

Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging

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Abstract In Scandinavia, an increased red fox *Vulpes vulpes* density during the last decades has been suggested to be caused by direct and indirect human influences on food availability. Recently, attention has been focused on the role of increasing scavenging opportunities due to intensified hunting of ungulates and the reestablishment of large carnivores. In our study, we investigated seasonal and annual variations in diet composition of red fox in Varaldskogen, SE Norway, an area with cyclic voles and a high density of moose *Alces alces*. Analyses of scats revealed significant differences among seasons in the occurrence of ungulates—mainly moose—and ungulates were the dominating food category during winter (44.9 % of all remains). Snow tracking of red fox (71 km) in winter confirmed the importance of ungulate carcasses, i.e. one case of scavenging per 3 km. The proportions of voles were high during all seasons (11.2–28.8 %); in spite of variation in available abundances, no significant seasonal or annual differences were detected. Other food categories with seasonal variation were birds, berries/seeds and amphibians/reptiles, all more common in snow-free seasons. Our study underlines the importance of ungulate remains during periods when the abundance and diversity of alternative food sources is low. Increased and stabilized populations of red foxes—mediated through remains from hunting and wolf kills from

high moose populations—might have an important effect on the population dynamics of small game. Hence, we recommend that this relationship be given attention in future studies.

Keywords *Vulpes vulpes* · Scat analyses · Ungulates · Carrion · Foraging

Red foxes (henceforth referred to as fox) are adaptable and opportunistic omnivores with a wide-ranging diet including invertebrates, mammals, birds, fruits and berries (Lindström 1982; Sillero-Zubiri et al. 2004). As predators, they typically kill birds and mammals up to about 3.5 kg and require approximately 500 g of food per day, often caching food that is in excess to their requirements (Sillero-Zubiri et al. 2004).

The fox rivals the grey wolf *Canis lupus* for having the greatest natural distribution of any living terrestrial mammal besides “man” (Nowak 2005). In northern Europe, this distribution includes areas with cyclic vole populations (O’Mahony et al. 1999), where the length of the cycle is 3–4 years with 50- to 500-fold differences between peak and lowest densities (Korpimäki et al. 2003). The diet composition of foxes seems to track the population cycles of small rodents (Lindström 1982; O’Mahony et al. 1999; Kjellander and Nordström 2003; Dell’Arte et al. 2007). Furthermore, Lindström (1982) showed that the fox density in the southern boreal forest follows the vole cycle with a time lag of 1 year, with densities ranging between two and four adults per 10 km² and concluded that vole abundance was the overriding influencing factor. He also reported that territory size was larger (6–7 km²) in a boreal forest area with cyclic voles than in an area south of the boreal region with higher diversity and abundance of food (4 km²).

In spring and summer, the diet of red foxes is small-mammal-based (Henttonen 1989; Dell’Arte et al. 2007). During the peak and decline phases of the cycle, field voles *Microtus agrestis* always dominated in the diet of adult foxes

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(Lindström 1982). Due to the cyclic patterns of voles, foxes and other medium-sized predators usually switch to alternative prey when their main prey declines, the so-called alternative prey hypothesis (Lack 1954; Hagen 1969; Angelstam et al. 1984). Thus, alternative prey species are less vulnerable to predation when the main prey population (voles) is large.

The importance of scavenging—especially on ungulate carcasses—has been documented (Jędrzejewski and Jędrzejewska 1992; Cagnacci et al. 2003; Wilmers et al. 2003a; Selva et al. 2005; Wikenros 2011). Winter severity, despite its constraints on foxes, may determine the availability of rich food resources, i.e. carcasses of ungulates that died of starvation (Cagnacci et al. 2003). Selås and Vik (2006) suggested that access to ungulate carcasses—depending on snow depth—may be of vital importance for both winter survival and spring condition and thus for the reproduction of foxes.

Three main mortality factors make ungulate carcasses available to scavengers (Selva et al. 2005): (1) Natural deaths supply scavengers with intact corpses in big pulses, usually at the end of the winter; (2) predation by resident large carnivores may have a strong influence on scavenging communities by constantly subsidizing them with the remains of their kills (Wilmers et al. 2003a); (3) human-caused mortality, mainly from hunting, is nowadays an important provider of carcasses in many areas (Wilmers et al. 2003a; Selva 2004) as well as vehicle-wildlife collisions. From south-central Scandinavia, Wikenros (2011) and Wikenros et al. (2013) reported that the largest food source for scavenging species was remains after hunter harvest of moose *Alces alces* in autumn, both in areas with and without wolf presence, whereas the remains stemming from vehicle collisions was relatively small. In areas with wolves, the biomass from hunting remains was approximately twice as high than from wolf kills. The use of carrion as a supplemental food resource during prey shortages may have substantial impacts on the population dynamics of predators and their prey (DeVault et al. 2003). This supports the hypothesis that hunters could well be providing a temporal resource pulse for scavenging mesopredators such as the red fox, thus contributing to maintaining dense populations of this predator, with subsequent impacts on alternative prey species like grouse.

