution and common status of *R. fuscipes* (Seebeck 1995), the lower level of predation on this species by foxes within the Snowy Mountains relative to predation on *M. fuscus* requires some explanation. However, to account for the lesser predation on *R. fuscipes* than *M. fuscus* simply on the basis of trap shyness, one would have to postulate an average of five times as many *M. fuscus*as *R. fuscipes* in the alpine zone and twice as many in the subalpine zone (Table 3). At alpine altitudes, the greatest disparity in captures of *M. fuscus* and *R. fuscipes* recorded was 1.6:1 (Caughley 1982). At Smiggin Holes, the subalpine trapping grid contains wet and dry heath, with parts of the grid extending into woodland and tussock grassland (Carron 1985). At this site, Hill

Table 5. Percentage of the estimated population of *Mastacomys fuscus* and *Rattus fuscipes* captured during trapping sessions by Carron (1985) at the Smiggin Holes grid

Trapping session	3	4	5	6	7	8	9	11	12	13	14	15	16	17
Population *M. fuscus*	5.4	11.9	10.6	8.2	6.7	5.4	3.8	12.4	16.3	19.7	21.6	28.0	22.6	20.0
Percentage captured	73.7	83.7	94.2	73.6	59.5	73.7	52.6	80.4	79.6	81.2	78.8	67.9	83.9	100.0
Population *R. fuscipes*	25.5	26.0	25.7	17.4	17.3	13.0	9.9	6.4	9.0	13.0	13.7	11.2	13.1	17.2
Percentage captured	86.4	80.9	74.0	63.4	86.7	100.0	90.8	93.2	100.0	84.6	80.5	89.6	76.6	92.9

(1996) found densities of *M. fuscus* of 21.8 ha^{-1} with 12.3 ha^{-1} for *R. fuscipes*, a ratio of 1.8:1. Carron (1985) recorded an average of 1.4:1 for the same site. In five woodland grids along the subalpine scat collection transect used in the present study, Sanecki (1999) found densities of 23.1 ± 3.4 ha^{-1} for *R. fuscipes* and 0.22 $ha^{-1}$for *M. fuscus*, a ratio of 105:1.

Given the low occurrence of *M. fuscus* along the subalpine transect, the high occurrence in scats was probably due to foxes foraging away from this transect. In the area contained within one home-range length of a fox from the subalpine transect, 17.6 km^2 or 44.6% was woodland (Fig. 1). If foxes were to forage randomly throughout this area of woodland and heath then, given the patterns of distribution of the two rodents in woodland and, taking the highest recorded disparity in densities in heath between them of 1.8 :1 from Hill (1996), there would still be a 1.4 times greater chance of encountering *R. fuscipes* than *M. fuscus* (for *R. fuscipes* $0.446 \times 23.1 + 0.554 \times 12.3$, for *M. fuscus* $0.446 \times 0.22 + 0.554 \times 21.8$). The greater predation by foxes on *M. fuscus* rather than on *R. fuscipes* must, therefore, have an explanation other than the accidental choice of a transect where the habitat for the former species predominates.

There are no data to show any significant difference in the behavioural responses of *M. fuscus* and *R. fuscipes* to traps in the present study area (Tables 4,5). However, to confirm that the relative trappability of two species reflects their abundance requires a second independent method of recording individuals. Macreadie *et al.* (1998) suggested that evidence from hair tubes showed that *M. fuscus* was more difficult to trap than *R. fuscipes*. However, unless genetic or other techniques are used, hair samples cannot measure the number of individuals. Wallis *et al.* (1982) suggested that using prebaiting and removal of *R. fuscipes* would improve the trapping results for *M. fuscus*. Wallis *et al.* did, in fact, improve the ratio of animals caught from 0.03:1 to 0.5:1, albeit with a small sample size (303 trap nights). However, at a time of high predation by foxes on the trapping grid used by Hill (1996), when foxes took animals directly from traps, many individually marked *M. fuscus* and *R. fuscipes* disappeared from the grid. These were 'quickly replaced by adults of both species' (Hill 1996). This suggests that if trapping grids are located in preferred habitat, then there is constant pressure from all species to occupy that habitat, and removal of animals of any species may result in immigration by others. This also occurs with *Antechinus swainsonii* (Waterhouse) in preferred habitat in the Snowy Mountains during the autumn when the species suffers a high mortality prior to the formation of the winter snowpack (Green 2001).

If the higher numbers of *M. fuscus* relative to *R. fuscipes* in fox scats generally are neither due to a higher number of *M. fuscus* nor to a greater amount of its preferred habitat within the home range of the foxes contributing to the sample, then the explanation must lie in the behaviour, either of the foxes or *M. fuscus*. In fact, the present study found no concentration of foraging effort by foxes in winter in areas where *M. fuscus* is most common and Bubela (1995) found only a slight bias towards non-wooded habitat in summer (at a time when foxes were feeding mainly on grasshoppers). By contrast, Halpin and Bisonette (1988) found that red foxes in winter snow in eastern Maine concentrated their foraging in open areas inhabited by voles rather than in hardwood forest inhabited by deer mice and shrews.

Two factors may predispose *M. fuscus* to greater predation than *R. fuscipes*. First, *M. fuscus* nests communally in winter beneath the snow, but above the ground (Green & Osborne 1994). Capturing more than one prey at a nest would be energetically more favourable for the fox, especially if digging is required, and might lead to a greater occurrence in scats (particularly if excess prey are cached and eaten later). However, this does not explain the greater abundance of *M. fuscus* in scats in seasons without snow (Table 3). Second, *M. fuscus* is slower and less aggressive than *R. fuscipes* (K. Green, pers. obs.) and may therefore be an easier prey to handle.

Menkhorst (1995) stated that at Bellell Creek near Lake Mountain, trapping results for *R. fuscipes* and *M. fuscus* were similar and they occurred in similar frequency in predator scats. He continued, 'thus discounting selective predation on Broad-toothed Rats'. In fact, the area trapped at Bellell Creek was only approximately 1 ha, surrounded by forest area unsuitable for *M. fuscus* (J. Seebeck, pers. comm., 2001). It is inconceivable that the foxes only foraged in this 1 ha, and to extrapolate the trapping results from this one grid over the entire foraging area of the foxes involved is invalid, and therefore the conclusion of Menkhorst (1995) is without foundation. Brunner and Wallis (1986) quoted data from fox scats and trapping data, and asked 'does the high percentage of *Mastacomys* in predator scats indicate a high population density of a difficult to trap mammal, or does it indicate strong preference by foxes for *Mastacomys* which occurs in low numbers?' The results of the present paper suggest the latter.

ACKNOWLEDGEMENTS

I thank David Happold, John Seebeck and Will Osborne for their discussions and for making critical comment on the manuscript. John Seebeck, Christine Hill, David Happold and Linda Broome provided access to unpublished material. Barbara Triggs identified approximately half of the hair samples.

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