BioOne COMPLETE

Can Supplemental Feeding of Red Foxes Vulpes vulpes Increase Roe Deer Capreolus capreolus Recruitment in the Boreal Forest?

Authors: Nordström, Jonas, Kjellander, Petter, Andrén, Henrik, and Mysterud, Atle

Source: Wildlife Biology, 15(2) : 222-227

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/08-030

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Wildl. Biol. 15: 222-227 (2009)
DOI: 10.2981/08-030
© Wildlife Biology, NKV
www.wildlifebiology.com

Short communication

Can supplemental feeding of red foxes *Vulpes vulpes* increase roe deer *Capreolus capreolus* recruitment in the boreal forest?

Jonas Nordström, Petter Kjellander, Henrik Andrén & Atle Mysterud

Red fox *Vulpes vulpes* predation on roe deer *Capreolus capreolus* fawns is regarded as a very important factor affecting recruitment of roe deer. Therefore from a hunting management perspective, it is of interest to find efficient ways to reduce predation. Because predator removal during summer is highly controversial and banned by law in Scandinavia, supplemental feeding of red foxes during the short, critical fawning period of roe deer has been proposed as a means to relieve predation on fawns. We performed a two-year study of providing red fox vixens with food, supplied as close to active dens as possible, and monitored recruitment of radio-marked roe deer in the vicinity of these dens at a realistic management scale (i.e. the size of a large hunting area; $\sim$65 km^2). Even though red foxes found and consumed the food supplied, we found no tendency towards increased recruitment of roe deer. We conclude that supplemental feeding of red foxes during the fawning period is not a solution to this management problem, at least not at the chosen management scale and with the current red fox predation levels.

Key words: incidental predation, lynx, predation, predator removal, red fox, roe deer recruitment, supplemental feeding

Jonas Nordström, Petter Kjellander & Henrik Andrén, Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences (SLU), S-730 91 Riddarhyttan, Sweden - e-mail addresses: jonas.nordstrom@ekol.slu.se (Jonas Nordström), petter.kjellander@ekol.slu.se (Petter Kjellander), henrik.andren@ekol.slu.se (Henrik Andrén) Atle Mysterud, Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway - e-mail: atle.mysterud@bio.uio.no

Corresponding author: Jonas Nordström

Received 14 April 2008, accepted 10 November 2008

Associate editor: Piero Genovesi

Red fox *Vulpes vulpes* predation is regarded as a very important factor affecting recruitment rates in roe deer *Capreolus capreolus* populations (Lindström et al. 1994, Jarnemo & Liberg 2005), mainly because of heavy predation on roe deer fawns during their first eight weeks of life (Aanes & Andersen 1996, Kjellander & Nordström 2003, Jarnemo et al. 2004). Red fox vixens with cubs are regarded as responsible for most roe deer fawn predation (Lindström 1994). From a hunting management perspective, roe deer harvest would benefit from finding ways to reduce red fox predation. One possible solution is predator removal but because non-territorial foxes take over territories as soon as territory holders are shot (Rushton et al. 2006), it is unlikely that control of red foxes in the hunting area during the autumn and winter hunting season is sufficient to reduce the predation on roe deer fawns which takes place during early summer, at least not at the scale of a typical hunting area. The effect, if there is one, of predator removal is likely to be short-term. If the aim of red fox control is to reduce predation on roe deer fawns, the killing of vixens with dependent cubs or of red fox juveniles during early summer would be necessary, a solution which would be extremely controversial and is in fact not allowed in either Sweden or Norway under the current hunting legislation.

In order to reduce red fox predation, a less controversial alternative might be to provide red foxes with additional food during the short, critical period

