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Diet and habitat selection of the pine marten in relation to competition with the red fox

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After a reduction in red fox *Vulpes vulpes* Linnaeus, 1758 density in south-central Sweden due to an epizootic of sarcoptic mange, which reached the study area in 1982, pine martens *Martes martes* Linnaeus, 1758 became more abundant. By scat analysis and by snow-tracking we compared winter diet and habitat selection of martens before (1979-80) and after (1987) the decline in foxes to test potential effects of relieved competition on martens. We also used radiotelemetry to study habitat selection after the fox decline in winter and in summer. We were able to show that, at least in the winter situation, martens and foxes do not compete over field voles *Microtus agrestis* which are a favoured prey of foxes. Probably snow conditions rather than competition limited the consumption of voles by martens in winter. The avoidance of clearcuts by martens seemed to be related to the martens' escape behaviour and had not changed after the decline in foxes. Our data did not contradict relieved interference- and resource-competition as causes of the increase in the marten population. Our study confirmed the role of the pine marten in the boreal forest as an opportunistic generalist predator which is largely bound to old successional stages.

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Introduction

During recent years the bag of pine martens *Martes martes* Linnaeus, 1758 in south-central Sweden has increased rapidly (Anonymous 1976–1986; Fig. 1). A higher frequency of observations of pine martens and their tracks supports the common notion that the density of the species has increased. During the 1970's, ten researchers of the Grimsö Wildlife Research Station had made a total of six observations of martens in south-central Sweden, but reported 23 observations during the 1980's (1980–88). From snow trackings, we made a tentative estimate of one marten per 10 km^2 in the Grimsö Wildlife Research Area during 1979–80. By 1987, this figure had at least doubled. Simultaneously, an epizootic of sarcoptic mange has caused the density of red foxes to decrease by at least 50% throughout Sweden (Lindström, in print), as also indicated by declining bag records (Fig. 1).

Red fox and pine marten co-occur throughout the Scandinavian boreal forest and show some pronounced differences in habitat and food selection. The fox preys upon

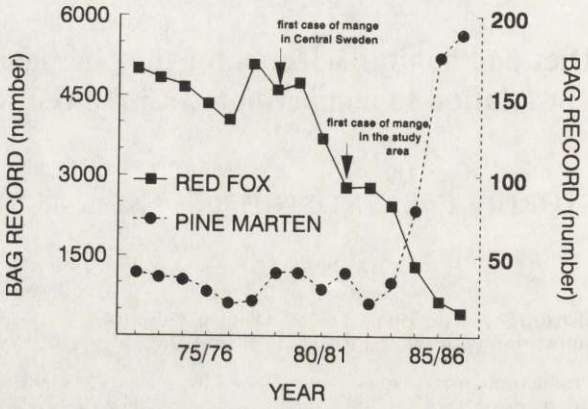

Fig. 1. Annual hunting bags of pine martens and red foxes in south-central Sweden (counties T and U) from 1972/73 to 1986/87 (after Anonymous 1976–86).

the grassland-adapted field vole (Hansson 1978, Lindström 1982). Foxes prefer *Microtus* as prey (Macdonald 1977) and accordingly they select *Microtus*-rich grassland habitat such as clearcuts (Christensen 1985) for hunting. The marten, however, is associated with mature forest and avoids young successional stages (Pulliainen 1981a, Wabakken 1985) regardless of high vole abundance. The forest--dwelling bank vole *Clethrionomys glareolus* is thus taken more frequently by martens than is *Microtus* (Höglund 1960, Pulliainen 1981a, Wabakken 1985).

This niche separation between fox and marten might result from interspecific competition over *Microtus*. Being bigger, the fox can be assumed to be the dominant competitor (see Wilson 1975), limiting prey and habitat availability for martens. Consequently, martens can be expected to gain better access to grasslands and to *Microtus* if the competition was relaxed by a reduction of competitors or by an excess of prey. The latter is supported by a study on the pine marten's American counterpart *Martes americana*: when high microtine populations had developed after forest burns in an area in Alaska, martens utilized these areas and increased in numbers (R.O. Stephenson, pers. comm.).

