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Pine marten — red fox interactions: a case of intraguild predation?

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We pursued the hypothesis that pine martens (*Martes martes* L.) suffer from intraguild predation by red foxes (*Vulpes vulpes* L.). An increase in population density of pine martens in Scandinavia was observed concomitant with a decline in the number of foxes due to an epizootic of sarcoptic mange during the 1980s. The increase was noted both as numbers of crossing marten tracks on snow along transects in a local area, and as number of martens harvested in Sweden. The latter could be linked county-wise by timing and amplitude to the occurrence of mange and decline in number of foxes harvested. We also compiled 16 cases of casually observed predation by red foxes on martens, and calculated a yearly mortality rate due to fox predation of 0.13 from >14 transmitter years of 26 radio-collared martens in three areas of Scandinavia during the period of high marten numbers. We conclude that the case against the fox is strong.

1. Introduction

During the 1980s, hunters and naturalists in southern Sweden noted a change in the pine marten (*Martes martes* L.) population. The number of observations of martens increased, and martens were also observed in areas where they previously had been absent (Strömberg 1987, Storch et al. 1990). Simultaneously, the population density of the red fox (*Vulpes vulpes* L.) decreased dramatically due to an epizootic of sarcoptic mange (Lindström 1991). The possibility that martens experienced a relieved competition with foxes was explored by Storch et al. (1990). However, they found no indication that the marten had taken over the food niche of the fox; martens did not utilise field voles (*Microtus agrestis* L.) for food or clearcuts for feeding more often after the decline in foxes than before. Storch et al. (1990) suggested that foxes previously had kept the marten population low by predation rather than by being more efficient foragers.

During recent years, the importance of such intraguild predation has gained increased attention (e.g. Kaikusalo 1982, Korpimäki & Norrdahl 1989, Polis et al. 1989, Stephenson et al. 1991, Doncaster 1992). In particular, Mulder (1990) reviewed several studies where circumstantial evidence pointed at red fox predation as an important limiting factor for populations of small mustelids. The possibilities to observe the event of predation or to manipulate the populations experimentally are small when dealing with elusive animals such as martens and foxes. Still, the credibility of the hypothesis that foxes influence the marten population density negatively by predation would be reinforced if

1) the increase in marten density could be closer linked both in time and in amplitude to the decrease in fox numbers
2) foxes could be shown to kill martens in a significant frequency

In this study we make use of track counts on snow to analyse the change in population density of martens, hunting statistics to test the correlation between the changes in the fox and marten populations, and casual observations of martens found dead as well as data on the fate of radio-equipped martens to evaluate the occurrence of fox predation.

2. Study areas and methods

2.1. Track counts

During December–March 1974–1980 (before mange in foxes) and 1990–1993 (mange epizootic prevalent), marten tracks in snow intersecting line transects were recorded in the southern part of Grimsö Wildlife Research Area within the southern part of the pure coniferous forest belt (Lindquist 1966, south-central Sweden, 59°40′N, 15°25′E). The exact location of the transects varied among years, but they covered in total an area of approximately 30 km^2 mainly consisting of managed mixed coniferous forest and bogs. The distance checked was calculated as actual number of km tracked each day times the number of nights since last snowfall, i.e. nights of marten activity on top of the snow. Most tracking was performed one night, and no tracking more than three nights, after last snowfall.

2.2. Hunting records

The Swedish Sportsmen's Association (1964–1991) reports yearly hunting records as number harvested per county in Sweden. We used these data (except those from the Baltic island of Gotland, which was never struck by mange, and where martens do not occur) for analyses of:

a) the relationship between the year the foxes of each county were first infected by mange, and the year of subsequent increase in the number of martens harvested.
b) the relationship between numbers of martens and foxes harvested after mange had appeared within each county.
c) same as b, but when pooling the counties according to how the number of foxes harvested reacted to the occurrence of mange.

