Lynx (*Lynx lynx*) killing red foxes (*Vulpes vulpes*) in boreal Sweden – frequency and population effects

J. O. Helldin[1], O. Liberg[1] & G. Glöersen[2]

1 Department of Conservation Biology, Swedish University of Agricultural Sciences, Grimsö Wildlife Research Station, Riddarhyttan, Sweden
2 Swedish Association of Hunting and Wildlife Management, Molkom, Sweden

Abstract

We studied the frequency and pattern of lynx *Lynx lynx* predation on red foxes *Vulpes vulpes* in boreal Sweden by the radio tracking of foxes and the snow tracking of lynx. We also assessed the population trend of red foxes after the re-establishment of lynx in the region, based on various population indices. Fifty per cent of recorded fox mortalities in the radio-tracking study (four of eight) were lynx kills. Adult-sized foxes killed by lynx during radio tracking were in normal condition and of prime age, and were killed after the assumed annual population bottleneck. Albeit based on a small number of kills, this pattern may suggest that lynx predation, at least to some extent, is additive to other mortality in foxes. The annual lynx predation rate was 14% on radio-tracked foxes and 4% on snow-tracked foxes. The population indices of foxes in the main study area decreased by about 10% annually during the study period. The population decrease could potentially be explained by lynx predation alone, but we acknowledge some alternative explanations. Our results point out the possibility that red fox populations can be significantly limited by allowing lynx populations to recover.

Introduction

Interspecific killing among mammalian carnivores (intra-guild predation) is a rare event, because of the generally low population densities of the species involved, and is therefore relatively sparsely reported. However, such killing appears ubiquitous, and has been noted for a variety of species in all major taxa (reviewed in Palomares & Caro, 1999). With the often dramatic changes in carnivore abundance reported from many areas in the world in the last decades (extinctions, reintroductions, re-establishments or boosts), increased attention has been paid to the effects of intra-guild predation on population dynamics and community structure (e.g. Polis, Myers & Holt, 1989; Mulder, 1990; Laurenson, 1995; Palomares *et al.*, 1995; Creel & Creel, 1996; Buskirk, 1999; Crabtree & Sheldon, 1999; Linnell & Strand, 2002). The importance of intra-guild predation for carnivore ecology and conservation has been stressed (Palomares *et al.*, 1996; Palomares & Caro, 1999; Linnell & Strand, 2002; but see Litvaitis & Villafuerte, 1996) and, on the basis of an extensive review, Palomares & Caro (1999) called for studies to quantify its population effects.

Eurasian lynx *Lynx lynx* killing red foxes *Vulpes vulpes* has been sporadically observed in several previous studies of lynx ecology (Haglund, 1966; Dunker, 1988; Sunde & Kvam, 1997; Linnell *et al.*, 1998; Jobin, Molinari & Breitenmoser, 2000; Sunde *et al.*, 2000), and hence appears to be a rare but regular phenomenon. Lynx may leave foxes they

have killed unconsumed (Sunde, Overskaug & Kvam, 1999), and foxes have never been reported to contribute more than marginally to the lynx diet (Haglund, 1966; Dunker, 1988; Sunde & Kvam, 1997; Jobin *et al.*, 2000; Sunde *et al.*, 2000; Moshøj, 2002).

Most observations of lynx predation on foxes have been anecdotal, and few studies have attempted to quantify lynx predation on foxes. A lynx radio-tracking study in the Swiss Jura Mountains is outstanding in this respect (Jobin *et al.*, 2000; Molinari-Jobin *et al.*, 2002), which reported annual kill rates of 1.5 foxes per lone female, 2.3 per lone male, 6.1 per lone subadult and 13.3 per lynx family group, with 4.8 foxes/lynx as a weighted average (own calculation). The study comprised 37 foxes killed during a total of 1156 lynx days. From northern Europe, only Sunde *et al.* (2000) have given data to allow for a similar calculation, resulting in an annual kill rate of 2.8 (own calculation, assuming a constant kill rate between seasons), but this estimate is highly uncertain because it is based on only one killed fox.

