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Where, why and how carnivores kill domestic animals in different parts of their ranges: An example of the Eurasian lynx

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ABSTRACT

Human-carnivore conflicts over predation on domestic animals are a global challenge. Knowledge of determinants and patterns of predation on domestic animals is an essential prerequisite to develop and apply effective interventions against carnivores. Yet, it is surprisingly little known about how these determinants and patterns vary across different parts of the distribution areas of individual carnivore species. We synthesized published information on Eurasian lynx (*Lynx lynx*) predation in terms of: (a) domestic prey species, (b) selectivity, kill rates and consumption; (c) problem seasons; (d) problem individuals and sex/age categories of lynx; (e) problem areas (hotspots); (f) predation in Europe and Asia; and (g) effects of livestock protection interventions. Using a global database of dietary profiles (104 cases from 39 publications), we found that the main domestic animals killed and consumed by lynx are semi-domestic reindeer (*Rangifer tarandus*) and sheep (*Ovis aries*). Predation patterns on these two species are very different. Reindeer tend to be predated as a main wild prey species, whereas sheep are primarily available during summer and appear to be killed upon chance encounters (mainly lambs), mostly by male lynx, in predictable hotspot areas. As sheep and especially reindeer graze over remote areas without human attendance, only few interventions can be effectively used, with a primary focus on hotspot areas and peak seasons associated with the highest losses to lynx. Electric fencing and herding have been recommended as practical tools for sheep protection on small to medium scales, whereas compensation of confirmed losses is mostly ineffective as poaching still remains to be the major cause of lynx mortality. Risk-based compensations and performance payments are promising, but their application in lynx has yet to be tested.

1. Introduction

Establishing and maintaining conditions for the coexistence of local people and wildlife are among the long-term challenges in modern conservation (Carter and Linnell, 2016; Nyhus, 2016). Wildlife can destroy crops, damage property, kill domestic animals and threaten public safety. The resulting financial, social and psychological losses violate the delicate balance between the needs of socio-economic development and biodiversity conservation (VerCauteren et al., 2012) and lead to complicated trade-offs between

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land-sparing and land-sharing approaches in conservation (Bruskotter et al., 2022). Losses also drive efforts to reduce contacts between humans and wildlife, encourage the destruction of encountered animals and lead to negative attitudes toward conservation (Fletcher and Toncheva, 2021). Practical, scientifically justified and non-lethal proactive measures are needed to reduce human-wildlife conflicts and promote coexistence which would secure viable livelihoods and avert wildlife extinctions.

Few species have such a strong reputation of conflict-makers with humans as mammalian carnivores. Conflicts with wolves (*Canis lupus*), coyotes (*C. latrans*), brown bears (*Ursus arctos*), American black bears (*U. americanus*), Asiatic black bears (*U. thibetanus*) and medium-sized and big cats are well-known and have been widely reported (van Eeden et al., 2018). These species can kill domestic animals and farmed wildlife, and bears can additionally destroy beehives, raid crop fields and tree plantations, and become a nuisance in human landscapes (VerCauteren et al., 2012). In addition, hunters and carnivores compete for ungulates and other game species (Nyhus, 2016; Červený et al., 2019). Due to the high value of damaged resources, financial losses can be substantial, especially for low-income households with no alternative means of subsistence (Dickman et al., 2011). Although cases of the aggressive behavior of carnivores and carnivore attacks on people are very rare, they receive disproportionately wide media coverage, thus provoking fear, lack of support for conservation and appeals for management actions (Penteriani et al., 2016; Nanni et al., 2020). Large-scale development leading to encroachment and fragmentation of natural areas also increases human-carnivore conflicts, with the appearance of carnivores in residential neighborhoods not uncommon (di Minin et al., 2016).

Finding solutions to human-carnivore coexistence requires dedicated efforts in applied scientific research and the synthesis of its results. Solid evidence of the effectiveness of carnivore-targeted interventions is limited (van Eeden et al., 2018; Khorozyan and Waltert, 2019; Khorozyan and Waltert, 2021), in spite of a plethora of site-specific studies of conflict patterns and applied mitigation tools (summarized in Moreira-Arce et al., 2018 and Ugarte et al., 2019, inter alia). Along with this, several aspects of human-carnivore interactions remain poorly understood. For example, it generally remains obscure why a particular carnivore species kills domestic species in different parts of its distribution area, what domestic species it kills, and what geographical, ecological and human factors can be responsible for this. In addition, the range-wide consumption by carnivores of wild prey and the associated factors have been well-examined (Lyngdoh et al., 2014; Newsome et al., 2016; Ferretti et al., 2020), but similar studies of domestic prey are limited and have largely focused on the relationships between predation on domestic species vs. the availability of wild prey (Khorozyan et al., 2015; Suryawanshi et al., 2017; Janeiro-Otero et al., 2020).

Obtaining information on intra-specific variation in predation on domestic animals is important from several perspectives. It can reveal large-scale features of conflict patterns and possible solutions that take into account regional aspects of carnivore ecology, landscape characteristics and even the socio-political settings in which solutions can be implemented, based on their record of success in similar conflict areas elsewhere. Moreover, knowledge on the type of damage inflicted by a species can facilitate the planning and implementation of relevant, practical and potentially effective solutions. And last but not the least, a given solution addressing a particular carnivore species may provide useful insights applicable to other, co-existing carnivores. While range-wide species studies often lack the quantitative information needed for comprehensive statistical analyses, this does not usually hinder a general view of human-carnivore conflicts. Rather, conservation-related decision-making, research and locally specific applications profit from the synthesis of many types of available information, including systematic reviews (Pullin et al., 2020).

The Eurasian lynx (*Lynx lynx*) is well-suited to explorations of the range-wide patterns of predation on domestic animals for three reasons. First, its distribution area covers northern Eurasia, where available options for predation are intrinsically scarce due to the limitations of the natural prey base, landscapes, domestic animals and livelihood practices, all of which result in predation patterns that are stable and predictable (Khorozyan and Heurich, 2023). Second, extrapolation of lynx predation patterns from its diet (scats, prey carcasses and stomach/intestine contents) is reliable as lynx mostly consume naturally killed prey and carrion does not make a significant part of its diet, although scavenging is possible (Sunde and Kvam, 1997; Matyushkin and Vaisfeld, 2003). The maximum contribution of carrion to the lynx diet reported in the literature is 15.7%, documented in the north of European Russia (Malafeev et al., 1986). Third, lynx predation on domestic animals can differ between Europe and Asia because: (i) lynx is threatened and protected in Europe but generally perceived as common and not prioritized in Asia (although often protected), therefore more published information on lynx-caused damage to domestic animals is expected to come from Europe while the Asian records would likely remain largely unreported (Namgail et al., 2007); and (ii) animal husbandry practices may differ between these two continents, which is most evident in sheep (*Ovis aries*) being grazed during summer in Europe and year-round in Asia (Gervasi et al., 2014; Din et al., 2015).

This study is a synthesis of the available published information on predation and consumption of domestic animals by lynx throughout its distribution area in northern Eurasia. It describes the domestic species targeted by lynx; how they are selected, killed and consumed; the problem seasons and areas in which losses to lynx are the highest; the lynx individuals (age, sex) most likely to kill domestic animals; how lynx predation on domestic animals differs between Europe and Asia; and the interventions that are, or can be, effective in reducing losses of domestic animals or lynx killing rates.

