

The spatio-temporal distribution of wild and domestic ungulates modulates lynx kill rates in a multi-use landscape

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Keywords

Capreolus capreolus; carnivore; *Cervus elaphus*; livestock; *Ovis aries*; red deer; roe deer; sheep.

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Abstract

Depredation on livestock and competition with hunters for game species are prominent among the conflicts that the return of large carnivores generates in multi-use landscapes. The relative magnitude of the conflict strongly depends on what prey selection patterns predators will adopt once established in a new area. We explored prey selection and kill rates from 24 Eurasian lynx *Lynx lynx* in Southern Norway, between 2006 and 2011, using Global Positioning System collars. We recorded 603 lynx predation events on a wide range of prey species, ranging from passerines to large ungulates. During summer, domestic sheep were the most frequent prey, representing 64% of the ungulates killed, for an average kill rate of 8.2/100 days, whereas roe deer *Capreolus capreolus* were killed in about 33% of cases (kill rate = 4.2/100 days). In winter, when sheep were unavailable, roe deer were the most frequent prey, accounting for about 73% of the kills, for an average kill rate of 9.4/100 days, whereas red deer were found at 17% of the kill sites, corresponding to a kill rate of 2.2/100 days. Lynx-killed prey provided an average of 400 kg of meat per 100 days, irrespective of prey density. In both seasons, the proportion of each species killed by lynx was determined by the combined effect of all prey densities, so that the density of wild ungulates had the potential to affect the rate of depredation on sheep, to the same extent as the abundance of sheep could influence the kill rate on wild ungulates. Our results underline the complexity of carnivore–ungulate trophic interactions in multi-use landscapes where livestock and wildlife co-occur, and suggest that changes in densities of prey, predators or both may produce undesired outcomes, if such complexity is not taken into account during the decision-making process for management and conservation.

Introduction

Large carnivores have returned or are returning to several densely populated areas of Europe and North America, as a consequence of the profound ecological and social changes of recent decades (Kellert *et al.*, 1995; Linnell, Salvatori & Boitani, 2008). Along such a recovery process, they have proved to be more tolerant and adaptable to human presence than many could have foreseen (Linnell, Swenson & Andersen, 2001; Treves & Karanth, 2003). As a result, large carnivores are now inhabitants of many multi-use landscapes, in which predation, reproduction and dispersal occur simultaneously and in sympatry with a diversity of human activities.

Among the conflicts that such co-occurrence generates, depredation on livestock and competition with hunters for game are prominent, and the relative extent to which recolonizing carnivores will affect the first or the latter conflict

depends on what type of predation patterns (especially concerning prey choice) they will adopt once established in a new area (Graham, Beckerman & Thirgood, 2005). In some instances, in fact, recolonizing carnivores rely almost exclusively on livestock, such as sheep or cattle, especially when they are abundant, lack anti-predatory behaviour and are not protected by appropriate herding practices (Odden *et al.*, 2002; Sangay & Vernes, 2008; Linnell, Odden & Mertens, 2012). This usually generates high social conflicts and economic costs, related to the implementation of compensation and mitigation actions (Treves & Karanth, 2003).

In other instances, carnivores rely mostly on the wild component of their prey spectrum, thus entering in direct competition with hunters for the harvest of game species (Breitenmoser *et al.*, 2010). In this case, while the combined effects of predation and human harvest have the potential to generate a decline in wild ungulate populations (Vucetich, Smith & Stahler, 2005; Gervasi *et al.*, 2012), a few individual

carnivores may, in some circumstances, show an inclination to kill livestock (Stahl *et al.*, 2002). These individuals often have the tendency to kill a surplus of domestic prey (Odden *et al.*, 2002), and to consume only a minor portion of them, so that a specific behavioural pattern by a few animals can generate high economic costs and a dramatic increase in the social and psychological perception of the conflict (Linnell *et al.*, 1999). For this reason, the effect of wild prey density on livestock predation has been widely studied and is a key debate in wildlife conservation and management (Meriggi *et al.*, 1996; Stahl *et al.*, 2001; Odden *et al.*, 2008).

In all instances, recolonizing carnivores, their wild and domestic prey, and humans (either as hunters or herders) are all part of an interconnected trophic system. Inside such a system, prey selection patterns by carnivores, and their functional response to prey density or accessibility, are the key underlying mechanisms, determining which specific part of the system will carry most of the costs related to allowing carnivore presence in a given landscape. Considering that large carnivores are still expected to expand and increase in numbers in the coming decades (Ray *et al.*, 2005), understanding which factors affect their prey selection patterns in a multi-use landscape is central to both biodiversity conservation and human well-being.

To this aim, the recovery and expansion of the Eurasian lynx *Lynx lynx* population in Southern Norway offers a good opportunity to explore the issue of predator–prey dynamics in a multi-use landscape (Linnell *et al.*, 2010). The interspersed forest ecosystem of Southern Norway hosts a diverse assemblage of wild and domestic ungulate species, in a context of intensive human use of the services provided by the ecosystem (grazing, hunting, logging, etc.). Moreover, a strong spatial gradient and seasonal variation in both domestic and wild prey distribution exist in the area, which exposes lynx to different conditions of prey availability and accessibility in space and time. Given these premises, we explored lynx prey selection patterns and kill rates in the area during a 6-year study period, focusing on the two most common wild ungulate prey, red deer *Cervus elaphus* and roe deer *Capreolus capreolus*, and on domestic sheep *Ovis aries*. We examine how the spatio-temporal variation in the availability of all prey species has the potential to affect lynx predation patterns and to shape the dynamics of the multi-prey system. We also discuss the consequences of such an interconnected trophic system on the management and conservation of carnivores in multi-use landscapes.

