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RED FOX REMOVAL AND ROE DEER FAWN SURVIVAL—A 14-YEAR STUDY

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Abstract: We studied the impact of red fox (*Vulpes vulpes*) predation on free-ranging roe deer (*Capreolus capreolus*) neonates during 14 years in a mixed forest/agricultural landscape in south central Sweden. A large-scale natural predator removal experiment occurred when an outbreak of sarcoptic mange (*Sarcoptes scabiei*) reduced the red fox population initially and caused subsequent variations in red fox abundance. We estimated relative red fox abundance by dividing number of fox observations with number of person-days in field. Red fox predation accounted for 88% of known mortality in roe deer fawns. Predation was closely correlated to red fox abundance, and there was a strong negative correlation between fox abundance and overall fawn survival. Fox abundance was the only factor with a significant effect on between year variation in fawn survival. Annual predation varied between zero and 90%. Our study recorded the highest predation rates for roe deer juveniles established to date. High fawn survival in years of low fox abundance suggested that predation mortality was additive during summer. Our results supported the conclusion that the large national increase of roe deer in Sweden during the 1980s and 1990s was related to lower fox predation on fawns and also indicated that the roe deer population density was well below habitat carrying capacity at the onset of the mange epidemic. In Sweden, in general, a thorough fox control will most likely result in increased fawn survival and higher potential roe deer harvest.

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Key words: *Capreolus capreolus*, deer population dynamics, juvenile survival, predation, predator abundance, predator removal experiment, red fox, roe deer, sarcoptic mange, Scandinavia, ungulates, *Vulpes vulpes*.

Predation is the most important mortality factor for neonatal ungulates in temperate regions (Linnell et al. 1995). Determining the magnitude and variation of this factor is crucial for understanding the life history and demography of ungulates (Keith 1974, Boutin 1992, Gaillard et al. 1998, Ballard et al. 2001). However, predation studies have some inherent methodological problems (Linnell et al. 1995). It is often difficult to identify species of predators and to differentiate between predation and scavenging. The role of predation as additive or compensatory mortality requires greater understanding of population dynamics. Clarifying this is crucial for a correct interpretation of how predation influences demographics and dynamics of the prey population. One approach to solving these types of problems is to experimentally remove predators, preferably with controls. However, predator removal is often a controversial issue. Even with no ethical or political restrictions, there are often practical difficulties relative to efficiency, especially for small and medium-sized predators (National Research Council 1997, Andelt et al. 1999, Ballard et al. 2001). Moreover, most studies cover only 1 or a few years (but see Byers 1997*a*), and effects are usually measured indirectly (e.g., changes in mother-offspring ratios; Beasom 1974, Guthery and Beasom 1977, Stout 1982, Stewart et al. 1985, Crête and Jolicoeur 1987, Ballard and Miller 1990). We report on a 14–year study of red fox predation on neonatal roe deer. We used radiotelemetry for direct measurement of mortality and benefited from a natural predator removal experiment caused by an outbreak of sarcoptic mange in the fox population.

The roe deer is the most common wild ungulate in Sweden. It is a small cervid with an adult body mass of 20–30 kg. Females normally first give birth at 2 years of age, and litter sizes vary between 1 and 3 (Borg 1970, Andersen et al. 1998). Fawn drop occurs in May and June. During the first 4 to 6 weeks post-birth, fawns are inactive and spend most of their time hidden in vegetation. The mother visits the fawn 3–7 times/day (Espmark 1969). The roe deer was near extinction in Sweden during the first decades of the 19th century, but it made a remarkable comeback in the following 150 years (Liberg et al. 1994). Introduction of hunting restrictions, near extinction of wolf (*Canis lupus*) and lynx (*Lynx lynx*), decreased use of forests for cattle grazing, and modern forestry and agriculture practices likely benefited roe deer during the 20th century (Cederlund and Liberg 1995). From the mid-1980s to the mid-1990s, total harvest in Sweden

