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ORIGINAL PAPER

Snow tracking reveals different foraging patterns of red foxes and pine martens

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Abstract Red fox (*Vulpes vulpes*) shares similar prey preferences and co-occurs with several other carnivores, and is together with pine marten (*Martes martes*), the most common mesocarnivore in the northern boreal forest. Voles are important prey for both species, but it is unclear to what extent they compete for the same food resources in winter. Here, we use 2139 km and 533 km of meticulous snow tracking of red foxes and pine martens to evaluate their food niches. We measured hunting and digging behaviour, whether successful or not, and the effect of snow depth and temperature. Pine martens were restricted to forested habitats, whereas red foxes used a wide range of habitats. Red foxes were found to dig more often than pine martens, 0.67 vs. 0.39 digging events per kilometre. Hunting was less common and similar in both species, about 0.1 hunting event per kilometre. Pine martens were more efficient in hunting and finding food remains compared to red foxes. Increasing snow depth reduced hunting success and also reduced dig success of red foxes. Food niche overlap was small. Red foxes used mostly voles and carrion remains of ungulates, whereas pine martens used cached eggs and small birds. We suggest that caching eggs is an important strategy for pine martens to survive winter in northern latitudes. Snow depth was important for capturing voles, and thick snow cover appeared to mask the effect of vole peaks. Intensified land use, as clear-cutting and leaving slaughter remains from harvest, will benefit red foxes on the expense of pine martens. The ongoing climate change with warmer winters and less snow will likely further benefit the red fox.

Keywords Niche · Competition · Red fox · Pine marten · Carcass · Egg · Voles

Introduction

Many medium-sized mammalian carnivores overlap in prey preferences, and the relative abundance of competing species is likely affected by interspecific competition (Holt 1977; Pianka 1981). Intraguild predation may further enhance the outcome of competition, even if it is only a small proportion of the predators' diet (Palomares et al. 1999). Red fox (*Vulpes vulpes*) shares partly similar prey preferences and co-occurs with several other carnivores (Brangi 1995; Kauhala et al. 1998; Carvalho and Gomes 2001; Elmhagen and Tannerfeldt 2002; Mitchell and Banks 2005; Lanszki et al. 2006; Sidorovich et al. 2010; Murdoch et al. 2010; Bassi et al. 2012). Increased competition from red foxes is proposed as an important factor eliminating the arctic fox (*V. lagopus*) from large parts of the Scandinavian tundra (Hersteinsson et al. 2003).

Red foxes and pine martens (*Martes martes*) are common mesopredators in the boreal conifer forests of northern Scandinavia (Kurki et al. 1998). At the turn of the last century, both species had been harvested down to substantially lower densities than today because of their valuable winter fur and as part of extensive predator control programs (Helldin 2000a; Selas and Vik 2006). Pine martens became completely protected during the 1930s in Sweden (Helldin 2000a), but the red foxes appear to have better sustained the intensive harvest programs and were never protected. Today, there is

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an open, but restricted season for both species, although the interest for population control and fur harvest is limited.

The red foxes are highly adaptable and found in a wide range of landscapes, including pine marten habitat, which is mostly restricted to the conifer forest (Storch et al. 1990). Only a few density estimates are available on red foxes and pine martens in Sweden: A range of 0.2–0.8 red fox km^{-2} was estimated from south and central parts of Sweden (Lindström et al. 1987), and winter densities of 0.2–0.4 km^{-2} were reported from a conifer-dominated area in northern Sweden (Willebrand 1988). The latter study recorded pine marten densities of 0.3–0.4 km^{-2}, which is similar to the 0.3 km^{-2} estimated by Helldin (1999). Both red foxes and pine martens show functional and numerical responses to the variation in vole (subfamily *Arvicolinae*) abundance (Englund 1970; Hanski et al. 1991; Helldin 2000b), which often exhibit geographically synchronized multiannual cyclic fluctuations (Hornfeldt et al. 1986; Marcstrom et al. 1990). Woodland grouse (subfamily *Tetranoinae*) and mountain hares (*Lepus timidus*) are alternative prey when voles are scarce (Small et al. 1993), and a negative effect of increased predation from red foxes and pine martens has been shown experimentally (Marcstrom et al. 1988a; Marcstrom et al. 1988b; see also Jahren et al. 2016).

