Journal of Applied Ecology 2001
38, 674–687

Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability

P. STAHL, J.M. VANDEL, V. HERRENSCHMIDT* and P. MIGOT
*Office national de la chasse et de la faune sauvage, 01330 Birieux, France; and *Ministère de l'environnement, 20 avenue de Ségur, 75302 Paris 07 SP, France*

Summary

1. In recent decades, the Eurasian lynx *Lynx lynx* has recolonized former habitat, bringing it into potential conflict with livestock. We studied the spatial and temporal distribution of lynx attacks on sheep in the French Jura between 1984 and 1998, during and after its population expansion. We estimated the local and regional impact of lynx predation on livestock.

2. The number of attacks increased from three in 1984 to 188 in 1989, concurrently with the colonization of the main sheep range by lynx. During subsequent years, 66–131 attacks were recorded annually (92–194 sheep killed per year).

3. On average, 1·6 sheep were killed per attack. Lynx preyed disproportionately on lambs and subadult sheep. A small percentage of flocks (9·5–22·9%) were attacked, most of which (75·2%) were attacked once or twice a year. At the regional level, annual sheep losses to lynx were 0·14–0·59% of the total number of sheep.

4. The major lynx–livestock problem was due to clustered attacks in a few small areas. Each year, two to six 'hot spots' (33–69% of the attacks) were identified. Hot spots covered 0·3–4·5% of the total area where attacks occurred (1835–4061 km^2). Roe deer abundance was higher in hot spots and, even here, sheep only made up 3·1% of the lynx diet. These data show that lynx were not killing sheep due to shortages of alternative prey or in response to an increased need for food when rearing young.

5. The concentration of hot spots in only nine small areas between 1984 and 1998 indicated that only a few individual lynx were involved. The reappearance of hot spots at the same sites, after years of interruption and despite the removal of lynx, suggested that the ultimate factors causing hot spots were factors inherent to those sites. Further investigation is needed to identify causal factors with a view to eliminating them. These may relate to landscapes features, animal husbandry practices or the behavioural ecology of lynx.

6. In future, where large predator reintroductions are planned, the potential for concentrated, localized, impact should be evaluated and mitigation measures put in place. For scattered and episodic lynx damage, financial compensation is the only realistic option at present. In hot spots, the cost-effectiveness of guard-dogs or the selective removal of some individual lynx should be evaluated.

Key-words: carnivore–livestock conflicts, France, Jura, *Lynx lynx*, management, species recovery.

Journal of Applied Ecology (2001) **38**, 674–687

Introduction

After a marked decline in Europe during the 18th and 19th centuries (Kratochvil 1968), the Eurasian lynx *Lynx lynx* Linné expanded its range in several western European regions during the 1980s and 1990s (Breitenmoser & Breitenmoser-Würsten 1990; Breitenmoser, Breitenmoser-Würsten & Capt 1998; Cop & Frkovic 1998; Stahl & Vandel 1998, 1999) and spread into livestock husbandry areas. As a result, lynx predation on domestic sheep led to conflict with farmers in several regions (Grosjean 1992; Kaczensky 1996; Capt 1998).

In a review of the data available for 11 European countries, Kaczensky (1996) estimated that lynx killed

Correspondence: Philippe Stahl, Office national de la chasse et de la faune sauvage, 01330 Birieux, France (fax 33 (0)4 74 98 14 11; e.-mail p.stahl@onc.gouv.fr).

annually 0·01–0·55% of the available stock. These percentage losses are similar to estimates given for other carnivore species in North America (Andelt 1996), Europe (Kaczensky 1996), Australia (Greentree *et al.* 2000) and for felids globally (Nowell & Jackson 1996). When taking into account this low level of depredation and the fact that damage compensation is paid in most countries (De Klemm 1996; Fourli 1999), lynx–livestock conflicts are sometimes considered a psychological rather than an economic problem (Breitenmoser *et al.* 1998). However, another factor of potential importance is the spatial and temporal pattern of the depredation events. Depending on factors such as habitat characteristics, herding techniques or the presence of 'problem individuals' (Linnell *et al.* 1999), some areas or flocks suffer higher levels of depredation than others (Suminski 1982; Fritts *et al.* 1992; Hoogesteijn, Hoogesteijn & Mondolfi 1993; Nédélec 1995; Cozza, Fico & Battistini 1996; Ciucci & Boitani 1998; Knowlton, Gese & Jaeger 1999). The sheep breeders' acceptance of a large carnivore's presence depends on the number and persistence of the attacks on individual sheep farms. The economic impact of local and repeated damage can be high for some sheep farmers, despite low levels of depredation at the national or regional level. Furthermore, from a conservation point of view, the methods of effectively managing carnivore–livestock conflicts are not the same if the attacks are more or less evenly distributed throughout a region, or if they concentrate on a small proportion of farms. The detailed patterns of the depredation events, for example the age and number of individuals killed and consumed per attack, are secondary factors that may exacerbate the impact of predation or affect the attitude of sheep farmers towards the predator.

There have been few detailed studies of the spatial and temporal distribution of lynx damage to livestock. Such data should be collected in a variety of habitat and husbandry contexts to estimate better the impact of lynx–livestock predation and to improve species management.

This study investigated lynx predation on sheep in the French Jura. The reappearance of the lynx in this region is due to reintroductions in the early 1970s (Breitenmoser & Baetig 1992; Breitenmoser, Breitenmoser-Würsten & Capt 1998). With a range covering 8000 km^2 in the French Jura (Vandel & Stahl 1998a) and 3500 km^2 in the Swiss Jura (Breitenmoser & Baetig 1992; Breitenmoser, Breitenmoser-Würsten & Capt 1998), this population is one of the largest reintroduced lynx populations in western Europe. Several aspects add interest to this case study. In the French part of the Jura, the investigation of lynx depredation events started soon after the first signs of lynx predation on livestock (Herrenschmidt & Léger 1987; Herrenschmidt & Vandel 1992) and an exhaustive census of lynx attacks on sheep is now available for a 15-year period, i.e. during and after the expansion of the lynx throughout the entire sheep–lynx range. Before lynx colonization, the Jura had been free of large carnivores for decades. After the lynx expanded in the region, no measures were taken to protect flocks against predators. The basic lynx predation pattern on sheep can thus be described with very limited interference due to livestock protection measures.

For lynx reintroduced into habitats that had long been free of large carnivores, Breitenmoser & Haller (1993) and Capt (1998) hypothesized predation on wild ungulates during the initial phase of settlement of the lynx would cause a decrease in prey availability, by decreasing prey number and altering prey behaviour. It was suggested that a temporary dietary shift to domestic ungulates would be observed during this stage. After the adjustment of the lynx population to the reduced wild ungulate availability, a decrease in livestock predation, followed by a stabilization at a lower level, would be observed. Despite being frequently invoked when explaining the lynx depredation pattern in western Europe (Kaczensky 1996; Linnell *et al.* 1996; Capt 1998), this hypothesis has never been supported by a detailed analysis of the lynx depredation events on sheep during and after the colonization of new areas.

The objectives of this study were to: (i) describe the characteristics of lynx predation events on sheep, as age and number of prey killed and consumed per attack; (ii) show the spatial and temporal pattern of lynx predation on sheep, in relation to the distribution and abundance of sheep and roe deer *Capreolus capreolus* Linné (L.), the main wild prey of lynx in the Jura (Weber & Weissbrodt 1999; Jobin, Molinari & Breitenmoser 2000); (iii) evaluate the percentage sheep loss to lynx at the local and regional scale; and (iv) examine in more detail the Breitenmoser & Haller (1993) hypothesis. We tested four predictions: (i) a time lag should be observed between the arrival of lynx and the initial increase in damage; (ii) the increase in damage should be observed over extensive areas because it is likely to be a lynx 'population' response to the reduced availability of prey; (iii) the spatial and temporal variability in the number of attacks should be related at least partly to the spatial and temporal variability of the main wild prey abundance; (iv) the sheep should make up an important part of the lynx diet.

Materials and methods

STUDY AREA

The French Jura, of 10 000 km^2, is situated in the northeast of France, and holds 36 000 ewes together with 347 000 cows and 4000 goats (Ministère de l'agriculture 1988a,b,c). Sheep husbandry is mainly carried out in the western and lower part of the Jura, 400–700 m a.s.l. The main sheep–lynx range (MSLR), of 6000 km^2, lies in the Ain and Jura counties. It contained 83% of the total sheep in the Jura and 97% of the 1984–98 lynx attacks on sheep (Fig. 1). Forests cover 32% of the MSLR, and agricultural land covers 47% (Ministère de l'agriculture 1988a,b,c). All results presented hereafter concern the MSLR.