The natural experiment of sarcoptic mange in foxes offered an opportunity to study the effects of interspecific competition on marten diet and habitat selection. In this paper we address the hypothesis outlined above by testing the following predictions:

1) The martens should feed on *Microtus* more frequently after the fox population had been reduced by sarcoptic mange.

(2) The martens should therefore also use clearcuts more often than before.

To test these predictions, we compare diet and habitat selection during winter before and after the reduction in fox density. We also consider seasonal effects by a comparison of marten diet and habitat selection in winter and summer.

Study area

The study was conducted during two periods, 1979-1980 and 1987, in the Grimsö Wildlife Research Area (14,000 ha; 59°40′N, 15°25′E) in south-central Sweden. The area is situated in the southern boreal zone (Lindquist 1966), and is dominated by coniferous forest in stands of varying successional stages. During the study periods approximately 10% of the area were classified as clearcuts (including plantations up to 1 m height), which ranged in size from a few to 150 ha. Bogs account for almost 20% of the area, farmland for less than 5%. Snow depth measured in mid February was approximately 0.5 m in all years of the study. Sarcoptic mange first occurred during 1982 in the study area, and by 1986 the fox population had decreased to half its former density (Lindström, in print). Vole densities were similar during both periods of study (see Fig. 2) (B. Hörnfeldt, pers. comm.).

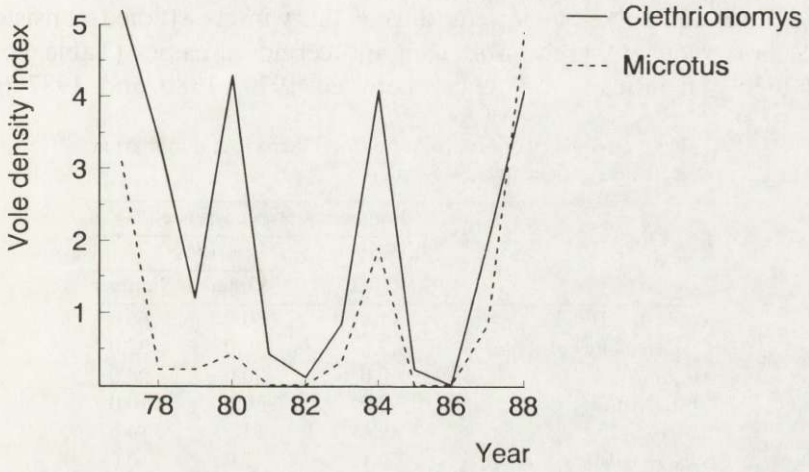

Fig. 2. Spring vole densities (numbers caught per 1000 traps during three nights with daily checking and resetting of traps) in the Grimsö Wildlife Research Area, south-central Sweden (data from B. Hörnfeldt, unpubl.).

Methods

Diet

Marten scats were collected during the two winters (January – March) of 1979 and 1980 (n = 51) and the winter of 1987 (n = 43). We also collected 50 scats in summer (June – July) 1987. Scats were found throughout the study area during snow-tracking, along forest roads, and at resting sites of radio-tagged martens, and were distinguished from fox scats by size and shape. Only scats that could be doubtlessly classified as marten scats were sampled. Food items were identified after drying and frequencies of occurrence were calculated.

Habitat selection

Marten tracks were followed on snow (January – March) for 126.0 (1979 – 80) and 76.3 km (1987). At intervals of 300 m the habitat was determined. The 300-m-interval was chosen because at least one other habitat type lies within this distance from almost every point in the study area. Areas of intensive hunting activity (an intricate network of tracks within a small confined area) were recorded during tracking. The trackings were plotted on forest maps (1 : 10,000). Habitat types were distinguished according to the system

used by the Swedish National Forest Service, which is largely corresponding to succession stages. We determined habitat availability through cross-points of a 250-m-grid laid over the map, considering only those parts of the study area where tracks had been followed. A selection index, the ratio of percent track-points (T) to percent habitat available (H), was calculated as log T/H for each habitat type.

In 1987, we also determined habitat selection of three martens by radiotelemetry. For account of materials and methods in radio-tracking of these martens, see Storch (1988). Also the radio-tracking data were analysed according to the method outlined above.