As a starting point, we used the year (year S) when 50% of the county was affected by the epizootic according to Lindström & Mörner (1985). In a), the year of increasing number of martens harvested was arbitrarily standardised as the first year (year I) after year S, when the number of martens harvested amounted to at least three times the previous ten years' average (years I–11 to I–1). In b), we transformed numbers of martens and foxes harvested to ln(x+1) and lnx, respectively (in some cases no martens were reported harvested, hence x+1). Because a time lag in the reaction of the marten population was to be expected [e.g. due to the high age (≥ 2 years) at first reproduction in martens], we tested the number of martens harvested against the number of foxes harvested with a lag of 0–6 years. Only the best correlation is reported. Finally, in order to make figures comparable when combining counties in c), numbers of martens and foxes harvested year S were standardised as 10 and 100, respectively, in each county. These figures approximate the relationship between numbers harvested in the whole of Sweden during the late 1970s.

2.3. Marten mortality

Reports of fox-killed martens were obtained from the literature and by appeals in hunter's magazines etc. We also made use of data on the fate of radio-equipped martens. During 1986–1992, adult-sized (i. e. > 0.5 years old) martens were followed for ≥7 days in Grimsö (n = 16), Varaldskogen (60°10′N, 12°30′E, n = 7), and Trondheim (63°20′N, 10°45′E, n = 3). Additionally, two juveniles were followed during their first summer in Varaldskogen. The Varaldskogen and Trondheim areas are both situated in the boreal zone in Norway, and are dominated by coniferous forest. The epizootic of sarcoptic mange reached the fox populations in all three study areas during the early to mid 1980s (own observations).

3. Results

3.1. Track counts

During the period 1990–1993, 5.4 times as many marten crossings were observed per km checked than during 1974–1980 (Table 1). In a one-tailed Mann-Whitney *U*-test of the sets of annual results, the difference between the two periods was significant at $P = 0.011$ ($n = 7+4$; z corrected for ties = –2.294). Average distance checked amounted to 12.1 ($SD = 5.7$) and 13.0 ($SD = 12.1$) km per tracking day (see methods) during the 1974–1980 and 1990–1993, respectively. The frequency of days with marten tracks was significantly lower during the first period (23 vs 82%, $P = 0.00001$, $\chi^2 = 20.5$, 2×2 contingency table test).

3.2. Hunting records

According to Lindström & Mörner (1985) and Lindström (1991), the initial large-scale spreading of mange was more rapid in the northern, boreal, areas of Sweden, whereas once mange had hit an area, the effect on the population density of foxes was more rapid in the southern, boreo-nemoral and nemoral, regions. Hence, we grouped the counties according to biogeographic region (i.e. roughly above and below 60°N, respectively, see Table 2).

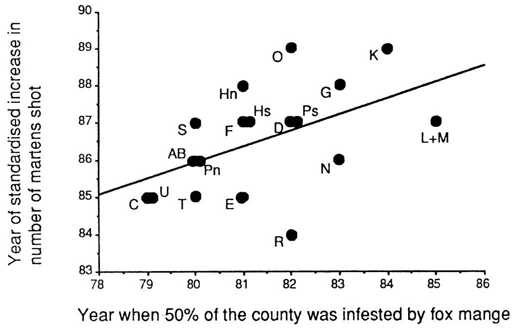

Fig. 1. The year of increase in number of martens harvested, arbitrarily standardised as the first year after the occurrence of mange when the number attained a value of ≥ 3 times the preceding 10 years average, in relation to the year when 50% of the county was included in the area infested by sarcoptic mange in foxes (Lindström & Mörner 1985). County codes as in Table 2. Hunting records from Swedish Sportsmens' Association (1964–1991).

The standardised year of increase in the number of martens harvested (year I) was possible to establish in all counties situated in the boreo-nemoral and nemoral regions, but only in one county of the boreal region. Among the 18 counties where the year I could be detected, this was significantly and positively related to the year S (when mange struck the foxes; Spearman rank correlation, Rho corrected for ties = 2.18, $n = 18$, one-tailed $P = 0.015$, Fig. 1).

Table 1. Frequency of marten tracks crossed while snow tracking transects in the Grimsö Wildlife Research Area during December–March 1974–1980 and 1990–1993.