During the last 50–60 years, moose populations in Fennoscandia increased dramatically. In Norway, the annual numbers of animals culled during the hunting seasons increased from c. 5,000 in early 1950s to >35,000 in 1990 (Statistics Norway 2013). During the same period, the populations of several small-game species declined markedly (Marcström 1979; Wegge 1979; Henttonen 1989), presumably caused by increased predation from increasing numbers of generalist predators, especially fox (Angelstam et al. 1984; Marcström et al. 1988; Henttonen 1989; Wegge et al. 1992; Helle et al. 2003). Predation by fox was found to be the main mortality factor on capercaillie *Tetrao urogallus* in the present

study area of Varaldskogen (Wegge and Rolstad 2011), and the role of fox as predator on forest grouse was well documented when an outbreak of sarcoptic mange *Sarcoptes scabiei* in the 1980s reduced fox populations dramatically over large areas in Fennoscandia, with subsequent increases in the grouse populations (Lindström et al. 1994; Smedshaug et al. 1999).

More recently than has the increase in moose, the wolf *C. lupus* population on the Scandinavian Peninsula has recovered dramatically in recent years. Between 1998 and winter 2010 wolf numbers grew from 50–72 individuals to an estimated 252–29 individuals (Wabakken et al. 2010). Undoubtedly, this increased the biomass available to scavengers, again with the potential to influence factors further down the food chain (Wikenros et al. 2013).

The objective of this study is to describe the seasonal diet of foxes in a boreal forest with cyclic voles and a dense population of moose. We hypothesize that scavenging on moose carcasses and remains from hunter-killed moose constitute a significant part of the foraging activity of foxes during late autumn and winter when other food sources are scarce. This may contribute to maintaining dense populations of foxes, with subsequent predation impacts on small game species.

Materials and methods

Study area

The study area is located in Hedmark County next to the Swedish border in southeast Norway (60°10' N, 12°30' E), and covers 100 km², of which the eastern part of the Varald State Forest (c. 40 km²) constituted an intensively monitored core area (Wegge and Rolstad 2011). The gently undulating terrain between 200 and 400 m above sea level consists of Norway spruce *Picea abies* (40 % standing volume) and Scots pine *Pinus silvestris* (58 % standing volume) forests interspersed with scattered birch *Betula spp.* (2 % standing volume) and aspen *Populus tremula*. In the older, semi-natural forest, ericaceous shrubs dominate the field layer, heather *Calluna vulgaris* and cowberry *Vaccinium vitis-idaea* in the less productive pine forest and forested peat bogs and bilberry *Vaccinium myrtillus* in the spruce-dominated forest on mesic sites (Wegge and Rolstad 2011). Varaldskogen has a moderate continental climate with average temperatures of 15.8 °C in July and −5.1 in January. The average annual precipitation is 700 mm, with snow covering the ground usually from November to late April. A few small farms and settlements are located along the periphery of the study area; except for logging operations and recreational activities, human impact and disturbance are low. Black grouse *Tetrao tetrix* and Capercaillie occur at moderately high densities with highly

patchy distributions of Hazel grouse *Bonasa bonasia* (Wegge and Rolstad 2011). The main predators in the study area are the fox, pine marten *Martes martes* and goshawk *Accipiter gentilis*. Wolf and lynx *Lynx lynx* have recently become regular visitors, and raven *Corvus corax* is the main avian scavenger. For more information on study area, see Wegge and Rolstad (2011).

In Hedmark County, with a forested area of c. 17,000 km², the moose population is quite dense with 7,284 animals culled during the 2006 hunting season (Statistics Norway 2011). In the 40-km² study area, the autumn populations were estimated at 70–80 animals during 2005–2010, of which >12 animals were harvested each year (Statistics Statskog 2013). No reliable density estimates exist for roe deer *Capreolus capreolus* in our study area. However, hunting statistics from the Kongsvinger municipality indicate that their density is far lower than the density of moose, as annual numbers of shot moose are approximately four times higher than the number of shot roe deer (Statistics Norway 2013). Red fox is common and distributed throughout the study area.