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

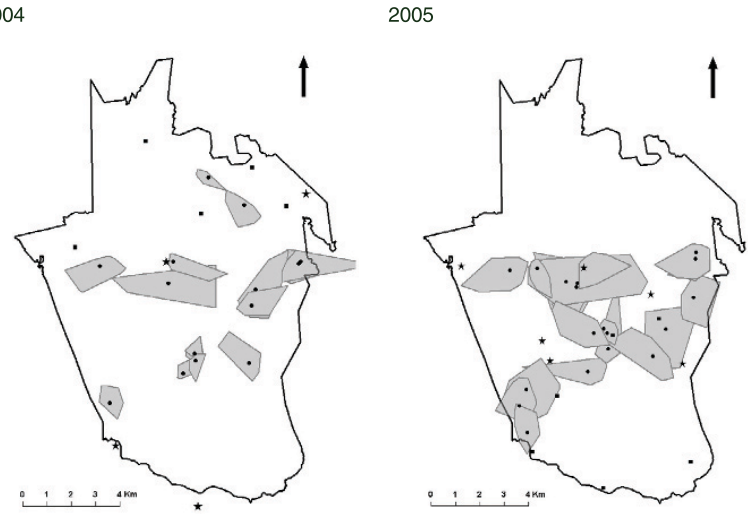


Figure 1. The Grimsö Wildlife Research area was divided into a northern and southern part for this study. Feeding plots were distributed over the northern area in 2004 (A) and over the southern area in 2005 (B). ■ denote feeding plots, ★ dens with fox litters, and ● the middle point of radio-marked roe deer doe's home ranges (grey shaded areas).

for roe deer fawns during early summer (Andersen et al. 2004). The idea being that red foxes would switch from fawn predation to the food supplied and that an increase in red fox numbers should be avoided by the shortness in duration of the feeding. The effect of supplemental feeding of red foxes on roe deer recruitment has never been tested, although Lindström et al. (1987) demonstrated that supplemental feeding of small and medium-sized predators, including red foxes, can have a positive effect on prey species survival in boreal Sweden. The aim of our study was, therefore, to test the idea that supplemental feeding of red foxes will improve recruitment of roe deer fawns. Our study was carried out during 2004-2005 in the Grimsö Wildlife Research Area using radio-marked roe deer females, and benefited from the knowledge accumulated by a long-term programme monitoring red fox dens in the area.

Material and methods

Study area

Grimsö Wildlife Research Area (130 km^2) is located in south-central Sweden (59°40'N, 15°25'E) in the southern part of the boreal forest. Norwegian spruce *Picea abies* and Scots pine *Pinus silvestris* forests cover 74% of the area, and bogs, mires and fens cover 18%. Farmland comprises 3% and lakes and rivers cover 5% of the area. The landscape is flat, rising altitudinally from 75 m a.s.l. in the south to 180 m a.s.l. in the north. For a more detailed description of the Grimsö Wildlife Research Area, see Swenson & Angelstam (1993).

Study design

Grimsö Wildlife Research Area was divided into a northern and a southern part of similar size (each ca 65 km^2), to mimic the attributes of a large hunting area. The supplemental feeding was conducted in the northern part in 2004 and in the southern part in 2005 (Fig. 1).

Because red foxes in Sweden are likely to abandon a den at the first disturbance, no den sites were visited *a priori* to determine the presence or absence of a fox litter. Instead, in order to target red fox vixens with cubs without causing them to abandon the den and to improve the likelihood of getting an effect as compared to random feeding, we established feeding plots close to denning sites known to be the most active during the previous five years, or where there had been fox litters present at least five times since 1973, i.e. the dens where it was most likely that a fox litter would be born. Based on these criteria, we established five feeding plots in the northern part (2004) and six in the southern part (2005; see Fig. 1). Meat from pig *Sus scrofa domesticus*, moose *Alces alces* and roe deer was placed on sand beds (about 1 m^2) for detection of scavenger tracks. As the nutritional needs of a vixen with cubs were largely unknown, we decided to place a 'large amount' of meat at the plots (approximately 20 kg/feeding plot/week) so that an over-abundance of food would be secured if foxes regularly visited the feeding plots, or if other scavengers competed for the meat. An

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 1. Feeding and visit details from supplemental feeding plots in the Grimsö Wildlife Research Area during early summer 2004 and 2005.