Materials and methods

Study area

The 25 000 km² Østafjells study area encompasses an environmental gradient (north-west–south-east) in Buskerud, Telemark and Oppland counties in Southern Norway (Fig. 1). The north-western part of the area is dominated by steep elevation gradients from valleys and up to mountains >1000 m above sea level, and it is marginally suitable for roe deer. The area is forested with a domination of Norway spruce *Picea*

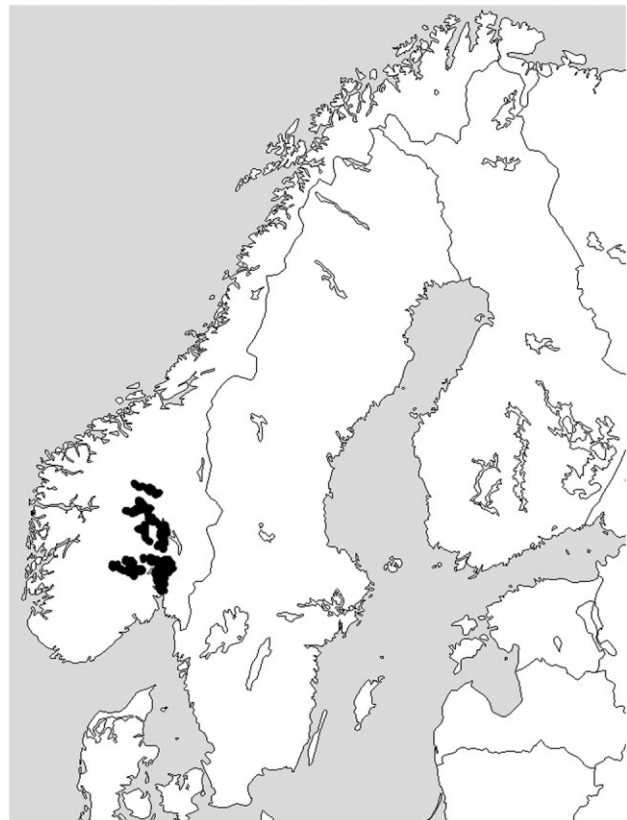


Figure 1 The study area in Buskerud, Telemark and Oppland counties, Southern Norway. The black dots represent all the 24 000 lynx Global Positioning System locations collected during the study in the period 2006–2011.

abies and Scots pine *Pinus sylvestris*. The south-eastern portion of the study area includes patches of deciduous forest, and the landscape is more human modified. Here, the forest is fragmented by cultivated land, and roe deer occur at higher densities. Red deer have recolonized the area within the last few decades and remain at low population densities partly due to harvesting. Furthermore, red deer perform an altitudinal movement from a low-elevation winter range to a high-elevation summer range (Myrsterud *et al.*, 2001), and they are therefore more available for lynx predation during winter. Roe deer also migrate, but to a lesser degree than red deer (Myrsterud *et al.*, 2012). All parts of the study area have free-ranging sheep grazing in forest and alpine habitats from June to September, with very limited supervision, no guarding and few constraints on their movements. However, the density and distribution of sheep vary considerably inside the area. The north and western parts have the widest distribution of grazing areas and the highest densities of sheep. Further south and east, the density of sheep can still be high locally, but sheep grazing areas are more patchily distributed. Wild mountain reindeer *Rangifer tarandus* are seasonally available at higher altitudes in the northern parts. Throughout the study

area, roe deer co-occur with moose *Alces alces*, mountain hares *Lepus timidus*, beavers *Castor fiber* and forest birds such as black grouse *Tetrao tetrix* and capercaillie *Tetrao urogallus*. Eurasian lynx are widespread throughout the area, having recolonized it in the 1980s. The population is controlled through hunter harvest, such that its size has fluctuated around 60–70 individuals since 2003 (Linnell *et al.*, 2010).

Animal capture

Between 2006 and 2011, we captured 14 female and 16 male lynx and monitored them using Global Positioning System (GPS) collars, summing up to almost 4000 tracking days and to a total of 76 kill rate sequences with intensive positioning. Adult lynx and juveniles (>5 months) were captured in wooden box traps and spring-loaded foot snares placed around lynx kills. All procedures were approved by the Norwegian Experimental Animal Ethics Committee, and permits for wild animal capture were obtained from the Norwegian Directorate for Nature Management. Based on snow tracking in winter and the marking of kittens in natal lairs, we were able to assess the reproductive status of each radio-collared female lynx in each year and season, and to determine if it was accompanied by dependent kittens.