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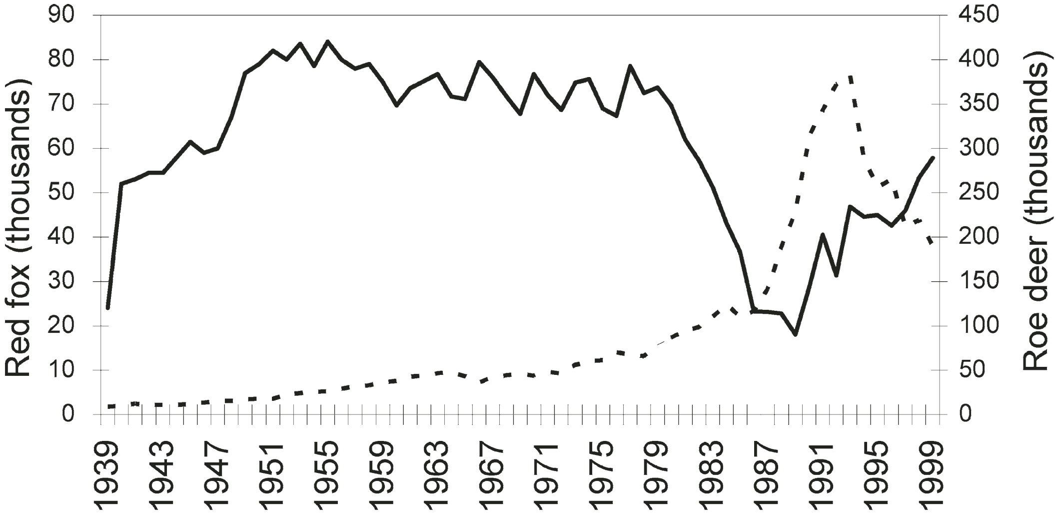

Fig. 1. Annual hunting bag of red fox (solid line) and roe deer (dashed line) in Sweden 1939–2000 (Kindberg 2003; K. Kultima, The Swedish Association for Hunting and Wildlife Management, personal communication.)

indicated a large population increase (Fig. 1). An outbreak of sarcoptic mange that decimated the red fox population (Fig. 1) and several mild winters likely contributed to this increase (Liberg et al. 1994, Lindström et al. 1994).

The red fox is a medium-sized generalist predator. In Scandinavia its main prey are rodents and lagomorphs (Lindström 1982). It is also a major predator on roe deer fawns (Strandgaard 1972, Liberg et al. 1993, Lindström et al. 1994, Aanes and Andersen 1996, Jarnemo et al. 2004), and the red fox is the smallest mammal reported as a major predator on ungulate neonates (Linnell et al. 1995).

Sarcoptic mange is a parasitic disease. The microscopic parasite lives most of its life cycle in the outer layers of epidermis and excavates tunnels in which females lay eggs. The total life cycle is 15–20 days, comprising egg, larvae, 2 nymph stages, and adults. Parasites of all stages might occur on the skin surface of the nose. Contamination occurs mainly through contact but may be indirect. The disease causes acute itching and skin lesions. The variety of sarcoptic mange that affects the red fox is *S. scabies varians canis* (Bornstein 1995). Victims eventually die from cold and starvation, combined with secondary infections in scratch wounds (Mörner and Christensson 1984, Bornstein et al. 1995). Sarcoptic mange was absent from Swedish wildlife for >100 years prior to 1972 when the first case was recorded in northern Sweden (Christensson 1972). It appeared to be spread by red foxes moving from nearby Finland. The next case was not reported until 1975 (Borg et al. 1976), after which the expansion was rapid and severe. The outbreak of mange in a red fox population with no immunity in Sweden during the late 1970s and 1980s created a large-scale predator removal experiment (Lindström and Mörner 1985, Lindström et al. 1994). The epidemic reached our study area in 1987. Mange not only severely reduced the red fox population initially but it also caused variations in fox numbers in subsequent years during the 1990s. Hence, an excellent opportunity arose to study the effects of red fox abundance on neonatal survival in roe deer. We investigated the relative importance of red fox predation as well as the effect of a variable red fox population size as a possible cause of between year variation in fawn survival.