Lindström *et al.* (1994) argued that the generally dense red fox population in Scandinavia during the last 50 years has in part been an effect of the lack of natural fox predators, mainly lynx and wolf *Canis lupus*, and they predicted a declining fox population if large predator numbers were allowed to recover. A negative spatial relation between lynx and red fox abundance was observed in some previous studies (Haglund, 1966; Bjärvall & Lindström, 1984), although it was not clear whether this was an effect

of foxes being killed or just avoiding areas of high lynx density. Therefore, the evidence for lynx predation limiting red fox abundance has remained circumstantial.

In this study, we describe the frequency and pattern of lynx predation on red foxes in boreal Sweden in order to assess its potential in controlling the fox population. We also test the prediction of a declining fox population in an area recently colonized by lynx. The study was based on the radio tracking of foxes and the snow tracking of lynx, and on various population density indices of the two species. The study was conducted in a period when the lynx population in central Sweden was rapidly increasing and expanding.

Materials and methods

Study area

The study was conducted in boreal Sweden during 1995–2004 – a period with an increasing lynx population in central Sweden (Liberg & Glöersen, 2000) and also an expansion southward (O. Liberg, unpubl. data). The radio-tracking study of foxes was performed in the 140 km^2 Grimsö Wildlife Research Area (59°40′N, 15°30′E; here-after called the Grimsö area), situated in the southern boreal region (area described in detail by e.g. Lindström, 1989). Lynx established in Grimsö in 1995–1996, with a dramatic shift from virtual absence to a high density ($> 1/100$ km^2) within < 1 year (O. Liberg, unpubl. data).

Fox mortality

Adult-sized red foxes were live trapped in autumn and winter (August–March) in 1999–2002 within the Grimsö area (Table 1). For the trapping, a traditional Swedish trap type was used ('the Värmland trap'), constituting a large box ($1 \times 1 \times 3$ m) open at both ends. Traps were baited mainly with remains of ungulates, and checked twice per day as a minimum. Trapped foxes were anesthetized with a mixture of ketamin and xylasin, and equipped with radio collars of VHS type and with ear tags. Most radio transmitters were equipped with a mortality indicator and had a life expectancy of 2 years (Telonics, Mesa, AZ, USA), but lightweight radios with short longevity and expanding collars (AVM, Livermore, CA, USA) were used for particularly small individuals (two cases). In addition, fox cubs were captured at or near dens within the Grimsö area in late June 2000 and 2001 (Table 2). Cubs were ear tagged and equipped with lightweight radios with short longevity and expanding collars (AVM). Young-of-the-year were arbitrarily considered of adult size at August 16 – after this date, most individuals could not be separated from adults by eye. In foxes captured in autumn, young-of-the-year were preliminarily age determined by tooth replacement and wear.

Foxes were normally radio tracked once or twice weekly, but cubs were tracked more frequently. Radio tracking was terminated at the end of December 2003 (at that time, only one radio-equipped fox remained). When a fox mortality was recorded, the place of the kill was searched for traces, and a preliminary autopsy (including assessment of condi-

Table 1 Adult-sized red foxes *Vulpes vulpes* (age > 4 months) radio tracked at Grimsö, Sweden, radio-tracking period and their fate

ID	Sex	Age[a]	Tracking period (y-m-d) Capture	Last contact	No. of days	Fate
9901	M	1	1999-08-19	2001-01-23	523	Dispersed?
9902	M	1	1999-08-19	1999-09-24	36	Dispersed
9903	M	1	1999-08-23	2000-01-04	134	Dispersed?
9904	F	1	1999-08-25	2002-02-22	912	Radio failure
9905	F	1	1999-09-02	2001-05-17	623	Killed by lynx
0001	F	5	2000-01-05	2000-07-04	181	Killed in traffic
0004	M	1	2000-08-16	2000-11-17	94	Radio failure
0005	F	1	2000-08-16	2000-09-07	20	Radio failure
0007	M	1	2000-09-11	2002-06-18	645	Unknown
0008	M	15	2000-10-03	2002-10-17	744	Killed by carnivore
0101	F	?	2001-03-17	2001-08-30	166	Dispersed
0101			2002-08-01	2002-12-05	127	Radio failure
0102	M	1	2001-09-23	2001-12-04	72	Dispersed
0103	M	1	2001-09-02	2002-09-02	365	Unknown
0103			2003-07-15	2003-11-03	111	Radio failure
0104	F	1	2001-09-05	2001-09-15	10	Killed in traffic
0105	F	1	2001-09-14	2002-01-02	110	Dispersed?
0106	M	1	2001-09-24	2003-05-15	598	Killed by lynx
0107	F	1	2001-10-08	(2003-12-22)	(805)	(Alive)
0108	F	1	2001-10-16	2003-01-22	463	Killed by lynx
0109	M	1	2001-10-16	2002-02-06	113	Dispersed?
0110	F	1	2001-11-02	2002-09-16	318	Killed by carnivore