2. Materials and Methods

2.1. Literature search

An intensive and systematic search of range-wide publications on the lynx diet was conducted from the IUCN Red List of Threatened Species account (Breitenmoser et al., 2015), national species status reports (Bao, 2010; Mousavi et al., 2016), thematic books (Nowell and Jackson, 1996; Breitenmoser and Breitenmoser-Würsten, 2008; Macdonald et al., 2010), reviews (Ferretti et al., 2020) and the online resources including the IUCN/SSC Cat Specialist Group digital library (<https://catsg.org>, 1950–2021), Web of Science (<http://apps.webofknowledge.com>, 1945–2021) and eLibrary (<https://elibrary.ru>, no time limits). No limitations were set on

publication types, study materials, countries or languages, and the longest possible periods were applied to the search. The search words included “lynx” (Russian equivalent – рысь; pronounced “rys”) and “lynx AND diet” (Russian equivalent – рысь, питание; pronounced “rys, pitanie”). As the first author is a native Russian speaker, the Russian-language literature was explored in detail. The search was stopped when no additional publications appeared.

The following types of studies were excluded: (1) studies lacking quantitative information on the lynx diet; (2) studies that focused on one or few prey species and did not describe the whole diet; (3) studies that used the same data that we collected and (4) studies that lumped together the lynx diet from scats, prey carcasses and stomach/intestine contents.

2.2. Analysis of the occurrence of domestic animals in the lynx diet

Data on the frequency of occurrence (FO, %) of wild and domestic prey items in lynx scats, prey carcasses and stomach/intestine contents were collected. To minimize biases from scat data (overestimation of small prey and underestimation of large prey), the FO in scats was converted to the percentage of biomass consumed (BC) using a lynx-specific correction factor (Wachter et al., 2012) (Eq. 1):

$$y_i = 1.045(1 - e^{-0.145W_i})$$

$$BC_i = \left(\frac{y_i n_i}{\sum_{i=1}^N y_i n_i} \right) 100 \quad (1)$$

where n_i is the number of collected scats containing the i -th prey, N is the total number of prey species in the study, W_i is the live body mass of the i -th prey (kg) and y_i is the biomass of the i -th prey species consumed (kg) to produce one scat.

For large prey species (≥ 40 kg), in which case lynx mostly prey on juveniles and females, the W_i was estimated as 0.75 of that of adult females (Hayward et al., 2012; Lyngdoh et al., 2014). For medium-sized ungulates and smaller prey (< 40 kg) not selected by lynx according to their sex/age, the W_i of adult individuals was used. The estimates of W_i were extracted from publications on the lynx diet, mammal (Jones et al., 2009; Smith et al., 2018) and bird (Storchová and Hořák, 2018) databases, species accounts in Mammalian Species, meta-analyses of the diets of co-existing big cats such as snow leopards (*Panthera uncia*) (Lyngdoh et al., 2014) and tigers (*P. tigris*) (Hayward et al., 2012), and other publications found in Google Scholar (<https://scholar.google.com>). For each prey species, W_i was the median of the body mass estimates extracted from different sources (see Appendix A1).

Semi-domestic reindeer (*Rangifer tarandus*) were distinguished from wild reindeer and considered only when their semi-domestic status was explicitly indicated by the authors or when they were reported from regions where wild reindeer are known to be extinct

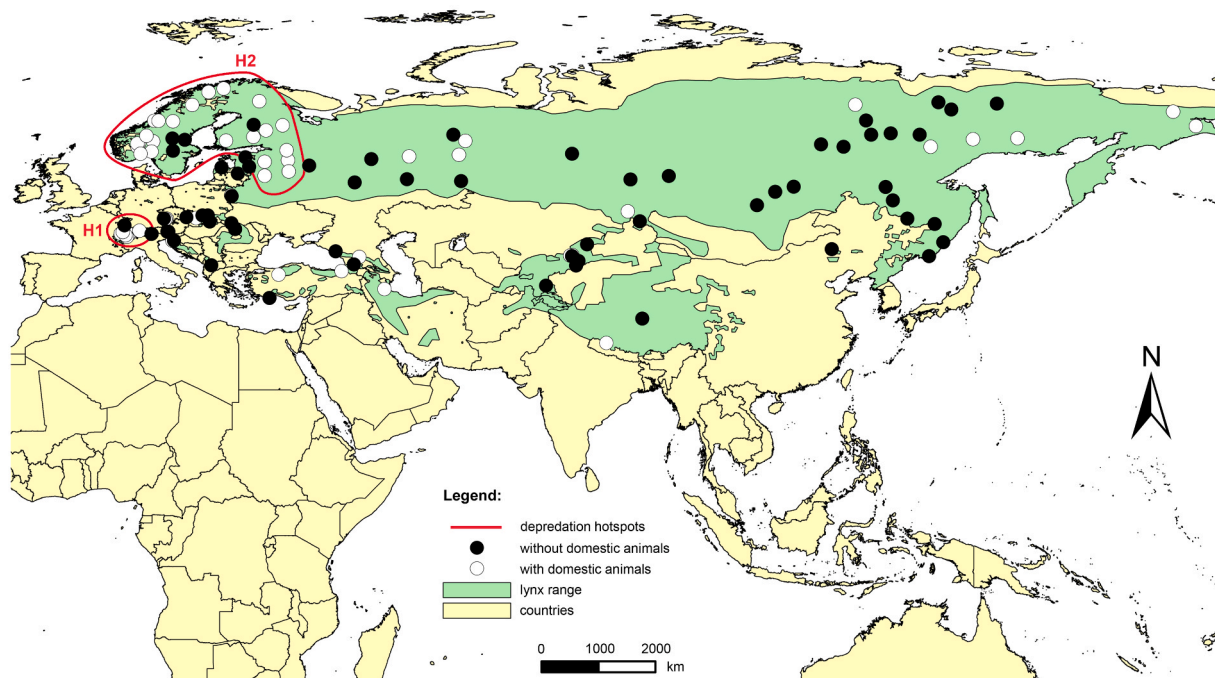


Fig. 1. Distribution of sites for which data on Eurasian lynx (*Lynx lynx*) diets, with and without domestic species, were included in this study. Tentative depredation hotspots delineated from the data are marked as H1 (Switzerland) and H2 (Fennoscandia/north of European Russia). The range map was obtained from Breitenmoser et al. (2015).

Table 1

Local contribution (%) of domestic species to the Eurasian lynx (*Lynx lynx*) diet revealed from differed published sources. It is shown as the percentages of consumed biomass from lynx scats and species occurrence in prey carcasses and lynx stomach/intestine contents. No locality names are provided to save space. Indication of the same country name several times for the same domestic species means several independent records for this country from different published sources. Data from Russia are provided for administrative units and geographical objects due to the large size of the country. The references are listed in Appendix A1. Abbreviations: n – total sample size. * – mixed cat and dog remains not further split into dog and cat remains, ** – while not explicitly indicated, these reindeer were presumed to be semi-domestic, given their high occurrence in the lynx diet.