STUDY AREA

We conducted our study at Ekenäs (58°58′N, 16°35′E), located approximately 100 km south of the boreal zone in south central Sweden in Söder–manland county. The core study area was 300 ha and was comprised of 53% forest and 47% farmland. The forest was largely dominated by intensively managed stands of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Common broad-leaved trees, normally found within coniferous stands or along edges, were aspen (*Populus tremula*), oak (*Quercus robur*), birch (*Betula* spp.) and alder (*Alnus glutinosa*). Ekenäs was a dairy farm, and much of the agricultural area was used for production of clover hay. Other crops were rye, oats, wheat, and rape. Approximately one third of the agricultural land was pasture. Other potential predators on roe deer fawns were badger (*Meles meles*) and pine marten (*Martes martes*). Roe deer hunting was prohibited at Ekenäs during the study, but it was allowed on neighboring estates.

METHODS

We typically caught fawns following maternal visits. We observed marked and unmarked does until they visited their hidden fawns. We captured fawns after they had bedded again and the mother had moved away. When there was a risk of losing sight of fawn and doe, we flushed the doe. In these situations fawns normally adopted a prone position as the female ran away. We also found fawns by searching in the vicinity of bed sites of previously marked siblings and, less frequently, in suitable bed site habitat. We weighed fawns at capture and estimated age using a mean body mass at birth of 1,500 g and a mean daily growth rate of 150 g (Andersen and Linnell 1998; O. Liberg, unpublished data). Male and female fawns do not differ in body mass or growth rate (Gaillard et al. 1993, Andersen and Linnell 1997). We equipped fawns with a radiotransmitter (Televilt TVP Positioning AB, Lindesberg, Sweden) attached to an expandable collar with a drop-off function. Transmitters weighed 65–70 g and had a range of ≤1.5 km and a battery life of approximately 1.5 years. We monitored marked fawns daily for up to 4–6 weeks of age and 1–2 times/week thereafter. We subtracted fawns known or suspected to have died as a consequence of marking (i.e., fawns abandoned or killed by foxes within hours after marking) from the data analyzed. We also subtracted fawns with failed transmitters (Jarnemo et al. 2004). We determined predation and predator species from assessing bite marks and carcass damage, buried carcasses and transmitters, carcasses and transmitters found at fox dens, tooth marks on transmitters, chewed off collars, and transmitters that smelled like foxes. We normally removed marked fawns from hay fields prior to mowing. Occasionally mowing occurred without our knowledge, and marked fawns were killed (Jarnemo 2002).

We estimated roe deer density using the Petersen estimate (Caughley 1977) based on resightings of marked and unmarked adult roe deer (Liberg et al. 1992). We recorded all visual observations of foxes we made while capturing and monitoring roe deer fawns. By dividing the number of fox observations with the number of person-days in the field at Ekenäs during May, June, and July, we determined an annual index of fox attendance. We collected harvest records of red fox and roe deer from 10 larger estates (total area 47,500 ha, range 1,100 to 16,500 ha) in Södermanland county, including 1 estate adjacent to Ekenäs (1,500 ha). We also collected data on precipitation, average temperature, and average minimum temperature in April, May, and June from the nearest weather station (Vingåker), which was 40 km from the study area.

We used the Mayfield method (Mayfield 1961, 1975; Johnson 1979) to analyze mortality, predation, and survival rates. This method considers the number of days (i.e., radio-days) each marked individual is at risk, and it is especially useful since fawns are born at different times and caught at varying ages.

RESULTS

We captured 233 fawns during 14 years. We fitted all fawns with transmitters except for 12 fawns that we only earmarked in 1996. Mean age at capture was 7 days (SD = 5). We included 216 in our study after the subtraction of capture-induced deaths, loss of transmitter, or disappearance (Jarnemo et al. 2004). Total predation was 42% (91 of 216 marked fawns; Table 1). Predation accounted for 81% (91 of 113 fawn deaths) of total mortality and 88% (91 of 103 fawn deaths) of known mortality causes. Other causes of mortality were hay mowing machines ($n = 5$) and starvation, hypothermia, and disease ($n = 7$). Ten fawns died from unknown causes, including 8 eartagged fawns in 1996. Since foxes were responsible for the vast majority of known mortality, the most likely cause of death for the eartagged fawns was red fox predation. In analysis, however, we treated these 8 fawns as dead by unknown causes.