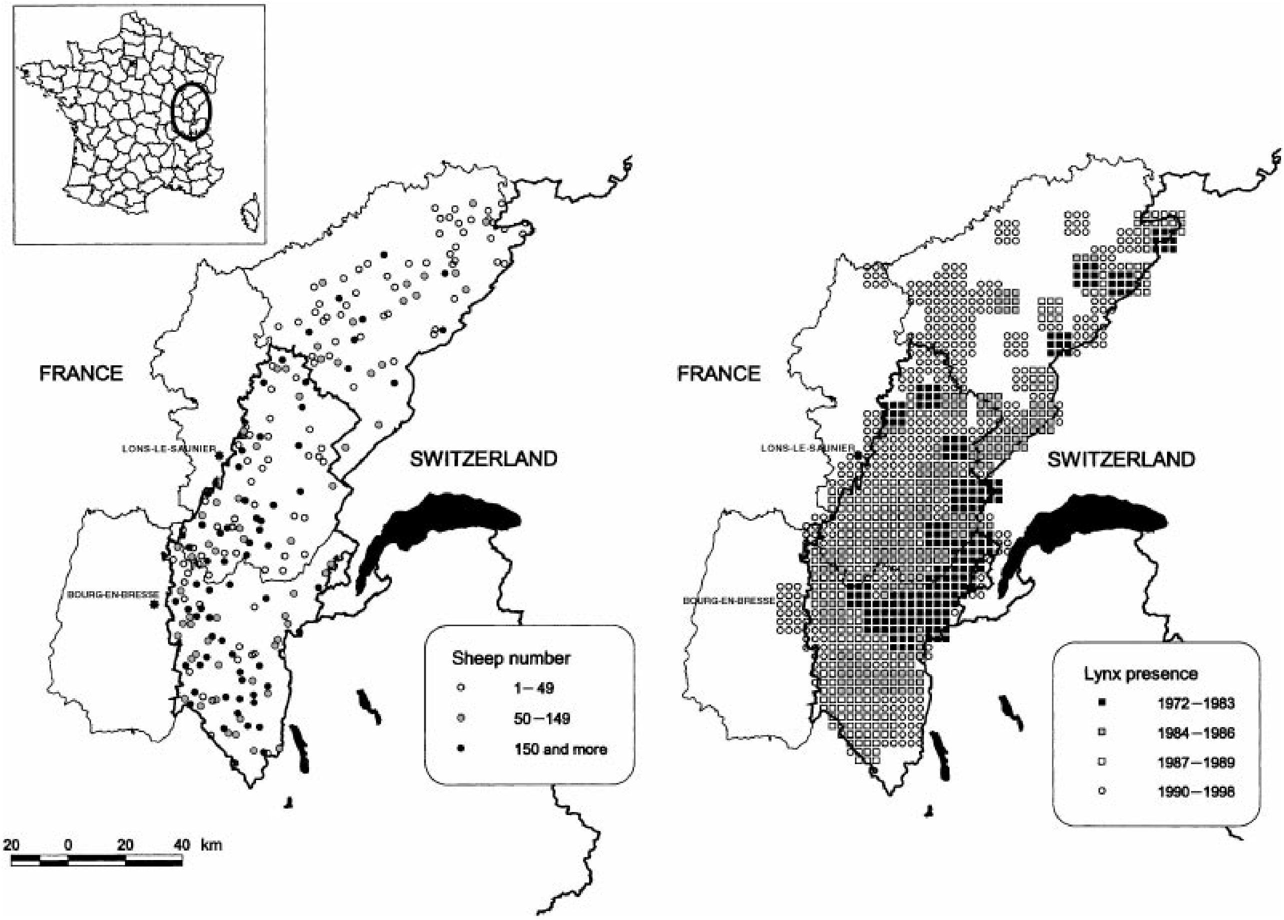

Fig. 1. Distribution of sheep in 1998 in the French Jura (left) and colonization by the lynx (right).

From early spring to late autumn, sheep and lambs are kept in pastures of 1–100 ha, surrounded with electric fences or 1·2-m high wire netting. These fences are designed only to constrain sheep movements and not to exclude large carnivores. Rams or cattle only rarely graze with ewes and lambs. Pastures are scattered around farms and human settlements (small villages and isolated farms) and are often bordered by forest or bushy areas. In the pastures, sheep are always unguarded and wander free by day and night. In winter, sheep are often housed. Most of the flocks number less than 100 ewes. Only 18% of the sheep producers are full-time farmers (Ministère de l'agriculture 1988a,b,c). Livestock guard-dogs are not present in the MSLR. Roe deer are the most numerous wild ungulates, and there are no red deer *Cervus elaphus*. Linné (L.) The chamois *Rupricapra rupricapra* Linné (L.) is abundant in the High Jura but is rare in the Low Jura where sheep are most numerous.

LYNX DISTRIBUTION

The lynx population was monitored by a network of trained lynx experts, most of whom were state-employed (Vandel & Stahl 1998b). Lynx experts collected and verified the presence of the lynx (tracks, wild prey remains, sightings). They also investigated each case of domestic livestock predation. Standardized identification and reliability assessment criteria were defined for each category of field sign (J.M. Vandel, P. Stahl & P. Migot, unpublished data). For spatial analysis, each data point was centred in a 3 × 3-km square. This method gives minimum estimates of the species range. As sheep farms were not evenly distributed in the MSLR, the total area colonized by lynx was only a rough index of lynx presence in sheep-herding areas. A more precise index of lynx presence in sheep-herding areas was calculated as the proportion of districts with sheep farms in which lynx signs were found. A district, also called 'commune', is the smallest French administrative unit, about 50 km^2 in size. The presence of sheep in districts was indicated by the agricultural administration (see below). Sign of lynx presence was attributed to a district when < 5 km from the centre of the district. This index was calculated each year from 1984 to 1998. As signs of presence were difficult to find, this index did not show the true proportion of districts with or without lynx presence. It was only designed to examine the temporal pattern of the colonization of sheep-herding areas by lynx, assuming that the probability of finding lynx signs remained constant.

CENSUS OF LYNX DAMAGE

The first detailed investigations of lynx depredation events by trained lynx experts were made in 1986, 2 years after the first cases of lynx depredation (Herrenschmidt & Léger 1987; Herrenschmidt & Vandel 1992). Every attack (i.e. one or several sheep killed or wounded in a pasture in one night) declared by a sheep breeder was investigated. Declaration and inspection was compulsory for sheep breeders if they wanted to be reimbursed for the damage. Missing animals (young lambs) were not taken into account.

Lynx experts attributed the cause of death to a predator if, after skinning, bite impacts associated with haematoma were found on the inside of the skin. The main criteria used to discriminate between dog and lynx attacks were the presence of bite holes around the larynx, the diameter of bite holes (in majority less than 3 mm in size), the presence of the typical 28–32 mm lynx canine spacing between couples of isolated bite holes (for dog canine spacing see Roberts 1986) and the prey consumption pattern. Depending on the number and quality of criteria observed on the carcasses or in the vicinity of the prey (tracks), attacks were classified as 'confirmed', 'probable', 'doubtful' or 'not attributed to lynx'. All analyses presented hereafter are based on confirmed and probable lynx attack. Doubtful attacks ($n = 71$) that could include domestic dog attacks were not taken into account even if compensation had been paid to sheep breeders.

A high damage area or 'hot spot' was defined as a cluster of ≥ 10 attacks recorded during one year (January to December) in neighbouring pastures belonging to one or several sheep breeders. The following procedure was used to identify clusters:

1. for each attack, defined by its x and y geographical coordinates, the number of attacks registered within a radius of 5 km during the year was computed;

2. the most important cluster of ≥ 10 attacks was then identified for the year;

3. attacks that belonged to this first cluster were eliminated and the procedure repeated with the remaining attacks in order to find the second order cluster, the third, and so on;

4. the procedure was stopped when all the clusters of ≥ 10 attacks had been identified for the year.

A 5-km radius (= a 7850-ha circle) was chosen because it is approximately half or one-third of an average lynx home range in this region (Breitenmoser *et al.* 1993; Office national de la chasse et de la faune sauvage, unpublished data). When taking the territorial behaviour of the lynx into account, clusters of attacks could have been due to a limited number of individuals. The minimum convex polygon method was used to estimate the size of hot spots and the annual size of the area with lynx attacks in the MSLR. Analyses were made with the RANGES V software for radio-tracking data (Kenward & Hodder 1996).