Domestic species	Europe			Asia			
	%	Country	n	%	Country	n	
Cat (<i>Felis catus</i>)	0.16	Switzerland	617	1.14	Türkiye	101	
	0.25	Czechia	1221				
	0.50	Switzerland	201				
	0.62	Sweden/Norway	1443				
	0.68	Norway	146				
	1.20	Russia (Karelia)	85				
	1.30	Russia (Kirov Oblast)	152				
	1.33	Germany/Czechia	39				
	1.60	Russia (Karelia)	63				
	1.87	Belarus	399				
	2.50	Russia (Novgorod Oblast)	40				
	3.90	Finland	390				
	4.10	Finland	88				
	7.50	Finland	107				
Cattle (<i>Bos taurus</i>)	0.49	Czechia	1221				
Dog (<i>Canis familiaris</i>)	0.58	Poland	172	2.33	Türkiye	101	
	0.65	Russia (Kirov Oblast)	152	2.70	Russia (Sverdlovsk Oblast)	113	
	0.80	Finland	88	9.73	Kazakhstan	44	
	1.45	Poland	139				
	1.60	Russia (Pskov Oblast)	61				
	1.91	Belarus	399				
	3.50	Russia (Karelia)	85				
	4.80	Russia (Karelia)	63				
	Domestic animals in general, not identified to species level	0.49	Norway*	205	2.90	Russia (middle Ural Mts.)	103
		4.00	Switzerland	99	18.20	Russia (middle Ural Mts.)	77
10.00		Switzerland	80				
13.60		Finland	3				
16.00		Slovenia/Croatia	37				
Farmed Arctic fox (<i>Vulpes lagopus</i>)	0.80	Finland	88				
Farmed rabbit (<i>Oryctolagus cuniculus</i>)	0.80	Finland	88				
Goat (<i>Capra hircus</i>)	0.16	Czechia	1221	5.87	Türkiye	69	
	0.19	Norway	492	11.88	Nepal	6	
	0.20	Switzerland	491				
	0.34	Belarus	399				
	0.50	Switzerland	201				
	0.56	Switzerland	179				
	0.84	Norway	358				
	0.88	Switzerland	114				
	0.90	Russia (Leningrad Oblast)	104				
	1.09	Switzerland	183				
	1.60	Russia (Pskov Oblast)	61				
	2.97	Norway	101				
	3.72	Russia (North Caucasus)	64				
	7.10	Switzerland	38				
	Pig (<i>Sus domesticus</i>)	0.68	Norway	146			
Semi-domestic reindeer (<i>Rangifer tarandus</i>)	18.54	Norway	205	22.18	Russia (Yakutia)**	28	
	23.08	Sweden	26	31.87	Russia (Magadan Oblast)	11	
	28.83	Sweden	26	33.49	Russia (Koryak Plateau)	9	
	30.68	Norway	111	38.54	Russia (Khabarovsk Krai)	26	
	39.04	Norway	146	39.57	Russia (Koryak Plateau)	19	
	42.45	Sweden	106	53.45	Russia (Khabarovsk Krai)	11	
	51.35	Sweden	37	54.62	Russia (Magadan Oblast)	5	
	69.19	Norway	396	56.19	Russia (Chukotka)	46	
	69.85	Sweden/Norway	1443	57.59	Russia (Chukotka)	19	
	93.43	Sweden	41	72.83	Russia (Yakutia)**	11	
	Sheep (<i>Ovis aries</i>)	0.74	Russia (North Caucasus)	64	3.50	Russia (central Altai Mts.)	56
		0.81	Switzerland	491	4.34	Kazakhstan	62
1.28		Czechia/Slovakia	78	9.86	Kazakhstan	44	
1.68		Czechia	773	23.53	Iran	17	
2.20		Russia (Tver Oblast)	91				
2.27		Switzerland	88				

(continued on next page)

Table 1 (continued)

Domestic species	Europe			Asia		
	%	Country	n	%	Country	n
Sheep (<i>Ovis aries</i>)	2.40	Russia (Karelia)	85			
	2.50	Russia (Novgorod Oblast)	40			
	2.90	Russia (Leningrad Oblast)	104			
	2.96	Norway	135			
	3.20	Russia (Karelia)	63			
	4.01	Czechia	1221			
	4.57	Sweden/Norway	1443			
	4.79	Norway	146			
	4.86	Russia (Tver Oblast)	142			
	6.14	Switzerland	114			
	6.15	Switzerland	179			
	6.35	Norway	111			
	6.60	Russia (Pskov Oblast)	61			
	11.67	Russia (Kirov Oblast)	19			
	11.73	Norway	358			
	11.87	Norway	396			
	23.19	Norway	69			
	25.00	Norway	40			
	30.37	Norway	492			
	31.68	Norway	101			
61.90	Norway	189				

(Sweden).

Information on interventions applied to protect domestic animals from lynx was retrieved from the search described above, and from the meta-analysis by Khorozyan and Waltert (2021). Data on seasonal variation in losses to domestic animals inflicted by lynx were collected from the text and tables of original publications, or from graphs using PlotDigitizer (<https://plotdigitizer.com/app>).

2.3. Statistical analysis

We used the Mann-Whitney test in IBM SPSS Statistics v. 26.0 to compare FO and BC between domestic species, continents (Europe and Asia) and for each species between continents. The effect size for the Mann-Whitney test was measured as Cohen's $r = |z|/\sqrt{N}$ and that for the χ^2 test as Cohen's $w = \sqrt{\chi^2/N}$, where z and χ^2 are the test statistics and N is the sample size (Fritz et al., 2012). The effect was considered to be strong for r and w values > 0.5 , moderate for values between 0.3 and 0.5 and weak for values between 0.1 and 0.3 (Fritz et al., 2012). We measured the median for each species sample and calculated its 99% confidence interval (CI) using the formula from Conover (1999). The species represented by only one sample (cattle *Bos taurus*, domestic Arctic fox *Vulpes lagopus*, pig *Sus domesticus* and rabbit *Oryctolagus cuniculus*) were excluded from the analysis.

3. Results and discussion

3.1. Domestic prey of lynx

This systematic review was based on 104 cases of consumption of domestic animals by the lynx throughout its range in northern Eurasia, as described in 39 publications (Fig. 1). Nine domestic or semi-domestic species in the lynx diet were recorded: sheep ($n = 31$ cases), reindeer ($n = 20$), goat (*Capra hircus*, $n = 16$), cat (*Felis catus*, $n = 15$), dog (*Canis familiaris*, $n = 11$), cattle ($n = 1$), farmed Arctic fox ($n = 1$), farmed rabbit ($n = 1$) and pig ($n = 1$). Unidentified domestic animals were grouped as a single diet category ($n = 7$). Other domestic animals locally killed and consumed by lynx included alpaca (*Lama pacos*), juveniles of yak (*Bos grunniens*), chicken (*Gallus domesticus*), and farmed European mouflon (*Ovis aries musimon*), fallow deer (*Dama dama*), sika deer (*Cervus nippon*), red deer (*C. elaphus*) and American mink (*Neogale vison*) (Danilov et al., 1979; Angst et al., 2002; Matyushkin and Vaisfeld, 2003; Breitenmoser and Breitenmoser-Würsten, 2008; Alexander et al., 2015), but studies of their contributions to the lynx diet are lacking.

Semi-domestic reindeer (hereafter, reindeer) grazing freely in polar and sub-polar regions of Norway, Sweden, Finland and Russia are consumed by lynx in much higher proportions (from 18% to $> 90\%$) of the overall diet than other domestic species (Table 1). This was confirmed statistically, as the median percentage of reindeer in the lynx diet (41.0%, 99% CI = 28.8–57.6%) estimated in this study was significantly higher than that of goat (0.9%, 0.2–3.7%, Cohen's $r = 0.85$), cat (1.3%, 0.5–2.5%, $r = 0.85$), dog (1.9%, 0.6–4.8%, $r = 0.82$), sheep (4.8%, 2.5–11.7%, $r = 0.75$) and domestic species in general (10.0%, 0.5–18.2%, $r = 0.75$). The number of reports documenting reindeer consumption was also high. Several reasons may explain why reindeer are more vulnerable to lynx predation: (i) in the northernmost areas of the lynx range, reindeer are the only ungulates that are abundant and available year-round (Danell et al., 2006; Mattisson et al., 2014a); (ii) reindeer have a low capacity to detect an approaching lynx, as domestication has resulted in their docile behavior; and (iii) because they spend much of their time digging for lichens in the snow during short polar days. As a result, the success rates of reindeer hunts by lynx are quite high, especially when individuals lagging behind the herd (Haglund, 1966) or hindered by deep snow (Pedersen et al., 1999) are selected as prey.