At the beginning of the study, roe deer density was approximately 10 animals/km^2. Within the following 3 years, it increased to 22–24 animals/km^2, and this density was maintained during the rest of the study with minor deviations. The fox population fluctuated considerably. We used an average of 52 (range 24–124) person-days to calculate a seasonal fox index, and the number of fox observations varied between zero and 36. The annual index varied between zero and 0.8 observations/person-day (Table 1, Fig. 2).

Average daily predation rate was 0.026 and varied between zero and 0.11 (Table 1). Predation on fawns and the red fox index at Ekenäs were positively correlated ($r = 0.76$, $P = 0.0016$; Fig. 2). Fawn survival was negatively correlated with the fox in-

Table 1. Fate of marked roe deer fawns, red fox index, and hunting bags of roe deer and red fox, Ekenäs and Södermanland, 1986–2000.[a]

Yr	No. fawns	Fox predation	Other deaths	Surviving fawns	Mortality rate, 10^{-2}	Predation rate, 10^{-2}	Fox observations	Person-days	Fox index	Roe deer density	Roe deer bag	Fawn bag	Fox bag
86	9	5	–	4	2.3	2.3	8	30	0.27	10.0	10.0	3.6	2.2
87	11	–	2	9	0.4	0.0	0	37	0	12.6	10.1	5.3	1.5
88	19	–	–	19	0.0	0.0	0	71	0	17.7	12.1	5.9	0.6
89	17	–	1	16	0.1	0.0	2	124	0.02	22.0	16.5	7.4	0.2
90	12	3	–	9	0.7	0.7	1	110	0.01	24.4	20.9	10.0	0.6
91	12	3	4	5	1.7	0.7	3	65	0.05	23.1	25.1	9.5	0.4
92	20	12	–	8	2.1	2.1	12	32	0.38	23.7	29.2	9.0	1.1
93	19	14	2	3	5.0	4.4	6	43	0.14	22.7	32.4	9.8	1.0
94	10	9	–	1	11.0	11.0	16	29	0.55	23.5	31.6	8.3	1.9
95	16	14	1	1	7.6	7.1	36	45	0.80	21.3	21.1	5.3	2.7
96	19	3	9	7	1.4	1.4	19	24	0.79	20.0	20.4	5.1	2.3
97	17	7	2	8	1.7	1.3	9	45	0.20	18.9	15.0	4.6	3.1
98	19	7	1	11	1.3	1.1	6	40	0.15	23.1	10.8	3.4	3.9
99	16	14	–	2	4.4	4.4	22	32	0.69	23.7	10.3	4.1	4.7
00											9.9	3.2	8.6
Σ	216	91	22	103									

[a] Number of marked, dead, and surviving fawns (up to 8 weeks old), daily mortality and predation rates, fox index (number of fox observations divided by person-days in field), roe deer density at Ekenäs (No./km^2), and hunting bags of roe deer and fox from 10 larger estates including Ekenäs (no./1,000 ha).

dex ($r = 0.76$, $P = 0.0016$; Fig. 3). There was no significant correlation between fawn survival and roe deer density ($r = -0.31$, $P = 0.29$) or any weather factor (P-values ≥ 0.33). A linear regression model between fox index and fawn survival explained 54% of the variation in survival ($F = 16.0$, df = 1, 12, $P = 0.0017$), whereas a negative exponential model explained 56% ($F = 17.4$, df = 1, 12, $P = 0.0013$). Mayfield estimates (Mayfield 1961, 1975; Johnson 1979) of daily mortality and predation rates (Table 1) were positively correlated with the fox index ($r = 0.74$, $P = 0.0026$; $r = 0.82$, $P = 0.0003$). Using linear regression models, the fox index explained 32% of the variation in the daily mortality rate ($F = 7.0$, df = 1, 12, $P = 0.021$) and 34% of the variation in daily predation rate ($F = 7.9$, df = 1, 12, $P = 0.015$).