SHEEP LOSSES

To receive agricultural subsidies, the sheep breeders declared the size of their flock (number of ewes) to the agricultural administration each year. To respect the individual's right to professional secrecy, the authorities would not give any information on the number of ewes belonging to each individual sheep breeder. The only data available were the number of ewes or goats for each district and the number of flocks per district. The MSLR encompasses 515 districts, 233 having sheep at least during one year. The annual percentage loss of sheep to lynx in the MSLR was estimated by relating the total number of sheep (ewes, subadults and lambs) killed by lynx to the total number of ewes present in the MSLR plus the estimated annual number of lambs or subadults produced. The estimated annual number of lambs and subadults produced was obtained by multiplying the total number of ewes by 1·4, the average fecundity for ewes in the study area.

The annual percentage loss of sheep in the flocks attacked by lynx was estimated by relating the number of lynx-killed ewes, subadults and lambs in the attacked flocks by the number of ewes in the flocks reported in the investigation forms, plus the estimated number of lambs or subadults produced in the flock. The annual number of lambs or subadults produced was estimated in the same way by multiplying the number of ewes present in winter by 1·4.

ROE DEER ABUNDANCE AND IMPORTANCE OF SHEEP TO LYNX

A roe deer abundance index was derived from the yearly hunting bag recorded in each district between 1986 and 1997. The index was the number of roe deer killed per 100 ha of forested and farm land. When hunting bags overlapped for more than one district (maximum = four districts), the number of roe deer killed in each district was estimated proportionally to the area of forest and farmland present in each district.

The potential importance of sheep in the diet of lynx attacking in hot spots was estimated by multiplying the number of attacks in the hot spots by the proportion of attacks with consumption of a sheep and by the number of days a lynx consumes a previously killed sheep. Because lynx rarely return to their domestic prey after the first night in this region, the average number of days a sheep was consumed by a lynx was set to 1.

Results

COLONIZATION OF THE MSLR BY LYNX

The first evidence of lynx in the High Jura was in 1974. The colonization of the south-western Jura, where sheep husbandry is widespread, began in 1984–86, and this region was almost entirely occupied by the end of 1989 (Fig. 1). Lynx expanded then to the north, where sheep were less numerous. From 1989, lynx presence was constantly recorded in the south-western MSLR, even if local or temporary absence of lynx cannot be excluded. The lynx index of presence in districts with sheep

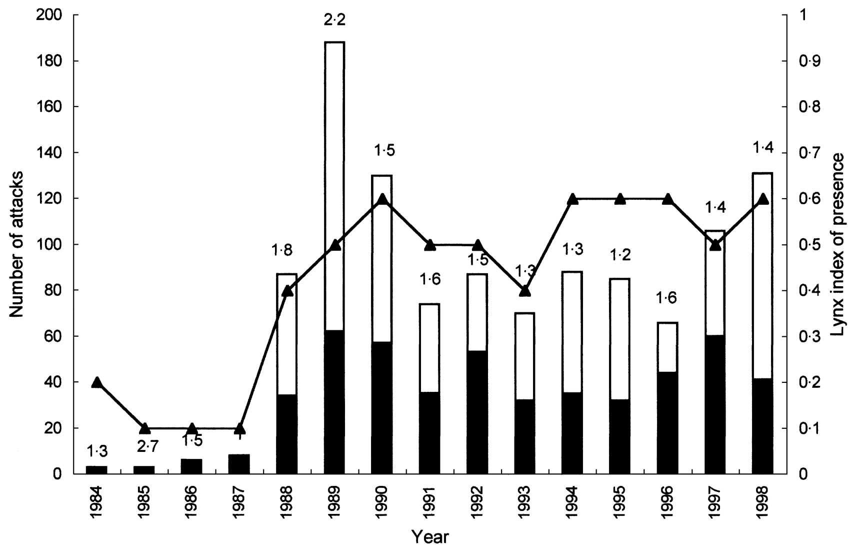

Fig. 2. Number of lynx attacks on livestock (bars) and lynx index of presence (line) in the main sheep–lynx range from 1984 to 1998. Numbers above bars indicate the annual average number of sheep killed or wounded per attack. Attacks situated in hot spot areas are in white. Attacks outside hot spot areas are in black.

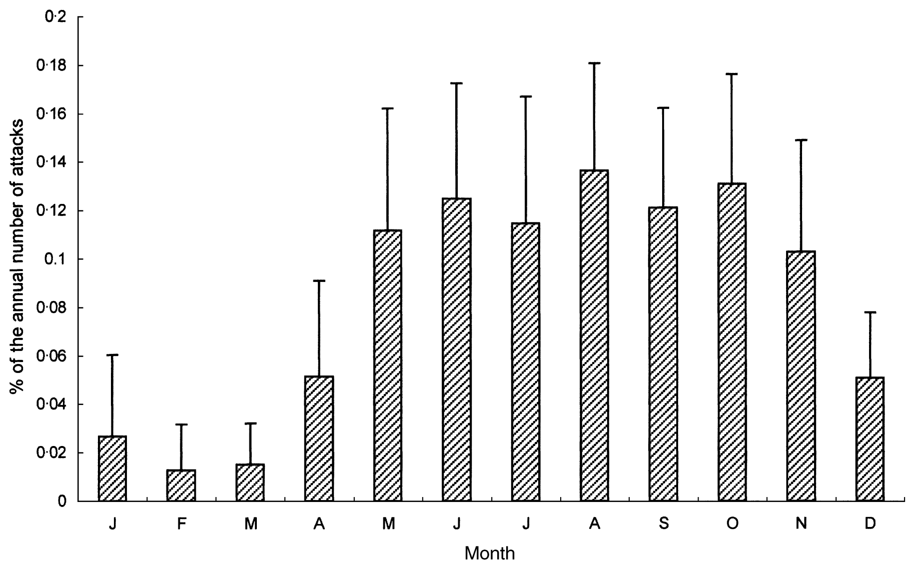

Fig. 3. Monthly distribution of lynx attacks (percentage of the total annual number ± SD) on livestock from 1988 to 1998.

increased from 1987 to 1990, and has fluctuated moderately thereafter (Fig. 2). Expressed as a percentage of the MSLR, lynx occupied 19% of the MSLR in 1983, 39% in 1986 and 62% in 1989.

MAIN CHARACTERISTICS OF LYNX ATTACKS

From 1984 to 1998, 1132 attacks were recorded on 206 flocks. A total of 1782 animals was killed (n = 1620) or wounded (n = 162). Goats were involved in 1·8% (n = 33) of the attacks, but neither cattle nor equid were involved.

Distances between attack sites and the nearest human settlements (village, hamlet, isolated farm) varied from a few metres (pasture adjacent to the sheepfold) to 6000 m (median = 500 m). Most attacks (84·5%) were recorded between May and November, when sheep were on pasture by day and night. During this period, attacks occurred without any monthly pattern (Fig. 3).

In most attacks, only one (68% of the attacks) or two sheep (18% of the attacks) were killed or wounded. Attacks on three sheep represented 8% of the cases and attacks on ≥ 4 sheep 6% of all cases. Only two exceptional attacks were recorded in 15 years, the first one on 10 sheep (including eight new-born lambs) and the second one on 11 adult sheep. The frequency distribution of the number of sheep killed or wounded per attack (1, 2, 3, ≥ 4) did not differ between flocks situated in hot spots and flocks situated outside hot spots (χ^2 = 0·45, d.f. = 3, P = 0·93), nor with month (χ^2 = 29·27, d.f. = 33, P = 0·48). For the 1988–98 period, there was a significant difference between years (χ^2 = 126, d.f. = 30, P < 0·001; Fig. 3), with a minimum average of 1·2