Little is known about the interaction between red foxes and pine martens in the boreal forest, but predation by red foxes on pine martens has been recorded (Lindstrom et al. 1995). Bag records of pine martens also increased dramatically during the severe outbreak of sarcoptic mange in red foxes in Sweden (Storch et al. 1990), although Kurki et al. (1998) suggested that the long-term effect on the pine marten population from red fox competition was limited. In addition, there are reported cases of predation by pine martens on red fox cubs (Brzeziński et al. 2014). It has been proposed that winter severity limits the distribution of red foxes (Bartoń and Zalewski 2007), when prey availability is at its minimum in northern Sweden. Abundance of birds is greatly reduced due to southward migration, and snow can make it difficult to hunt remaining potential prey. Especially the voles are protected by occupying the subnivean space, and Lindstrom and Hornfeldt (1994) showed that the amount of small rodents in fox stomachs declined with increasing snow depths. Studies using camera traps and scat analysis have shown that remains of ungulate carcasses are an important food source for red foxes (Lund 1962; Englund 1965; Jedrzejewski and Jedrzejewska 1992; Needham et al. 2014; Selas and Vik 2006). Pine martens also appear to be a generalist predator with a winter diet similar to the red fox. Pine marten will also catch prey in trees, and red squirrels (*Sciurus vulgaris*) can be a regular finding in pine marten scats, but it is rarely found in red fox scats or stomachs from the same area (Storch et al. 1990; Helldin 2000b).

Here, we use data from extensive snow tracking of red foxes and pine martens in northern Sweden to evaluate whether red foxes are more limited by snow than pine martens and expect that red foxes should utilize carrion more than pine martens. Registering events, frequency and success during tracking were compared to snow depth and temperature. We expect red foxes and pine martens to have only partial overlap in food niche, and red foxes should be more opportunistic and use a broader range of habitat and food niche compared to pine martens.

Methods

Study area

This study was done in the coastal area of Gulf of Bothnia in northern Sweden (65.717 lat., 22.83 long.), and data were collected as part of the large-scale predator removal experiment described in Marcstrom et al. (1988a, b). Most tracking was done on the islands of Bergön (18.0 km^2) and Rånön (23.5 km^2) between 3 and 4 km from the mainland. Red foxes and pine martens were also tracked on the mainland north of Bergön and Rånön close to Kalix municipality.

The average winter temperature was − 10 °C, and the sea ice was frozen between November and early June. The ground was snow-covered between 160 and 180 days. The large part of the study area, including the islands, was commercially managed boreal conifer forest with clear-cutting and replanting practices. Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*) were the most common tree species, with less than 10% birch (*Betula* spp.). Other deciduous trees, mostly along the coastline, were alder (*Alnus incana*) and willow (*Salix* spp.). Open bogs were only present in low proportions (Elveland 1976).

Density of red fox and pine marten were 0.2–0.6 and 0.1–0.3 km^{-2} respectively (Marcstrom et al. 1988a,b). Moose (*Alces alces*) were common in the area and regulated by hunting to minimize the risk of extensive forest damages. Capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), hazel grouse (*Tetrastes bonasia*) (hereafter grouse) and mountain hare were common small game species. Voles showed a 3–4-year fluctuation pattern, with peaks in 1977, 1980 and 1984. Goshawks (*Accipter gentilis*) were rare in the area. There were no permanent settlements on the islands, but small villages and boat landings could be found on the mainland. The islands did not have any roads, but the mainland was transversed both by public and forest roads. The communities in this part of Sweden utilize both fish and wildlife as a contribution to their subsistence. Entrails, including lungs and heart, from harvested moose were left at the kill sites.

Snow tracking

Tracks were followed 1–4 days after snowfall depending on wind and temperature. There were 436 (330 red fox and 107 pine marten) tracking events between the winters of 1975–1981 and 1985–1987; 293 of these occurred on Bergön and Rånön. Tracking and data recording were done by three to six experienced trappers in different years. The trappers were hired through the predator removal project and had several years' experience of trapping and shooting red foxes and pine martens. Areas of the island that were subjected to predator control were excluded from our tracking dataset. Each trapper followed a prescribed route until a track of a red fox or a pine marten was located. On Bergön and Rånön, line transects for estimating mountain hare density were used. On the mainland, snowmobiles were used to find tracks by travelling on unploughed forest roads, clear-cut edges and bogs. This probably resulted in somewhat more fox encounters on the mainland than the islands, 86 vs. 70% fox tracks. Each track was followed in both directions. All events were recorded carefully as (1) hunting attempts (successful/unsuccessful chase) and (2) dig sites to find voles, cached food or scavenging on different remains under the snow. Pounces through the snow with no subsequent digging were categorized as a hunting attempt. Tracks in the snow from hunting and potentially killing prey, presence of blood, remains at dig sites, hair, bones and feathers were all recorded. It was possible to differentiate hunting attempts on grouse from small birds. It is possible that small items or a vole kill occasionally could go undetected.