Lynx kill rates

We collected data on kill rates between November and April in winter, and between May and September in summer. During the period 2006–2008, we monitored four lynx using ‘store-on-board’ GPS collars with a schedule of two locations per day. Thus, we identified potential kill sites using GIS software (ArcGIS 9.2, ESRI, Redlands, CA, USA) and visited them after the collars had dropped off. After 2008, we fitted lynx with GPS-GSM (Global System Communication) collars, which allowed us to visit potential kill sites right after the animal had left the area. Furthermore, the monitoring schedule was increased up to 19 locations per day during predation sequences. We defined clusters as a set of at least two locations within 100 m, and visited them to confirm a predation event. When a carcass was found, we identified the species, and whenever possible its sex and age class (calf/fawn, yearling, older individual). We defined seasonal species-specific kill rates for each individual lynx as the number of individuals of a given species killed in 100 days. To convert kill rates into an overall prey biomass, we used values of 26, 150 and 70 kg for adult roe deer, red deer and sheep, respectively (Silva & Downing, 1995; Andersen, Duncan & Linnell, 1998). We also used a monotonic growth model to estimate the body mass of juvenile and yearling prey in each month of the year (Tjorve & Tjorve, 2010).

Prey density

To model the spatial and temporal variation in sheep density during our study, we used data from the Norwegian Forest and Landscape Institute (<http://www.skogoglandskap.no/>) for the years 2006–2011, which reports the number of sheep

released in spring in each grazing area. The average size of grazing areas was about 50 km², about one-tenth of an average lynx home range (Herfindal *et al.*, 2005); therefore, we assumed homogeneous sheep density inside grazing areas. For roe and red deer, we did not have direct estimates of the spatial variation in their density. We used predictive density maps with a 1 km resolution (Bouyer *et al.*, unpublished data) for each of the two prey species, derived from a set of pellet count surveys, performed along 430 transects during the study period. The maps were inferred from hurdle models (Zuur *et al.*, 2009) applied on environmental and anthropogenic variables, such as altitude, road density, human density, habitat composition, average snow depth, etc. The models were validated using cross-validation and two independent datasets related to prey densities. The models allowed us to predict the spatial variation of prey density inside each lynx home range, and thus provided an index of roe and red deer density to be associated with each lynx kill. We estimated roe deer and red deer density at increasing buffer distances around each kill, ranging from 1 to 10 km, and found that the closest relationship between prey density and kill probability was observed when using a 4 km buffer, which we used for all subsequent analyses.

Statistical analyses

Given the seasonal variation in the spatial distribution of both wild and domestic prey in our study area, we performed separate analyses of prey selection patterns on winter and summer kills. In summer, we focussed on roe deer and sheep, which comprised the vast majority of lynx kills, whereas in winter, we analysed the roe deer/red deer prey selection patterns because sheep were largely unavailable. Before performing successive analyses, we used binomial generalized linear model (Zuur *et al.*, 2009) to test for any variation in the proportion of other species among lynx kills, and found that their proportion was constant across the gradient of all prey densities, across sexes and seasons, and independent of the reproductive status of female lynx. This assured that no bias was introduced in the prey selection analysis by the exclusion of this group of prey species. Then, we used binomial generalized linear mixed-effects models in R (R Development Core Team, 2008), using the package *lme4* (Bates, Maechler & Bolker, 2011), to test what factors affected the proportion of the two main prey among lynx kills in each season. As some individuals were followed for more than 1 year and had multiple kill rate estimates, we fitted mixed-effects logistic regression models with individual lynx as a random effect, to account for pseudo-replication (Hurlbert, 1984). We used the density of each of the two focal prey species as explanatory variables, and for each of them fitted a linear, logarithmic, quadratic and second-order polynomial function. We also tested for a difference in prey selection patterns among males, solitary females and females with dependent kittens. In each season, we performed a preliminary variance inflation analysis (Zuur *et al.*, 2009) to assess the degree of collinearity among explanatory variables, which highlighted a negative correlation between roe deer and red deer density (Pearson's $\rho = -0.5$). Thus,

Table 1 Seasonal composition of the prey species killed by solitary females, females with kittens and male lynx in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

Prey type	Solitary females (%)		Females with kittens (%)		Males (%)	
	Summer (16)	Winter (64)	Summer (73)	Winter (87)	Summer (188)	Winter (64)
Beaver <i>Castor fiber</i>	0	0	0	0	0	0.5
Domestic goat <i>Capra aegragus</i>	0	0	0	0	0.5	0
Hare <i>Lepus timidus</i>	10.5	12.5	13.7	16.5	12.9	4.3
Moose <i>Alces alces</i>	0	0	0	0	0	1.2
Red deer <i>Cervus elaphus</i>	5.4	7.8	2.7	6.2	1.1	22.6
Red fox <i>Vulpes vulpes</i>	0	1.5	0	0	0	1.8
Wild reindeer <i>Rangifer tarandus</i>	0	0	0	0	0.5	0.6
Roe deer <i>Capreolus capreolus</i>	52.6	67.2	24.7	67.0	23.1	56.7
Domestic sheep <i>Ovis aries</i>	10.5	0	45.2	3.1	55.4	12.3
Squirrel <i>Sciurus vulgaris</i>	0	0	0	1.0	0	0
Tetraonids	10.5	9.4	12.3	6.2	3.8	0
Other birds	10.5	1.6	1.4	0	2.7	0

Numbers in parentheses indicate the total number of kills for a given lynx category and season.

to avoid overfitting the models and underestimating the variance, we fitted a linear regression model between roe deer and red deer density, and used the residuals from this model as an independent estimate of red deer density in the study area (Jakob, Marshall & Uetz, 1996). Thus, the resulting contribution of this variable represents the effect of red deer on lynx prey selection, after accounting for the proportion of variance already explained by roe deer density.

After generating reduced models, we selected the most parsimonious one using the Akaike information criterion (AIC_c) of model fit (Burnham & Anderson, 2002).