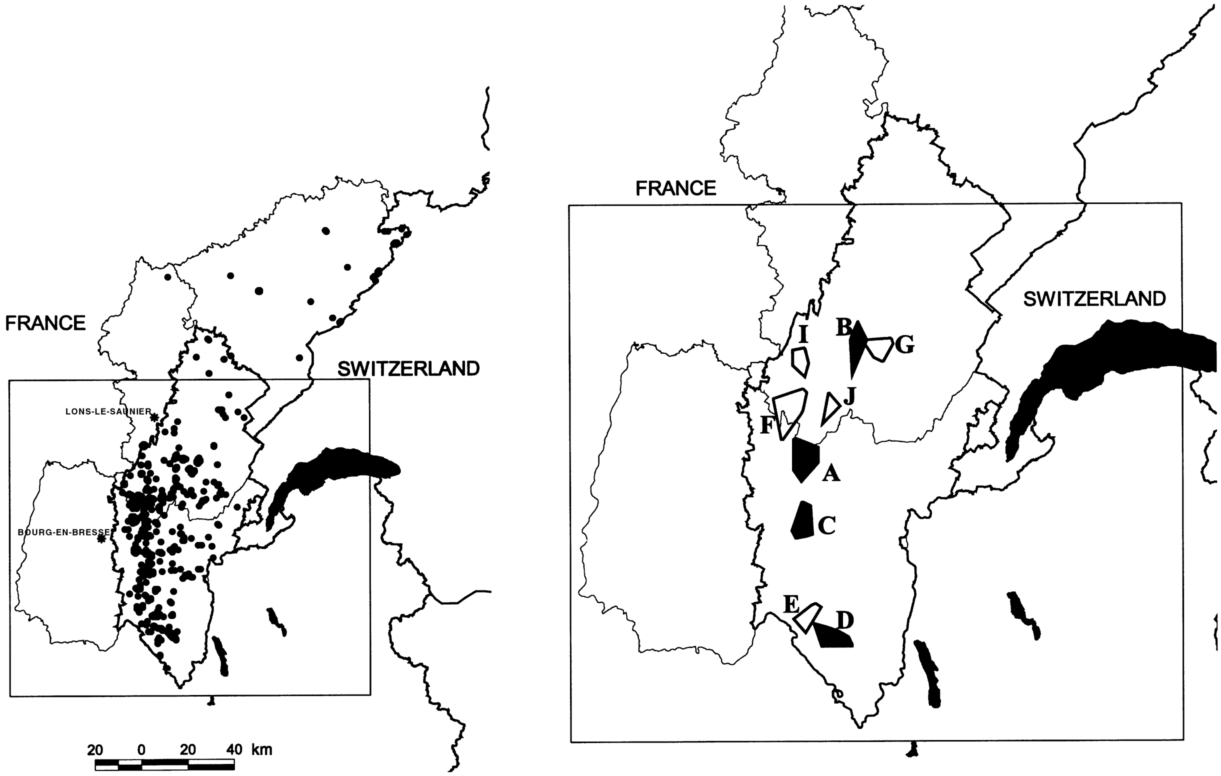

Fig. 4. Distribution of lynx attacks (left) and sites with hot spots (right) in the French Jura from 1984 to 1998. Areas with legal lynx removal are in black.

individuals killed or wounded per attack in 1995 (n = 85, SD = 1·1) and a maximum average of 2·2 individuals in 1989 (n = 188, SD = 1·4). The average number of sheep killed or wounded per attack was not related to the annual number of attacks (Spearman's coef. corr.: $r_s = 0{\cdot}14$, $P = 0{\cdot}67$, n = 11).

On average, 48·5% of the sheep killed or wounded were adults (≥ 12 months), 13·5% were subadults (6–12 months) and 38% lambs (< 6 months). Lynx preyed disproportionately upon lambs in flocks comprising lambs and adults: 63% of the animals killed were lambs for 36% available ($\chi^2 = 90{\cdot}34$, d.f. = 1, $P < 0{\cdot}001$). A similar preference for subadults vs. adults was observed in subadult–adult flocks: 57% of the animals killed or wounded were subadults for 28% available ($\chi^2 = 16$, d.f. = 1, $P < 0{\cdot}001$). Lambs were not selected against subadults when only the two age class were present ($\chi^2 = 1{\cdot}92$, d.f. = 1, $P = 0{\cdot}16$).

NUMERICAL AND SPATIAL DISTRIBUTION OF LYNX ATTACKS

The first attacks on sheep were registered in 1984, but there was a dramatic increase in the number of attacks in 1987–89 (Fig. 2). After a decrease in 1990, the number of attacks stabilized at about 70–90 attacks per year for a 6-year period. A slight increase was observed in 1997 and 1998. The 1987–89 increase correlated with an increase in the lynx index of presence in sheep areas (Fig. 2). From 1990 to 1998, no significant correlation was found between the lynx index of presence in sheep areas and the annual number of lynx attacks (Kendall's coef. rank corr.; $\tau = 0{\cdot}39$, n = 9, $P = 0{\cdot}14$).

Lynx attacks were not evenly distributed in space (Fig. 4). From 1988 onwards, two to six hot spots were identified each year (Tables 1 and 2). The size of the hot spots was always smaller than their maximum possible size (i.e. 78·5 km^2) because sheep were clustered in several small proximate pastures (mean = 13·4 km^2, n = 35, SD = 11·2 km^2, range 0·7–42·2 km^2). On average, hot spots covered 1·5% (range 0·3–4·5%) of the area with attacks in the MSLR (Table 1).

Between 1988 and 1998, the percentage of attacks in hot spots (range 33–69%) and the percentage of attacked flocks in hot spots (range 13–57%) varied significantly from year to year (attacks: $\chi^2 = 60$, d.f. = 10, $P < 0{\cdot}001$; flocks: $\chi^2 = 28{\cdot}4$, d.f. = 10, $P = 0{\cdot}002$; Table 1). The highest percentages of attacks and flocks in hot spots were recorded in 1989 and 1998 (Table 1). These were also years with the maximum number of attacks. When hot spots were not taken into account, there was no trend in the number of attacks between 1988 and 1998 (Fig. 2).

Hot spots often reappeared in the same places from year to year. When grouping the annual hot spots overlapping more than 50% of their surface area, only nine different sites (range 15·9–64·9 km^2) were identified throughout the whole MSLR for the 1984–98 period (Fig. 4). The cumulative area of these nine sites was 323·3 km^2 (Table 2), 5·9% of the cumulated total area with attacks (minimum convex polygon = 5525 km^2). In relation to lynx home range size, hot spots belonging

Table 1. Hot spots in the main sheep–lynx range (MSLR) of the French Jura between 1988 and 1998. Hot spots are sites with ≥ 10 attacks per year within a 5-km radius. No hot spot was identified before 1988

	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	Mean value ± SD
Number of hot spots	2	5	5	3	2	2	4	3	1	2	6	3·2 ± 1·6
Number of flocks attacked in the MSLR	34	71	49	32	39	25	36	31	32	36	51	39·6 ± 12·9
Number of flocks in hot spots	9	28	17	10	5	5	11	7	9	8	29	12·5 ± 8·5
(%)	(26·5)	(39·4)	(34·7)	(31·3)	(12·8)	(20)	(30·6)	(22·6)	(28·1)	(22·2)	(56·9)	(29·5 ± 11·7)
Number of attacks in the MSLR	87	188	130	74	87	70	88	85	66	106	131	101·1 ± 36·1
Number of attacks in hot spots	53	126	73	39	34	38	53	53	22	46	90	57 ± 29·5
(%)	(60·9)	(67)	(56·2)	(52·7)	(39·1)	(54·3)	(60·2)	(62·4)	(33·3)	(43·4)	(68·7)	(54·4 ± 11·4)
Total area with attacks in the MSLR (km^2)	1835	2976	2946	2657	3014	2542	3656	3008	2010	4061	3114	2893 ± 641
Hot spot area (km^2)	15·2	134·6	50·0	38·1	8·8	10·8	31·4	15·0	35·9	38·3	89·7	42·5 ± 38·2
(%)	(0·8)	(4·5)	(1·7)	(1·4)	(0·3)	(0·4)	(0·9)	(0·5)	(1·8)	(0·9)	(2·9)	(1·5 ± 1·3)

Table 2. Annual number of lynx attacks in the nine sites where hot spots were identified between 1988 and 1998. Years with hot spot are in bold. For years without hot spots, the number of attacks is the number of attacks within a 5-km radius around the centre of the site (arithmetic mean of the *x*, *y* coordinates of attacks during hot spot years). Where lynx were legally removed, the number is indicated in parentheses