Habitat was recorded during tracking, and the following habitat classes were used: (1) conifer forest; (2) clear-cuts, bogs and young pine plantations (< 1.5 m); (3) ice-covered lakes and sea; (4) shoreline (within 75 m from water edge); and (5) rock outcrops with scattered trees. We have no information on the overall landscape composition and therefore only compare relative habitat use of the species. Temperature and snow depth were recorded at each tracking event.

Data analysis

We evaluated the difference between the foraging behaviour of red foxes and pine martens and to what extent snow depth and air temperature affected the foraging. The frequencies of hunting and digs, as well as whether these attempts were successful or not, were used as response variables in a negative binomial and binomial regression models respectively. We used a Bayesian approach to model our data, because it provides a full posterior distribution, and the credible interval of the parameters shows the chance that it has captured the correct value. The four models were developed in the JAGS language (Plummer 2003), and R2Jags (Su and Yajima) was used as an interface to R (R Core Team 2017). Year was used as a random intercept in all models. Snow depth and temperature were standardized by subtracting the mean and dividing with twice the standard deviation. Temperature and snow depth were not significantly correlated, Pearsons $r = -0.009$ ($t = -0.190$, df = 433, p value = 0.849). We ran three chains, with a thinning rate of three and a burn-in of 6000. Only non-informative priors were used. The full models are presented in Appendix 1. The number of iterations was increased until convergence, R-hat < 1.1 (Gelman et al. 2013). Trace plots were used to visually evaluate the mixing of the chains. A posterior predictive check (i.e. a Bayesian p value) was used to evaluate if the model fit was acceptable (Hooten and Hobbs 2014). The squared residuals of the data points were compared to the squared residuals of a randomly generated data set from the fitted distribution. A value less than 0.05 or larger than 0.95 was considered a poor fit that required another distribution and/or additional parameters. For each model, we explored four alternative covariate sets: (1) intercept only, (2) species only, (3) species, snow and temperature and (4) species interaction with snow and temperature in addition to 3. The *leave-one-out cross-validation* (Vehtari et al. 2016) was used to explore the four models by calculating the loo information criteria and its standard error. The function logdensity.*foo* in JAGS was used to extract the posterior log likelihood for each data point and joined into a matrix that was parsed to the loo function. The difference between the highest ranking models was larger than 2.7 except in one case. The model of hunting success with only species effect was favoured by a difference of 1.1 compared to including snow depth and temperature, but we choose to present the latter model. We did not consider model averaging (Cade 2015).

The frequency of hunting and digs was initially analysed using a Poisson distribution with a log link and distance tracked (logged) as an offset variable. Results revealed a large over-dispersion, and both zero-inflated Poisson and negative binomial models were explored as alternatives. The Bayesian p value was 0 for the zero-inflated Poisson models but was within the acceptable range for the negative binomial models. The potential success of digs and hunting events following a track was modelled using a binomial distribution and a logit link. Dig success showed large over-dispersion and an initial Bayesian p value < 0.05, and we therefore added the individual observation as a random variable (Harrison 2014).