Scat collection and analysis

Fox scats were collected along forest roads and trails in April and July 2005, May and August 2006, and December 2009 to March 2010. Snow tracking in January to February 2009 provided an additional sample. The samples collected in April and May are hereafter referred to as “spring samples”, although some may stem from late winter, i.e. before the snow melted. July and August are referred to as “summer”, whereas scats from December to March are termed “winter samples”. Collection sites were spread out across the whole study area in order to minimize autocorrelation and to obtain scats from as many different individuals as possible. The scats were stored in paper envelopes with their unique GPS location and frozen prior to analysis. In the laboratory, the scats were oven-dried at 90 °C for 24 h in order to destroy harmful parasites. Once desiccated, soaking in water in individual containers for 24–48 h rehydrated the scats. This enabled a gentle breakdown of the scat to avoid potential damage to identifiable macro-components. Micro and macro-components were then separated through a sieve of 0.5 mm, and the micro components subsequently discarded.

The macro components were analysed following the point-frame method developed by Chamrad and Box (1964) later modified by Ciucci et al. (2004) and Wegge et al. (2012). This method assumes a random distribution of the macro-components, and the contents were therefore thoroughly mixed and subsequently evenly spread over a clear gridded plastic tray before analysis. Subsequently, 50 individual macro-components were selected from the grid. Hits of macro-components were selected closest to the intersections of the grids.

The selected macro-components were identified using a dissecting microscope and consulting reference manuals (Day 1966; Brom 1986; Teerink 1991) and a selection of reference samples compiled by the Norwegian University of Life Sciences. Hairs were initially examined visually looking at hair colour, length and thickness and thereafter—using a compound microscope—identified on the basis of medullar pattern and cuticle scale (Teerink 1991). Remains from ingested birds do not emerge from the digestive process as well preserved as do mammalian hairs, only quill bases are more readily detected (Reynolds and Aebischer 1991). However, Galliformes have a unique feature where the feather resembles splitting into two just above the base of the quill, which enabled a fast identification of grouse remains. Hence, whenever possible, feathers from the order Galliformes were identified according to Brom (1986) and Day (1966).

Small mammals were pooled together except when it was possible to identify *Microtus*, *Myodes* and *Sorex* species using teeth or mandibles (Yalden and Morris 1990). Ungulates, including roe deer and moose, were also pooled together. Roe deer were present in the study area, but in very low numbers. It was assumed that ungulate hair had originated from carcasses. At the time of the sampling sessions, ungulates were most likely to be consumed as carcasses as roe deer calves had grown up and could normally move fast and escape from predation by foxes (Cagnacci et al. 2003) and moose are not in danger from predation by foxes. When bones were recorded in scats with hair purely from one species, they were counted as hits for that species.

The macro-components were identified to species or species group (Table 1). The number of times each species or group classification occurred in the scat samples of each sampling period was recorded and henceforth referred to as its frequency of occurrence (FO). The sum of all FOs exceeded 100 % because nearly all scats contained more than one food item. We used log-linear likelihood models (*G* tests) on contingency tables (Reynolds and Aebischer 1991) in order to test for differences in overall diet composition between sampling periods. We grouped food items into five categories, i.e. “voles”, “ungulates”, “berries/seeds”, “birds” and “other” (other mammals, invertebrates, reptiles and amphibians), and converted FOs into “whole scat equivalents” (WSEs) following the method described by Angerbjörn et al. (1999). This method allows for direct comparisons of proportions of ingested of different food items in scats without altering the total sample size. For instance, if 10 scats contained proportions of 90 % ungulates and 10 % berries, they would be converted to nine scats of 100 % ungulates and one scat of 100 % berries. We used logistic regression models for analysing temporal variation in the occurrence of specific food categories, using presence/absence of the given food items as a binomial response variables. Explanatory variables were as follows: YEAR (year of sample collection, i.e. 2005,

Table 1 Frequency of occurrence (%) of food categories in the scats of red fox collected in different sampling periods and years in Varaldskogen, southeast Norway. (*n*)=Number of scats examined

Category	April 2005 (50)	July 2005 (50)	May 2006 (50)	August 2006 (50)	February 2009 (40)	Winter ^a 2010 (42)
Small rodents	56	64	31	48	35	60
Ungulates ^b	60	14	38	2	77	74
Other mammals ^c	12	16	18	2	8	5
Birds ^d	16	38	22	30	13	21
Amphibians and reptiles	8	14	64	26	0	0
Invertebrates	28	68	33	68	3	5
Berries and seeds 50	50	70	71	98	5	43