			Number of attacks											
Site	Area (km^2)	Number of flocks attacked	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	Total
E	24·6	9	5	**13**	6	0	0	0	2	0	0	2	0	28
F	64·9	22	2	7	6	3	5	1	**14**	**12**	**22**	2	**31**	105
C	38·3	9	**10**	**31**	**16**(1)	4	3	4	2	4	1	0	3	78
H	15·9	11	2	7	1	0	4	3	2	3	2	9	**11**	44
D	38·0	7	**43**	**45**	**24**(2)	1	5	4	**14**	**31**	6	9	**10**	192
A	54·7	14	6	**26**(1)	**13**(1)	**10**	**11**	**19**	**12**	3	3	**33**	6(1)	142
G	30·1	3	1	2	**10**	**14**	**23**	**19**	**13**	**10**	6	**13**	**11**	122
I	22·2	8	0	0	3	0	0	0	0	0	1	0	**11**	15
B	34·8	7	1	**11**	**10**(3)	**15**(1)	3	4	6	6	5	6	**16**	83
Total	323·3	90	70	142	89	47	54	54	65	69	46	74	99	809

to sites E and D could have been included in the same lynx range (Fig. 4). The other sites were separated by open landscapes and valleys or were far apart from each other and could have been in different home ranges. The history of these nine sites showed alternate periods with and without hot spots. Presence of hot spots was noticed for 1–6 successive years (Table 2). From 1989 to 1999, eight lynx and two unidentified predators thought to be lynx were legally removed in four of the nine sites (Stahl *et al*., in press; Table 2). Hot spots persisted or reappeared after lynx removal in three sites (sites A, B, D). In the fourth site (site C), no hot spot reappeared after one male was caught in 1990, but evidence was obtained that the main attacked flocks disappeared in 1991.

RELATIONSHIP BETWEEN THE NUMBER OF ATTACKS, SHEEP NUMBERS AND ABUNDANCE OF ROE DEER

The number of sheep registered in the MSLR remained stable between 1988 and 1998 (22 046 ± 985; range 20 277–23 659) despite a 3·4% annual decrease in the number of flocks. Over the 1988–98 period, the annual number of attacks was not related to the number of sheep present in the MSLR (Kendall's coef. rank corr.: $\tau = 0{\cdot}37$, $n = 11$, $P = 0{\cdot}12$). The same was true in districts with at least one lynx attack on sheep ($\tau = -0{\cdot}037$, $n = 11$, $P = 0{\cdot}88$), i.e. with proof that lynx were present in a specific year.

The average number of sheep per district was lower in the districts with sheep but with no lynx attacks ($n = 131$, range 10–556, median = 45) than in the districts with attacks but without hot spots ($n = 64$, range 10–900, median = 64), which in turn was lower than in the districts with attacks and hot spots ($n = 38$, range 13–1081, median = 138; Kruskal–Wallis test, $P < 0{\cdot}001$). However, within these categories, there was only a slight overall relationship between the number of attacks per district and the number of sheep present (districts without hot spots: $r^2 = 0{\cdot}054$, $P = 0{\cdot}065$; districts with hot spots: $r^2 = 0{\cdot}114$, $P = 0{\cdot}047$).

Roe deer hunting bags increased gradually between 1986 and 1997 (Fig. 5): 1712 roe deer were killed in 1986 and 7116 in 1997. During this period, the annual number

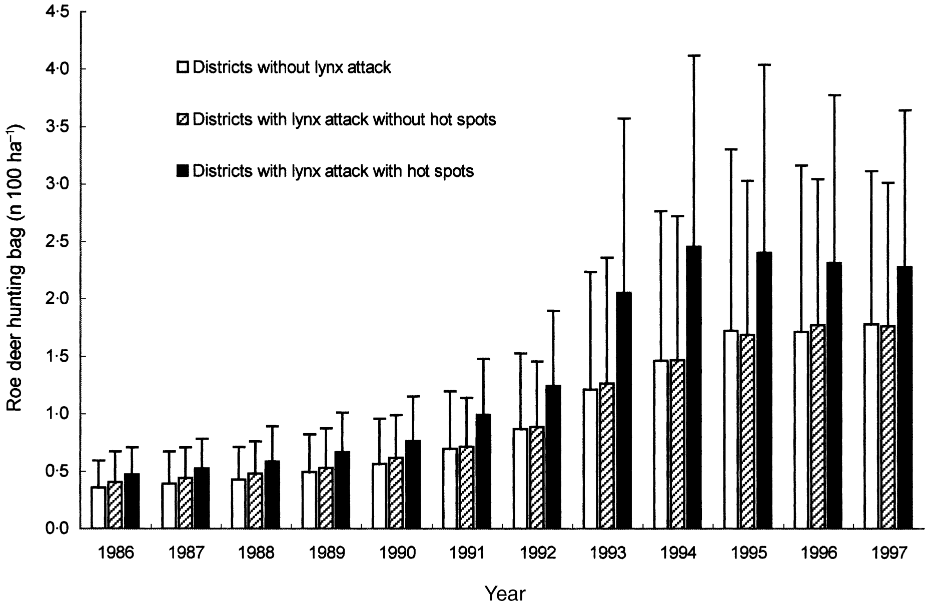

Fig. 5. Roe deer hunting bag (number of roe deer killed per 100 ha) from 1986 to 1997 in districts with hot spots, districts with lynx attacks but no hot spots and districts without any lynx attacks on sheep.

Table 3. Sheep losses to lynx in the main sheep–lynx range (MSLR) of the French Jura between 1988 and 1998

	Mean annual value ± SD (minimum – maximum)
Number of flocks in the MSLR	265 ± 26 (227–310)
Number of flocks attacked	40 ± 13 (25–71)
% attacked	14·9 ± 4·3 (9·5–22·9)
Number of ewes, lambs and subadults in the MSLR	52911 ± 2364 (48665–56782)
Number of ewes, lambs and subadults killed by lynx	137 ± 73 (76–337)
% killed	0·26 ± 0·13 (0·14–0·59)

of attacks in the MSLR was not related to the roe deer hunting bags (Kendall's coef. rank corr., $\tau = 0{\cdot}17$, $n = 12$, $P = 0{\cdot}45$). The same was true in districts with at least one lynx attack on sheep ($\tau = 0{\cdot}14$, $n = 12$, $P = 0{\cdot}54$).

The highest roe deer hunting bags were always in districts with attacks and hot spots (Fig. 5). Roe deer hunting bags were lower in districts with lynx attacks but no hot spots and in districts without any lynx attack. The difference between these three categories was significant for all the years (Kruskal–Wallis test, $P < 0{\cdot}05$).

MAGNITUDE OF LIVESTOCK LOSSES TO LYNX PREDATION

From 1988 to 1998, an average of 15% of the flocks present in the MSLR were attacked each year (range 9·5–22·9%; Table 3). From 1988 to 1998, the average annual livestock losses to lynx was estimated at 0·26% ($n = 11$, SD = 0·13%, range 0·14–0·59%) of the total number of sheep present in the MSLR (Table 3).

Complete data on flock size were available for 179 out of the 206 flocks attacked by lynx and for a total of 403 flock-years. When taking into account the flocks that had been attacked for the first time before 1997 ($n = 176$), to get a 3-year history of the attacks on each flock, 70·5% of the flocks were attacked for 1 or 2 years between 1984 and 1998, and 29·5% were attacked for 3 years or more (maximum = 11 out of 15 years). Most of the flocks regularly attacked were situated in hot spots (Table 4).

During one specific year, 94% of the flocks were attacked once or twice a year (Table 5). In hot spots, repeated attacks were more frequent: 23·3% of the flocks were attacked ≥ 5 times per year (maximum = 31).

In the smallest flocks (< 50 ewes), 50% suffered > 5% annual losses (range 0–100%) although the absolute numbers of killed sheep remained low (maximum = 15; Fig. 6). In flocks comprising > 100 ewes, only 4% had > 5% annual losses (range 0–6·8%) but the absolute number of sheep killed was higher: 13·4% of the flocks had losses of > 10 sheep per year (maximum = 54).