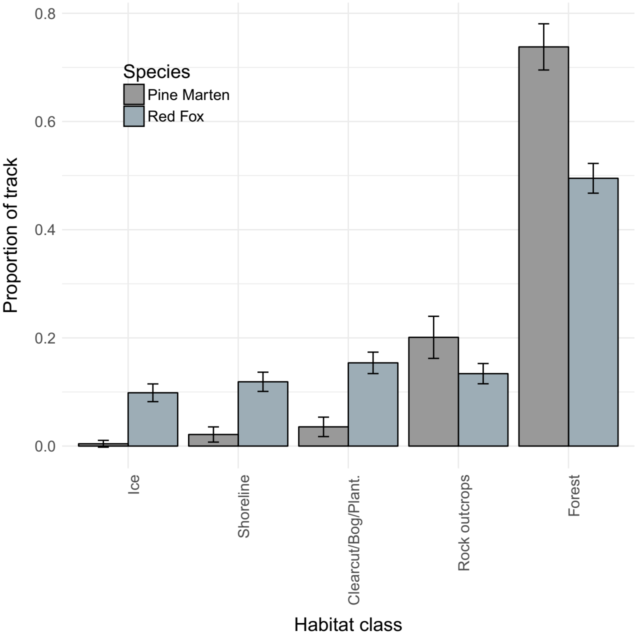

Fig. 1 The proportion of different habitat classes along the tracks of red fox and pine marten summarized for all tracks. The ± 1 standard error is included at top of each bar

Frequencies of prey species and scavenging objects for pine martens and red foxes were tested by Fischer exact test and computing *p* values by Monte Carlo simulations with 2000 replicates. The proportions of the five habitat classes for each tracking event were calculated, and the average and standard error were presented. The general niche concept has multidimensional properties, but here, we used it to describe the number of different food items utilized. We calculated Pianka's standardized index for niche breadth and overlap (Krebs 1999) for digs and hunting for red foxes and pine martens respectively. All calculations were made using R (R Core Team 2017).

Results

The total distance tracked was 2139 and 533 km for red foxes and pine martens respectively. The average length of each followed track was longer for red foxes compared to pine martens, 6.5 vs. 5.0 km respectively (Student's *t* test (two-sided), $t = -4.03$, df = 199, $P < 0.001$). The majority of tracks were followed between rest sites. A larger proportion of the pine martens tracks went through forest and tree covered rock outcrops (94%) compared to red foxes (63%). Red foxes used shorelines and sea ice to about 20% (Fig. 1).

Figure 2 shows the density plots of the predictions for red fox and pine marten foraging behaviour from the four different final models (Table 1) at average snow depth and temperature. The posterior distributions of the model parameters were used to calculate predictions (Table 1), which then were back transformed using the appropriate link function. Red foxes were more often engaged in digs (0.67 km^{-1}) compared to pine martens (0.39 km^{-1}). Snow depth had a negative effect on dig frequency by red foxes but not for pine martens. Parameter values were − 0.39

Fig. 2 Density plots of the model estimates for red fox and pine marten digging (**a**) and hunting (**b**) frequency and digging (**c**) and hunting (**d**) success rates, assuming average snow depth and temperature. The predictions were based on the posterior distribution of the model parameters (Table 1), back transformed using the appropriate link function

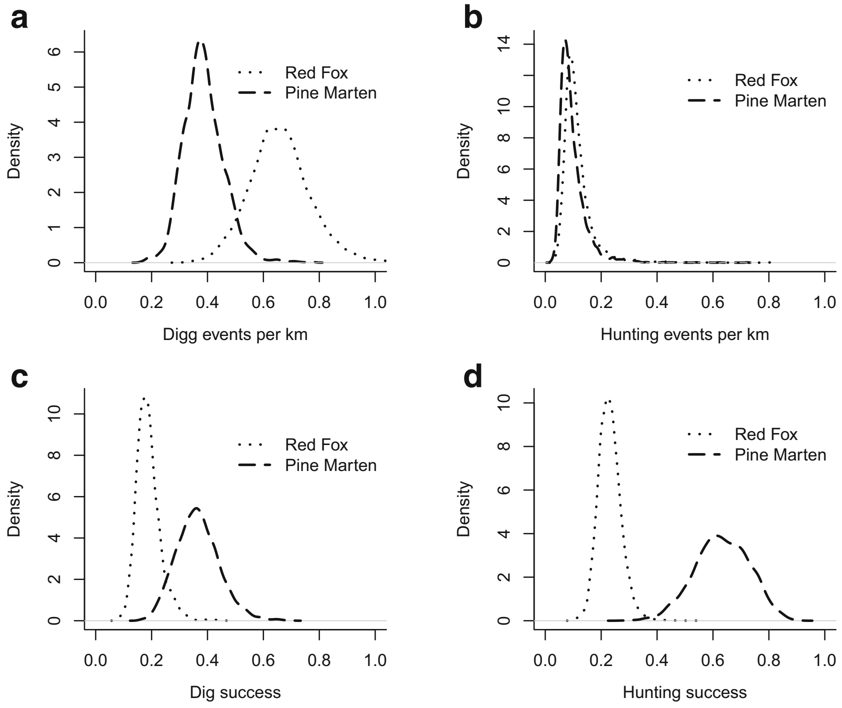

Table 1 Parameter values of the four selected models of dig and hunting events, and their probability of success