Year	Feeding plot	Mean food consumed* (%)	Total food (kg)	Feeding events	Fox visits			Fox frequency	Corvid	
					Known	Likely	Total		Visits	Frequency
2004	1**	75.00	118.0	17	3	1	4	0.24	10	0.59
2004	2	84.69	139.0	17	6	3	9	0.53	13	0.76
2004	3	86.76	143.0	17	3	1	4	0.24	8	0.47
2004	4	71.47	107.5	17	3	0	3	0.18	9	0.53
2004	5***	81.76	123.5	17	8	0	8	0.47	4	0.24
2005	6	94.06	165.0	17	6	0	6	0.35	7	0.41
2005	7	89.00	100.0	11	1	1	2	0.18	7	0.64
2005	8	57.00	68.0	11	3	0	3	0.27	6	0.55
2005	9	96.47	180.0	18	4	1	5	0.28	5	0.28
2005	10	73.82	153.0	18	1	0	1	0.06	6	0.33
2005	11	68.44	125.0	17	3	1	4	0.24	6	0.35

*or removed, **visited once by a dog, ***visited once by a badger.

estimated total of 1,422 kg of meat was placed in the feeding plots during the two years of our study (Table 1).

In order to avoid a numerical response in red foxes, e.g. an increase in the number of fox territories or increased litter size, we kept the period of feeding as short as possible. In 2005, feeding started earlier than in 2004 in order to further assure high fox-use of the feeding plots at the birthing time of roe deer fawns. Feeding started on 5 May 2004 and 15 April 2005, and ended on 24 June 2004 and 23 June 2005 to minimise the long-term effects on survival of red fox cubs.

It was important to assess whether red foxes used the extra food, or if most of it was consumed by other scavengers. The sand beds were used to identify tracks of the species which had utilised the feeding plots. We visited the feeding plots roughly twice weekly and the percentage of meat consumed from the last visit was then estimated and replaced. When fox tracks or scats were found on the sand bed, as well as when the sand smelled of fox urine, we concluded that foxes had visited the feeding plots and carried away and consumed the missing food. Likewise, when rainfall had erased tracks, but when all large bones had been removed, we concluded that foxes had visited the plots, carried away and consumed some of the missing food, because only two visits by other mammalian scavengers or predators were recorded at the feeding plots (see Table 1). In contrast, if large bones were still present, we assumed that avian scavengers such as ravens *Corvus corax* and European jays *Garrulus glandarius* had visited the site and consumed the meat. Other mammalian predators and scavengers at the Grimsö Research Area large enough to carry away bones include wolves *Canis lupus*, lynx *Lynx lynx*, hunting dogs *Canis familiaris*, wild boar *Sus scrofa* and badgers *Meles meles*.

It was important to assess, not only that foxes made use of the food, but also that vixens with cubs did. Therefore in early July each year, a fox den survey was performed within the research area in which all known fox dens and several potential fox dens (in total 201 dens) were visited and searched for signs of presence of a fox litter as well as remains of supplemental food from feeding plots (e.g. sawn-off bones) to determine which dens, if any, were targeted by additional feeding.

Recruitment of roe deer was measured as the number of fawns per radio-marked roe deer doe in autumn. Roe deer does equipped with VHF radio-collars were stalked and observed from 18 August to 15 October (median date 19 September) in order to determine the number of fawns per doe, and thereby the loss of fawns to predators. If a doe was observed alone at the first stalking, two more observations of that doe without fawns were required to conclude that she had lost all her fawns. A total number of 37 does were observed during the two years of supplemental feeding (Table 2). For comparison of fawns/doe index in years with and without additional feeding, we observed a further 18 does in 2003 and 2006. We assumed that roe deer doe recruitment output was equal over years. This could, unfortunately, not be tested because of the small sample size of roe deer does shot during 2003-2006 (0-3 yearly).

Triangulation of does was performed twice weekly from early May until late August to provide data for the determination of summer home-range size and location of each doe. The centre of the does' summer home range was calculated as the mean of all triangulation locations. This centre of home range

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 2. Recruitment of radio-marked roe deer (fawn/doe), expressed as mean (SE) in areas of supplemental feeding (With) and areas without supplemental feeding (Without) during 2003-2006. The northern part of the study area (see Fig. 1) was used as the supplemental feeding area in 2004 and the southern part was used for supplemental feeding in 2005. In 2003 and 2006 no supplemental feeding was conducted.

Year	With	Without
2003		0.60 (0.221), N = 10
2004	1.25 (0.366), N = 8	1.57 (0.297), N = 7
2005	0.91 (0.285), N = 11	0.88 (0.333), N = 8
2006		1.13 (0.350), N = 8

was used to calculate distances to the closest active red fox den as well as mean distances to all active red fox dens and distances to feeding plots for all observed roe deer does. Distance matrixes were calculated in PASSAGE 1.0 (Rosenberg 2003). Voles were caught in snap traps each spring to get an index of vole density.