^a Winter, December 2009 to April 2010

^b Mainly moose, only few roe deer (<10 %)

^c Mountain hare, red squirrel and unknown mustelid

^d Mainly Capercaillie and black grouse

2006, 2009 and 2010), WINTER (whether samples were collected in the winter months of 2009 and 2010 or in any other season), SUMMER (collected in the summer months of July 2005 and August 2006, or in any other season), SEASON (grouping the samples into winter, summer and spring, where the latter were samples from April 2005 and May 2006) and PERIOD (i.e. six sampling periods). The explanatory variables were not independent, and thus, we used only one variable per model and evaluated their relative performance based on comparison of Akaike information criterion (AIC) values (Burnham and Anderson 2002).

Small-rodent snap trapping has been carried out annually for several years in late summer in the study area (see Wegge and Rolstad 2011). As seen in Fig. 1, the abundance of small rodents has changed over the years with a strong peak in 2010 and two smaller peaks in 2004 and 2007

Snow tracking

During January to February 2009, roads and trails were surveyed for fox tracks by car, snow scooter and on foot during the day. When found, tracks were followed on snowshoes and

mapped. The tracks were backtracked so as not to disturb the study subjects and were followed for 1–2 km, aiming for a minimum of 1 km and a maximum of 2 km. These guidelines were implemented to efficiently sample as many different track sets as possible.

Sixty-two fox tracks were mapped with an average length of 1,150 m. Hunting attempts and evidence of scavenging were recorded and mapped, and the types of prey were identified whenever possible. Digging into snow where prey remains were present confirmed a successful hunt. Diggings into the snow where no prey remains were found were recorded as hunting attempts. Evidence of scavenging was clear because the tracks would lead to a carcass or a part thereof. Occasionally, remains of prey would be found randomly along the fox track, and depending on the species, this would be recorded as either depredation or scavenging.

Results

Scat analysis

Temporal variation

The overall diet composition differed significantly both among seasons ($G=72.67$, $DF=8$, $P<0.001$) and years ($G=73.65$, $DF=12$, $P<0.001$). However, the analyses of temporal patterns in the occurrence of each food category separately with logistic regression models revealed that seasonal rather than annual variations in diet composition were the most pronounced, as none of the best models included the factor YEAR (Tables 1, 2 and 3).

The occurrence of ungulate remains in scats was best explained by the factor SUMMER (Table 2 and 3), i.e. this food category was rarely recorded in summer samples, but far more frequently in spring and winter. During winter, ungulates

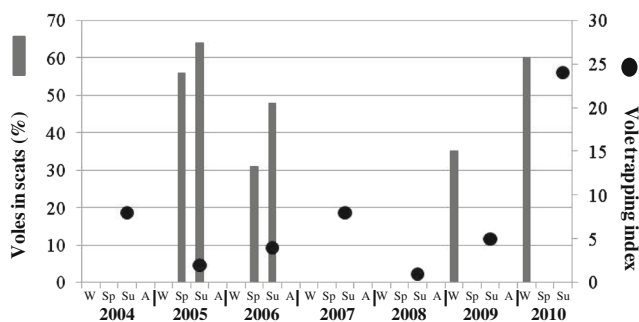


Fig. 1 Vole abundance indices (no. trapped per 100 trap nights) and the frequencies of occurrence (%) of voles in red fox scats collected in Varaldskogen SE Norway. W winter, Sp spring, Su summer, A autumn

Table 2 Results from logistic regression models of contents in red fox scats collected in Varaldskogen, SE Norway, during the springs and summers of 2005 and 2006 and the winters of 2009 and 2010. Thebinomial response variable were presence/absence of different food categories in scats ($n=277$), whereas explanatory variables were time of collection

Parameter	Ungulates		Birds		Amphibians reptiles		Invertebrates		Berries seeds	
	Δ AIC	w	Δ AIC	w	Δ AIC	w	Δ AIC	w	Δ AICw	w
SEASON	75.92	0.00	8.66	0.01	4.67	0.09	58.31	0.00	34.88	0.00
SUMMER	0.00	1.00	0.00	0.87	42.20	0.00	0.00	0.84	9.09	0.01
WINTER	31.57	0.00	5.62	0.05	0.00	0.91	3.39	0.16	0.00	0.99
YEAR	57.07	0.00	6.95	0.03	36.83	0.00	27.26	0.00	37.97	0.00
PERIOD	75.61	0.00	8.22	0.01	38.20	0.00	50.67	0.00	47.30	0.00
NULL	83.76	0.00	6.69	0.03	40.28	0.00	67.64	0.00	53.44	0.00

