LYNX DEPREDATION ON DOMESTIC SHEEP IN NORWAY

JOHN ODDEN,^{1, 2} Hedmark College, Evenstad, N-2480 Koppang, Norway

JOHN D. C. LINNELL, Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway

PÅL FOSSLAND MOA, Nord-Trøndelag College, Post box 145, N-7701 Steinkjer, Norway

IVAR HERFINDAL, Department of Zoology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

TOR KVAM, Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway

REIDAR ANDERSEN, Department of Zoology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway, and Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway

Abstract: We studied depredation rates on free-ranging domestic sheep (*Ovis aries*) by Eurasian lynx (*Lynx lynx*) in 2 areas in Norway to test whether selected individuals or a demographic group within a lynx population kill a disproportionate share of livestock. During 6 grazing seasons from 1994 to 1999, we monitored 34 radiocollared lynx during 641 tracking periods (either all night or during a full 24-hr period). Sixty-three domestic sheep and 3 domestic goats were killed by radiocollared lynx during these periods. All of the radiocollared lynx had access to free-ranging domestic sheep within their annual home ranges. Male lynx killed sheep more frequently than females and were responsible for 12 out of 13 cases of surplus killing. After adjusting for number of nights monitored, sheep-killing rates among males differed slightly, whereas the differences between individual females were correlated with the number of sheep available. There were no indications of any special "problem individuals," but rather a "problem sex." Therefore, it seems to be intrinsic in their behavior that males are likely to kill domestic animals more frequently than females. The lack of specific problem individuals in this study might depend on the livestock-herding technique used in Norway, where sheep generally are free-ranging and unattended throughout a lynx's home range. Selective removal of depredating males requires that the gap in the social mosaic either remains unfilled or is filled by an individual that causes less damage to livestock. The effects of such removal on sheep depredation are likely to be only temporary since all adult and yearling male lynx appear to kill sheep.

JOURNAL OF WILDLIFE MANAGEMENT 66(1):98-105

Key words: carnivore–livestock conflicts, domestic sheep, Eurasian lynx, Lynx lynx, Norway, Ovis aries, predation, problem individuals, radiotelemetry, surplus killing.

Depredation on livestock by large carnivores has been a problem since wild ungulates were first domesticated. This conflict is now a management concern because many large carnivore populations are recovering (Blanco et al. 1992, Quigley and Crawshaw 1992, Mech 1995, Aanes et al. 1996, Cozza et al. 1996, Kaczensky 1996). Because of their generally large home ranges and low densities, viable populations of large carnivores in the developed world depend on their integration into multi-use landscapes (Fritts and Carbyn 1995, Mech 1995). Past extermination policies are no longer an option in the management of large carnivores. New methods are needed to facilitate the integration of carnivores into the modern multi-use landscape. Conflict with domestic sheep husbandry can be mitigated through changes in husbandry and/or separating carnivores and livestock (zoning; Linnell et al. 1996, 1997; Smith et al. 2000a,b). Experience

has shown, however, that some form of removal of individual carnivores is needed in response to depredation (Dorrance 1983; Fritts et al. 1985, 1992; Mech 1995; Linnell et al. 1997, 1999).

The paradigm of selective removal of problem individuals arose as an alternative to nonselective control. Its basic assumption is that only a small proportion of the individuals in a carnivore population engages in livestock depredation. Yet the question of the existence of problem individuals has rarely, if ever, been directly tested (Linnell et al. 1999). The only way to test this is to study depredation rates of individual carnivores.

The conflict between large carnivores and domestic sheep is high in Norway compared with other European countries (Kaczensky 1996). From 2 to 2.5 million sheep and lambs are grazed annually in forest and mountain habitats during May–September in Norway. Sheep generally are allowed to graze freely, with little supervision from the owner. In many regions, sheep are occasionally or chronically subjected to predation by remnant and recovering populations of wolf (*Canis lupus*), brown bear (*Ursus arctos*), wolverine (*Gulo gulo*), golden eagle (*Aquila chrysaetos*),

¹ Present address: Norwegian Institute for Nature Research, Tungasletta 2, N-7485, Trondheim, Norway.