Results

Diet

The dominating food of martens during the winters studied consisted of red squirrel *Sciurus vulgaris*, shrews *Soricidae* and cervid carcasses (Table 1). The diet exhibited highly significant differences between 1979–1980 and 1987 ($p<0.001$, contingency table test). Shrews and cervid carcasses occurred more frequently during the latter period; red squirrel, which dominated in the diet during 1979–1980, occurred much less frequently in 1987. We found no increase in the use of *Microtus* during winter after the reduction of foxes. Voles, birds, and insects were more important in the marten diet in summer than in winter (Table 1).

Table 1. Frequency of occurrence of food items found in marten scats from south-central Sweden.

Food item	Frequency of occurrence (%)		
	1979-1980	1987	
	Winter	Winter	Summer
Voles (total)	11.8	0.0	66.0
Clethrionomys glareolus	9.8	0.0	32.0
Microtus agrestis	0.0	0.0	24.0
Undet. voles	2.0	0.0	10.0
Sorex spp.	19.6	53.5	14.0
Sciurus vulgaris	50.1	7.0	0.0
Lepus timidus	0.0	4.7	14.0
Lepus europaeus	0.0	0.0	4.0
Cervidae carcasses	15.7	48.8	2.0
Birds	9.8	11.6	30.0
Eggs	13.7	14.0	8.0
Insects	0.0	0.0	24.0
Seeds	0.0	0.0	4.0
n	51	43	50

Habitat selection

Martens in the Grimsö Wildlife Research Area exhibited significant preferences in their choice of habitats. Mature forests were used more than expected, whereas clearcuts were avoided (Table 2). There was no difference in this pattern between the

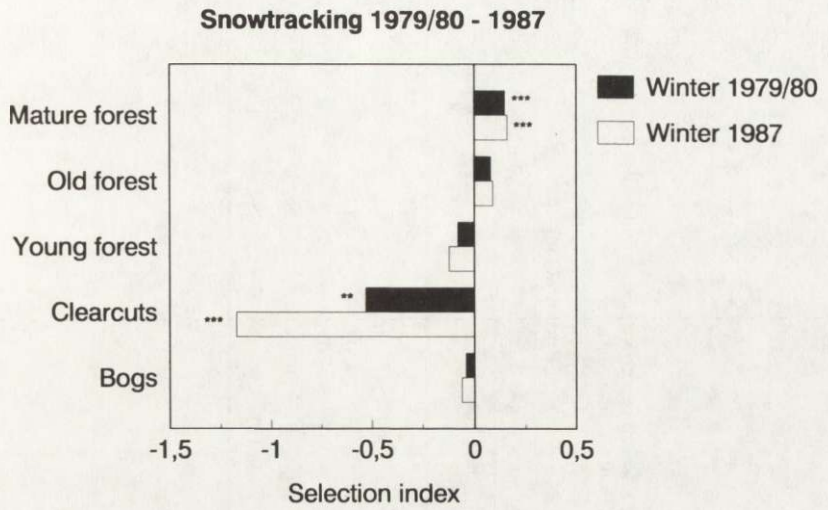

Fig. 3. Habitat selection by martens as determined by snow tracking in winters 1979–80 and 1987. Stars indicate significant preferences and avoidances (Bonferroni-z-test, * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