Year	tracking days	days with tracks	km checked	crossing marten tracks	crossings/ km checked
1974	5	2	52.9	2	0.038
1975	4	0	41.0	0	0.000
1976	6	1	112.1	4	0.036
1977	23	8	301.9	38	0.130
1978	4	0	35.3	0	0.000
1979	7	0	55.8	0	0.000
1980	5	2	56.6	7	0.120
Total period 1	54	13	654.6	51	0.078
1990	1	1	8.0	5	0.630
1991	9	9	65.5	40	0.610
1992	3	1	34.2	3	0.092
1993	9	7	183.7	82	0.450
Total period 2	22	18	291.3	130	0.450

Table 2. Details of the strongest negative regressions between the number of martens and foxes harvested in different counties of Sweden after the year 50% of the county was infested by mange (both variables ln-transformed). The material was tested with 0–6 years of time lag in marten numbers. Nemoral and boreo-nemoral zones (above) separated from boreal zone (below). Hunting records from Swedish Sportsmens Association (1964–1991). Year of mange from Lindström & Mörner (1985).

	County code	*r*	*p* (1-tail)	*F*	*df*	lag
Boreo-nemoral and nemoral zones	AB	–0.92	0.0001	50.6	1/9	2
	C	–0.94	0.0001	73.8	1/10	3
	D	–0.62	0.037	4.50	1/7	3
	E	–0.94	0.0001	66.1	1/8	2
	F	–0.97	0.0001	119	1/8	0
	G	–0.97	0.0001	96.3	1/6	2
	Hn	–0.98	0.0001	241	1/8	3
	Hs	–0.97	0.0001	129	1/8	4
	K	–0.97	0.0002	67.9	1/5	2
	L+M	–0.94	0.003	31.0	1/4	1
	N	–0.88	0.002	20.9	1/6	1
	O	–0.82	0.004	14.2	1/7	2
	Ps	–0.92	0.0002	40.4	1/7	0
	Pn	–0.89	0.0002	32.5	1/9	3
	R	–0.84	0.003	16.9	1/7	2
	T	–0.93	0.0001	57.3	1/9	3
	U	–0.93	0.0001	59.1	1/10	2
Boreal zone	S	–0.91	0.0001	43.6	1/9	1
	W	–0.87	0.0001	35.2	1/11	3
	X	–0.82	0.0002	24.6	1/12	1
	Y	–0.74	0.001	14.2	1/12	3
	Z	–0.85	0.0002	27.5	1/11	1
	AC	–0.66	0.008	8.38	1/11	2
	BD	+	.	.	.	.

Table 3. Account of 16 martens found killed by red foxes. Data collected after appeals in hunters' magazines and from notes in the same magazines.

Circumstances	Number	Sources
Found dead, subcutaneous haemorrhages & marks of fox teeth	5	Rudolf Johansson, Sävsjöström, Lenhovda, S Lars Lövgren, Sävsjön, S Reinhold Virdeskog, S, (Svensk Jakt 1941: 225) Kristian Overskaug, Trondheim (2 cases), N
Fatal fight tracked on snow	6	Lennart Hansson, Uppsala, S Rune Johansson, Limedsforsen, Malung, S (2 cases) Sten Persson, Hemshyttan, Söderbärke, S Verner Olsson, Drevdagen, Idre, S Otto Wibeck, S, (Svensk Jakt 1953: 118)
Warm marten dropped by fox	2	C. G. Gustavsson, Ryd, Skillingaryd, S Sven-Erik Pårs, Delsbo, S
Other, unspecified	3	Daniel Vikström through Torbjörn Lövbom, Burträsk, S Anonymous person to E. R. L. at meeting with Mörbylånga jaktvårdskrets, S (2 cases)