	Intercept	Species	Snow depth	Temperature	Snow + species	Temp. + species	SD year	BP	Loo
Dig events	− 0.969 (− 1.336, − 0.615)	0.541 (0.307, 0.783)	0.066 (− 0.354, 0.481)	− 0.641 (− 1.015, − 0.252)	− 0.455 (− 0.898, − 0.010)	0.270 (− 0.179, 0.420)	0.484 (0.254, 0.914)	0.927	1955.7 (51.4)
Dig success	− 0.556 (− 1.206, 0.128)	− 0.950 (− 1.479, − 0.426)	0.759 (0.350, 1.188)	0.475 (0.080, 0.896)	–	–	0.641 (0.272, 1.304)	0.267	889.8 (27.2)
Hunting events	− 2.424 (− 3.093, − 1.465)	0.181 (−0.310, 0.649)	− 0.554 (− 0.888, − 0.229)	− 0.209 (− 0.569, 0.152)	–	–	0.917 (0.390, 1.953)	0.498	754.2 (39.0)
Hunting success	0.567 (− 0.240, 1.442)	− 1.788 (− 2.715, − 0.930)	− 0.196 (− 0.770, 0.372)	0.462 (− 0.201, 1.120)	–	–	0.306 (0.108, 1.120)	0.323	229.1 (19.4)

Events were analysed using negative binomial model with logarithmic link. Success was analysed using a binomial model with a logit link. The loo information criterion was used to rank the models. The 95% credible interval of the parameter values is shown in parenthesis. SD year shows the random effect of year on the intercept. BP is the Bayesian probability, and Loo is the information criteria and associated standard error in parenthesis

and 0.07 respectively (Table 1). Increasing temperature had a negative effect on the frequency of digs by both species, − 0.37 and − 0.64 respectively. Note that the positive interaction parameter (0.27) for red foxes had a wide credible 95% interval including zero effect. Hunting events occurred at a similar rate for both species, 0.11 and 0.09 hunting events per kilometre for red foxes and pine martens respectively (Fig. 2b). Snow depth and temperature reduced the number of hunting events, − 0.55 and − 0.21 respectively. Not that the 95% credible interval for temperature includes zero effect.

Pine martens were more successful than red foxes in both digs and hunting (Fig. 2c, d). Pine martens were successful in 0.39 of the dig events, whereas the corresponding value for red foxes was 0.18. The success of digs was positively affected by both snow depth and temperature with parameter values of 0.76 and 0.48 respectively. The difference in successful hunting attempts was large, 0.64 vs. 0.23 successful attempts for pine martens and red foxes respectively. The parameter value was − 0.20 for snow depth and 0.46 for temperature, but the credible interval included zero effect in both cases.

Red fox successful digs ($n = 261$) prey items contained voles (37%), ungulate remains (26%) and mountain hares (11%), whereas pine marten successful digs ($n = 77$) prey items contained eggs (48%), small birds (22%) and voles (21%) (Table 2). Prey proportion in successful hunting also showed differences between red foxes ($n = 54$) and pine martens ($n = 17$). Voles (48%) and mountain hare (22%) dominated red fox successful hunting events, whereas pine marten hunts contained principally small birds (54%), although the sample size was low. The contingency tables of both digs and hunting showed a significant difference between red fox and pine marten (Fisher's exact test, $P < 0.001$).

The pooled number of all vole catches in different years showed a peak in 1977 and 1978 but was lower in the other years of the study (Fig. 3a). More captures of voles were registered at shallow snow depths, and 23 of 26 occasions when red foxes captured voles by pounces occurred when snow depth was below 25 cm. Pine martens were never registered to catch voles on snow or by pouncing through the snow as red foxes. Red foxes showed a wider niche breadth than pine martens, that was wider for digs than for hunting events. Niche overlap between red foxes and pine martens was low for both digs (0.14) and hunting (0.11) events.