The food categories “Rodents” and “other mammals” (see Table 1) were excluded due to a low performance of all candidate models. Values from the best models are in italics

SEASON Spring, summer or winter; *SUMMER* Summer or in any other period; *WINTER* Winter or in any other period; *YEAR* 2005, 2006, 2009 or 2010; *PERIOD* sampling period (six periods); *NULL* Null model with only intercept. Δ AIC the Akaike Information Criterion of each model minus the AIC value of the best model; w Akaike weight, i.e. the relative likelihoods of each model

was the dominating food category, 44.9 % of all identified material (%WSE), whereas the proportion in spring samples was 20.2 %, and in summer samples only 2.8 % (Fig. 2).

SUMMER was also the best factor explaining the occurrence of the two food categories birds and invertebrates although occurrences were higher during summer than in lower in spring and winter (Tables 2 and 3, Fig. 2).

The factor WINTER (i.e. whether samples were collected during winter or in spring/summer) was included in the best models of the occurrence of both berries/seeds and amphibians/reptiles, with the lowest numbers in winter. Surprisingly, berries showed up rather frequently during spring, probably due to a quite extensive consumption of over-wintering berries, such as cowberry and cranberry *Vaccinium oxycoccos*, soon after the snow melted.

The food category “other mammals” (all mammal species except ungulates and small rodents) showed a weak tendency

to vary according to sampling PERIOD, whereas none of the models explained the occurrence of small rodents. The proportions of the former food category in the scats were generally low, whereas the proportions of the latter were relatively high in all sampling periods (Fig. 2, Tables 1 and 2).

Snow tracking

Of 44 scats collected during winter 2009, only 40 were suitable for analysis (4 scats contained no macro-components). Hunting attempts on various species, dominated by small mammals, were recorded 71 times (Table 4), suggesting a hunting attempt on average once per kilometre. Scavenging was evident on average every 2.8 km with 25 cases, of which ungulates represented 92 % of the cases.

Discussion

This study demonstrates that scavenging on moose carcasses/remains was a main foraging activity during winter. The

Table 3 Parameter estimates and significance values from the best logistic regression models (lowest AIC) of contents in red fox scats collected in Varaldskogen, SE Norway. The binomial response variable was presence/absence of different food categories in scats. Explanatory variables are further explained in Table 2

Category	Parameter estimates (SE)	P value
Rodents	-0.58 (0.36) INT +0.41 (0.25) SUMMER	0.109
Ungulates	3.39 (0.48) INT -2.91 (0.40) SUMMER	<0.001
Other mammals	-1.39 (0.41) INT -0.26 (0.13) PERIOD	0.001
Birds	-2.36 (0.44) INT +0.85 (0.29) SUMMER	<0.001
Amphibians/reptiles	2.42 (1.06) INT -3.41 (1.02) WINTER	0.001
Invertebrates	-3.78 (0.45) INT +2.26 (0.29) SUMMER	<0.001
Berries/seeds	3.05 (0.41) INT -2.09 (0.30) WINTER	<0.001

INT intercept, *SUMMER* if scats stemmed from summer or any other season, *WINTER* scats from winter or any other season, *PERIOD* sampling period (six periods), irrespective of season

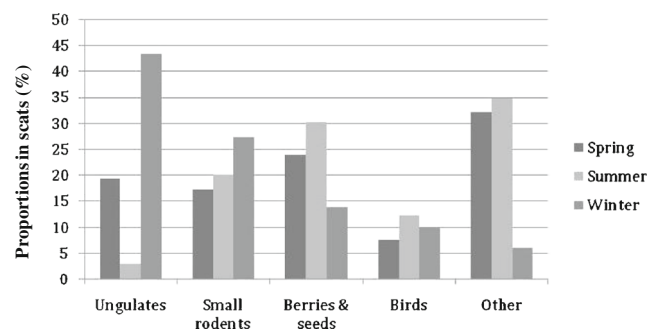
**Fig. 2** Seasonal changes in the major food groups in the diet of red fox in the Varaldskogen study area in 2005–2009, expressed as proportions of recognized material in scats. *Ungulates* mainly moose, *Small rodents* field voles and bank voles, *Birds* mainly capercaillie and black grouse

Table 4 Hunting attempts (71 times) and scavenging (25 times) recorded along 62 different red fox tracks followed in a total of 71 km during winter 2009 at Varaldskogen, SE Norway

Species	Hunting attempts (%)	Scavenging (%)
Rodent	64 (90)	
Frog	2 (3)	
Black grouse	3 (4)	
Capercaillie	2 (3)	
Moose		15 (60)
Roe deer ^a		8 (32)
Grouse		2 (8)

^a A few roe deer carcasses from traffic deaths were distributed within the study area to attract foxes for live trapping. Foxes frequently visited them, and the recorded roe deer scavenging probably stemmed from these feeding stations

occurrence of this food item decreased successively during spring and summer. Small rodents were common in scats from all seasons, whereas all other food categories were most common in scats from snow-free periods.