[a]Age at first capture (1 = first year of life).

Table 2 Red fox *Vulpes vulpes* cubs (age <4 months) radio tracked at Grimsö, Sweden, radio-tracking period and their fate

| ID | Sex | Litter[a] | Tracking period (y-m-d) | | No. of days | Fate |
			Onset	Last contact		
0002	F	a	2000-06-19	2000-06-30	11	Killed by lynx
0003	F	a	2000-06-19	2000-07-21	32	Radio failure
0004	M	b	2000-06-21	2000-08-16	55	(Transferred to Table 1)
0005	F	b	2000-06-21	2000-07-11	20	Radio failure
0005			2000-08-09	2000-08-16	7	(Transferred to Table 1)
0006	F	b	2000-06-21	2000-07-12	21	Radio failure
0102	M	c	2001-06-28	2001-07-03	5	Radio failure

[a]Same letters denote litter mates.

Table 3 Snow tracking of lynx *Lynx lynx* conducted in mid-Sweden (separated between lone lynx and family groups) and number of fox attacks recorded during the tracking

| Winter | Area censused (km²) | Lone lynx[a] | | | | Lynx family groups[b] | | | |
		Km tracked	No. of lynx days	No. of fox kills	No. of failed fox attacks	Km tracked	No. of group days	No. of fox kills	No. of failed fox attacks
1995	81 900	1057	167	0	0	283	71	1	0
1996	38 700	988	187	1	0	507	104	0	1
1998	75 900	1528	385	1	0	522	140	2	1
2000	56 600	1558	297	0	2	446	174	1	0
2001	67 300	1136	285	0	2	314	111	1	1
Total		6267	1321	2	4	2072	600	5	3

[a]Adult males, non-reproducing females and subadults of both sexes.
[b]Adult females with kittens.

tion, based on subcutaneous and visceral fat deposits) was conducted at Grimsö Wildlife Research Station. The cause of the deaths could be established by a combination of bite and claw marks on the body, subcutaneous haemorrhages and other circumstances in the finding place. In most cases, a complete autopsy was conducted at the Swedish Institute for Veterinary Medicine (SVA). Dead foxes were age determined by cementum analysis (Matson's Lab., Milltown, MT, USA). There was no regular human hunting or trapping of foxes in the area during the study period.

Lynx were snow tracked in the winters of 1995, 1996, 1998, 2000 and 2001 in major parts of mid-Sweden (*c*. 150 000 km²; Table 3) during national lynx censuses performed in those years (Liberg & Glöersen, 1995, 2000, 2001; Glöersen, 1996; Glöersen & Liberg, 1998). Censuses were performed on fresh snow during one weekend in January or February. Censused areas were searched for lynx trails along a dense network by car, snowmobile, ski or foot, simultaneously by several thousands of volunteers, under the direction of the Swedish Association for Hunting and Wildlife Management. Most lynx trails found were back-tracked until covered by the last snowfall. Carcasses and failed hunting attempts along the trail were recorded. Lone lynx were distinguished from family groups (female with kittens) in analyses. Estimates of the number of lynx days that the tracked distance corresponded to were derived from information on date and hour for the last snowfall. From this estimate and number of carcasses found, kill rates on

foxes were derived for the two lynx categories. Sex, age, condition or degree of consumption was not recorded for the fox carcasses found during snow tracking.