Discussion

Our results suggest several differences in winter foraging strategies between red foxes and pine martens, when

Table 2 The proportion of different prey and remains identified from successful digs and hunting events of red fox and pine marten tracked in northern Sweden during winter

Activity	Species	Vole	Hare	Small birds	Ungulate	Grouse	Egg	Other	Niche breadth	Niche overlap
Digging	Red fox (261)	37%	11%	8%	26%	–	8%	8%	0.54	0.14
	Pine marten (77)	21%	–	22%	1%	–	48%	8%	0.34	
Hunting	Red fox (54)	48%	22%	6%	–	20%	–	6%	0.34	0.11
	Pine marten (17)	–	24%	59%	–	12%	–	6%	0.23	

Values are presented as proportion of total number of successful events for each species. The total number is given in parenthesis. Pianka's niche breadth and overlap was calculated according to Krebs (1999)

prey availability is at its lowest and potential competition for food is high. As shown earlier by Storch et al. (1990), pine martens almost exclusively used forested habitat, whereas the red foxes can be found in all types of habitats.

Several studies have shown the importance of scavenging and use of cached food for both pine martens and red foxes. In Norway, Lund (1962) found 0.56 digs km^{-1} by red foxes similar to this study, whereas Halpin and Bissonette (1988) found on average 1.8 digs per kilometre in eastern Maine, USA. In southern Norway, red foxes dug for ungulate carrion 0.35 times per kilometre (Needham et al. 2014). In this study, digs resulted in finding food more often than at hunting attempts, and both species would on average find food from digs 3 out of 4 days. Compared to red foxes, digs appeared less opportunistic by pine martens because of fewer digs but with higher success. We lack estimates of the probability to miss an attempt to dig or kill a prey, but we do not believe our estimates of time between kills and digs to be significantly over-estimated.

Pine martens were about three times more successful in chasing and killing prey compared to red foxes, although hunting events were only recorded about once every 10 km in both species. Red foxes are larger than pine martens, and it is possible that a smaller size is advantageous to approach potential prey undetected. Using the average distance between rest sites to estimate time between kills resulted in about 3 days for pine martens but more than 6 days for red foxes. Similar to our results, Jędrzejewski et al. (1993) found that pine martens were successful in 65% of hunting attempts on small rodents. Other studies on hunting success of red foxes in winter are unfortunately not available.

Niche breadth of red foxes was higher for digs (0.54) than hunting (0.34), and similar to other studies: 0.36–0.6 (Kauhala et al. 1998; Brangi 1995; Cagnacci et al. 2003). Low values (0.03–0.16) have been reported in two studies (Lanszki et al. 2006; Lanszki et al. 2007), where the diet was dominated by small mammals. Niche breadths can also vary greatly among seasons and years in the same area (Murdoch et al. 2010; Sidorovich et al. 2010), supporting an opportunistic feeding. We did not observe tracks of red foxes killing pine martens or smaller mustelids as has been reported earlier (Lindstrom et al. 1995; Dell'Arte et al. 2007). In our study, pine martens had lower niche breadths in digs and hunting compared to red foxes, and previous studies have shown a wide range of niche breadths, 0.2–0.7 (Jędrzejewski et al. 1993; Helldin 2000b). The low overlap could indicate a strategy by pine martens to avoid foraging competition with red foxes. Voles are an important food source for both red foxes (Englund 1970) and pine martens