The main alternative prey to reindeer is the mountain hare (*Lepus timidus*), but it is an unstable food resource due to periodical population fluctuations making lynx rely on reindeer, or to undertake long-distance forays in search of sufficient food (Zheleznov-Chukotsky, 2010; Sedalischev et al., 2014). As reindeer are seasonally migrating, lynx have to maintain extremely large home ranges to prey on alternative species such as mountain hares and grouses (*Lagopus* sp.) (Danell et al., 2006; Linnell et al., 2021). Towards the south of reindeer grounds, lynx also prey on wild ungulates, primarily European (*Capreolus capreolus*) and Siberian (*C. pygargus*) roe deer, which become more common along the north-south gradient (Jędrzejewski et al., 1993; Danilkin, 2014; Khorozyan and Heurich, 2023). In contrast to semi-domestic reindeer, wild reindeer have a limited distribution and are larger and more vigilant, such that their contribution to the lynx diet is low (< 10%) (Matyushkin and Vaisfeld, 2003; Odden et al., 2013; Gervasi et al., 2014).

Sheep are the second most intensively killed and consumed domestic species (0.7–61.9% in the lynx diet, Table 1), but their predation cases make up the majority of literature reports (29.8% of all reported cases). Sheep consumption (median 4.8%, 99% CI = 2.5–11.7%) was much higher than that of cat (Cohen's $r = 0.56$) and moderately higher than that of goat ($r = 0.50$) or dog ($r = 0.43$), which are shown above. Sheep are widely grazed but patchily distributed, mostly on deforested mountain slopes and alpine meadows from spring to autumn (May–June to September–October; Odden et al., 2006; Alexander et al., 2015) or even until late autumn (Stahl et al., 2001a) or year-round (Din et al., 2015). The two countries with the highest rates of sheep consumption by lynx are Norway and Switzerland (Fig. 1). In both, sheep are free-ranging, without attendance by shepherds and dogs, and are thus often targeted if they encroach on lynx habitat (Odden et al., 2006; Molinari-Jobin et al., 2007). Like many other European countries, Switzerland experienced a long-term absence of large carnivores due to human persecution leading to the loss of knowledge and skills in sheep protection from reintroduced lynx (Breitenmoser and Haller, 1993). However, the situation is gradually improving due to the pan-European efforts to bring back traditional methods of livestock protection in response to the ongoing conservation-led recovery of the continent's large carnivore populations (Dory, 2017).

For the above-mentioned domestic species that make up an insignificant part (< 10%) of the lynx diet, records are very rare (Table 1). Few data are available on goat predation by lynx and it remains unclear whether the low consumption rate of goats is related to their low availability or to their vigilance in avoiding lynx attacks (in contrast to sheep, which frequently graze together with goats). Sometimes, it is not possible to discern cases of goat predation from those of scavenging (Mengülluöglu et al., 2018). Occasional consumption of dogs and cats may result from inter-specific competitive killing, suggesting that the number of cases of cats and/or dogs killed but not consumed by lynx can be higher than reported. However, the possibility of hunger-driven consumption should not be excluded, which implies that lynx may visit villages deliberately to kill roaming cats and small to middle-sized dogs for food (Danilov et al., 1979; Matyushkin and Vaisfeld, 2003). The lack of published information about the relationships between lynx, cats and dogs suggests this topic as an area of research.

In single cases, lynx have consumed farmed Arctic fox, rabbit, pig, and calves. While lynx can indeed kill Arctic foxes, rabbits, chickens and farmed American minks in villages during lean times (Danilov et al., 1979; Pullianen, 1981; Matyushkin and Vaisfeld, 2003), the consumption of pigs and cattle reported in the literature occurred under unusual circumstances. Particularly, a pig was consumed when it served as bait in a trap placed in lynx habitat (Birkeland and Myrberget, 1980) and the consumed calves were the newborns of free-grazing cows in the wild (Červený et al., 1998). As cattle are too large for lynx, they are most likely consumed by scavenging, particularly when slaughtered individuals are placed in the wild as a supplemental food resource to avert brown bear attacks on livestock (Krofel et al., 2011). In such cases, the presence of cattle remains in the stomach or intestine of a lynx killed while consuming a carcass bait will overestimate cattle consumption (Krofel et al., 2011). Supplemental feeding with the carcasses of domestic animals is prohibited in some countries because it is ineffective and expensive, but it is allowed and practiced in others (Kavčić et al., 2015).

3.2. Selectivity, kill rates and consumption of domestic prey

Patterns of prey selection by lynx for particular domestic species and the sex/age categories of those species have been published only for reindeer and sheep. Sheep are usually taken when their densities are high and their protection is loose or absent, but even in this case lynx may preferentially select wild prey, such as roe deer, despite their low densities (Odden et al., 2006). Most sheep kills occur in forest habitats used by lynx and its wild prey rather than in sheep grazing areas, implying that sheep predation is due to incidental encounters rather than to active searches by lynx (Moa et al., 2006; Odden et al., 2008). On a larger scale, however, the scarcity of wild prey has a more profound impact, and estimated sheep losses are the highest in areas where wild prey densities are low (Odden et al., 2013).

In contrast to sheep, which are more likely to be killed in chance encounters, reindeer are purposefully hunted by lynx like a wild species and are thus the preferred prey in tundra and forest-tundra habitats, similar to roe deer in forests (Mattisson et al., 2011b; Mattisson et al., 2014b).

In terms of age preferences, in the case of sheep lynx kill mostly lambs (≤ 1 year; Odden et al., 2002; Breitenmoser and Breitenmoser-Würsten, 2008; Odden et al., 2008; Odden et al., 2013) and juveniles (1–2 years; Li et al., 2013; Gervasi et al., 2014), but also can prey on adults (Alexander et al., 2015). Lynx kill adults when lambs are absent, but once lambs become available, they are actively selected (Stahl et al., 2001a). However, whether these age categories of killed sheep reflect true selection or proportional availability is impossible to determine unless the number of initially available prey is reported. In some cases, a strong selectivity can be inferred from the complete dominance of a certain category among the kills, e.g., when all sheep killed by lynx are lambs and juveniles (Din et al., 2015). The role of lynx predation in overall lamb mortality depends on how long the lambs graze within forests, the main habitat of lynx (Warren et al., 2001).