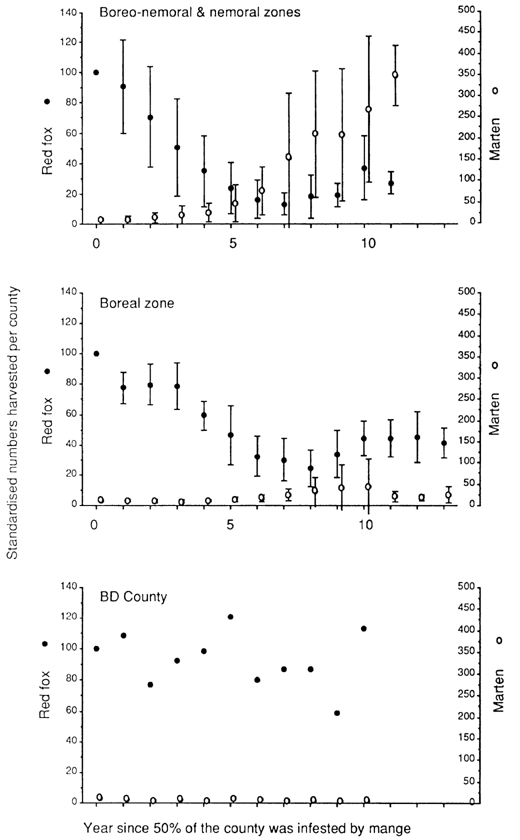

Fig. 2. Average number ± *SD* of martens and foxes harvested per county in Sweden (Swedish Sportsmens' Association 1964–1991) after the arrival of sarcoptic mange (year S = 0 on the x-axis) in the boreo-nemoral and nemoral zones, the boreal zone except BD County (northernmost Sweden), and the BD County. To facilitate comparison, the number harvested when mange hit each county was standardised as 100 foxes and 10 martens. Other figures were recalculated according to this.

The number of martens harvested after mange had struck the foxes was significantly and negatively related to the number of foxes harvested in all counties of mainland Sweden except the northernmost one (BD County, Table 2). However, the average *r*-value was significantly lower in the boreal zone than in the boreo-nemoral and nemoral zones (0.81 vs. 0.91; $t = 2.37$, two-tailed $P = 0.03$). The best correlation was obtained with a time lag of the reaction in marten numbers averaging 2 years. The indication in Fig. 1 of a longer time-lag in the counties first struck by mange than later was not supported by the actual time-lags of the best correlations in Table 2 ($r = 0.09$, $F(1/21) = 0.172$, $P = 0.68$ in a regression analysis of the relationship between year S and time-lag).

The reaction of the average number of martens harvested per county after the occurrence of mange was quantitatively related to the reaction in numbers of foxes harvested (Fig. 2, note that in each diagram fox and marten numbers during year 0 are standardised to 100 and 10, respectively). Here, we have treated the northernmost county (BD, where no negative correlation between numbers of martens and foxes harvested could be discerned) as a group of its own. The strongest effects in both species occurred in the counties of the boreo-nemoral and nemoral regions, whereas there was no reaction in the numbers of either foxes or martens harvested in the northernmost county.

3.3. Marten mortality

We were able to obtain data on 16 cases of fox killed martens distributed over much of the Scandinavian peninsula (Table 3). Thirteen of these were first hand observations by our informers, one secondhand report and two from articles in hunter's magazines. Most (14) concerned adult-sized martens (i.e. > 1/2 yr old), which presumably were detected more easily (e.g. tracks on snow), than cases of juveniles killed in their first summer. The most detailed accounts were from marten tracking on snow. For example, one hunter, who had tracked down a marten to an underground resting site, also observed fox tracks going into and out of the den. Some ten metres away along the foxtrail, he found a marten tail. Another hunter observed the tracks of a fight between a fox and the marten he had been tracking. He followed the fox tracks and found where the fox was laying on top of a large stone. The fox dashed away, but in front of its bed there was a pile of snow within which the dead marten was buried. Yet another hunter shot at a fox which disappeared, but "dropped its tail" as it appeared. Instead, he found a dead marten which the fox had been carrying.

Two of the adult-sized martens we radio-tracked were killed by foxes while the radios were still functioning (Table 4). Both were found buried and uneaten; one with the tail bitten off. In both instances subcutaneous haemorrhages and the size and spacing between tooth marks revealed the culprits to be red foxes. One of the martens (Grimsö 10) was buried in a clearcut over 1 km outside the boundary of its home range, and the moss covering the marten was garnished with fresh fox urine. During tracking at Varaldskogen, 3 instances were observed of red fox trying to get into the underground daybed of an adult radio collared marten. On one occasion the fox camped on the daybed site for a period of two days. In total, we followed martens with radios for more than 14 marten-years. A calculation of the yearly mortality rate due to foxes from these data (Trent & Rongstad 1974) yielded a figure of 0.13. In addition, one out of two marten juveniles followed for a total of 26 days during summer was killed by a fox.

4. Discussion

The alleged increase in the population density of martens during the 1980's was supported by our track counts. This as such did not imply that the increase was caused by the concomitant decrease in the number of foxes. However, we could also establish a qualitative (timing, Fig. 1) and quantitative (amplitude, Table 2, Fig. 2) connection between numbers harvested of each species. It

Table 4. Account of number of tracking days and the fate of adult-sized (≥ 0.5 yr.) radio-collared martens in the areas of Grimsö, Varaldskogen, and Trondheim.