The annual mortality rate of adult-sized foxes was calculated from (1) radio-tracking data following Trent & Rongstad (1974) and (2) the kill rate derived from snow tracking, an estimated population density ratio of foxes to lynx of 30:1 (ratio estimate based on a lynx density of 0.1/1000 ha; Liberg & Glöersen, 2000; and assuming an average red fox density of 3/1000 ha, as reported by Lindström, 1982). In both mortality calculations, we arbitrarily assumed a constant mortality between seasons and ages. Because of the small sample size, no mortality rate was calculated for fox cubs.

Population indices

Population indices of red fox and lynx were derived from the Grimsö Wildlife Monitoring Program, and were thus also collected before 1995. Red fox population density within the Grimsö area was measured annually by two indices: (1) minimum number of fox litters, assessed as number of active dens found during the annual check of all known dens (about 200) in early June, in combination with incidental observations of the young later in the summer, and (2) number of foxes (young in summer excluded) incidentally observed annually during fieldwork. Here the observation time was assumed to be constant between years. No

estimates of variance were available to these indices. Data on the number of fox litters in 1996–2000 have been previously published by Kjellander & Nordström (2003).

Population trends of lynx and red fox from Örebro County (9300 km^2 surrounding the Grimsö area) were derived by an annual questionnaire to hunters ($n = 163$–250) from all over the county. For lynx, the hunters reported occurrence (yes or no) on each hunter's hunting ground. For red foxes, hunters reported perceived changes of the population on their hunting grounds since the previous hunting season. The fox population reports were transformed into an annual relative population density (ranging from 0 to 1) by giving 'increase' a value of 1, 'stable' 0.5 and 'decrease' 0, and dividing the annual sum of the reports by the total number of reports that year.

Results

Twenty adult-sized foxes were captured (most of them less than 1 year old) and radio tracked for a total of 7173 fox days (Table 1). Seven of these foxes were found dead during the period in which they were radio tracked: three were killed by lynx, two by an unknown carnivore (probably a fox or domestic dog) and two in traffic. None of the foxes killed by carnivores was consumed to any per cent by the predator. Six fox cubs from three different litters were captured, but because of frequent radio failures, these could only be followed for a total of 151 days (Table 2). During this time, the only mortality was one cub that was killed by lynx. The cub was 50% consumed by the lynx.

Two of the lynx kills of adult-sized foxes took place in May, and one in January (Table 1). All these three foxes were in their second or third year of life. Autopsies did not reveal any diseases or other physical disabilities among them, except for the injuries causing the death. The vixen killed in May (ID 9905) was lactating and had five fresh placental scars. She was found at a distance of 2 km from what was probably the maternal den. All three dead foxes were residents and were found within their regular home ranges. Their condition was good except for the lactating vixen, who was judged undernourished.

The annual adult fox mortality due to lynx predation as calculated by radio-tracking data was 0.142 [95% confidence interval (CI): 0.041–0.338]. Annual mortality due to other causes was 0.184 (95% CI: 0.067–0.387).

Lynx were snow tracked for a total distance of 8339 km, equaling 1921 lynx days (both lynx categories pooled; Table 3). Along this cumulative trail, seven red foxes killed by lynx (and additionally seven unsuccessful hunting attempts on red foxes) were found. The annual kill rate based on snow tracking was 1.3 foxes/lynx (95% CI: 0.6–2.8) and annual fox mortality was 0.044 (95% CI: 0.021–0.095).