² E-mail: john.odden@chello.no

and Eurasian lynx (Warren and Mysterud 1995, Aanes et al. 1996). Lynx and wolverine cause most of the damage. During 1997 and 1998, farmers were compensated for >9,000 sheep killed by lynx (Norwegian Department of the Environment, unpublished data).

Our objective was to test whether selected individuals or a demographic group within a lynx population kill a disproportionate share of livestock. This was done by taking into account livestock availability and intensively following movements and predation behavior of individual lynx of different age and sex classes in 2 areas in Norway with free-ranging domestic sheep.

STUDY AREA

Our study was conducted in Hedmark and Nord-Trøndelag counties, Norway. Hedmark County is in southeastern Norway (61°15'N, 11°30'W) and covers approximately 8,600 km² (Fig. 1). The topography consists of several parallel hills and river valleys running from north to south at about 200-900 m above mean sea level. Vegetation of this region is predominantly boreal coniferous forest; 72% of the study area is forested. Scotch pine (Pinus sylvestris) and Norwegian spruce (Picea abies) dominate the forest. Birch (Betula sp.) also is well represented, especially in the forest-alpine interface and along rivers. Most of the coniferous forest was logged and replanted at least once during the past 2 centuries, resulting in a mosaic of even-aged stands. The preferred lynx prey is roe deer (Capreolus capreolus), which is widely distributed throughout the study area but occurs at very low densities (<1 per km²). Wild reindeer (Rangifer tarandus) are found in the northwestern part of the area, while red deer (Cervus elaphus) occur sporadically. Moose (Alces alces) occur in high numbers, but are only rarely killed by lynx (J. Odden, J. D. C Linnell, and R. Andersen, unpublished data). The distribution of domestic sheep within the area is widespread but patchy, and sheep density is highest in the western and northern parts. Other small prey species include hare (Lepus timidus), red fox (Vulpes vulpes), capercaillie (Tetrao urogallus), and black grouse (Tetrao tetrix). The density of lynx in the study area was estimated to be 0.34 per 100 km², including dependent offspring (Odden et al. 2000). Other carnivores include a pack of wolves in the study area, and wolverines and brown bears in areas adjacent to the study area. The climate is continental with average January and July temperatures of -10 °C



Fig. 1. The study area in Hedmark and Nord-Trøndelag, Norway, 1994–1999.

and 15 °C, respectively. Average annual precipitation is 500–1000 mm; the ground is covered with 50–200 cm of snow from November until April.

Our second study area is approximately 7,000 km² and is located in Nord-Trøndelag County (64°30'N, 12°20'W) in central Norway. The topography varies from sea level to a maximum elevation of 1,160 m above mean sea level. The tree line is 300-400 m above mean sea level. In the lowlands, snow is present from mid-November to early May and often is more than 1 m deep in forest habitats. Cultivated fields, coniferous forests, and alpine vegetation cover 4%, 32%, and 64% of the land area, respectively (Norwegian Yearbook of Statistics 1996). The Nord-Trøndelag study area differs from the Hedmark study area in the greater distribution of semidomestic reindeer, which are herded in alpine habitats throughout the year. Lynx feed primarily (81% of their diet) on roe deer, semidomestic reindeer, and domestic sheep (Sunde et al. 2000a). The approximate densities of ungulates in the Nord-Trøndelag study area were 0.06-0.20 roe deer km⁻², 1.6 reindeer km⁻², and 2.5 sheep km⁻² (during Jun–Sep; Sunde et al. 2000a). The density of lynx in the county during January 1996 was estimated to be 0.5 per 100 km² including dependent cubs (T. Kvam, unpublished data). Wolverine and brown bear occur in very low densities, and wolves have been absent since ca. 1940. Hunting for lynx was permitted in both study sites between 1 February and 31 March.