Statistical analysis

We used general linear models (GLM) to analyse the relationship between roe deer recruitment and log distance to fox den sites, as well as log distance to feeding plot sites and year; as the dependent variable consisted of count data (number of fawns, 0-3), a Poisson link function was used. We conducted analyses using the statistical package R version 2.3.0 (R Development Core Team 2006), and we used the Akaike Information Criterion (AIC_c) corrected for sample size for model selection (Burnham & Anderson 1998). We assessed model fit using standard diagnostic tools. As might be expected, the effect of distance to fox den is non-linear, being smaller the further away from the active den until a threshold is reached, so we also used generalised additive models (GAM) to explore possible non-linearity graphically (Hastie & Tibshirani 1990). Similarly, we used ordinary linear models and GAMs to analyse how much food (percentage removed, arcsine square-root transformed) had been consumed at feeding sites as a function of Julian date, to determine whether red fox use varied over the period observed. We analysed the relationship between the number of fox visits and distance from feeding plots to dens using a simple regression model. We also investigated the overall effect of supplemental feeding on fawn-per-doe ratio in autumn for years with (2004-2005) and without (2003 and 2006) supplemental feeding, and differences in fawn-per-doe ratio between years of supplemental feeding (2004-2005) using unpaired t-tests.

Results

The fox den survey revealed that four red fox litters were born in the research area in 2004 and six in 2005. The distance from fox dens with litters to feeding plots was on average 8,433 m (990-12,060 m) in 2004, and 5,751 m (1,056-6,644 m) in 2005. In 2004, bones or other remains from feeding plots were later found in one of the dens with litters in the northern area of supplemental feeding (distance between the den and the closest feeding plot was 8,321 m) and, in 2005, in two inhabited dens in the southern area of supplemental feeding (distance between dens and the closest feeding plots was 2,111 and 1,477 m, respectively). Red foxes visited all of the feeding sites frequently (see Table 1). Corvids also used feeding plots frequently but only one visit by a badger and one by a dog were recorded (see Table 1). We found no tracks or scats of wolves, lynx or wild boar at or near a feeding site. Use of the extra food (percentage of food removed) increased sharply after feeding began and reached a threshold level before or very early in the critical fawning period for roe deer. Estimated mean birth date for fawns of marked roe deer at the Grimsö Wildlife Research Area is 27 May $\pm$ 9 days (SD; J. Nordström, P. Kjellander, H. Andrén & A. Mysterud, unpubl. data). In 2004, supplemental feeding started on 5 May; the percentage of food removed increased sharply after this date (estimate = 0.0022, $P < 0.001$) until a threshold level of food-use was reached by 20 May. After that date, the percentage of food removed was stable (estimate = 0.000042, P = 0.85). In 2005, feeding started on 15 April and the threshold level of food-use was reached on 25 April (estimate = 0.0073, $P < 0.001$). Thereafter, use of food more or less levelled off (estimate = 0.000088, P = 0.54). There was no relationship between the number of fox visits and the distance between fox dens and feeding plots (P = 0.86, $R^2 = 0.004$). There was no overall difference in fawn-per-doe ratio among years during the study period (2004 vs 2005; t = 2.074, P = 0.046). Supplemental feeding did not significantly increase the fawn-per-doe ratio in autumn when comparing years with supplemental feeding (2004-2005; mean = 1.14, N = 37) to years without supplemental feeding (2003 and 2006; mean = 0.83, N = 18, t = 1.142, P = 0.26; see also Table 2).

The best GLM (with the lowest AIC_c) was the one containing year only (estimate = -0.45, SE = 0.33). The second best GLM to explain variation in the fawn-per-doe ratio included distance between

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 3. Results from model selection performed on recruitment based on observations of radio-marked roe deer at Grimsö Wildlife Research Area in Sweden during 2004-2005. AIC_c = Akaike Information Criterion corrected for small sample size. ΔAIC_c = difference in AIC_c value relative to the model with the treatment effect and effect of distance to the closest red fox den.