Both the annual number of fox litters and the annual number of fox observations at Grimsö showed negative trends after 1996, when lynx had established in the area (linear regression, $R^2 = 0.75$, $n = 9$, $P = 0.003$ and $R^2 = 0.35$, $n = 9$, $P = 0.09$, respectively; Fig. 1). The annual
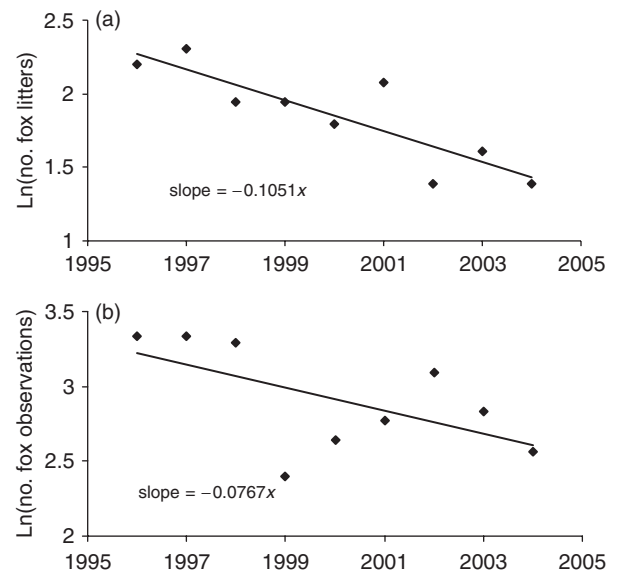

Figure 1 Indices of red fox *Vulpes vulpes* population density [(a) annual number of fox litters and (b) fox observations] at Grimsö, Sweden, after the establishment of lynx *Lynx lynx*. Annual population increase rates were calculated as the slope of the fitted regression line.
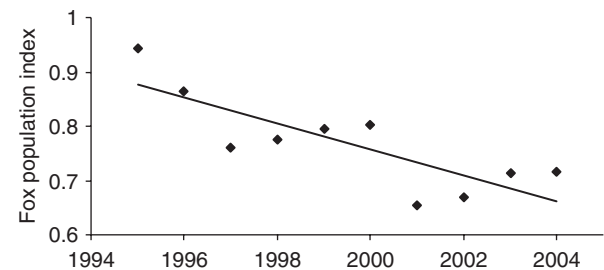

Figure 2 Relative index of red fox *Vulpes vulpes* population density (derived from hunters' reports) in Örebro County, Sweden, after the establishment of lynx *Lynx lynx*.

population increase rates (measured as the slope of the regression line) were −0.11 (SE ± 0.02) for number of fox litters and −0.08 (SE ± 0.04) for number of fox observations.

Hunters in Örebro County reported an increasing lynx distribution during the 1990s. From 1995 onwards, lynx were reported from > 75% of the county. After this year, the annual population index of red foxes in Örebro County decreased (linear regression, $R^2 = 0.66$, $n = 9$, $P = 0.004$; Fig. 2).

Discussion

The two independent measures of red fox mortality due to lynx predation in the present study (14% annually due to radio tracking of foxes, 4% due to snow tracking of lynx, both measures with wide confidence limits) did not appear dramatic, and the figures as such were within the limits of

what the fox population should be able to compensate for with an increased recruitment. However, in the radio-tracking study, lynx predation constituted 50% (four of eight) of the observed mortalities. Although mortality by human hunting was underrepresented in our sample, regular hunting or trapping is generally not intense in the region; therefore, this should not have caused a large bias to the result. Comparable proportions of intra-guild predation (43–68% of mortalities) have been observed in a number of other carnivores alleged to be limited by such predation (Laurenson, 1995; Lindström et al., 1995; Ralls & White, 1995; Creel & Creel, 1996; Crabtree & Sheldon, 1999; Palomares & Caro, 1999).

More important than the actual mortality figures is the question of whether the observed mortality is additive or compensatory. All observed lynx-related mortalities occurred in winter or spring, that is after the main period of territory establishment for the red fox (Niewold, 1980) and, therefore, after the assumed bottleneck for population regulation in the territorial red fox. The three lynx-killed foxes in the radio-tracking study were resident, in prime age (early reproductive period, long life expectancy) and apparently in normal condition (which should also hold for the lean lactating vixen). The inference from this small number of kills is not strong, but suggests that the mortality in red foxes caused by lynx predation should be at least in part additive, and thus have a potential to cause a decline in the fox population.

Our data supported the prediction that fox numbers may go down when lynx become abundant (Haglund, 1966; Lindström et al., 1994). The negative rates of increase calculated from Grimsö fox indices ($r \approx -0.1$) could potentially be explained by lynx predation alone.