Results

Seasonal predation patterns

During the study period, we recorded 603 lynx predation events on a wide range of prey sizes, spanning from small birds up to ungulates as large as moose (Table 1). In both seasons, ungulate prey constituted about 80% of lynx diet, whereas most of the remaining proportion of kills involved hares, black grouse and capercaillie. Among ungulates, a clear difference in predation patterns emerged between the two seasons. During summer, sheep were on average the most frequent prey, representing 64% of the ungulates killed, but large differences between individuals were evident. Some lynx, especially males and females with dependent offspring, relied almost totally on sheep predation, whereas others, including several solitary females, showed the opposite tendency to almost exclusively kill roe deer (Table 1). Only five red deer and one wild reindeer were killed in summer during the whole study period. In winter, roe deer were the most frequent prey species, accounting for about 73% of the kills, whereas red deer were found at 17% of the kill sites. Also in this case, we observed a large individual variation around the average values, with a general tendency for males to kill a larger proportion of red deer than females (Table 1).

Table 2 Age distribution of the ungulates killed by lynx in summer and winter in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

Age class	Winter				Summer			
	Red deer		Roe deer		Sheep		Roe deer	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
Juvenile	18	52	47	47	75	93	20	41
Yearling	11	31	16	16	1	1	9	18
Adult	6	17	38	37	5	6	20	41
Unknown	11	23	100	50	57	41	32	39

The proportion of ungulates killed in each age class was calculated on the total number of individuals for which we were able to determine age, whereas the proportion of 'unknown' was calculated on the total number of prey items for a given species and season.

We were able to attribute an age class to about 65% of the ungulate prey found. Among them, 93% of the sheep killed by lynx were lambs (Table 2). Predation on juvenile red and roe deer accounted for 52 and 45% of all the kills, respectively, but lynx killed a larger proportion of adult roe deer (~40%) than adult red deer (17%; Table 2).

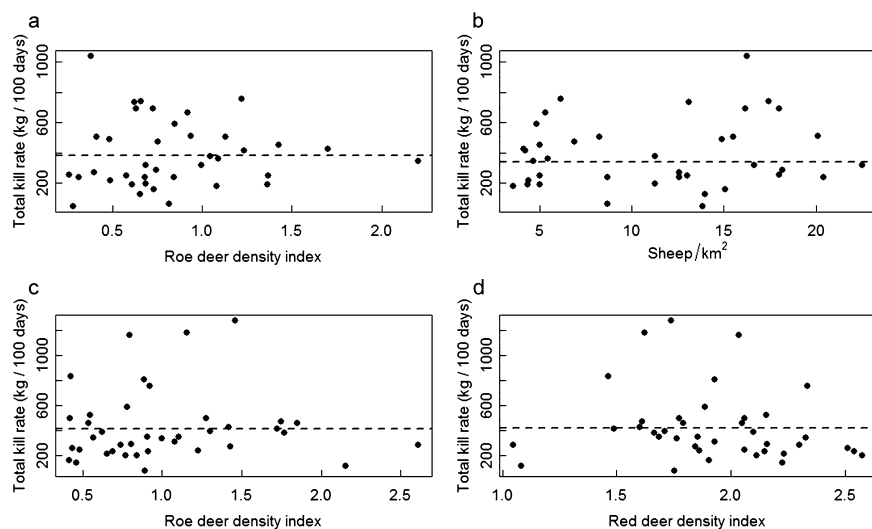
Kill rates and the effect of prey density

Lynx kill rate on roe deer was on average 4.2/100 days in summer and 9.4/100 days in winter (Table 3), but a large variation was evident around these mean values, with some individuals killing up to 23 roe deer every 100 days, whereas others did not kill any roe deer (Table 3). As expected from the seasonal variation in their availability, sheep were killed by lynx to a larger extent in summer than in winter, as the summer kill rate was on average 8.2/100 days, but only 1.0/100 days in winter. Also in this case, some individual lynx showed extremely high kill rates on sheep, with up to 54 kills in a 100-day period, whereas several other individuals killed no

Table 3 Average kill rate estimates (number of prey killed/100 days) on wild and domestic ungulates for solitary females, females with kittens, and male lynx in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

Lynx type	Roe deer		Red deer		Sheep	
	Summer	Winter	Summer	Winter	Summer	Winter
Solitary females	5.5 (0–9.3)	8.9 (1.8–13.8)	0.2 (0–0.9)	1.0 (0–3.4)	9.4 (0–14.3)	0.0 (0–0)
Females with kittens	3.5 (0–14.3)	10.8 (3.1–21.2)	0.6 (0–4.8)	0.4 (0–2.7)	6.4 (0–13.3)	0.2 (0–2.6)
Males	7.2 (0–22.7)	9.0 (0–20)	0.4 (0–3.4)	3.1 (0–12.5)	14.6 (0–54.5)	1.6 (0–20.7)
Mean	4.2	9.4	0.2	2.2	8.2	1.0

Numbers in parentheses indicate the range of observed kill rates for each season, lynx category and prey species.

**Figure 2** Seasonal relationship between prey density and the individual lynx total kill rate expressed as kilograms of meat. The graphs show the functional relationship between roe deer density and roe deer kill rate in summer (a) and winter (c), between sheep density and sheep kill rate in summer (b), and between red deer density and red deer kill rate in winter (d). Dotted lines are regression curves between prey density and total kill rate, whose slopes are all not significantly different from zero.

sheep (Table 3). Lynx predation on red deer emerged especially as a winter habit for males. The average winter kill rate was 2.2 red deer killed/100 days, but reached 3.1/100 days for males and only about 0.5–1.0/100 days for females (Table 3).