The validity of the fox index was supported by the fox harvest on the estate adjacent to Ekenäs. Trends in the red fox abundance index agreed with trends in the number of foxes shot the preceding hunting season on the adjacent estate (Fig. 4). The total harvest of roe deer at the 10 larger estates (Table 1) showed a >3-fold increase, and the fawn (<1-yr-old) harvest showed an almost 3-fold increase from the beginning of the study to the peak in 1992–1993. The subsequent decrease in roe deer harvest coincided with an increase in the numbers of fox harvested. At the end of the study, the harvest of roe deer and fawns returned to levels almost identical to levels before the increases, whereas the fox bag was almost 4 times higher in the last year of the study than in the first.

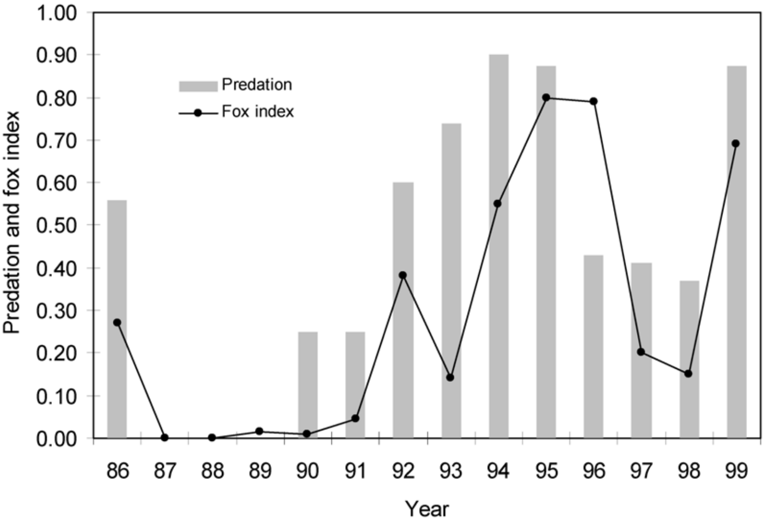

Fig. 2. Predation rate (gray bars) and red fox index (black line) at Ekenäs, Sweden, 1986–1999. In 1996, 12 of 19 fawns were eartagged and not equipped with radio transmitters.

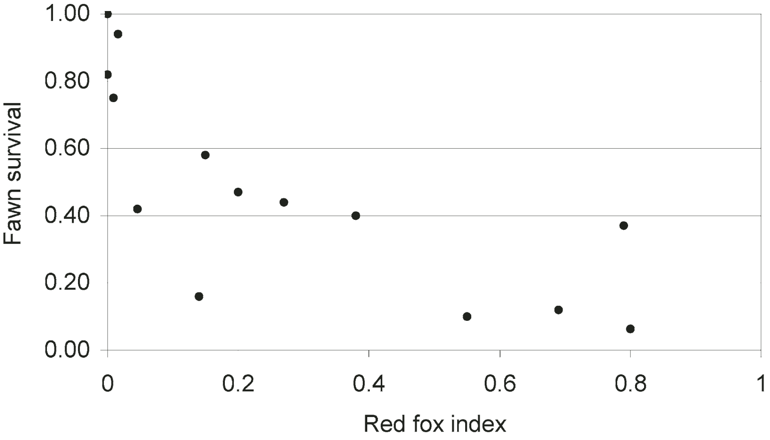

Fig. 3. Overall fawn survival in relation to red fox index, Ekenäs, Sweden, 1986–1999.

The number of fawns harvested was negatively correlated with fox bag ($r = -0.70$, $P = 0.0033$).

DISCUSSION

Predation and total mortality rates tracked the fox population closely and demonstrated conclusively that fox abundance was the major determinant of fawn survival. The only other Scandinavian study on predation on roe deer fawns using telemetry also found that fox predation was the greatest mortality factor (Aanes and Andersen 1996). The 2-year study by Aanes and Andersen (1996) did not include predator removal, but in a Danish study, Strandgaard (1972) noted that in autumn the fawn:doe ratio decreased from 1.10 to 0.45 immediately following termination of a fox removal program.