METHODS

We captured lynx during winter with snares set around fresh roe deer kills, in large box traps, by treeing them with dogs, darting them from a car, or taking 5-week-old kittens from the natal dens of radiocollared females at the lair (Nybakk et al. 1996). Kittens younger than 6 months were implanted with a radiotransmitter (Arnemo et al. 1999). Kittens older than 6 months and adults were fitted with radiocollars (150 g; Telonics Inc., Mesa Arizona, USA).

During each intensive tracking period, we located lynx every 0.5 hr in either a full 24-hr cycle or during night. We located kills using telemetry points where lynx were stationary for >1 hr. We searched for kills, often with dogs, when the lynx left the area to minimize disturbance. When lynx were observed moving within sheep flocks without stopping to eat, we searched for possible uneaten sheep kills. Several sheep kills were found by the sheep farmers after we notified them about radiocollared lynx movements and possible kill sites. We probably did not find all uneaten sheep, but this error should be expected to be the same among individual lynx. Relative consumption of sheep was classified as 0, 0-75%, or >75 % of edible parts. We used a Mann-Whitney U-Test to compare relative consumption of sheep killed for different age and sex categories of lynx.

Sheep-killing rate, the number of sheep killed per 100 intensive tracking nights, was estimated for adult (>2 yr old) and yearling lynx (<2 yr old). We pooled data for individuals in each age–sex category. Number of nights between a sheep-killing event, that is 1 kill or multiple kill at the same time, was estimated for age and sex categories.

Because male lynx have larger territories and move longer distances than female lynx (Sunde et al. 2000*b*, Linnell et al. 2001), we adjusted sheep-killing rates to reflect possible individual differences in sheep–lynx encounter rates by considering only nights when lynx moved through sheep-grazing areas.

Because the number of nights monitored varied among individuals, we compared sheep-

killing rates for lynx monitored >5 nights. Data from all tracking seasons were pooled when a lynx was monitored for more than 1 grazing season. Because sheep-killing rates of male lynx were correlated with number of nights monitored (r_{e} = 0.969, P < 0.001, n = 8; Spearman rank order correlation), we compared sheep-killing rates for individual lynx by comparing the residuals of a regression line for number of sheep killed per number of days monitored per individual. We used a nonparametric Mann-Whitney U-Test to compare sheep killing rates among adult males (>2 years), adult females (>2 years), and yearlings (1 year, both sexes pooled). A Mann-Whitney U-Test also was used to compare frequency of sheep-killing events; that is, 1 kill or multiple kill at the same time, among adult males (>2 years), adult females (>2 years), and yearlings (1 year, both sexes pooled).

We used Spearman rank correlation to investigate relations between the residuals of the regression for number of sheep killed per number of days monitored and home range size, availability of sheep, and proportion of sheep-grazing areas within lynx summer ranges. We mapped sheepgrazing areas based on interviews of sheep farmers, drawn on a map (scale 1:250,000), and digitized using ARC/INFO (ESRI 1999). We calculated summer home ranges (1 May-1 Sep) using the 100% minimum convex polygon method (Hayne 1949) and RANGESV computer software (Kenward and Hodder 1996). We calculated availability and distribution of sheep within each home range using overlay operations in ARC/INFO (ESRI 1999).

Because number of individuals and number of nights monitored per individual differed between study areas, because farmers used the same sheep husbandry technique, and because the number and distribution of sheep available were similar, we pooled the data for both areas.

RESULTS

We intensively monitored 34 radiocollared lynx during 6 grazing seasons from 1994 to 1999 to determine kill rates (Table 1). All radiocollared lynx had sheep available within their annual home range. Radiocollared lynx killed 63 domestic sheep (4 ewes, 58 lambs, and 1 unknown) and 3 goats (1 mature female and 2 kids) during 641 monitoring nights. Only 8% of sheep and goat carcasses were completely consumed (>75% of all edible tissue), 56% were partially consumed (75% >0%), and 36% were not eaten at all. Sheep killed Table 1. Age and sex of lynx radiocollared and radiomonitored in Hedmark and Nord-Trøndelag study areas, Norway, 1994–1999.