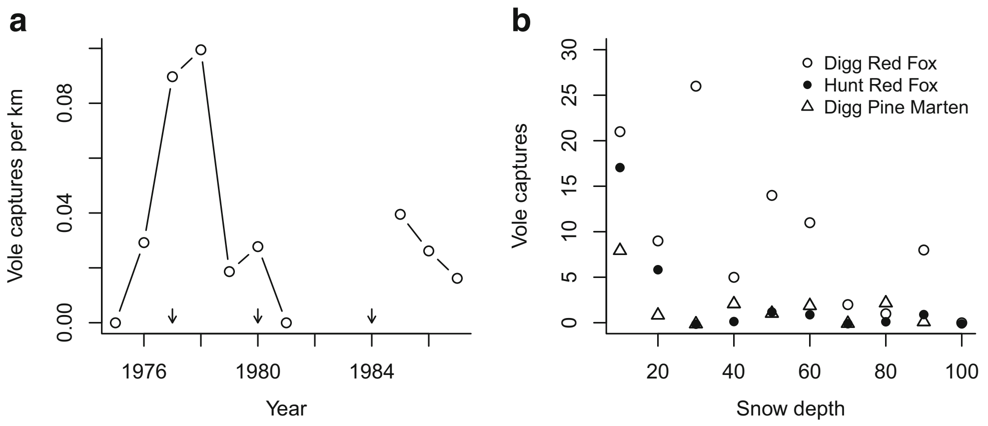

Fig. 3 **a** Pooled vole captures per kilometre for red foxes and pine martens during different years of the study. The *arrows* indicate the peaks of the vole cycle. **b** The sum of vole captures by red fox (digs and hunting) and pine marten (digs) at different snow depth intervals (5–15, 15–25, 25–35 cm, etc.)

(Pulliainen and Ollinmaki 1996; Helldin 1999), although the latter author suggested that pine martens were less affected than red foxes by the variation in vole abundance probably because pine martens prey less on voles in winter.

The suggestion that the common behaviour of caching eggs (Hoglund 1960; Storch et al. 1990) is an important alternative resource in winter for pine martens is in agreement with our findings. In an unpublished pilot study, one of the authors cached frozen chicken eggs at 16 points in 1 × 1 km grid with camera traps in central Norway. The eggs were hidden just under the topsoil when temperature was constantly below 0°, about a week before the ground was snow-covered. Throughout the winter, all cached eggs were found and removed. At 15 points, the eggs were removed by pine martens and one by wolverine. Red foxes were only observed investigating the dig sites after the eggs had been removed. Further south, where winters are fairly mild and short, the food overlap between pine marten and red fox was substantially larger than in this study (Sidorovich et al. 2000; Sidorovich et al. 2010). In these studies, both red foxes and pine martens were found to use a wide range of food items in winter, for example, fruits and beetles. We expect both species to have a different foraging behaviour in our study area during summer and likely show a larger overlap. The difference in foraging efficiency between the two could then be insignificant or even reversed.

Increasing snow depth reduced the number of hunting attempts and their probability of success for both species. Snow depth affected the relative high frequency of dig events for red foxes negatively but did not affect pine martens. Snow conditions are important for the consumption of voles by pine martens (Storch et al. 1990) and red foxes (Lindstrom and Hornfeldt 1994) and probably explain why only the first of the three vole peaks was revealed in the amount of voles captured in different years. Red foxes pounced through the snow to capture voles up to about 25 cm, but the negative effect of snow depth on digs for voles was less pronounced. The biomass of voles in the stomachs of red foxes decreased with snow depth (Lindstrom and Hornfeldt 1994), and they found a substantially lower vole biomass below 70 cm of snow. The proportion of birds in the diet of pine martens in autumn/winter has been found to increase with latitude (Jędrzejewski et al. 1993), and we propose that birds become important for pine martens as snow depth increases and impedes the killing of voles. Unlike red foxes, pine marten can capture prey in trees. Several woodpeckers (*Dendrocopos major*) were caught in trees, but we only found one case of a killed red squirrel, probably due to the lack of suitable red squirrel habitat as old spruce stands (Andren and Delin 1994).

Small birds and cached eggs were common food of pine marten, a likely competitive advantage in relation to red fox in undisturbed conifer forests at northern latitudes in winter. Pine martens were efficient in killing prey and finding food under the snow. It seems that the smaller size of pine martens compared to red foxes is an advantage that makes it possible to catch prey in trees and search for voles under stones and stumps. We speculate that pine martens prefer to cache eggs from capercaillie and black grouse nests to use the subsequent winter; these eggs are larger and more abundant compared to eggs of other birds in the boreal conifer forest. The declining populations grouse (Jahren et al. 2016) would then likely affect pine martens more than red foxes. In addition, ongoing human land use probably favours red foxes. Clear-cutting practices reduce the preferred habitat for pine marten but increase the grassy habitat preferred by the field vole (*Microtus agrestis*), which is a common prey for red foxes (Lindstrom 1992; Dell'Arte et al. 2007). Sidorovich et al. (2010) showed that red fox consumption of field vole increased after clear-cutting but less so for pine martens. Large populations of moose regulated through hunting provide entrails at kill sites, and sometimes whole carcasses of moose and domestic reindeer (Henden et al. 2010; Gomo et al. 2017), that will support the scavenging red foxes.