The ratio of food (nutritional value, e.g. meat) to waste (no nutritional value, e.g. hair, feathers and bone) products will vary between prey species, depending on their individual size (Klare et al. 2011). In carnivore scats, the proportion of waste to food will be greater for a small mammal than it will be for larger animals such as ungulates. Hence, in general, the frequency of occurrence (FO) overestimates the importance of small mammals as food compared to larger animals. However, our foxes ingested mainly material from left-over body parts from hunter-killed moose and—presumably—some from consumed and deserted wolf kills. Thus, the ratio of food to waste from moose was less distorted relative to that of small mammals than it would have been if derived from whole animals. Nevertheless, there is little doubt that remains from moose constituted a main source of food during winter and early spring. This conclusion is also supported by the results from the snow tracking, as scavenging on ungulate carcasses occurred on average every 3 km.

From the north temperate Biolowieza forest, Jędrzejewski and Jędrzejewska (1992) and Kidawa and Kowalczyk (2011) reported that the main foraging activity of foxes was scavenging on ungulate carcasses, and Selås and Vik (2006) showed that the growth in red fox populations in Norway during the previous century was positively associated with the growth in cervid numbers. Kidawa and Kowalczyk (2011) also observed an increasing consumption of ungulate carrion with increasing forest cover. These findings support our results as they underline the importance of ungulate carrion, especially in forested areas, during winter.

Skonhoft (2006) and Selva (2004) found that wolves display a preference for moose. Wikenros (2011) found that from wolf-killed moose, approximately 30 % of the available

biomass was left for scavengers. The latter is an important factor considering the recent re-establishment of wolves and the high densities of moose within the study area. Not only do wolves provide food for foxes during the critical winter period, but wolves also appear to reduce the variability, both within and between years, of winter food availability (Wilmers et al. 2003b; Wikenros 2011; Wikenros et al. 2013).

With a high density of moose, hunting pressure is high: within the general study area during 2005–2010, an average of 14 animals was harvested per year in 65 km² (Statistics Statskog 2013). Hence, in the smaller area where scats were collected, 8–10 animals were slaughtered each autumn, providing foxes and other scavengers with supplemental food. Except for discarded stomachs and intestines, which are consumed quickly, left-over legs, heads and skin are relatively low in nutritional value, but since they make up a large quantity distributed across the forest, they may constitute an important food source for foxes. Unfortunately, some animals are also wounded during hunting and then die later. Just one such carcass, with a body weight of >200 kg, may sustain a fox for several months during the critical winter season (Selva et al. 2003). Although not a common occurrence, non-systematic observations during >30 years of fieldwork indicate that such deaths occur once every 3–4 year in the study area (Wegge, unpubl.). Moose remains from vehicle collisions probably did not exist in our study area, as the area only have some few forestry roads with very little vehicular traffic.

Cyclic patterns of small rodents determine their availability as prey. In our study, small rodents were the most frequently recorded prey item in the scats, but the variation did not match their fluctuating pattern of abundance. The proportion tended to be lower in the year when rodents were in the increasing phase of their cycle, but the highest frequency in scats was recorded in the crash year in 2005. In winter scats, small rodents made up a large proportion of the prey items, nearly doubling their frequency of occurrence from winter 2009 to 2010. As they were then increasing in numbers towards the large peak in summer 2010, small rodents were probably more abundant than in 2009. However, a more likely explanation for the pronounced difference is that the two winters were quite different: in 2009, snow cover was low with temperatures frequently shifting between warm and cold, causing an icy ground layer in the forest. Winter 2010 was quite opposite, with a thick layer of loose snow and consistently cold temperatures, producing dry, insulating snow down to the ground. Presumably, small rodents suffered much higher mortality from exposure during winter 2008–2009 than in the following winter season.

Wilmers et al. (2003a) suggested that the consumer species that are able to respond to brief food pulses are usually generalist species. Ostfeld and Keesing (2000) went on to suggest that positive numerical responses by consumers to such pulsed resources may have strong trophic consequences.