Study area	Sex	Age category	Number of individuals
Hedmark	Males	Adult	6
		Yearling	4
	Females	Adult	10
		Yearling	4
Nord-Trøndelag	Males	Adult	3
		Yearling	1
	Females	Adult	3
		Yearling	3 ^a

^a Two yearling females were monitored also as adults, but are listed here only as yearlings.

by adult male lynx were utilized less than those killed by adult females (U = 93.0, n = 44, P = 0.002). No difference occurred in utilization of carcasses between adult males and yearling males (U = 124.5, n = 40, P = 0.633), but yearling females consumed less of each carcass than adult females (U = 35.0, n = 26, P = 0.003). We observed 13 cases of multiple killing of 2 to 8 sheep. Adult males were associated with 9 multiple killings, yearling males with 3, and a yearling female with 1. Multiple killing was recorded for 3 out of 6 adult males monitored for more than 10 nights.

Adult males killed more sheep per night than adult female lynx (U=21.0, n=21, P=0.036; Table 2). No difference in the number of sheep killed per night were found between yearling and adult males (U=14.0, n=14, P=0.178) or between yearling and adult females (U=37.5, n=21, P=0.390).

Adult males killed more sheep per night in a grazing area than adult females (U = 2.0, n = 12, P = 0.017). We observed no differences between

Table 2. Estimated kill rates of sheep (number of sheep killed / 100 nights) by lynx in Hedmark and Nord-Trøndelag, Norway, 1994–1999. Data for all individuals, seasons, and study areas are pooled. Inside grazing area (IGA) includes only monitoring nights where lynx moved through at least 1 grazing area.

yearling males and adult males (U= 4.0, n = 9, P = 0.142), but yearlings (of both sexes pooled) tended to kill more sheep per night in grazing areas than adult females (U = 7.0, n = 13, P = 0.056). Presence of kittens did not affect sheep-killing rates of adult females (U = 5.0, n = 10, P = 0.136).

The frequency of sheep-killing events did not differ between adult males and adult females (U = 24.0, n = 21, P = 0.062; Table 3), between yearlings of both sexes and adult males, or between yearlings (U = 13.0, n = 14, P = 0.140) and adult females (U = 39.5, n = 21, P = 0.478).

The differences in number of sheep killed per adult male were not correlated with home range size ($r_s = 0.429$, P = 0.397, n = 6), availability of sheep ($r_s = 0.143$, P = 0.787, n = 6), or the proportion of summer range that consisted of sheep-grazing areas ($r_s = -0.667$, P = 0.219, n = 5).

Sheep-killing rates for individual adult females were correlated with the number of sheep available inside the summer area ($r_s = 0.740$, P = 0.009, n = 11). Sheep-killing rates tended to correlate with proportion of summer range consisting of sheep-grazing area ($r_s = 0.619$, P = 0.056, n = 11). No significant relationship was found between sheep-killing rates and size of summer home range ($r_s = 0.516$, P = 0.104, n = 11) or proportion of summer range consisting of sheep-grazing areas ($r_s = 0.619$, P = 0.056, n = 11).

DISCUSSION

Male lynx killed sheep more frequently than female lynx, and they killed more sheep per killing event. This pattern conforms to other studies of depredation by carnivores, including leopard (*Panthera pardus*), cougar (*Puma concolor*), and black bear (*Ursus americanus*; see Linnell et al. 1999 for a review). Sacks et al. (1999) radiotracked 14 coyotes (*Canis latrans*) in a sheep-ranching

Table 3. Number of nights between sheep-killing events in Hedmark and Nord-Trøndelag, Norway, 1994–1999. Data for all individuals, study areas, and years are pooled. Inside grazing area (IGA) includes only monitoring nights where lynx moved through at least 1 grazing area.

li	ndividuals	6			Killir	ng rate
	in		Tra	cking	(she	ep/100
Age-sex	each	Sheep	nights		nights)	
category of	category	killed	All	IGA	All	IGA
Adult males	9	31	171	81	18	38
Yearling males	5	9	34	17	27	53
Adult females	15	13	371	163	4	8
Yearling female	es 7	13	65	50	20	26