Long winters and deep snow probably limit red foxes more than pine martens that are more adapted to soft dry snow and more easily move on the snow surface compared to red foxes. One pine marten used the soft snow to approach a capercaillie male by moving under the snow the last few meters. The ongoing climate change has already resulted in warmer and more humid winters with less snow. This will further benefit red foxes and increase their importance in the northern boreal forest ecosystem at the expense of pine marten. However, the long-term effects of climate change is difficult to predict because the species composition of the ecosystem will gradually change and individual species will adapt at different speeds forming new biotic communities (Pecl et al. 2017).

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Appendix 1.

a) Model code in jags for running negative binomial regression with year as random intercept. Log link was used and the logged values for kilometre were added as an offset. Code shows the full model with interaction.

```
model
{
  # Priors
  alpha1 ~ dnorm(0, 0.001)
  beta1 ~ dnorm(0, 0.001)
  beta2 ~ dnorm(0, 0.001)
  beta3 ~ dnorm(0, 0.001)
  beta12 ~ dnorm(0, 0.001)
  beta13 ~ dnorm(0, 0.001)
  r ~ dunif(0, 50)

  for (y in 1:Nyear){ a[y]~dnorm(0, tau.year) }
  tau.year<-1/(sigma.year*sigma.year)
  sigma.year ~dunif(0,18)

#Likliehood
   for (y in 1:Nyear){
    for (i in 1:n[y]) {

      D[i,y] ~ dnegbin(p[i,y], r)
      log(mu[i,y]) <- a[y]+logA[i,y]+alpha1 +
beta1*x1[i,y]+beta2*x2[i,y]+beta3*x3[i,y]+beta12*x1[i,y]*x2[i,y]+beta
13*x1[i,y]*x3[i,y]

    # Transforms mu into p,
    p[i,y] <- r/(r + mu[i,y])

# Bayesian p-value and likelihood to loo
    ExpY[i,y] <- mu[i,y]
    E[i,y]    <- pow((D[i,y] - ExpY[i,y]),2)
    Y2[i,y] ~ dnegbin(p[i,y], r)
    E2[i,y]    <- pow((Y2[i,y] - ExpY[i,y]),2)
    loglik[i,y]<-logdensity.negbin(D[i,y],p[i,y],r)
    }
       fit1[y]<-sum(E[1:n[y],y])
       fit1.new[y]<-sum(E2[1:n[y],y])
     }
      # Add up discrepancy measures
      fit <- sum(fit1[1:10])
      fit.new <- sum(fit1.new[1:10])
}
```

b) Model code in jags for running logistic regression with logit link, and year as a random intercept. Code shows the full model with interaction.

```
model {
# Priors
  alpha1 ~ dnorm(0,0.001)
  beta1 ~ dnorm(0,0.001)
  beta2 ~ dnorm(0,0.001)
  beta3 ~ dnorm(0,0.001)
  beta12 ~ dnorm(0,0.001)
  beta13 ~ dnorm(0,0.001)

for (y in 1:Nyear){ a[y]~dnorm(0, tau.year) }
tau.year<-1/(sigma.year*sigma.year)
sigma.year ~dunif(0,18)

# Likelihood
for (y in 1:Nyear){
  for (i in 1:n[y]) {
    C[i,y] ~ dbin(p[i,y], N[i,y])
logit(p[i,y]) <-
alpha1+a[y]+beta1*x1[i,y]+beta2*x2[i,y]+beta3*x3[i,y]+
beta13*x3[i,y]*x1[i,y] + beta12*x2[i,y]*x1[i,y]+ind[i,y]

#  Bayesian p-value and likelihood to loo
   pred[i,y]<-N[i,y]*p[i,y]
   Presi[i,y] <- (C[i,y]-pred[i,y]) / sqrt(N[i,y]*p[i,y]*(1-p[i,y]))
   C.new[i,y] ~ dbin(p[i,y], N[i,y])
   Presi.new[i,y] <- (C.new[i,y]-pred[i,y]) / sqrt(N[i,y]*p[i,y]*(1-
p[i,y]))
   loglik[i,y] <- logdensity.bin(C[i,y], p[i,y], N[i,y])
 }
 fit1[y]<-sum(Presi[1:n[y],y])
 fit1.new[y]<-sum(Presi.new[1:n[y],y])
}
 fit <- sum(fit1[1:10])
 fit.new <- sum(fit1.new[1:10])
}
```

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