Partial R^2							
Log-distance doe to closest							
Feeding plot	Fox den	Year	Total R^2	ΔAIC_c	ΔDeviance	df	P(model)
		0.07	0.070	0.00	1.90	1	0.17
0.01		0.10	0.110	1.19	2.95	2	0.23
0.01			0.010	1.64	0.26	1	0.61
	0.004		0.004	1.79	0.11	1	0.74
	0.004	0.07	0.080	2.09	2.05	2	0.36
0.01	0.030	0.08	0.120	3.15	3.03	3	0.39
0.03	0.004		0.040	3.48	0.98	2	0.61

observed doe and feeding plot, and year (estimate (doe-feeding plot distance) = -0.48, SE = 0.46; estimate (year) = -0.57, SE = 0.35). None of these models had a statistically significant effect on the number of fawns per doe, and R^2 values were very small for all models (Table 3).

Discussion

We found no evidence that roe deer recruitment was affected by supplemental feeding of red foxes in this study. There are several explanations for this result. Negative results are always difficult to explain because they depend on sample size, which in our case was marginal. The measure of fawn-survival used may also be debated. The best way to measure mortality in roe deer fawns is likely to monitor radio-marked fawns directly, but we failed to obtain a sufficient sample. Fawn-per-doe ratio as a recruitment measure cannot distinguish between fawn losses due to predation by other predators and fawn losses due to predation by red foxes. Re-established lynx kill 12.5% of radio-marked roe deer fawns in our study area (J. Nordström, P. Kjellander, H. Andrén & A. Mysterud, unpubl. data), and this may partly mask effects of supplemental feeding of red foxes. Voles *Microtus* sp. are supposedly a main prey of red foxes in our study area, and fluctuations in vole population density may influence fox predation on roe deer fawns (Kjellander & Nordström 2003) but, in spite of the fact that the population density of voles was low in 2004 (0.25 voles/100 trap nights) and high in 2005 (1.51 voles/100 trap nights), there were no significant differences in fawn-per-doe ratio between the two years. This result may be interpreted as being in support of the effects of supplemental feeding, as differences in predation pressure on roe deer fawns between years of high and low vole population densities might have been leveled out by supplemental feeding. However, mean fawn-per-doe ratio was actually lower in 2005 (0.85 fawns per doe) than in 2004 (1.47 fawns per doe), indicating a negative relationship between vole density and number of fawns per doe.

Furthermore, the lynx is an intra-guild predator on the red fox and may affect red fox behaviour and numbers (Sunde et al. 1999, Helldin et al. 2006). However, since the lynx is an integral part of the situation facing managers, the main result of our study, that supplemental feeding of red foxes during the roe deer fawning season does not increase overall roe deer recruitment, is likely to be valid for the current multi-predator system which exists in boreal Sweden.

The lack of effects of supplemental feeding on roe deer recruitment may not apply in areas with higher densities of roe deer and red foxes. The low density of roe deer in our area may mean that red foxes are not actively searching for roe deer fawns because these are a fairly rare prey item. Red fox predation on fawns at the Grimsö Wildlife Research Area amounts to about 17% of fawns of radio-marked roe deer does (J. Nordström, P. Kjellander, H. Andrén & A. Mysterud, unpubl. data), which is much lower than reported from more agricultural areas (Aanes & Andersen 1996 (50%), Jarnemo & Liberg 2005 (42%)) where foxes may be roe deer fawn specialists during early summer (Panzacchi et al. 2008). The low predation rate in the Grimsö Wildlife Research Area is most likely related to low population densities of both red foxes and roe deer, as well as to the landscape structure, and is likely to be representative for large parts of the boreal forest in Scandinavia. For this reason, we suggest that red fox predation on roe deer fawns in the boreal forest might be purely incidental (Vickery et al. 1992), in which case predation may occur, albeit at a low level, even if red foxes are provided with supplemental food.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Our study was designed to fit a scale relevant to local managers or keen hunters. The study areas used each year were about the size of a large hunting area (~65 km^2). Arguments can always be raised that the supplemental feeding effort could have been greater, with more feeding plots and larger amounts of food. However, given the initial premise that a manager or hunter would be carrying out the supplemental feeding in a typical size hunting area, this argument is unrealistic. We simply do not think that the average hunter would spend more time, money and effort on supplemental feeding than we did. We also had a better knowledge of the locations of fox dens than most landowners would have, and thus were better able to target the feeding than the average landowner would be. Indeed, red foxes frequently used the supplemental food, and bones and other remains from feeding sites were found at fox dens suggesting that red fox vixens with cubs were eating the food, clearly documenting that the treatment as such was successful.