The population trend differed from what is reported from Switzerland, where fox and lynx populations have increased simultaneously (U. Breitenmoser, pers. comm.), despite the frequent killing of red foxes by Swiss lynx (Jobin et al., 2000). The density ratio of foxes to lynx in Switzerland is, however, considerably higher (probably about 10–100 times) than in Scandinavia (U. Breitenmoser, pers. comm.); therefore, fox mortality due to lynx predation should still have been low ($< 1\%$ on an annual basis). The effect of lynx predation on fox population may therefore depend on the density ratio between the two species. Accordingly, Stephenson, Grangaard & Burch (1991) suggested that when the density of Canada lynx Lynx canadensis in Alaska was high, and the fox:lynx ratio approached 1, lynx predation could contribute to declines in red fox populations.

Alternative explanations for the fox decline include altered habitat structure or habitat preferences, a mange outbreak, low food abundance and increased food competition from lynx. Foxes have previously been found to benefit from the large-scale changes in landscape structure produced by farmland abandonment and small-scale forestry transformed into industrial forestry (Christiansen, 1979), but both these processes were completed many years ago, and there are no large-scale habitat changes in recent years that could explain the recent fox decline. Foxes, however, have changed habitat preferences in recent years, and now concentrate their activity on areas close to farmland and human settlements (L. Silversund & J. O. Helldin, unpubl. data). Whether this behaviour is to escape lynx predation (as suggested by e.g. Haglund, 1966) or not, it may have resulted in areas not used by foxes, and accordingly in a decreased fox population density on a larger scale.

An epizootic of sarcoptic mange caused a nationwide dramatic decrease in the fox population in the 1980s (Lindström et al., 1994). The recovery of the fox population started in the late 1980s (Lindström et al., 1994), and fox density appears to have reached a new maximum in the mid-1990s (Kjellander & Nordström, 2003). Although mange was still present in the fox population during the present study, and infected foxes were observed occasionally, no local or regional outbreak large enough to explain the declining fox population was noted.

Also food supply has previously been shown to be of importance to red fox abundance in the area – foxes may fluctuate in accordance with microtine cycles, and medium-sized herbivores such as mountain hare Lepus timidus, capercaillie Tetrao urogallus and black grouse Tetrao tetrix may be important alternative food during microtine lows (Lindström, 1982, 1989). The average microtine abundance was low during most of the 1990s (Kjellander & Nordström, 2003). During the first 7 years of low microtine abundance (1989–1995), the fox population however increased or peaked. Hence, there seems to be little correlation between vole and fox numbers.

Hares and forest grouse declined dramatically between 1989 and 1993, explained as an effect of predation from the increasing red fox population (Lindström et al., 1994). Accordingly, in the mid-1990s, foxes may to some degree have suffered from their own overexploitation of these species. However, hares and forest grouse have started to recover with the fox decline (Å. Pehrson, pers. comm.), and therefore appear to have been governed by the fox density rather than governing it.

We exclude increased food competition from lynx as a possible explanation for the fox decline. Foxes and lynx may compete for hares and forest grouse, but lynx consumption of these species has recently been low in our study area (Moshøj, 2002) and hardly been able to affect their abundance. Furthermore, the frequent killing of roe deer Capreolus capreolus by lynx resulted in a large number of carcasses (Moshøj, 2002), which should have supplied foxes with a rich extra food resource year round (Helldin & Danielsson, in press). Thus, lynx presence should have resulted in an increased rather than decreased food abundance for foxes.

In conclusion, we cannot exclude the possibility that the recent decrease in the fox population was at least in part due to some other factor than predation. The concordance between the observed mortality rate due to lynx predation and the population decrease rate for red foxes does, however, suggest the possibility of a causal relationship between them. We furthermore find the alternative explanations for the fox decline less likely.

Except for Eurasian lynx, other lynx species and wolves may also kill foxes (Stephenson *et al.*, 1991; Peterson, 1995; Palomares *et al.*, 1996). The results from our study suggest that the present deficit of large carnivores over most of their former ranges may have resulted in an over-abundance of red foxes in many areas. Allowing large carnivores to re-establish may thus be an efficient way of limiting fox populations.

Acknowledgements

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