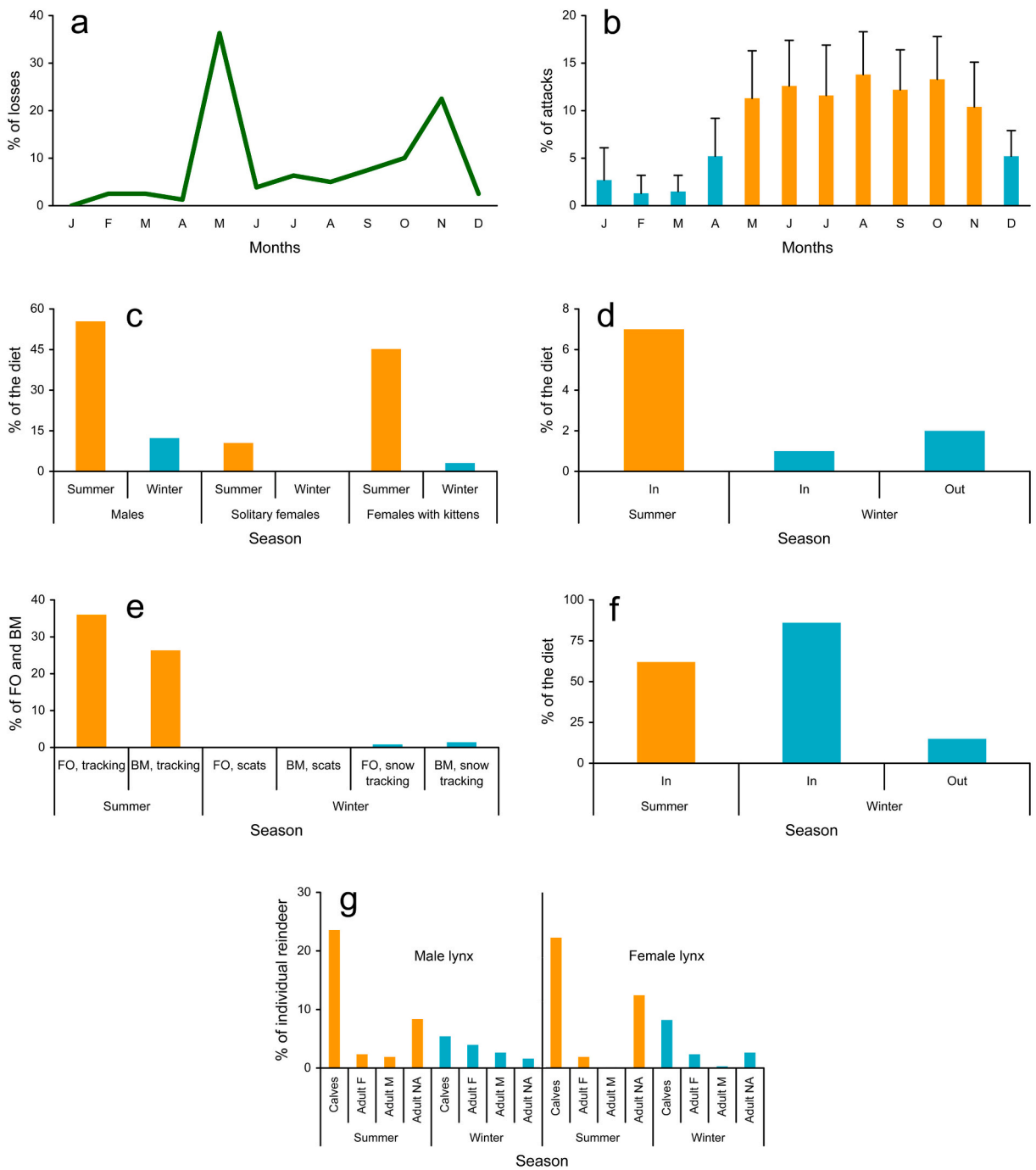


Fig. 2. Seasonal variation in lynx predation on domestic animals: (a) Monthly distribution of sheep and goat losses in Pakistan (Din et al., 2015); (b) Monthly distribution of the number of attacks on sheep in France, with bars of standard deviation (converted from proportions; Stahl et al., 2001a); (c) Contribution (%) of sheep to the diets of males, solitary females and females with kittens in summer and winter in southern Norway (Gervasi et al., 2014); (d) Contribution (%) of sheep to the lynx diet in summer and winter depending on whether grazing grounds are in or out of lynx home ranges, northern Scandinavia (Mattisson et al., 2011b); (e) Frequency of occurrence (FO, %) and percentage of ingested biomass (BM, %) of sheep in the lynx diet in summer and winter, southeastern Norway (Odden et al., 2006); (f) Contribution (%) of reindeer to the lynx diet in summer and winter depending on whether grazing grounds are in or out of lynx home ranges, northern Scandinavia (Mattisson et al., 2011b); (g) Proportions (%) of reindeer sex (males M, females F, not available NA) and age categories in summer and winter diets of male and female lynx, northern Scandinavia (converted from absolute numbers; Mattisson et al., 2014a). Summer months are colored dark orange and winter months are turquoise.

Studies of reindeer suggest that adult females (≥ 1.5 years) are the preferred prey but also adult males (≥ 1.5 years) and calves, mainly in poor physical condition (Pedersen et al., 1999). In other studies, lynx actively selected newborns (≤ 1 month; Mattisson et al., 2011a) and calves (< 1 year; Mattisson et al., 2011b; Mattisson et al., 2014a).

GPS-tracking allows estimates of domestic animal kill rates, i.e., the number of individuals killed by a carnivore per unit of time. In one study, lynx killed 4–4.45 reindeer/month, with the higher number killed when accompanied by wolverine (*Gulo gulo*) scavenging of the kills (Andrén et al., 2011). Higher reindeer kill rates by lynx indicate a much shorter interval between consecutive kills (Mattisson et al., 2011a) and thus more energy expended for hunting. In another study, mean kill rates were 1.2 sheep/month regardless of sheep densities and 7.1 reindeer/month, which increased with reindeer densities (Mattisson et al., 2014b). The average reindeer kill rate in yet another study was 0.2 reindeer/day, which varied from 0 to 0.41 reindeer/day between individual lynx (Pedersen et al., 1999). Similar lynx-dependent variation has also been observed in sheep kill rates, which ranged from 8.2 sheep/100 days in summer, when these animals were most available, to 1 sheep/100 days in winter, when they were at their lowest density; however, they also varied substantially between individual lynx within 0–54 sheep/100 days in summer and 0–20 sheep/100 days in winter independently of sheep densities (Gervasi et al., 2014). Pooled sheep kill rates were 4–27 sheep/100 days across all study areas and 8–53 sheep/100 days within grazing areas, although lynx spent much less time in the latter (Odden et al., 2002). Other authors reported sheep kill rates of 0–12.4 sheep/100 days; lynx that did not kill sheep had fewer sheep available in their home ranges (Stahl et al., 2002). On a large scale, kill rates varied from 0.2 to 7.9 sheep/30 days, depending on the sex of lynx, and they increased with increasing sheep densities and decreasing wild prey (roe deer) densities (Odden et al., 2013).

Like many other carnivores, lynx can kill multiple domestic animals per event during a single hunting rush but then consume none or only one of them (Breitenmoser and Haller, 1993). This “surplus killing” mostly involves domestic animals confined to limited spaces (fences or barns) or trapped by harsh conditions (e.g., deep snow) that cause them to panic or hinder them from defending themselves or escaping (Haglund, 1966; Odden et al., 2002; Breitenmoser and Breitenmoser-Würsten, 2008). It also may involve wild prey not regularly exposed to carnivores and thus lacking defensive behaviors (Dunker, 1988; Breitenmoser and Haller, 1993). Surplus killing events cannot be inferred from carnivore scats or stomach/intestine contents. As a result, their occurrence may be underestimated if the carnivore diet is assessed using these two sources (Odden et al., 2006); rather, only prey carcasses and observations can evidence surplus killings and their intensity. In studies of reindeer predation, surplus killing by lynx was documented in four events (2 animals killed/event, Pedersen et al., 1999) and accounted for 5.5% of all killing events (2–3 animals killed/event, Mattisson et al., 2011b). For sheep, the frequencies of surplus killing events by lynx were higher: 13 events (2–8 animals killed/event, Odden et al., 2002), accounting for 10% of all killing events (2–5 animals killed/event, Odden et al., 2013) and 32% of all killing events (2–11 animals killed/event, Stahl et al., 2001a). Higher frequencies of surplus killing events involving sheep and larger numbers of sheep killed per event show the greater vulnerability of sheep than reindeer to these events.