IMPORTANCE OF SHEEP TO LYNX

Lynx consumed their prey, at least partly, in 75% of the successful attacks (maximum = 4 prey partly consumed; $n = 1085$). Logistic regression showed a significant effect of the 'number of attacks over the year in a 5-km radius' (< 10, 10–20, > 20) and of the 'number of animals killed

Table 4. Distribution of the flocks according to the number of years in which they were attacked by lynx between 1984 and 1998. Flocks attacked for the first time after 1996 were not taken into account

Number of years with lynx attacks		Flocks in hot spot areas	Flocks outside hot spot areas	Total
1 years	*n*	12	83	95
	(%)	(21·4)	(69·2)	(54·0)
2 years	*n*	11	18	29
	(%)	(19·6)	(15·0)	(16·5)
3 years or more	*n*	33	19	52
	(%)	(58·9)	(15·8)	(29·5)
Total	*n*	56	120	176
	(%)	(100)	(100)	(100)

Table 5. Annual number of lynx attacks per flock. The same flocks may be involved several times

Annual number of lynx attacks per flock		Flocks in hot spot areas	Flocks outside hot spot areas	Total
1–2	*n*	134	169	303
	(%)	(60·1)	(93·9)	(75·2)
3–4	*n*	37	10	47
	(%)	(16·6)	(5·6)	(11·6)
≥ 5	*n*	52	1	53
	(%)	(23·3)	(0·6)	(13·2)
Total	*n*	223	180	403
	(%)	(100)	(100)	(100)

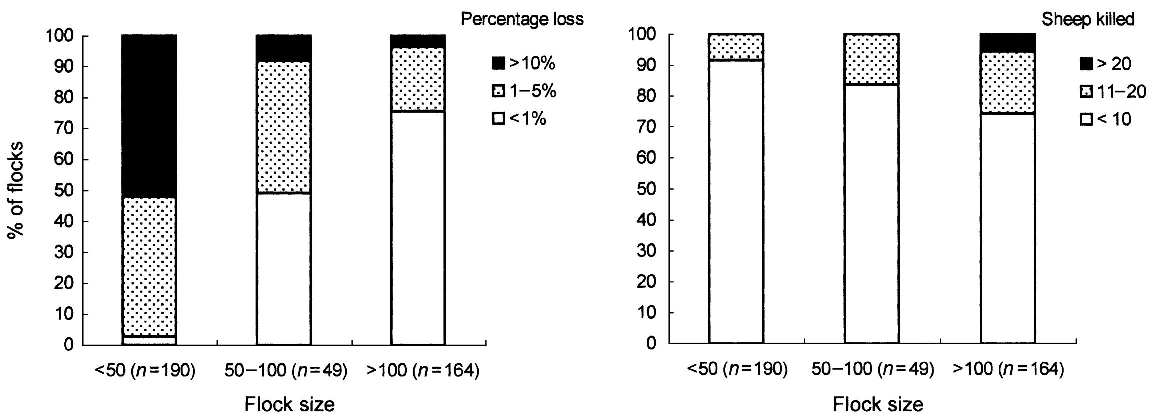

Fig. 6. Annual percentage loss of sheep and annual number of sheep killed with respect to various flock sizes.

during the attack' (1, 2, ≥ 3) on the probability of a sheep being consumed. Prey consumption was less frequent on sites with numerous attacks ($\beta = -0{\cdot}205 \pm 0{\cdot}058$, $P < 0{\cdot}01$): the proportion of successful attacks without any consumption of a sheep increased from 19% on sites with less than 10 attacks during the year, to 33% on sites with more than 20 attacks. Prey consumption was also less frequent in attacks with a large number of animals killed ($\beta = -0{\cdot}219 \pm 0{\cdot}095$, $P = 0{\cdot}022$): the proportion of successful attacks without any consumption of a sheep increased from 24% in attacks with one sheep killed to 34% in attacks with ≥ 3 sheep killed. The 'age of the prey killed' (< 12 month, ≥ 12 month) had no effect.

For the 35 hot spots identified between 1984 and 1998 in nine sites, the median delay between successive attacks on the same hot spots was 7 days. The average number of days with a sheep-based diet for lynx was 11·4 days year^{-1} (n = 35, SD = 5·3 days, range 5·2–24·8 days; Fig. 7), i.e. 5·5% of the days between the first and the last attack in the hot spot (n = 35, SD = 2·6%, range 1·6–14·8%). In only two cases was this percentage higher than 10%. On an annual basis (365 days), this percentage was 3·1% of the days (SD = 1·5%, range 1·4–6·8%).

Discussion

In most western European countries, lynx damage on sheep varies between some tens of sheep killed per country and per year to a few hundred (Cerveny & Bufka 1996; Breitenmoser, Breitenmoser-Würsten & Capt 1998; Cop & Frkovic 1998; Huber & Kaczensky 1998; this study) and livestock are never the main prey of lynx (Breitenmoser & Haller 1987; Capt *et al.* 1993;

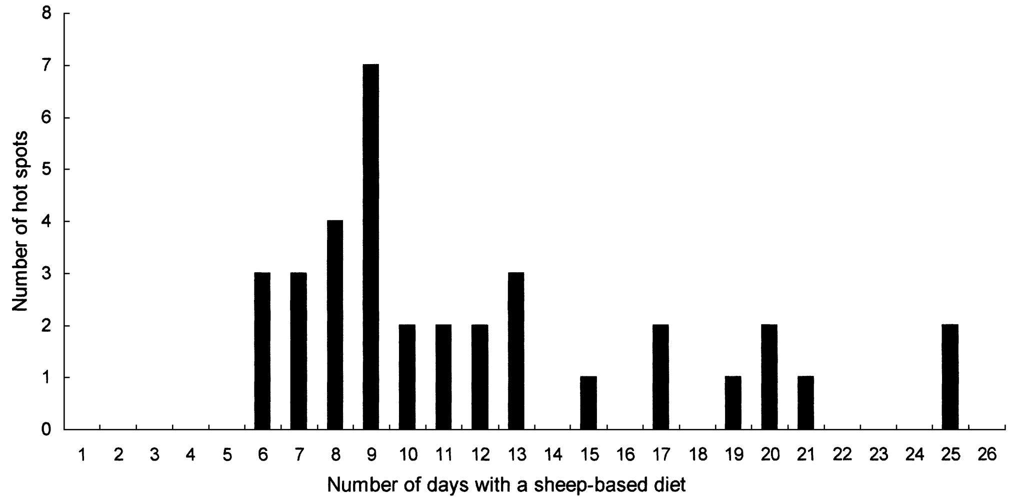

Fig. 7. Annual number of days with a sheep-based diet for lynx attacking in hot spots.

Jedrzejewski *et al.* 1993; Okarma *et al.* 1997; Sunde & Kvam 1997; Pedersen *et al.* 1999; Jobin, Molinari & Breitenmoser 2000). Greater damage has only been reported in Norway, where large flocks of unattended sheep graze in forests during the summer season (Kaczensky 1996), and over 9000 sheep per year were killed by lynx from 1996 to 1999 (J. Linnell, personal communication). Compared with the damage that occurs in Norway, the French husbandry system of keeping sheep in fenced fields is probably a successful deterrent. In the Jura, there was no general lynx–livestock problem in spite of the absence of measures to protect livestock. At the regional scale, sheep losses to lynx were low, i.e. less than 0·5% of the available stock. Many flocks were not affected and, among those suffering attacks, most were only sporadically attacked. With an average of 1·6 animals killed per attack and few wounded animals, lynx attacks differ from dog or wolf attacks, where the number of individuals killed and the frequency of mass attacks is higher (Fico, Morosetti & Giovanni 1993; Ciucci & Boitani 1998).

As already suggested by Breitenmoser *et al.* (1998) and Breitenmoser (1998), lynx–livestock conflicts in France and in Switzerland were partly due to the psychological impact of the sudden return of large carnivores in habitats where, for a long time, large predators had been absent. The absence of traditional methods of herd protection, or the delay of implementation of a procedure of compensation, certainly also influenced the reaction. Nevertheless, the high concentration of lynx damage to certain flocks is a factor that has been underestimated. These localized and year-to-year persistent hot spots represent the major lynx–livestock problem. In hot spots, lynx attacks can completely decimate the smallest flocks. Among the bigger flocks, only a minority suffered sheep losses up to 5% but these flocks were attacked almost every year. These losses, which made up about 50% of lambs and subadults, can lead to a loss of annual income, but the greatest problems are probably linked to the difficulty of herding. These large flocks often occupy vast and scrubby parks, situated near wooded hillsides far from human settlements. These conditions make the discovery of killed sheep more difficult. Furthermore, as has been established by radio-tracking studies (Warren & Mysterud 1990; Neale *et al.* 1998), very young lambs that are killed by predators are difficult to find. To limit their economic losses, i.e. for compensation to be paid, the breeders should regularly patrol their parks to collect the corpses of killed animals, which are often overlooked without a thorough search. In these hot spot areas, the year-to-year persistence of lynx predation may become a real handicap to the breeders.