Once a pulse has dissipated, high consumer densities frequently lead to high levels of predation on alternative prey (Ostfeld and Keesing 2000). This has been proposed as a main cause of grouse population cycles in Fennoscandia (Myrberget 1974; Angelstam et al. 1984; Lindström 1982; Lindström et al. 1994). Our study demonstrates the importance of moose remains during winter when food availability is generally low. Furthermore, other authors have shown that the consumption of ungulate carrion increases in periods with low availability of small rodents (Jędrzejewski and Jędrzejewska 1992; Killengreen et al. 2011). Hence, if wolves and man are now supplementing the diet of foxes during years of low small-rodent abundance, the annual fluctuations in the density of foxes is likely to stabilize, subsequently presenting higher predation pressure on alternative prey species such as Tetraonidae during years of low rodent abundance. Regrettably, our bird sample sizes in the scats were too small and distributed irregularly across the rodent cycle to confirm or refute this. Hence, we recommend that more research be focused on the importance of human-induced subsidies for red fox population density and dynamics, and its effect on small-game populations.

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References

- Angelstam P, Lindström E, Widen P (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62:199–208
- Angerbjörn A, Tannerfeldt M, Erlinge S (1999) Predator–prey relationships: arctic foxes and lemmings. *J Anim Ecol* 68:34–49
- Brom TG (1986) Microscopic identification of feathers and feather fragments of Palearctic birds. *Bijdragen tot de Dierkunde* 56(2):181–204
- Burnham KP, Anderson RD (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag, New York
- Cagnacci F, Lovari S, Meriggi A (2003) Carrion dependence and food habits of the red fox in an alpine area. *Italian J Zool* 70:31–38
- Chamrad AD, Box TW (1964) A point-frame method for sampling rumen contents. *J Wildl Manag* 28:473–477
- Ciucci P, Tosoni E, Boitani L (2004) Assessment of the point-frame method to quantify wolf *Canis lupus* diet by scat analysis. *Wildl Biol* 10:149–153
- Dell’Arte GL, Laaksonen T, Norrdahl K, Korpimäki E (2007) Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta Oecol* 31:271–281
- DeVault TL, Rhodes OR Jr, Shivik JA (2003) Scavenging by vertebrates: behavioural, ecological and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102: 225–234
- Day MG (1966) Identification of hair and feather remains in the gut and faeces of stoats and weasels. *J Zool* 148:201–217
- Hagen Y (1969) Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent fluctuations. *Fauna* 22: 73–126
- Helle P, Belkin V, Bljudnik L, Danilov PI, Jakimov A (2003) Changes in grouse populations in Finland and Russian Karelia during past decades. *Suomen Riista* 49:32–43
- Henttonen H (1989) Does an increase in the rodent and predator densities, resulting from modern forestry, contribute to the longterm decline in Finnish tetraonids? *Suomen Riista* 35:83–90, In Finnish with English summary
- Jędrzejewski W, Jędrzejewska B (1992) Foraging and the diet of the red fox *Vulpes vulpes* in relation to variable food resources in Białowieża National Park, Poland. *Ecography* 15: 212–220
- Kidawa D, Kowalczyk R (2011) The effect of sex, age, season and habitat on diet of the red fox *Vulpes vulpes* in northeastern Poland. *Acta Theriol* 56:209–218
- Killengreen ST, Lecomte N, Ehrich D, Schott T, Yoccoz NG, Ims RA (2011) The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. *J Anim Ecol* 80:1049–1060
- 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
- Klare U, Kamler JF, MacDonald DW (2011) A comparison and critique of different methods for determining carnivore diet. *Mammal Rev* 41(4):294–312
- Korpimäki E, Klemola T, Norrdahl K, Oksanen L, Oksanen T, Banks PB, Batzli GO, Henttonen H (2003) Vole cycles and predation. *Trends Ecol Evol* 18(10):494–495
- Lack D (1954) The natural regulation of animal numbers. Oxford University Press, Oxford
- Lindström ER (1982) Population ecology of the red fox (*Vulpes vulpes* L.) in relation to food supply. Ph.D. Thesis, University of Stockholm, Sweden
- Lindström ER, Andrén H, Angels P, Cederlund G, Hörmfeldt B, Jäderberg L, Lemnell PA, Martinson B, Sköld K, Swenson JE (1994) Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. *Ecology* 75:1042–1049
- Marcström V (1979) A review of the tetraonid situation in Sweden. *Proc Int Grouse Symp* 1:13–16
- Marcström V, Kenward RE, Engren E (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. *J Anim Ecol* 57:859–872
- Myrberget S (1974) Variations in the production of willow grouse *Lagopus lagopus* (L.) in Norway 1963–1972. *Ornis Scand* 5:163–172
- Nowak RM (2005) Walker’s carnivores of the world. The John Hopkins University Press, Baltimore, Maryland
- O’Mahony D, Lambin X, MacKinnon JL, Coles CF (1999) Fox predation on cyclic field vole populations in Britain. *Ecography* 22:575–581
- Ostfeld RS, Keesing F (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol Evol* 15(6):232–237
- Reynolds JC, Aebischer NJ (1991) Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the red fox *Vulpes vulpes*. *Mammal Rev* 21(3): 97–122
- Selås V, Vik JO (2006) Possible impact of snow depth and ungulate carcasses on red fox (*Vulpes vulpes*) populations in Norway, 1897–1976. *J Zool* 269:299–308
- Selva N (2004) The role of scavenging in the predator community of Białowieża Primeval Forest (E. Poland). Ph.D. Thesis, Polish Academy of Science, Poland, and the University of Sevilla, Sevilla, Spain