When kill rates were expressed in terms of total biomass killed, we found that variation in prey density did not contribute to explain differences among individuals. Both in winter and in summer, lynx-killed ungulates summed to an average of about 400 kg per 100 days irrespective of prey density, with significant inter-individual variation (Fig. 2). This is notable if we consider that the study area included an almost threefold spatial variation in red and roe deer density and up to a fivefold variation in sheep density. Therefore, differences among kill rates of lynx individuals were predominantly the result of different prey selection patterns, rather than of a limitation in predation efficiency due to the effect of prey density.

Seasonal models of prey selection

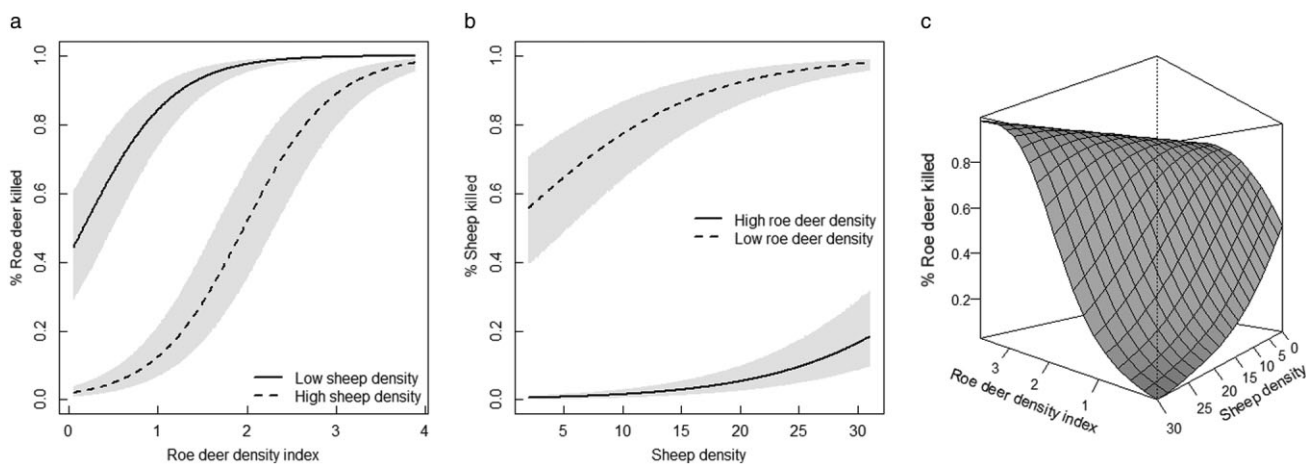
The logistic regression analysis of summer prey selection patterns showed that the proportion of roe deer and sheep killed by lynx was determined by the combined effect of both prey densities. The best supported model (model 1 in

Table 4) included a linear effect of the two variables, whereas a quadratic effect was slightly less supported. Furthermore, an effect of lynx sex and reproductive status was included in all the best models, showing an increased probability for males and females with kittens to kill sheep. Figure 3 shows a positive response by lynx to roe deer density, but also that sheep abundance had the potential to modulate such responses, especially at low and intermediate roe deer densities. In areas with low sheep density (continuous line in Fig. 3a), the prey selection function rapidly reached an asymptotic level, at which lynx were predicted to kill almost exclusively roe deer. In contrast, in areas where sheep were abundant (dashed line in Fig. 3a), lynx exhibited a reduced response to roe deer density, so that sheep were the main prey along a substantial portion of the roe deer density gradient. The other side of the coin is that roe deer density also strongly modulated the response of lynx to sheep density (see Fig. 3b). Lynx showed almost no response to variation in sheep density, when roe deer were abundant in their home range (continuous line in Fig. 3b), but exhibited a typical positive asymptotic response when roe deer density was low (dashed line in Fig. 3b). The functional relationship between prey density and lynx prey selection patterns in summer was best described by a surface, whose determinants were local densities of both roe deer and sheep (Fig. 3c).

Table 4 Model selection results for the binomial GLM analysis of summer prey selection patterns of lynx in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

N	Model	AICc	Δ AICc	Weight
1	Roe deer + Sheep + Sex*Reproductive status	423.06	0	0.43
2	Roe deer + Sheep + (Sheep) ² + Sex*Reproductive status	425.04	1.98	0.16
3	Roe deer + (Roe deer) ² + Sheep + Sex*Reproductive status	425.05	1.99	0.16
4	Roe deer + (Sheep) ² + Sex*Reproductive status	425.55	2.49	0.12
5	(Roe deer) ² + Sheep + Sex*Reproductive status	426.51	3.45	0.08
6	Roe deer + Log(Sheep) + Sex*Reproductive status	427.98	4.92	0.04
7	Log(roe deer) + Sheep + Sex*Reproductive status	429.94	6.88	0.01
8	Roe deer + Sheep	441.78	18.72	0.00
9	Roe deer + Sex*Reproductive status	446.52	23.46	0.00
10	Sheep + Sex*Reproductive status	457.74	34.68	0.00
11	Roe deer	461.15	38.09	0.00

GLM, generalized linear model.