Area	Marten No	Captured	Last contact	Days	Fate
Grimsö	1	87-01-26	87-03-22	55	
	2	87-01-31	87-08-03	184	
	3	87-03-18	87-07-17	121	
	3	91-03-21	91-09-13	176	
	4	88-12-18	89-05-17	150	
	5	88-12-18	89-05-12	145	
	5	89-12-12	90-05-02	141	
	6	89-03-16	89-08-07	144	
	7	89-03-01	89-09-21	204	
	8	89-11-25	90-08-23	271	
	9	89-12-04	90-01-19	46	found dead
	10	89-12-21	90-03-10	79	killed by fox
	11	90-03-15	90-03-29	14	
	12	90-03-16	90-08-15	152	
	13	90-03-17	90-12-18	276	
	14	91-01-18	91-02-07	20	trapped
	15	91-02-01	91-11-14	286	
	16	91-03-06	91-10-16	224	
				Σ 2688	
Varaldskogen	1	90-02-25	91-11-11	624	
	2	90-03-01	91-03-06	370	
	3	90-03-09	90-08-08	152	
	4	90-12-25	91-09-30	279	
	5	91-01-30	91-05-20	110	
	6	91-03-04	91-10-15	225	
	7	91-03-14	91-10-29	229	
				Σ 1989	
Trondheim	1	88-12-04	89-02-25	83	
	2	90-12-08	92-07-12	582	
	3	91-01-03	91-02-09	37	killed by fox
				Σ 702	

should be noted that the population densities of martens and foxes was not equal all over Sweden before the mange outbreak. Hence, we suggest that the extraordinary reaction in the harvest of both species in the nemoral and boreo-nemoral zones may be explained by originally high fox densities concomitant with low marten densities. The time lag of two years in the reaction in number of martens harvested could be caused by the late start of reproduction.

An alternative explanation to the increase in the number of martens harvested is that this was an effect of the hunters' reaction to the decreasing population density of foxes. Assuming that hunters react like any switching predator, this could indeed also have caused the observed changes. On the other hand, prior to the mange outbreak >50% of all foxes harvested were shot at night at baits (Lindström 1982a). Only 20% were taken in traps. Ninety-four percent of all martens were taken in killing traps during 1989–1993 (Helldin, unpubl.). The difference, between sitting and watching in a cold barn for a fox to come to a moon-lit bait in the middle of the night, and setting traps to be checked once a week, is as great as between fly fishing and setting nets. Furthermore, it seems likely that hunters should react also to the general situation in the country, being influenced by reading hunters' magazines etc. During the 1980's the use of killing traps for small furbearers became legal in Sweden and there were many articles on this subject. This campaign certainly increased the interest in marten trapping, but could not explain why the county-wise increase in marten harvests was linked in time and amplitude to the decrease in the number of foxes harvested. Hence, it is not obvious that all fox hunters should have changed to marten trapping two years after foxes became scarce in their areas. However, we do not dismiss the possibility that the increase in marten harvests was amplified by the hunters' behaviour.

Foxes do actively pursue and kill martens as confirmed by our own and other's observations (Tables 3 and 4). We estimated the winter density of martens during the second period in the Grimsö Wildlife Research Area to 2.9 per 10 km^2 (unpubl.). According to the tracking data this was 5 times higher than before the mange outbreak. The increase could have been caused by a relieved yearly mortality rate of approximately 0.15. This can be compared with the observed remaining mortality rate caused by foxes of 0.13. The density of foxes was estimated to 2–4 per 10 km^2 before the outbreak (Lindström 1982b). If previously each fox on average killed 0.054 (= [(2.9/5)*(0.13+0.15)]/3) martens per year (one marten per 18 fox years), this would have been enough to prevent the marten population from increasing. The fact that killing has been recorded at all, makes it not unlikely that the mortality rate of martens due to fox predation may have been substantially higher. On the other hand, this mortality might also have been partly compensatory. Although no final evidence can be presented, we conclude that the case against the fox as limiting marten numbers through predation is strong. Eventually the recovery of the fox population, which now has been possible to observe for some years, will provide the answer. We predict that the marten population density will decrease once again as a response to increased fox densities.

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