The causes of hot spots, which were suggested in detailed studies of large carnivore depredation on cattle, often are the result of a combination of factors: cattle-orientated predatory behaviour of a few individual predators (Stander 1990; Camarra *et al.* 1993; Mizutani 1993; Anderson *et al.* 1997; Sacks *et al.* 1999; but see Linnell *et al.* 1999), sometimes with signs of injury (Rabinowitz 1986; Hoogesteijn, Hoogesteijn & Mondolfi 1993), the particulars of the herding techniques (Nass, Lynch & Theade 1984; Rabinowitz 1986; Nédélec 1995; Cozza, Fico & Battistini 1996; Ciucci & Boitani 1998; Espuno 1998), the local abundance of sheep (Nass, Lynch & Theade 1984), habitat characteristics (Pearson & Caroline 1981; Robel *et al.* 1981; Rabinowitz 1986; Fritts *et al.* 1992; Hoogesteijn, Hoogesteijn & Mondolfi 1993; Mizutani 1993; Sunde, Overskaug & Kvam 1998), the rarity of wild prey (Mech, Fritts & Paul 1988; Meriggi & Lovari 1996; Meriggi *et al.* 1996) or the abundance of predators (Sagør, Swenson & Røskaft 1997). In the Jura massif, the history of hot spots was characterized by a succession of episodes with damage over several seasons, followed by durable interruptions. The very small areas covered by the hot spots and the persistence of damage for several years suggest that these hot spots were caused by a small number of individual lynx. The reappearance of damage on the same sites after years of interruption, during which there was proof that lynx had been eliminated, suggests that different individuals living in the same sites have developed the same predatory behaviour on sheep. Therefore, even if the proximate factor causing the appearance of a hot spot could have been linked to the presence of a lynx with an individual predatory behaviour on sheep, the reappearance of attacks in the same sites and the concentration of hot spots within only a few areas clearly indicates that the ultimate factors causing hot spots are factors that are inherent to these sites.

Among the factors inherent to specific sites, the local availability of domestic and wild ungulates is potentially important. Predation on domestic ungulates by large carnivores may be higher when the availability or the diversity of wild ungulates is low because predators switch from wild to domestic prey depending on their relative availability (Mech, Fritts & Paul 1988; Meriggi & Lovari 1996; Meriggi *et al.* 1996). A positive relationship between the abundance of food and the magnitude of predation on domestic animals has been suggested in other cases, because of an increase in predator density in response to a high food supply (Nass, Lynch & Theade 1984; Yom-Tov, Ashkenazi & Viner 1995). In the Jura, roe deer abundance was greater in hot spots. Areas rich in roe deer may be more intensively used by lynx, producing higher encounter rates between lynx and sheep. A high local abundance of ungulates may be especially important to females with young (Schmidt, Jedrzejewski & Okarma 1997). As regards sheep, there was only a slight correlation between the abundance of sheep and the number of attacks. However, a simple relationship between their abundance and the number of attacks can only be expected in sites where sheep are free-ranging and unattended in natural carnivore habitat (Linnell *et al.* 1996; Landa *et al.* 1999). In other cases, herding methods, or environmental factors such as the proximity of forests, the presence of forested slopes or resting areas rarely frequented by humans (Warren & Mysterud 1990; Sunde, Snorre & Kvam 1998), or the proximity of dens (Schmidt 1998; Reinhardt & Halle 1999) may increase the encounter rate between lynx and sheep, independently of sheep abundance.

According to the Breitenmoser & Haller (1993) hypothesis, the long-term trend in the number of attacks, i.e. the initial peak of predation on sheep followed by a decrease and stabilization, could be explained by a temporary dietary switch of lynx from wild ungulates to sheep because of a lesser availability of wild ungulates and temporal high density of lynx. This hypothesis seems to be rather implausible for this expanding lynx population, if one examines our four predictions.

1. In accordance with the hypothesis, the dramatic increase in the number of attacks was followed by a decrease and stabilization in damage. Nevertheless, the increase in the number of attacks seems to be concomitant with the settlement of lynx in the sheep-breeding region. We cannot exclude the possibility of a bias in the method by which the process of colonization was monitored. However, lynx tracks, sightings, remains of wild prey and discoveries of dead animals were collected at regular intervals by the observers, even in the absence of attacks on domestic prey (Stahl & Vandel 1999). Sightings provided a valuable source of information about lynx distribution and habitat for the Iberian lynx *Lynx pardinus* (Palma, Beja & Rodrigues 1999). Furthermore, data collected on radio-collared lynx showed that all lynx were detected by the network of observers (Office national de la chasse et de la faune sauvage, unpublished data).

2. In the French Jura, the increase in the number of attacks was mainly caused by the appearance of clustered attacks in a few hot spots. Numerous flocks have never been attacked. Therefore, the trend in the number of attacks was not due to the whole lynx population, but was an isolated phenomenon involving only a few individuals on a few sites.

3. The constant spatial heterogeneity of damage, observed during and after the massif's colonization, cannot be explained by the lesser abundance of wild ungulate populations. On the contrary, throughout the whole French Jura, the numbers of wild ungulates have been growing, as indicated by the large increase in the hunting bag, and the abundance of wild ungulates was consistently higher in the areas with numerous attacks than in the areas without attacks.

4. Lynx did not depend on sheep for its annual dietary needs. Even in sectors where the most numerous attacks occurred, sheep only represented a small proportion of the lynx diet. Lynx rarely returned for several consecutive nights to the same spot to consume sheep, even when these were not moved away, and during about one-quarter of the attacks no prey were consumed. A summer increase of the number of attacks on sheep was not observed, as was suggested in Norway where females must satisfy the increasing need for food of their young (Warren & Mysterud 1990). Furthermore, the highest proportion of attacks without prey consumption was recorded in hot spots and during the most severe attacks. This surplus killing behaviour (Kruuk 1972) occurs in other felids (Fox & Chundawat 1988; Stuart 1988).

We suggest that the spatial and temporal variability in the number of attacks cannot be explained by functional and numerical responses of the predator population to the respective availability of wild and domestic prey, as Breitenmoser & Haller (1993) have attempted. The initial increase in the number of attacks, and the subsequent changes over time in the number of lynx attacks, were mainly caused by the appearance of clustered attacks on a few sites. This pattern could simply be explained by the development of the lynx population throughout the sheep-herding area and the occasional appearance of individuals that regularly killed sheep in some very specific environments. In these hot spot areas, further studies are needed to ascertain more precisely the causal connection between habitat characteristics, lynx use of space and the development of an individual predatory behaviour on sheep.

Journal of Applied Ecology, **38**, 674–687

MANAGEMENT IMPLICATIONS

There are two main ways in which conflict and damage can be minimized: financial compensation for damage caused by predators and the development of herding methods to protect flocks. In addition to these fundamental measures, direct control of 'problem individuals' is sometimes proposed when damage is concentrated and linked to individuals (Boitani 2000; Breitenmoser *et al*. 2000; Swenson & Dahle 2000). In the Jura, more than 70% of the flocks attacked suffer rare and non-regular lynx attacks. In that case, the implementation of protective measures is not cost-effective, and damage compensation is the only available tool. Furthermore, compensation payments cannot justifiably be conditional on the implementation of expensive protective measures for the flocks. In hot spots, which are a sporadic but recurrent problem, the costs, benefits and practicality of different measures of prevention should be evaluated: capture of animals causing large amounts of damage if it is clear that the hot spots are indeed due to a few specialized predators; subsidized use of dogs to guard the flocks if damage is linked to a particular environment; or a combination of these two methods.

Acknowledgements

We thank the members of the lynx networks for their co-operation and intensive field work. The 'Direction Départementale de l'Agriculture et de la Forêt' provided us with sheep data. The 'Fédération Départementale des chasseurs' of Ain and Jura provided us with the roe deer hunting bags. Maps were prepared by Philippe Landry. Eveline Taran improved the English. John Linnell, Ben Sachs and an anonymous referee provided helpful comments and suggestions that improved an earlier version of the paper. This study was supported by the Ministry of Environment, Nature and Landscapes Directorate.

References

Andelt, W.F. (1996) *Carnivores* (ed. P.R. Krausman), pp. 133–135. Rangeland Wildlife, Society for Range Management, Denver, CO.

Anderson, C.R., Ternent, M.A., Moody, D.S., Bruscino, M.T. & Miller, D.F. (1997) *Grizzly Bear–Cattle Interaction on Two Cattle Allotments in Northwest Wyoming*. Final Report. Wyoming Game and Fish Department, USA.

Boitani, L. (2000) *Action plan for the conservation of wolves in Europe* (Canis lupus). Nature and Environment, No. 113, Council of Europe, Strasbourg.

Breitenmoser, U. (1998) Large predators in the Alps: the fall and rise of man's competitors. *Biological Conservation*, **83**, 279–289.