**Figure 3** Functional relationship of roe deer (a) and sheep density (b) with the proportion of roe deer *Capreolus capreolus* killed by lynx in summer in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011. (c) shows the surface describing the overall functional response of lynx to both roe deer and sheep density in summer. Sheep density is expressed as number of sheep /km².

A similar pattern was revealed by the analysis of winter prey selection patterns. The most supported model (model 1 in Table 5) included a linear effect of both roe deer and of the residuals of red deer density. A slightly less supported model (model 2 in Table 5; Δ AIC_c = 1.19) also included the effect of lynx sex and reproductive status, corresponding to a higher probability for male lynx to kill red deer, with respect to both solitary and accompanied females. Given the negative correlation between roe and red deer densities, separating the effects of the two prey species in winter was not as straightforward as in summer. Still, model predictions show that an increase in roe deer density (and coincident decrease in red deer density) corresponded to a higher proportion of roe deer killed (Fig. 4), whereas the residual effect of red deer density, after accounting for the portion of variance already explained by the correlated part, was relatively weak, although signifi-

cant. Figure 4c shows the shape of the surface, describing lynx functional response to prey density in winter.

Discussion

Managing carnivore-ungulate communities (especially with a mix of wild and domestic ungulates) in multi-use landscapes is a challenging task. Different cultural approaches, resulting in competing goals, usually drive the actions directed at the different members of the community: (1) wild ungulates are usually managed to ensure that their harvest is sustainable, balancing population persistence and yield, while minimizing the potential damage that high ungulate densities can cause to forestry interests or with vehicle collisions; (2) livestock herding mainly responds to the goals of animal production, in which any loss of capital (a depredation event) reduces the

Table 5 Model selection results for the binomial GLM analysis of winter prey selection patterns of lynx in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

N	Model	AICc	Δ AICc	Weight
1	Roe deer + Red deer	271.91	0	0.36
2	Roe deer + Red deer + Sex*Reproductive status	273.1	1.19	0.20
3	Roe deer + (Roe deer) ² + Red deer + Sex*Reproductive status	274.07	2.16	0.12
4	(Roe deer) ² + Red deer + Sex*Reproductive status	274.14	2.23	0.12
5	Log _(Roe deer) + Red deer + Sex*Reproductive status	274.56	2.65	0.09
6	Roe deer + Log _(Red deer) + Sex*Reproductive status	275.69	3.78	0.05
7	Red deer	277.45	5.54	0.02
8	Roe deer + (Red deer) ² + Sex*Reproductive status	278.12	6.21	0.02
9	Roe deer	278.56	6.65	0.01
10	Roe deer + Red deer + (Red deer) ² + Sex*Reproductive status	279.25	7.34	0.01

AICc, Akaike information criterion; GLM, generalized linear model.

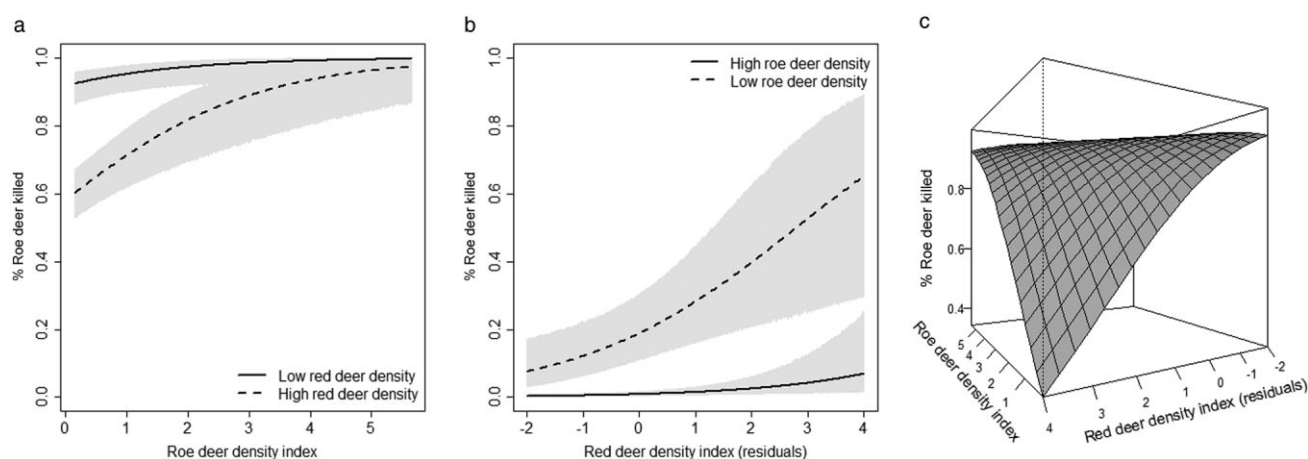


Figure 4 Functional relationship of roe deer (a) and red deer density (b) with the proportion of roe deer *Capreolus capreolus* killed by lynx in winter in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011. (c) shows the surface describing the overall functional response of lynx to both roe deer and red deer density in winter.

potential profit of the economic activity, and is therefore to be minimized via protection measures or compensation using alternative financial mechanisms (Schwerdtner & Gruber, 2007); (3) under the protection of international legislation, carnivores have progressively gained a right to exist in multi-use landscapes (Linnell *et al.*, 2010; Trouwborst, 2010), but often only within the boundaries of certain population targets, aimed at limiting the economic and social impact of their presence (Linnell *et al.*, 2010).