The rates of domestic animal consumption by lynx are generally lower than those of wild prey, as only 8% of all killed sheep and goats were completely consumed and 36% were not consumed at all (Odden et al., 2002). In other reports, 3.5 kg were consumed per killed sheep, 6 kg per killed goat (Odden et al., 2006) and 61% of reindeer biomass (Pedersen et al., 1999). These low rates can be explained by human disturbance, such as during the verification of fresh kills required to receive compensation for losses (Mattisson et al., 2011b) or during attempts to drive a carnivore away, but also by surplus killing (Dunker, 1988; Pedersen et al., 1999; Stahl et al., 2001a). Human disturbance may cause lynx to go away still hungry and thus hunt again, thereby increasing the kill rates of domestic animals.

3.3. Problem seasons of predation on domestic animals

Sheep are not actively searched by lynx but rather killed in chance encounters, without preference for sheep grazing areas (Moa et al., 2006; Odden et al., 2008); thus, their predation will increase during seasons when sheep availability and the odds of sheep-lynx interactions are the highest. This is confirmed by high sheep kill rates from late spring to early autumn (Odden et al., 2006; Gervasi et al., 2014; Alexander et al., 2015) or late autumn without monthly differences (Stahl et al., 2001a) (Fig. 2b–e). Sheep predation in winter is lower than in summer, most likely because of the rare occurrence of sheep on winter grazing grounds, since the animals are mainly sold or confined in barns (Stahl et al., 2001a; Mattisson et al., 2014b; Alexander et al., 2015). In areas of year-round grazing, sheep losses are still low in winter, but sharply increase in spring and autumn, when sheep move between winter and summer pastures (Din et al., 2015; Fig. 2a). In winter, when sheep are not available, lynx hunt on wild ungulates, particularly favoring those areas where ungulate dispersal is limited by snow cover and confined to certain feeding sites (Odden et al., 2008; Nilsen et al., 2009).

Because reindeer are actively searched by lynx, they might be expected to be killed according to their catchability rather than availability, but these two aspects are difficult to distinguish. For example, most of the lynx diet in July–September consists of reindeer calves, the easiest and most available prey, before most of the animals are harvested in October–January (Mattisson et al., 2014a; Fig. 2g). Additionally, reindeer bulls can be actively killed by lynx during January–June (Fig. 2g), when they lose their antlers and thus become more vulnerable to predation (increased catchability). However, during this period bulls stay within the forested lynx habitat, such that they may also be taken due to their increased availability, in contrast to reindeer cows with calves, which move up above the tree line (Mattisson et al., 2014a). In general, in areas where reindeer live at high densities and are thus easily available, lynx kill more reindeer in winter (Mattisson et al., 2011b; Fig. 2f), possibly due to the increased vulnerability caused by deep snow and low vigilance (see above).

Visitations of lynx to villages for predation on hunting dogs, cats, chickens or other small domestic animals can be quite frequent in northern parts of the lynx range, where mountain hare is the main prey. Populations of mountain hare undergo periodic fluctuations due to ecological and climatic reasons, such that lynx face hunger during seasons and years of low hare numbers, which drives them to

move widely in search of food (Matyushkin and Vaisfeld, 2003). Cases of lynx approaching and penetrating human settlements are most common in winter, when subadult lynx learn to hunt independently, hares are very scarce and snow conditions may restrict successful hunting. A majority of these lynx encounters involve animals that are in poor physical condition and end with the killing of the lynx by people or dogs (Matyushkin and Vaisfeld, 2003).

3.4. Problem individuals and sex/age categories of lynx

Lynx predation on domestic animals strongly depends on the sex and age of individual lynx. This is most evident in sheep predation by lynx. Adult male lynx (> 2 years; Sunde and Kvam, 1997) have higher sheep kill rates than females and are responsible for most cases of surplus killing, but their sheep consumption rates are low and they typically visit the kills only once (Sunde et al., 2000; Odden et al., 2002; Odden et al., 2006; Odden et al., 2013; Gervasi et al., 2014). This pattern is caused by high mobility of males and their higher tolerance of human disturbance, which increase the chances of encountering sheep (Breitenmoser and Haller, 1993; Mattisson et al., 2014b). Consequently, males are more likely to kill more sheep. Since it is usually impossible to recognize problem individuals, males can instead be regarded as a “problem sex” (Odden et al., 2002). Although in some cases habitual sheep killing may be carried out by individuals of both sexes exhibiting bold behavior and high tolerance of human landscapes, males are more likely to be the culprits (Stahl et al., 2002; Breitenmoser and Breitenmoser-Würsten, 2008).

Yearlings of both sexes may also engage in the surplus killing of sheep, especially in sheep grazing areas, such that kill rates are even higher than those of male lynx (Odden et al., 2002). This could be perhaps attributed to the wide-ranging exploratory movements and inexperience of yearlings, leading them to hunt sheep as easy prey.

Adult female lynx (> 2 years; Sunde and Kvam, 1997), whether solitary or accompanied by kittens, are least likely to kill sheep but when they do it is only in areas where sheep and grazing areas are most available (Odden et al., 2002). Some females may select for sheep and become habitual sheep killers, suggesting that individual preferences rather than sex alone can determine sheep killing by lynx (Stahl et al., 2002; Mattisson et al., 2014b). However, information on surplus killing by adult females is lacking. Adult lynx of both sexes avoid sheep grazing areas and thus exploit them much less than suggested by their availability, as they prefer forested habitats where their main wild prey, especially roe deer, live (Odden et al., 2006; Odden et al., 2008; Mattisson et al., 2014b).

Sex- and age-related variations are less evident in reindeer-killing lynx than in sheep-killing lynx. Male lynx may kill more reindeer bulls and preferentially target them than female lynx (Mattisson et al., 2014a), but kill rates are higher only in summer (Mattisson et al., 2011b). Surplus killing of reindeer by lynx is neither sex- nor age-biased (Mattisson et al., 2011b) such that the term “problem sex” cannot be applied to lynx predation on reindeer. Foraging on reindeer by male and female lynx is similar to that on wild prey (roe deer), with males exhibiting a slightly higher preference than females for reindeer, but generally the effect of lynx sex on reindeer predation is very weak (Sunde and Kvam, 1997). The lack of strong differences in the sex/age categories of lynx predation on reindeer is most likely explained by the fact that reindeer are an irreplaceable food resource for lynx in northern regions, and all lynx are intensively dependent on these animals for their survival.

3.5. Problem areas (hotspots)

The killing of domestic animals by lynx is not spatially random but is usually confined to certain hotspots, where recurrent attacks and the resulting damage are prominent. These hotspots are generally few, smaller than most grazing grounds and persistent over years, even if problem lynx are removed, which implies that their status depends on inherent conditions rather than on individual lynx (Stahl et al., 2001a). Site-specific high losses are a significant economic obstacle to sheep breeding, especially in the mountains where carcass detection, a requirement for financial compensation to sheep owners, is problematic (Stahl et al., 2001a). Moreover, surprisingly little is known about the spatial, ecological and social determinants of hotspots characterized by high losses of domestic animals to lynx, in contrast to those favored by other carnivore species (Miller, 2015). The probability of sheep killing by lynx is higher in areas located close to forests, that have no human population, contain high abundance of wild prey (roe deer) and comprise attacked pastures within ≤ 2 km from the electric fence of the pastures (Stahl et al., 2002). The proximity of grazing areas to forest, or their coverage by patches of forest or shrubs, is a prerequisite of lynx predation on sheep (Breitenmoser and Breitenmoser-Würsten, 2008).