We did not find any significant effect of precipitation or temperature on roe deer fawn survival. However, weather has been shown to affect fawn survival in other studies. A delayed spring (Andersen and Linnell 1998) or cold and wet weather after birth (Wotschikowsky and Schwab 1994) can increase mortality. Conversely, cool and wet conditions before and during the birth period may positively influence survival through enhanced vegetation growth and food quality (Gaillard 1994, Gill 1994, Thor 1995).

Few fawn deaths were due to causes other than predation. The close correlation between fawn survival and fox abundance, especially the almost complete absence of mortality during years when foxes were absent, was strong evidence that foxes not only scavenged on fawns but also killed them, and that foxes were the only significant fawn predators in the area. Although badger and pine marten were unaffected by fox mange and were often observed during low fox years, fawn survival during those years was still almost total.

Our finding that red fox predation on roe deer neonates is the most important mortality factor is in accordance with the general pattern observed for other ungulates in temperate closed stems (Linnell et al. 1995). However, the predation rates we documented during years of peak fox population are among the highest reported. In their review of 68 studies, Linnell et al. (1995) did not find any predation rates >85%; most were <60% (but see Byers 1997*a,b*). We recorded mortality rates >85% in 3 different years. Several factors may contribute to the extremely high predation we observed, in-

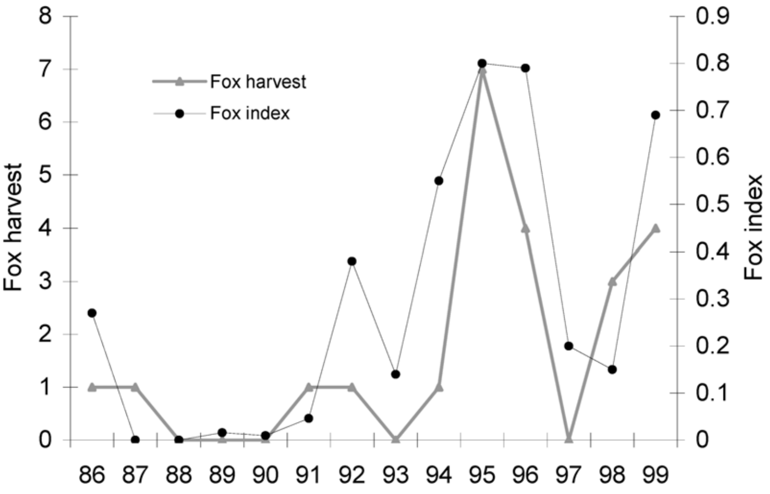

Fig. 4. Fox index (right axis) at Ekenäs, Sweden, and number of foxes harvested (left axis) at the neighboring estate Lagmansö (1,500 ha), 1986–1999.

cluding the type of landscape. The Ekenäs area was fragmented by agricultural fields that were heavily used by roe deer as foraging habitat. Several authors argue that lack of cover and open landscapes make neonates in hider species (Lent 1974) more vulnerable to predation (Carroll and Brown 1977, Autenrieth 1980, Barret 1981, Aanes and Andersen 1996, Canon and Bryant 1997). Observations at Ekenäs indicated that this type of landscape favored foxes in their search for fawns (Jarnemo 2004).

High fox and roe deer densities could also contribute to high predation. The mixed forest/agricultural landscape at Ekenäs is considered optimal fox habitat (Erlinge et al. 1983, Kurki et al. 1998). Although we have no data on absolute fox density, we believe it was high during peak index years. Also, as roe deer at Ekenäs were not hunted, roe deer density at Ekenäs was higher compared to surrounding estates where hunting was allowed (K. Wahlström, Stockholm University, unpublished data; O. Liberg, Swedish University of Agricultural Sciences, unpublished data). We found 2 fawn transmitters at fox dens 4–5 km from the study area, which may indicate forays into the Ekenäs area. It is likely that the high roe deer density generated an improved search image for fawns and a temporary specialization on this prey. Fawning is concurrent with the annual low of the fox's main prey species, the field vole (*Microtus agrestis*) and bank vole (*Clethrionomys glareolus*; Lindström 1982, Hansson 2002), which increases the importance of fawns for fox and leads them to switch prey from voles to fawns (Kjellander and Nordström 2003).