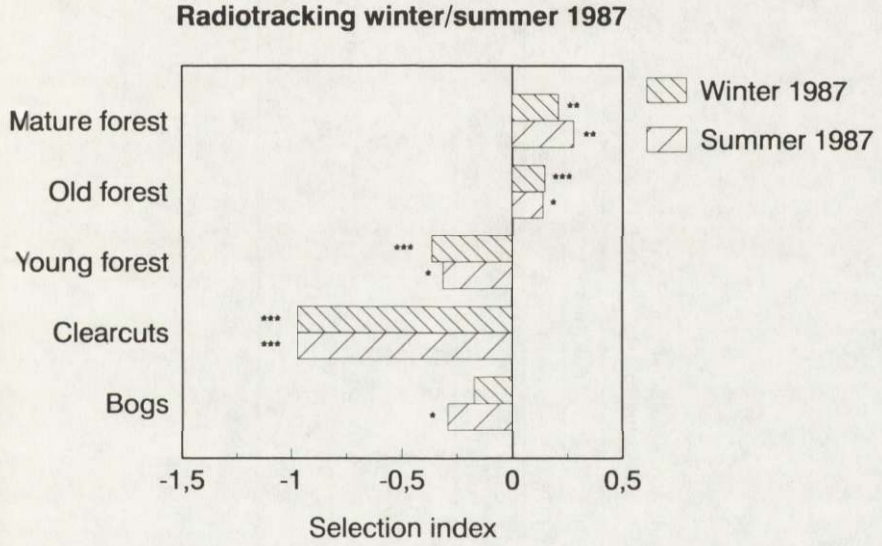

Fig. 4. Habitat selection by martens determined by radio telemetry in winter and summer 1987. Stars indicate significant preferences and avoidances (Bonferroni-z-test, * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

two periods of study (Fig. 3). The areas of intensive hunting activity were almost exclusively found in old and mature forest (34 out of 40 during 1979-1980, and 13 out of 14 during 1987, respectively). Only one area of intensive hunting was found on a clearcut (during 1979–1980).

Radio-tracking of one male and two female martens in winter 1987 (137 locations)

Table 2. Habitat availability and utilization by martens (track points) in south-central Sweden assessed by snowtracking and radiotracking in 1979/80 and 1987, respectively. p – values indicate differences between utilization and availability (Bonferroni-z-test).

Habitat	Snowtracking						Radiotracking					
	1979/80			1987			Winter 1987			Summer 1987		
	habitat %	track points %	*p*	habitat %	track points%	p	habitat %	locations %	*p*	habitat %	locations %	*p*
Mature forest	32	45	<0.01	30	44	<0.001	16	26	<0.01	17	33	<0.01
Old forest	18	22	ns	19	23	ns	40	56	<0.001	37	50	<0.05
Young forest	18	15	ns	19	14	ns	17	7	<0.001	13	7	<0.05
Clearcuts	5	2	<0.01	12	1	<0.001	7	0	<0.001	8	1	<0.001
Bogs	19	17	ns	21	18	ns	14	1	ns	18	9	<0.05
n	521	380		253	254		549	137		287	108	

resulted in the same pattern of habitat selection as obtained by snow-tracking, and we were thus confident in the comparability of the two methods. The two females were also tracked in summer 1987 (108 locations), and habitat selection was the same as in winter (Fig. 4).

Discussion

Diet

The present study confirms the notion of the marten as an opportunistic feeder (see Yurgenson 1947, Höglund 1960, Weckwerth and Hawley 1962, Yazan 1970; Morozov 1976, Danilov and Tumarov 1976, Moors 1980, Pulliainen 1981b) with great between-year variations in diet composition. According to Weckwerth and Hawley (1962), the use of a particular food item is affected by: (1) the availability to the marten, (2) the preference by the marten, and (3) the availability of alternative food. The availability of a food item depends on its abundance, but also on the hunting behaviour of the predator. Hence, an opportunist should choose high quality food which is abundant and easy to obtain. This explains the great variation in the marten diet in a fluctuating environment such as the boreal forest.

The high frequency of squirrels in the diet during 1979 – 1980 was related to a peak in squirrel density, whereas the population experienced a low in 1987 (P. A. Lemnell, unpubl.), when squirrels were rarely eaten by martens. The shrew populations peaked during autumn 1986 and crashed that winter (B. Hörnfeldt, unpubl.). Shrews were presumably obtainable in excess throughout the crash, which could explain their high frequency in the marten diet during this particular winter. The availability of cervid carcasses — notably those of roe deer *Capreolus capreolus* — also varies greatly between winters depending, for example, on snow depth (Cederlund and Lindström 1983). However, cervid (roe deer and moose *Alces alces* mortality was considered as similar during the years of this study (G. Cederlund, unpubl.). Hence, the higher frequency of cervid remains in 1987 might be explained as an effect of relieved competition by foxes.