- Selva N, Jędrzejewska B, Jędrzejewski W, Wajrak A (2003) Scavenging on European bison carcasses in Białowieża Primeval Forest (eastern Poland). *Ecoscience* 10(3):303–311
- Selva N, Jędrzejewska B, Jędrzejewski W, Wajrak A (2005) Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Can J Zool* 83:1590–1601
- Sillero-Zubiri C, Hoffmann M, Macdonald DW (2004) Canids: foxes, wolves, jackals and dogs: Status Survey and Conservation Action Plan. IUCN/SSC Canid Specialist Group
- Skonhøft A (2006) The costs and benefits of animal predation: an analysis of Scandinavian wolf re-colonisation. *Ecol Econ* 58(4): 830–841
- Smedshaug CA, Selås V, Lund SE, Sonerud GA (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildl Biol* 5:157–166
- Statistics Norway (2011) <http://www.ssb.no>
- Statistics Norway (2013) <http://www.ssb.no>
- Statistics Statskog (2013) <http://www.statskog.no>
- Teerink BJ (1991) Hair of West European mammals: Atlas and identification key. Cambridge University Press, Cambridge
- Wabakken P, Aronson Å, Strømseth TH, Sand H, Maartman E, Svensson L, Flagstad O, Hedmark E, Liberg O, Kojola I (2010) The wolf in Scandinavia: status report of the 2009–2010 winter. Oppdragsrapport4-2010. Høgskolen i Hedmark, Elverum. (In Norwegian with English summary, figures and tables.)
- Wegge P (1979) Status of capercaillie and black grouse in Norway. *Int Grouse Symp* 1:17–26
- Wegge P, Rolstad J, Gjerde I (1992) Effects of habitat fragmentation on capercaillie grouse: empirical evidence and management implications. In: McCullough DR, Barrett RH (eds) *Wildlife 2001: Populations*. Elsevier Science Publishers, Amsterdam, pp 738–749
- Wegge P, Rolstad J (2011) Clearcutting forestry and Eurasian boreal forest grouse: long-term monitoring of sympatric capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* reveals unexpected effects on their population performances. *Forest Ecol and Manag* 261:1520–1529
- Wegge P, Shrestha R, Flagstad Ø (2012) Snow leopard *Panthera uncia* predation on livestock and wild prey in a mountain valley in northern Nepal: implications for conservation management. *Wildl Biol* 18:131–141
- Wikenros C (2011) The return of the wolf—effects on prey, competitors and scavengers. Ph.D. Thesis, Swedish University of Agricultural Sciences, Uppsala
- Wikenros C, Sand H, Ahlqvist P, Liberg O (2013) Biomass flow and scavengers use of carcasses after Re-colonization of an apex predator. *PLoS One* 8(10):e77373. doi:10.1371/journal.pone.0077373
- Wilmers CC, Stahler DR, Crabtree RL, Smith DW, Getz WM (2003a) Resource dispersion and consumer dominance: scavenging at wolf and hunter killed carcasses in Greater Yellowstone, USA. *Ecol Lett* 6:996–1003
- Wilmers CC, Crabtree RL, Smith DW, Murphy KM, Getz WM (2003b) Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *J Anim Ecol* 72:909–916
- Yalden DW, Morris PA (1990) The analysis of owl pellets. *Mammal Society Occasional Publications* 13. Mammal Society, London