In this context, our increasing understanding of the complexity of trophic interactions in terrestrial communities suggests that changes in densities of prey, predators or both may produce undesired management outcomes (Sinclair & Byrom, 2006) if such complexity is not taken into account during the decision-making process. The results of our study provide empirical evidence of such complexity in a trophic system in which wild ungulates, livestock and an efficient opportunistic predator occupy an ecosystem at a high economic and social cost. The multivariate nature of lynx prey

selection patterns (Figs 3 and 4) shows that the density of wild ungulates in Southern Norway has the potential to affect the rate of depredation on livestock, to the same extent as the abundance of sheep in the study area can influence the level of potential competition between lynx and wild ungulate hunters. If we consider that roe deer density in many parts of Southern Norway has been generally decreasing over the last decade (Melis *et al.*, 2010), that red deer are in turn expanding in range and numbers (Milner *et al.*, 2006), while about 30 000 sheep are annually compensated in Norway as being predated by large carnivores (Linnell *et al.*, 2010), the potential economic and social consequences of failing to account for the complexity of lynx–prey interactions during such a modification of the community structure are evident.

Our study site provided a diverse prey base for lynx. At least 16 prey species occurred in the diet of 24 individuals over a 6-year period, and we did not detect any effect of variation in prey density on the amount of biomass that lynx were able

to obtain when hunting. In all respects, lynx seemed to kill what they needed, likely based on their energetic requirements, whereas the relative abundance of each prey species in their home range determined to a large extent the proportions of species killed.

The structure and the dynamics of the lynx–ungulate system in Southern Norway are similar to several other multi-use landscapes, in which large carnivores are returning or have recently returned across Europe and North America. As the expansion of carnivore populations is accompanied by a similar trend in several species of large herbivores (Putman, Apollonio & Andersen, 2011), prey availability is likely to be not a limitation for most of the carnivore populations settling in new areas, whereas the prey selection patterns they will adopt will determine to a large extent the cost and the potential conflicts associated with their presence in the landscape. This is the case for the recolonizing wolf population of the Western Alps in Italy and France, which occupies an area with four wild and two domestic ungulate species (Marucco, Pletscher & Boitani, 2008; Marucco & McIntire, 2010), and for the expansion of pumas *Puma concolor* in the Patagonia region, which hosts a complex assemblage of domestic and wild prey, some of them seriously threatened with extinction (Wittmer, Elbroch & Marshall, 2012). This further underlines the need to explore the main factors driving predation patterns of recolonizing carnivores and their potential demographic impact on wild and domestic prey species in a multi-prey context. If prey availability is unlikely to be a limiting factor in most of these socioecological contexts, traditional functional response approaches (Holling, 1959; Vucetich, Peterson & Schaefer, 2002), based on the limitations imposed by searching and handling time on predation efficiency, are likely to fail in properly addressing the issue. While the results of our study highlight the importance of further exploring the main ecological drivers of prey selection in large carnivores, they also suggest that the underlying energetic requirements of carnivores might be a unifying approach to the study of predator–prey interactions in a multi-prey context (Carbone, Teacher & Rowcliffe, 2007; Jeschke, 2007). Understanding the mechanisms linking individual energy budgets to prey selection, to kill rates and, ultimately, to predation impact, can potentially provide a theoretical framework to inform the decision-making process for the management and conservation of human–wildlife communities in multi-use landscapes.

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References

- Andersen, R., Duncan, P. & Linnell, J.D.C. (1998). *The European roe deer: the biology of success*. Oslo: Scandinavian University Press.
- Bates, D., Maechler, M. & Bolker, B. (2011). Linear mixed-effects models using S4 classes. R package.
- Breitenmoser, U., Ryser, A., Molinari-Jobin, A., Zimmermann, F., Haller, H., Molinari, P. & Breitenmoser-Wursten, C. (2010). The changing impact of predation as a source of conflict between hunters and reintroduced lynx in Switzerland. In *Biology and conservation of wild felids*: 493–506. Macdonald, D.W. & Loveridge, A.J. (Eds). London: Oxford University Press.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference*. New York: Springer-Verlag.
- Carbone, C., Teacher, A. & Rowcliffe, J.M. (2007). The costs of carnivory. *PLoS Biol.* **5**, 363–368.
- Gervasi, V., Nilsen, E.B., Sand, H., Panzacchi, M., Rauset, G.R., Pedersen, H.C., Kindberg, J., Wabakken, P., Zimmermann, B., Odden, J., Liberg, O., Swenson, J.E. & Linnell, J.D.C. (2012). Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore–ungulate systems in Scandinavia. *J. Anim. Ecol.* **81**, 443–454.
- Graham, K., Beckerman, A.P. & Thirgood, S. (2005). Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biol. Conserv.* **122**, 159–171.
- Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B. & Andersen, R. (2005). Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *J. Zool. (Lond.)* **265**, 63–71.
- Holling, C.S. (1959). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Entom.* **91**, 293.
- Hurlbert, S.H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**, 187–211.
- Jakob, E.M., Marshall, S.D. & Uetz, G.W. (1996). Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61.
- Jeschke, J.M. (2007). When carnivores are 'full and lazy'. *Oecologia* **152**, 357–364.
- Kellert, S.R., Black, M., Rush, C.R. & Bath, A.J. (1995). Human culture and large carnivore conservation in North America. *Conserv. Biol.* **10**, 977–990.
- Linnell, J.D., Broseth, H., Odden, J. & Nilsen, E.B. (2010). Sustainably harvesting a large carnivore? Development of Eurasian lynx populations in Norway during 160 years of shifting policy. *Environ. Manage.* **45**, 1142–1154.
- Linnell, J.D.C., Odden, J. & Mertens, A. (2012). Mitigation methods for conflicts associated with carnivore depredation