However, the effects of individual lynx characteristics on the presence of hotspots cannot be excluded, particularly when the hotspots are small and persist for a few years during the lifetime of a lynx (Vandel and Stahl, 1998). Juvenile lynx can learn to kill domestic animals from their mothers, and especially to kill reindeer, which is common among adult females (Mattisson et al., 2011b). Female lynx seldom predate sheep, but habitual sheep-killing females accompanied by cubs (Stahl et al., 2002) might train their offspring to do so.

The risk of sheep predation by lynx is much higher on farms that have already experienced attacks on sheep, but it sharply decreases at least 2–3 months after the first attack (Karlsson and Johansson, 2010). Stahl et al. (2002) also claim that the presence of attacked pastures is a significant determinant of further lynx attacks on sheep, which implies a certain level of spatial conservatism in the sheep-killing behavior of lynx.

3.6. Predation on domestic animals in Europe and Asia

Our survey covered the lynx range in northern Eurasia, without visible biases (Fig. 1). It showed that European records of consumption of domestic animals by lynx are significantly more numerous ($n = 82$) than those from Asia ($n = 22$; Cohen's $w = 0.58$). However, domestic animals comprised a larger proportion of the lynx diet in Asia (median 20.2%, 99% CI = 3.5–39.6%) than in Europe

(2.7%, 1.3–4.8%, $r = 0.38$) (Table 1). As there was no evidence that the consumption of a particular domestic species differed between these two continents, this pattern may be due to numerous publications on lynx from Europe and caused by the dominance of intensively killed and consumed reindeer in the Asian sample (Table 1).

Active scientific reporting of lynx depredation on domestic animals in Europe is caused not only by the protected status of this carnivore throughout the continent, but also by strong enforcement and funding of its conservation (Chapron et al., 2014). In contrast, information on lynx-caused damage to domestic animals in Asia should be more intensively collected and analyzed to make a more reliable comparison with the European counterpart. In Asia, lynx is officially protected in many countries and Russian federal territories, but it is not a priority species; rather, funding is directed towards more threatened flagship species co-existing with lynx, such as the tiger, leopard (*P. pardus*), snow leopard and polar bear (*U. maritimus*) (WWF Russia, 2022). Also, in-depth research in northern Asia is expensive or unfeasible, as the areas of lynx occurrence are much larger than those in Europe, extensively covered by mountains, deep coniferous forests or swamps (Hytteborn et al., 2005) and often lack the infrastructure allowing access. Consequently, the scope and rate of losses to domestic animals due to lynx predation are likely to be underestimated, particularly when compensation programs for lynx, as an incentive for reporting, are non-existent (S. Naidenko, pers. comm.) or ineffectively managed (Alexander et al., 2015). Lynx are naturally rare and their damage is low in marginal areas of their range in Asia (Namgail, 2004; Namgail et al., 2007; Li et al., 2013; Mousavi et al., 2016), but sheep losses to lynx can still be under-reported because owners tend not to report them as the economic value of sheep is relatively low (Namgail et al., 2007). Finding lynx kills, especially of juveniles, in challenging and remote landscapes also leads to under-reporting of lynx predation on domestic animals. Such non-detection of losses is reported for Europe (Stahl et al., 2001a; Mattisson et al., 2011b), but is expected to be higher in Asia due to vast scopes and less intense effort.

3.7. Effects of livestock protection interventions

3.7.1. Livestock protection as a condition to reduce lynx poaching

Lynx tend to kill domestic animals when they are unprotected, as well-exemplified by high lynx-related losses of sheep in grazing areas of Norway where shepherds and guard dogs are absent (Breitenmoser and Breitenmoser-Würsten, 2008). Practical and effective interventions to protect domestic animals, especially economically valuable livestock, from lynx attacks are essential to reduce the preventive or retaliatory poaching of lynx (Linnell et al., 2012). Admittedly, lynx poaching may be independent of livestock losses, being motivated instead by socio-psychological factors such as fear, desire to destroy a perceived competitor, feeling of impunity, or pride in gaining a valuable trophy (Lescureux et al., 2011; Červený et al., 2019; Arlettaz et al., 2021). Nonetheless, the reduction of lynx damage to livestock is a vital step to support local livelihoods and mitigate the perceived threat posed by lynx.

As demonstrated in Europe, the compensation of livestock losses to carnivores, including lynx, can improve human tolerance of, and coexistence with, wildlife (Linnell and Cretois, 2018), but the effectiveness of this approach is arguable as poaching remains the main threat to lynx throughout Europe (Andrén et al., 2006; Heurich et al., 2018). In Asia, compensation programs are rarely implemented because they depend on national policies that are poorly enforced (Namgail et al., 2007; Alexander et al., 2015) or favor threatened flagship carnivore species other than lynx (S. Naidenko, pers. comm.), such that lynx poaching levels continue to be high (Matyushkin and Vaisfeld, 2003). The intrinsic inadequacies of compensation programs, such as moral hazard, high transaction costs, long lag times and the lack of transparency (Zabel and Holm-Müller, 2008), are widespread in Asia (Harihar et al., 2014; Karanth et al., 2018). Therefore, participatory and motivated livestock protection rather than the passive receipt of compensations is likely to be more effective in promoting the coexistence of humans and lynx.

Since reindeer and sheep are the domestic animals most affected by lynx predation, all stages of protective interventions, beginning with the search for practical tools and ending with their applications, should focus on these two species, considering their husbandry practices and landscape conditions. Interventions require time and financial, technical and human resources and may therefore well be economically inexpedient in areas where lynx-related damage is random, low-level and unpredictable (Breitenmoser and Breitenmoser-Würsten, 2008). Priority in intervention applications should be given on two scales: (1) on a spatial scale – to high-risk hotspot areas, including recurrently attacked farms, where losses are disproportionately high and concentrated in relatively small areas, and (2) on a temporal scale – to site-specific peak seasons of losses, especially when juveniles are most available and catchable (see above). Furthermore, the acceptance of interventions by livestock owners is critical in translating knowledge into practice and requires close communication with owners to identify the interventions most suitable to a particular case (Eklund et al., 2020). For this reason, interventions should be finely tailored to local conditions, predation patterns and acceptance by local people.

3.7.2. Sheep protection from lynx

Sheep graze in areas where wild prey, primarily ungulates such as roe deer, are usually present in quantities sufficient to maintain lynx populations (Odden et al., 2013). Due to this, sheep can be potentially protected up to the levels when they become fully unavailable to lynx without sacrificing lynx viability as these felines have enough wild resources to subsist on. The most common interventions used for sheep protection against lynx are electric fences in Europe, herding and guard dogs in Asia and parts of Europe, and lethal removal in both continents. The effectiveness of these interventions for lynx and other wild cats was summarized in a meta-analysis (Khorozyan and Waltert, 2021) that examined data from six lynx studies conducted in sheep and fallow deer breeding sites. Electric fences were shown to reduce losses by 100% and were the most effective means of protection (Angst, 2001), followed by guard dogs (reduced by 100% – Otstavel et al., 2009 and 86% – Landry and Raydelet, 2010) and herding (65% – Angst et al., 2002). The effectiveness of lethal removal is controversial, as in one study it decreased lynx attacks by 51% (Stahl et al., 2001b) but in another study losses of lambs increased by 2% (Herfindal et al., 2005).