		Number of nights		
	Individuals	between		
	in each	sheep killing		
Age-sex category	category	All	IGA	
Adult males	9	11	5	
Yearling males	5	6	3	
Adult females	15	37	16	
Yearling females	6	13	10	

er 1996, Linnell et al. 1999).

area in California and found breeding coyotes, especially males, were the principal predators. In contrast, Knight and Judd (1983) found that both male and female grizzly bears (*Ursus arctos*) killed sheep when bear and sheep ranges overlapped. Males also predominate among animals shot or trapped following depredation (Fairaizl and Stiv-

Among carnivores that prey on large livestock, body size of males may explain their increased tendency to kill livestock. Although female Eurasian lynx also kill sheep and goats, male lynx have larger territories and travel longer distances than females (Breitenmoser et al. 1993, Schmidt et al. 1997, Sunde et al. 2000b, Linnell et al. 2001), and likely have higher encounter rates with livestock. During our study, males killed more sheep even after adjusting for the greater sheep encounter rate. This tendency suggests that lynx depredation is an intrinsically male behavioral pattern. Sukumar (1991) argued that the males of polygynous large mammals exhibit greater variance in reproductive success than females. This suggests that selection favors a high-risk, high-gain reproductive strategy that brings these species into greater conflict with humans.

The greatest difference in predation rates between sexes was that males were responsible for almost all multiple killing. Surplus killing of livestock is common among large carnivores, including cougar (Anderson et al. 1992), leopard (Stuart 1988), covote (Andelt et al. 1980), gray wolf (Bjärvall and Nilsson 1976, Fritts et al. 1992), black bear (Horstman and Gunson 1982), and brown bear (Mysterud 1980). While making multiple kills may be adaptive in some situations, Kruuk (1972) hypothesized that whereas killing and satiation may inhibit searching behavior, continued killing at the same site is less likely to stop if other prey are still easily available. Such a situation is unlikely to occur in wild ungulate herds but is typical among domestic species such as sheep and cattle. Curio (1976) also regarded searching and prey recognition to be hunger dependent. The antipredator behavior of most wild prey species (Caro and Fitzgibbon 1992) presents few opportunities for kills. In virtually all cases of surplus killing of wild prey, some factor or unusual condition increases prey vulnerability. Some of these factors include thunderstorms (Kruuk 1972), deep snow (Eide and Ballard 1982, Patterson 1994), or concentrations of vulnerable neonates (Miller et al. 1985). Unusual conditions prevail in almost all circumstances where livestock are concerned (Linnell et al. 1999).

When a lynx is faced with such abundant, vulnerable prey, there does not seem to be an adaptive reason why a lynx should limit killing, unless there is a threat of injury incurred by the prey.

Unattended free-ranging sheep are easy prey for inexperienced juvenile lynx. Nonetheless, sheep constituted only a relatively small amount of the yearling diet (Sunde and Kvam 1997, Sunde et al. 2000*a*). No radiocollared juveniles in Hedmark starved during the first 3 months after independence (Henriksen 1999); therefore, domestic sheep do not seem important for lynx survival.

Female lynx with kittens killed fewer sheep than might be expected to support their high energetic needs. Several females gave birth to kittens within areas of high sheep densities, but they virtually ignored this abundant resource. Instead of killing sheep that were only a few hundred meters away, females often traveled over 10 km from the kittens to kill a hare or a roe deer (J. D. C. Linnell, unpublished data). In fact, sheep constitute only a small part of the summer diet of male and female lynx (Sunde and Kvam 1997, Sunde et al. 2000*a*). This phenomenon might be rooted in the ontogeny of search image and prey recognition, inasmuch as all sheep are confined when kittens begin hunting with their mothers during late autumn and winter.