- on livestock. In *Carnivore ecology and conservation: a handbook of techniques*: 314–332. Boitani, L. & Powell, R.A. (Eds). Oxford: Oxford University Press.
- Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R. & Swenson, J.E. (1999). Large carnivores that kill livestock: do ‘problem individuals’ really exist? *Wildl. Soc. Bull.* **27**, 698–705.
- Linnell, J.D.C., Salvatori, V. & Boitani, L. (2008). Guidelines for population level management plans for large carnivores in Europe. In: *A Large Carnivore Initiative for Europe report prepared for the European Commission (contract 070501/2005/424162/MAR/B2)*.
- Linnell, J.D.C., Swenson, J.E. & Andersen, R. (2001). Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Anim. Conserv.* **4**, 345–349.
- Marucco, F. & McIntire, E.J.B. (2010). Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: wolves in the Italian Alps. *J. Appl. Ecol.* **47**, 789–798.
- Marucco, F., Pletscher, D.H. & Boitani, L. (2008). Accuracy of scat sampling for carnivore diet analysis: wolves in the Alps as a case study. *J. Mammal.* **89**, 665–673.
- Melis, C., Basille, M., Herfindal, I., Linnell, J.D.C., Odden, J., Gaillard, J.-M., Høgda, K.-A. & Andersen, R. (2010). Roe deer population growth and lynx predation along a gradient of environmental productivity and climate in Norway. *Ecoscience* **17**, 166–174.
- Meriggi, A., Brangi, A., Matteucci, C. & Sacchi, O. (1996). The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography* **19**, 287–295.
- Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Csányi, S. & Stenseth, N.C. (2006). Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *J. Appl. Ecol.* **43**, 721–734.
- Mysterud, A., Bischof, R., Loe, L.E., Odden, J. & Linnell, J.D.C. (2012). Contrasting migration tendencies of sympatric red deer and roe deer suggest multiple causes of migration in ungulates. *Ecosphere* **3**, art92.
- Mysterud, A., Langvatn, R., Yoccoz, N.G. & Stenseth, N.C. (2001). Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *J. Anim. Ecol.* **70**, 915–923.
- Odden, J., Herfindal, I., Linnell, J.D.C. & Andersen, R. (2008). Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. *J. Wildl. Manage.* **72**, 276–282.
- Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T. & Andersen, R. (2002). Lynx depredation on domestic sheep in Norway. *J. Wildl. Manage.* **66**, 98–105.
- Putman, R., Apollonio, M. & Andersen, R. (2011). *Ungulate management in Europe: problems and practices*. Cambridge: Cambridge University Press.
- R Development Core Team. (2008). R: A language and environment for statistical computing. R. F. f. S. Computing (Ed.). Vienna, Austria.
- Ray, J.C., Redford, K.H., Steneck, R.S. & Berger, J. (2005). *Carnivores and the conservation of biodiversity*. 200th edn. London: Island Press.
- Sangay, T. & Vernes, K. (2008). Human–wildlife conflict in the Kingdom of Bhutan: patterns of livestock predation by large mammalian carnivores. *Biol. Conserv.* **141**, 1272–1282.
- Schwerdtner, K. & Gruber, B. (2007). A conceptual framework for damage compensation schemes. *Biol. Conserv.* **134**, 354–360.
- Silva, M. & Downing, J.A. (1995). *Handbook of mammalian body masses*. Boca Raton, FL: CRC Press Edition.
- Sinclair, A.R. & Byrom, A.E. (2006). Ecosystem dynamics for conservation of biota. *J. Anim. Ecol.* **75**, 64–79.
- Stahl, P., Vandel, J.M., Herrenschmidt, V. & Migot, P. (2001). Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability. *J. Appl. Ecol.* **38**, 674–687.
- Stahl, P., Vandel, J.M., Ruetz, L., Coat, L., Coat, Y. & Balestra, L. (2002). Factors affecting lynx predation on sheep in the French Jura. *J. Appl. Ecol.* **39**, 204–216.
- Tjorve, E. & Tjorve, K.M. (2010). A unified approach to the Richards-model family for use in growth analyses: why we need only two model forms. *J. Theor. Biol.* **267**, 417–425.
- Treves, A. & Karanth, K.U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* **17**, 1491–1499.
- Trouwborst, A. (2010). Managing the carnivore comeback: international and EU species protection law and the return of lynx, wolf and bear to Western Europe. *J. Environ. Law* **22**, 347–372.
- Vucetich, J.A., Peterson, R.O. & Schaefer, C.L. (2002). The effect of prey and predator densities on wolf predation. *Ecology* **83**, 3003–3013.
- Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005). Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos* **111**, 259.
- Wittmer, H.U., Elbroch, L.M. & Marshall, A.J. (2012). Good intentions gone wrong: did conservation management threaten endangered huemul deer *Hippocamelus bisulcus* in the future Patagonia National Park? *Oryx* **47**, 393–402.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.