Roe deer mothers aggressively defend their offspring against small and medium-sized predators including the red fox (Raesfeld et al. 1985, Cederlund and Liberg 1995, Jarnemo 2004). However, fawns of young, inexperienced mothers might be more vulnerable to predation (Ozoga and Verme 1986, Mech and McRoberts 1990, Nixon and Etter 1995, Kjellander 2000). Early in the mange epidemic, several cohorts of roe deer females may have grown up with little or no experience with foxes. As a consequence, these does may have been less effective in defending their fawns.

Our method of finding fawns by watching does in open terrain could have biased our sample towards fawns that predominantly used open habitats; thus, these fawns might have faced a higher predation risk (Aanes and Andersen 1996). However, most fawns had home ranges covering forest and farmland. The fragmented landscape made it less likely that we could find forest-living roe deer. Another potential bias was that foxes benefited from the marking procedure by locating marked fawns more easily, and we had 1 case (excluded from the data) where this was suspected. We tested possible effects of marking by comparing autumn fawn:doe ratios between does with marked fawns and does with unmarked fawns, and we found no difference ported by others (Ballard et al. 1981, Garrott et al. 1985, Ozoga and Clute 1988, Byers 1997*a*).

The high survival of fawns in years of low fox abundance provided evidence that predation mortality was additive during summer and was consistent with other studies where predators were experimentally removed (Beasom 1974, Stout 1982, Smith et al. 1986, Crête and Jolicoeur 1987, Byers 1997*a*). When compensatory mortality occurs during the postpartum period, it seems to be related to high deer density and deteriorated range conditions (Carroll and Brown 1977, Steigers and Flinders 1980, Singer et al. 1997). Deer density may thus be crucial to determining the impacts of predation (Ballard et al. 2001). In another study area in central Sweden, Kjellander (2000) recorded density dependent effects on body mass, growth, fecundity, and survival when roe deer density was 30–36 deer/km^2. On a fox-free island, no density dependence in fawn summer survival could be detected as density increased from 10 to 40 roe deer/km^2 (Andersen and Linnell 1998). In Scandinavia, good-quality forage is abundant during summer. Roe deer therefore typically show little density dependence in variables such as postnatal investment or postnatal mortality (Andersen and Linnell 1997, 1998), suggesting that the effect of fox predation will be additive.

During our study, the roe deer population at Ekenäs never reached these high densities. It is possible that the mortality from fox predation would generate a less additive effect in a high-density roe deer population subject to density dependent effects, but in that case, the compensatory process would most likely act between summer and winter mortality. So far, evidence on the red fox:roe deer system, including our study, implies there are additive effects of fox predation (Strandgaard 1972, Liberg et al. 1994, Lindström et al. 1994) and supports the conclusion that the nationwide increase of roe deer in Sweden during the mange period was related to lower fox predation on fawns. The national increase of roe deer and our results indicate that the roe deer population density was below habitat carrying capacity at the onset of the mange epidemic. We found that the enormous impact of mange on fox density and the strong effect of fox predation on fawn survival made it likely that the driving force in this system was sarcoptic mange.

MANAGEMENT IMPLICATIONS

The roe deer is the most common cervid in Scandinavia, and fox predation is not a threat to the roe deer population. However, fox may suppress the population and decrease hunter harvest. Wildlife managers and hunters wanting to sustain a high yield of roe deer might consider reducing fox density. Our data did not indicate any threshold values in the relationship between fawn survival and fox abundance but rather identified a continuous decrease in fawn survival with increasing fox numbers. In general, roe deer populations in Sweden are well below densities where density dependent effects may occur, so thorough fox control will likely result in increased fawn survival and higher potential harvest in any given area, regardless of initial roe deer density. Hunting of roe deer should perhaps be adjusted to fox abundance. Following resurgence of the fox, hunters maintained the high roe deer harvest they had become accustomed to during fox-free years. This may have exacerbated the decline in roe deer numbers seen in the late 1990s. Wildlife managers and hunters can construct a fox index during early summer and estimate a fawn:doe ratio during late summer and early autumn to foresee status and potential harvest of the roe deer population.

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