Although there were individual differences among lynx in number of sheep killed, even after we corrected for sheep availability and number of nights monitored, all male lynx probably kill sheep. In these areas, it seems to be more like a problem sex rather than problem individuals. A prerequisite for the existence of problem individuals among carnivores that kill livestock is the existence of individuality among wild carnivores. Although patterns of personality are difficult to ascribe to individual carnivores (e.g., Feaver et al. 1986, Fagen and Fagen 1996, Gosling 1998), it should be clear that in such complex and longlived organisms, a potential exists for individuality, and therefore the formation of problem individuals (Linnell et al. 1999). Our inability to identify problem individuals may depend on the livestock-herding techniques in Norway. Where sheep are free-ranging and left unattended within a carnivore's hunting area, all lynx may have an opportunity to kill livestock without a need to develop specialized hunting behavior. Where livestock are herded, kept on open fields, or are confined at night (Kruuk 1980, Mizutani 1993, Linnell et al. 1996), predation requires a specialized hunting behavior. These behaviors all require a process of learning and are unlikely to develop in young animals or more cautious females (Sukumar 1991). This may explain why domestic sheep depredation is higher in Norway than in other countries (Warren and Mysterud 1995, Aanes et al. 1996, Kaczensky 1996, Sagør et al. 1997). Recent evidence for this has been obtained from a reintroduced lynx population in eastern France, where Stahl et al. (2001a,b) found clear evidence for the existence of problem individuals of both sexes in an area where sheep were kept on pastures, and the overall depredation rates were much lower than in Norway.

MANAGEMENT IMPLICATIONS

All radiocollared lynx had free-ranging domestic sheep available inside their annual home ranges. Although male lynx were the primary predators of domestic sheep, we could not identify problem individuals. In Norway, sheep depredation by lynx appears to be a male phenomenon. Thus, management will be successful only if it targets adult and yearling males. In practice, removal of depredating individuals is difficult. Toxic livestock protection collars mounted on sheep may be the only guaranteed method for targeting a specific depredating individual (Connolly and Burns 1990, Burns et al. 1996). However, this method is not suitable where husbandry is lax and where most male lynx may occasionally kill livestock. Because males almost never return to a sheep kill, trapping on the carcass will not often target the problem male. On the contrary, trapping lynx at sheep carcasses will almost certainly capture females. They rarely kill sheep but often return to carcasses. Although the sexes cannot be distinguished by track size, hunting of an offending male may be done during winter with the aid of snow and hunting dogs.

Even if a depredating male is removed, the benefits likely will be only temporary. Further, there is no guarantee that the replacement lynx will not engage in depredation. A home range vacancy may be filled by a neighbor, a dispersing juvenile, or a mature transient. Since all male lynx appear equally likely to kill sheep, the effect of the removal on sheep depredation levels is dependent on how fast this gap will be closed. When considering these scenarios, we concur with Stahl et al. (2001*b*) that the most effective management solution for rare or endangered species is to proactively modify husbandry techniques or zone land-use to prevent depredation, rather than to react to individual depredation events.

ACKNOWLEDGMENTS

We thank J. M. Arnemo, T. Berg, T. Bjørkli, R. Bjørnstad, J. P. Bolstad, M. Bredvold, S. E. Bredvold, M. Bronndal, K. Brøndbo, B. T. Bækken, M. Dötterer, K. Fische, P. Fossum, L. Gangås, H. Henriksen, G. Jacobsson, J. Karlsen, M. Kjørstad, E. Maartmann, E. Mømb, A. Negård, E. Ness, P. Nijhuis, K. Nybakk, K. Overskaug, E. T. Pedersen, A. Rognstad, H. Rogogjerd, L. Rotelli, R. Røsvoll, S. Sandodden, K. Schmidt, H. Solvang, S. Ø. Stener, O. K. Steinset, O. G. Støen, P. Sunde, S. O. Swenson, A. Söderberg, I. Teurlings, T. Udø, P. Wabakken, S. Wedul, and L. Øvrem. The study was supported by the Norwegian Research Council, the Norwegian Directorate for Nature Management, the Norwegian Institute for Nature Research, Hedmark Collage, and the Nature Protection Division of the County Governor's Office for Sør-Trøndelag, Hedmark, Buskerud, and Telemark.

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Received 17 July 2000.

Accepted 15 July 2001.

Associate Editor: Maehr.