Nevertheless, the negative result holds only for the scale we chose as relevant and for the level of red fox predation common to our area. Thus, results from this study clearly suggest that supplemental feeding of red foxes will most likely not be a solution to this management issue or an alternative to predator removal. However, in agriculturally dominated areas where roe deer density and red fox predation rates are higher, and where foxes may act as specialist predators on roe deer fawns (Panzacchi et al. 2008), we cannot exclude that supplementary feeding may increase roe deer recruitment, especially if lynx predation is low.

Acknowledgements - we are grateful to H. Hensel, L. Jäderberg and R. Schneider for help with collection of recruitment data. We also thank L. Jäderberg and K. Sköld for carrying out the fox den survey funded by 'Olle and Signhild Engquists stiftelse'. Thanks to Johan Månsson for constructing distance matrixes in PASSAGE and to G. Samelius for help with Figure 1. This study was supported by a grant to J. Nordström from the private foundation of 'Oscar and Lili Lamms minne'.

References

Aanes, R. & Andersen, R. 1996: The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. - Canadian Journal of Zoology 74: 1857-1865.

Andersen, R., Mysterud, A. & Lund, E. 2004: Rådyret det lille storviltet. - Naturforlaget, Oslo, 134 pp. (In Norwegian).

Burnham, K.P. & Anderson, D.R. 1998: Model selection and inference: a practical information theoretic approach. - Springer Verlag, New York, USA, 353 pp.

Hastie, T. & Tibshirani, R. 1990: Generalized additive models. - Chapman & Hall, London, 356 pp.

Helldin, J-O., Liberg, O. & Glöersen, G. 2006: Lynx (*Lynx lynx*) killing red foxes (*Vulpes vulpes*) in boreal Sweden - frequency and population effects. - Journal of Zoology (London) 270: 657-663.

Jarnemo, A. & Liberg, O. 2005: Red fox removal and roe deer fawn survival - A 14 year study. - Journal of Wildlife Management 69: 1090-1098.

Jarnemo, A., Liberg, O., Lockowandt, S., Olsson, A. & Wahlström, K. 2004: Predation by red fox on European roe deer fawns in relation to age, sex, and birth date. - Canadian Journal of Zoology 82: 416-422.

Kjellander, P. & Nordström, J. 2003: Cyclic voles, prey switching in red fox, and roe deer dynamics - a test of the alternative prey hypothesis. - Oikos 101: 338-344.

Lindström, E., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P-A., Martinsson, B., Sköld, K. & Swenson, J.E. 1994: Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. - Ecology 75: 1042-1049.

Lindström, E., Angelstam, P., Widén, P. & Andrén, H. 1987: Do predators synchronize vole and grouse fluctuations? - An experiment. - Oikos 48: 121-124.

Lindström, E.R. 1994: Large prey for small cubs - on crucial resources of a boreal red fox population. - Ecography 17: 17-22.

Panzacchi, M., Linnell, J.D.C., Odden, J., Odden, M. & Andersen, R. 2008: When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. - Canadian Journal of Zoology 86: 116-126.

R. Development Core Team 2006: Available at http://www.r-project.org/ (Last accessed on 9 March 2009).

Rosenberg, M.S. 2003: Available at: http://www.passagesoftware.net/ (Last accessed on 9 March 2009).

Rushton, S.P., Shirley, M.D.F., Macdonald, D.W. & Reynolds, J.C. 2006: Effects of culling fox populations at the landscape scale: a spatially explicit population modelling approach. - Journal of Wildlife Management 70: 1102-1110.

Sunde, P., Overskaug, K. & Kvam, T. 1999: Intraguild predation of lynxes on foxes: evidence of interference competition? - Ecography 22: 521-523.

Swenson, J.E. & Angelstam, P. 1993: Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. - Canadian Journal of Zoology 71: 1303-1310.

Vickery, P.D., Hunter, M.L. Jr. & Wells, J.V. 1992: Evidence of incidental nest predation and its effects on nests of threatened grassland birds. - Oikos 63: 281-288.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use