Although these results provide a useful guide for future interventions against lynx predation on livestock, they largely represent

single-site efforts and may therefore succeed or fail in other locations. Furthermore, the respective studies employed case-control (Angst et al., 2002) and before-after (all others) study designs, such that the effectiveness of the examined measures in other areas can be poorly inferred (Christie et al., 2019). In the absence of proper study controls, factors other than the interventions themselves may have been responsible for the changes in livestock losses. Specifically, in before-after design, the roles of factors that change over time, such as weather, landscape and husbandry practices, cannot be ruled out. As an example, lynx attacks on herded sheep in Slovakia decreased in the 1990 s compared to the 1950–1960 s, but whether this was caused by shepherds and dogs is unclear, since during the same period lynx numbers were reduced by hunting and an economic recession decreased sheep stocks (Hell and Slamečka, 1996). Similarly, in case-control design, the treated “case” sheep stocks may intrinsically differ from the “control” stocks in terms of the numbers of animals, land areas, proximity to lynx habitat and other factors. Therefore, robust experimental study designs, such as randomized controlled trials, before-after-control-impact and crossover, should be used to accurately and realistically estimate the effectiveness (Khorozyan, 2022). However, we are not aware of such studies in lynx.

The lethal removal of lynx, aimed at the reduction of lynx population size or the elimination of habitual killers, appears to be readily accepted by farmers and hunters (Eklund et al., 2020), but sound evidence of its effectiveness is very limited and possibly site-specific. Removal leads to a substantial decrease in lynx-related lamb mortality only when the lynx population is significantly reduced (Herfindal et al., 2005), which would violate the standards and principles of the conservation agenda. The selective removal of reliably identified livestock-killing individuals reduces the numbers of lynx attacks on farms and in hotspot areas, but its impact is only short-term, as kills will resume with the arrival of other lynx (Stahl et al., 2001b). Moreover, when habitual killers cannot be confidently identified, lethal removal is very likely to target innocent individuals, particularly females, thus disrupting local populations (Odden et al., 2002). Therefore, proactive improvement of sheep husbandry is suggested as a strong alternative to the reactive killing of lynx (Stahl et al., 2001a; Odden et al., 2002).

Herding, further reinforced by the use of guard dogs, is an age-old method to protect livestock from carnivores, including lynx. It is widely practiced throughout Asia (Alexander et al., 2015; Din et al., 2015) and in Eastern and Southern Europe (Dorresteijn et al., 2014) but it is also undergoing a revival in Western Europe (Dory, 2017) in response to the recovery of regional carnivore populations (Chapron et al., 2014). Its economic practicality is debatable in areas where lynx-induced damage is limited. Moreover, its effectiveness in areas of traditional use varies depending on the shepherd’s skills. The main duty of shepherds is to keep sheep and other livestock within their field of view, but they may fail to deter carnivores or to ensure that livestock are grazed away from high-risk carnivore habitats. In these situations, herding will be ineffective or even counter-productive, by increasing animal exposure and therefore losses instead of reducing them (Alexander et al., 2015). Simply moving sheep flocks to habitats seldom or not used by lynx may significantly reduce sheep losses (Odden et al., 2008). The promotion of professional herding through stakeholder cooperation, teaching and education, as is being done in Europe (Dory, 2017), and the development of conservation-oriented herding (Molnár et al., 2016) have been the innovative practices that can be adopted in other regions of the lynx range.

Electric fencing is among the most effective interventions for separating carnivores from livestock and farmed wildlife (Linnell et al., 2012; Khorozyan and Waltert, 2019), and it is a method largely accepted by sheep farmers (Eklund et al., 2020). However, it is technically and economically ineffective for large land plots, cold areas with frozen soil, and if owners are reluctant to maintain fence functionality by keeping the voltage low or occasionally switching it off to save time and money. When fences are designed to keep animals inside but do not properly prevent the intrusion of carnivores from the outside, they will be ineffective and may even provoke surplus killing (Angst, 2001). Technical specifications ensuring the performance of electric fences against carnivores are available (Linnell et al., 2012), but it is also practically important to understand the roles of landscape (especially in the mountains) and weather conditions in the effectiveness of electric fencing, the topics that have yet to be adequately studied.

3.7.3. Reindeer protection from lynx

Unlike sheep, reindeer are a non-alternative stable food resource for lynx and also a key element of traditional local livelihoods in the northernmost parts of Eurasia. Reindeer graze freely, usually unattended, and are managed by the owners mostly during seasonal migrations between summer and winter pastures (Mattisson et al., 2011b). As the protection of reindeer is inevitably incomplete, herders should accept a certain level of losses in order to ensure the survival of local lynx populations (Pedersen et al., 1999; Andrén et al., 2011; Mattisson et al., 2011b). Moreover, the minimization of reindeer losses poses many challenges, as grazing areas are vast and herds are large and seasonally migratory. Fencing females during the calving season in spring is a good temporary measure to reduce lynx predation on newborns, but once the females and juveniles are released back into the tundra, juveniles will be intensively preyed upon by lynx (Mattisson et al., 2011b). Acceptance of fencing varies greatly between individual herders (Eklund et al., 2020). Local acceptance of interventions and their compliance to sensitive indigenous cultures of reindeer-keeping societies are critically important to secure human-lynx coexistence.

Compensation payments for reindeer losses to lynx are still the most common method to mitigate local human-lynx conflicts, but they are associated with a significant uncertainty regarding the actual number of losses, due to the difficulty in finding reindeer carcasses as evidence (Mattisson et al., 2011b; Mattisson et al., 2014b). Compensations based on valid evidence may cause local resentment because a significant part of indirect costs, such as additional labor costs and the reduced productivity of stressed animals, is not eligible for compensation or is only minimally compensated because such losses are hard to prove (Widman et al., 2019). Recent development in GPS tracking of reindeer allows individual animals to be tracked via mobile phones but it also allows the detection of a dead animal when its GPS signal remains suspiciously unchanged (Middleton, 2018). However, other problems with compensations remain. For example, reindeer herders generally prefer compensation based on potential risk rather than on actual losses, as the allocated resources could be spent to improve husbandry and reduce poaching instead of searching for killed reindeer (Andrén et al., 2011; Mattisson et al., 2011b). Whether risk-based compensation reduces lynx poaching has yet to be studied.

Performance payments are another approach used to stimulate tolerance and coexistence between reindeer herders and local carnivores. Under this scheme, payments are made to local villages on the basis of confirmed carnivore reproduction on their grazing grounds (Zabel and Holm-Müller, 2008; Dickman et al., 2011). In other words, funds are granted for projected losses inflicted on reindeer by identified carnivore offspring once they become adults. Like risk-based compensation, performance payments are not related to carnivore-caused losses but are instead intended to encourage reindeer protection and reduce poaching. An added advantage is that they do not involve measures that disturb the traditional lifestyle of local indigenous people (Dickman et al., 2011). The effectiveness of performance payments to reindeer herders was demonstrated in an area where wolverines co-exist with lynx, in which the number of wolverine reproductions more than doubled in a decade and the population expanded to previously unoccupied areas (Persson et al., 2015). However, performance payments are not yet tested on lynx. It should be kept in mind that this approach is sensitive to uncertainties in terms of local land tenure, the roles of uncontrolled ambient factors affecting carnivore reproduction (Dickman et al., 2011) and the natural spatial heterogeneity in reproduction sites, all of which may create conflicts between local communities.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data is in the supplementary material.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02585](https://doi.org/10.1016/j.gecco.2023.e02585).

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