Our data indicated that at least in winter, martens did not use *Microtus* more frequently after the fox population had declined. This result conflicts with the basic hypothesis that competition by foxes limits the martens' access to this prey. However, it has been argued that field voles are not available to martens during winter, because they spend most of their time under the snow-layer (Powell 1982). Shrews and bank voles spend less time under the snow and are probably easier for a marten to obtain. Koehler and Hornocker (1977), and Hargis and McCullough (1984) suggested that it is too energy-demanding for martens to obtain prey from beneath the snow-cover in open areas. Since the snow-cover in these areas often is deep and crusty, prey can be virtually inaccessible to a marten. Red foxes localize field voles acoustically and pin-point them through the snow after a high leap in the air (see *e.g.* Henry 1986). Martens are presumably too small and not morphologically adapted to use this technique. Thus,

snow conditions rather than competition by foxes probably limits the consumption of *Microtus* by martens in winter.

Accordingly, *Microtus* should be more available to martens in the snow-free season, and competition might be more intense then. We tested this *ad hoc* hypothesis by the sample of 50 marten scats from summer 1987, and voles including *Microtus* were indeed more important in the diet then. Regrettably, there was no comparable data-set from the period of high fox density.

Habitat selection

Our data on habitat selection confirm previous studies on the European pine marten (Pulliainen 1981b, Wabakken 1985) and the American marten (Koehler and Hornocker 1977, Soutiere 1979, Hargis and McCullough 1984, Bateman 1986, Snyder and Bissonette 1987, Thompson and Colgan 1987). Martens avoid clearcuts and prefer mature forests. In accordance with the lack of dietary response concerning *Microtus* to the decreased fox density, at least in the winter situation, martens neither exhibited any change in habitat choice. To test the *ad hoc* hypothesis derived in the discussion above – that competition over field voles was more likely to have prevailed during the snow-free season – we examined habitat choice of two radio-tracked female martens during summer 1987. However, the habitat choice of martens was the same in summer and winter, thus contradicting the prediction of increased use of *Microtus*-rich clearcuts during summer after the decline in fox density.

The pine marten is an opportunistic generalist predator. Compared with the other mammalian generalist predator in the boreal forest, the red fox, the marten's ability to climb trees enables it to feed more frequently on prey species which are bound to the canopy layer such as birds and squirrels. The marten, however, seems to be less well adapted to take field voles during times of deep snow cover than the fox.

In this study, we were able to show that the two predators – at least in the winter situation – do not compete over field voles occurring on clearcuts. Although snow conditions may limit the martens' access to voles, this does not explain why they also avoid vole-rich clearcuts in summer. Thus, the martens' avoidance of open areas has to be explained in other terms.

Although being a predator itself, the marten is small enough to fall prey to several other predators. Its strategy to escape its foes is to climb up in trees, and consequently the marten avoids treeless areas. This also explains why the martens in this study completely avoided clearcuts but not bogs, which provide at least some smaller trees for escape.

The only nocturnal predator which is common in south-central Sweden and which might interfere with martens is the red fox. Foxes occasionally chase or kill martens (Pulliainen 1981b, H. Christensen, pers. comm.), and were found to have a regulating influence on other mustelids (Latham 1952). Hence, the decrease in fox density might have resulted in increased survival of martens and also in better access to food-rich

patches such as cervid carcasses to martens. Thus, the enhancement of marten numbers during recent years in south-central Sweden might still have been ultimately caused by the epizootic of sarcoptic mange in foxes in terms of both relieved interference- and resource-competition, although the predicted change in marten habitat selection did not take place. There are several possible reasons why martens still avoid clearcuts after the reduction of foxes:

(1) Foxes might still be abundant enough to make open areas dangerous for martens. This hypothesis could be tested by a comparison between areas where martens live with and areas where they permanently live without predators. In the latter case treeless areas should be used more frequently by martens.

(2) The five years of reduced fox density may have been too short a period to change marten habitat selection to an already detectable extent. If this is the case, an increase in the use of clearcuts by martens can be expected if fox density remains low for a still longer time.

(3) Also, the behaviour might be genetically fixed, and it could not be changed by a temporary decline in the density of predators as considered here. In this case, martens should avoid treeless habitats regardless of the presence of predators.

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