Breitenmoser, U. & Baetig, M. (1992) Wiederansiedlung und Ausbreitung des Luchses, *Lynx lynx*, im Schweizer Jura. *Revue Suisse de Zoologie*, **99**, 163–176.

Breitenmoser, U. & Breitenmoser-Würsten, C.H. (1990) *Status, Conservation Needs and Re-Introduction of the Lynx (*Lynx lynx*) in Europe*. Nature and Environment Series No. 45. Council of Europe, Strasbourg, France.

Breitenmoser, U. & Haller, H. (1987) Zur Nahrungsökologie des Luchses, *Lynx lynx*, in den Schweizerischen Nordalpen. *Zeitschrift für Säugetierkunde*, **52**, 168–191.

Breitenmoser, U. & Haller, H. (1993) Patterns of predation by reintroduced European lynx in the Swiss Alps. *Journal of Wildlife Management*, **57**, 135–144.

Breitenmoser, U., Breitenmoser-Würsten, C.H. & Capt, S. (1998) Re-introduction and present status of the lynx, *Lynx lynx*, in Switzerland. *Hystrix*, **10**, 17–30.

Breitenmoser, U., Breitenmoser-Würsten, C.H., Okarma, H., Kaphegyi, T., Kaphygyi-Wallmann, U. & Müller, U.M. (2000) *Action plan for the conservation of the Eurasian lynx in Europe* (Lynx lynx). Nature and Environment, No. 112, Council of Europe, Strasbourg.

Breitenmoser, U., Kaczensky, P., Dötterer, M., Breitenmoser-Würsten, C., Capt, S., Bernhart, F. & Liberek, M. (1993) Spatial organization and recruitment of lynx, *Lynx lynx*, in a reintroduced population in the Swiss Jura mountains. *Journal of Zoology, London*, **231**, 449–464.

Camarra, J.J., Salinas, R., Larras, J.P., Migot, P. & Stahl, P. (1993) *Bilan d'intervention sur un ours problème dans les Pyrénées Atlantiques*. Actes du colloque de la SFEPM, 17–18 octobre 1992. Musée d'histoire naturelle, Grenoble, France.

Capt, S. (1998) Conflicts with the lynx: depredation and competition with hunters. *The Re-Introduction of the Lynx into the Alps*. Environmental Encounters No. 38, pp. 55–58. Council of Europe, Strasbourg, France.

Capt, S., Bernhart, F., Breitenmoser, U., Breitenmoser-Würsten, C.H., Haller, H., Liberek, M., Vandel, J.M. & Herrenschmidt, V. (1993) Prédation du lynx (*Lynx lynx*) sur les ongulés sauvages et domestiques. *Actes du colloque prédation et gestion des prédateurs, Dourdan 1–2 dec. 1992* (eds P. Migot & P. Stahl), pp. 85–92. Office national de la chasse-Union nationale des fédérations départementales de chasseurs, Paris, France.

Cerveny, J. & Bufka, L. (1996) Lynx *Lynx lynx* in south-western Bohemia. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemicae Brno*, **30**, 16–33.

Ciucci, P. & Boitani, L. (1998) Wolf and dog depredation on livestock in central Italy. *Wildlife Society Bulletin*, **26**, 504–514.

Cop, J. & Frkovic, A. (1998) The re-introduction and development of the lynx in Slovenia and its present status in Slovenia and Kroatia. *Hystrix*, **10**, 65–76.

Cozza, K., Fico, R. & Battistini, M.L. (1996) The damage–conservation interface illustrated by predation on domestic livestock in central Italy. *Biological Conservation*, **78**, 329–336.

De Klemm, C. (1996) *Compensation for Damage Caused by Wild Animals*. Nature and Environment No. 84. Council of Europe, Strasbourg, France.

Espuno, N. (1998) *Facteurs influençant la prédation du cheptel domestique par le loup (*Canis lupus*) dans le Massif du Mercantour.* Diplôme d'études approfondies. University of Montpellier II, Montpellier, France.

Fico, R., Morosetti, G. & Giovanni, A. (1993) The impact of predators on livestock in the Abruzzo region in Italy. *Revue Scientifique et Technique de l'Office International Des Epizooties*, **12**, 39–50.

Fourli, M. (1999) *Compensation for Damage Caused by Bears and Wolves in the European Union*. DG XI. European Commission, Bruxelles, Belgium.

Fox, J.L. & Chundawat, R.S. (1988) Observations of snow leopard stalking, killing and feeding behaviour. *Mammalia*, **52**, 137–140.

Fritts, S.H., Paul, W.J., Mech, L.D. & Scott, D.P. (1992) *Trends and Management of Wolf–Livestock Conflicts in Minnesota*. Resource Publication No. 181. United States Fish and Wildlife Service, Washington, DC.

Greentree, C., Saunders, G., Macleod, L. & Hone, J. (2000) Lamb predation and fox control in south-eastern Australia. *Journal of Applied Ecology*, **37**, 935–943.

Grosjean, D. (1992) The impact of lynx on livestock. *The Situation, Conservation Needs and Reintroduction of the Lynx in Europe, 17–19 oct. 1990*. Environmental Encounters No. 11, pp. 69–73. Neuchâtel Fac. des lettres, Council of Europe, Strasbourg, France.

Herrenschmidt, V. & Léger, F. (1987) Le Lynx *Lynx lynx* (L.) dans le Nord-est de la France. La colonisation du massif jurassien français et la réintroduction de l'espèce dans le massif vosgien. Premiers résultats. *Ciconia*, **11**, 131–151.

Herrenschmidt, V. & Vandel, J.M. (1992) The reintroduction of the lynx in France: scientific and sociological aspects. *The Situation, Conservation Needs and Reintroduction of the Lynx in Europe, 17–19 oct. 1990*. Environmental Encounters No. 11, pp. 58–61. Neuchâtel Fac. des lettres, Council of Europe, Strasbourg, France.

Hoogesteijn, R., Hoogesteijn, A. & Mondolfi, E. (1993) Jaguar predation vs. conservation: cattle mortality caused by felines on three ranches in the Venzuelan Llanos. *Mammals as Predators* (eds N. Dunstone & M.L. Gorman), pp. 391–407. Proceedings of the 65th Symposium. Zoological Society of London, Oxford, UK.

Huber, T. & Kaczensky, P. (1998) The situation of the lynx *Lynx lynx* in Austria. *Hystrix*, **10**, 43–54.

Jedrzejewski, W., Schmidt, K., Milkowski, L., Jedrzejewska, B. & Okarma, H. (1993) Foraging by lynx and its role in ungulate mortality: the local (Bialowieza Forest) and Palearctic viewpoints. *Acta Theriologica*, **38**, 385–403.

Jobin, A., Molinari, P. & Breitenmoser, U. (2000) Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. *Acta Theriologica*, **45**, 243–252.

Kaczensky, P. (1996) *Large Carnivore–Livestock Conflicts in Europe*. Münich Wildlife Society, Ettal, Germany.

Kenward, R.E. & Hodder, K.K. (1996) *Ranges. V. An Analysis System for Biological Data*. Institute of Terrestrial Ecology, Dorset, Wareham.

Knowlton, F.F., Gese, E.M. & Jaeger, M.M. (1999) Coyote depredation control: an interface between biology and management. *Journal of Range Management*, **52**, 398–412.

Kratochvil, J. (1968) Survey of the distribution of populations of the genus *Lynx* in Europe. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemicae Brno*, **2**, 5–12.

Kruuk, H. (1972) Surplus killing by carnivores. *Journal of Zoology, London*, **166**, 233–244.

Landa, A., Gudvangen, K., Swenson, J.E. & Røskaft, E. (1999) Factors associated with wolverine *Gulo gulo* predation on domestic sheep. *Journal of Applied Ecology*, **36**, 963–973.

Linnell, J.C., Odden, J., Smith, M.E., Aanes, R. & Swenson, J.E. (1999) Large carnivores that kill livestock: do 'problem individuals' really exist? *Wildlife Society Bulletin*, **27**, 698–705.

Linnell, J.C., Smith, M.E., Odden, J., Kaczensky, P. & Swenson, J.E. (1996) Strategies for the reduction of carnivore–livestock conflicts: a review. *NINA Opdragsmelding*, **443**, 1–118.

Mech, L.D., Fritts, S.H. & Paul, W.J. (1988) Relationship between winter severity and wolf depredations on domestic animals in Minnesota. *Wildlife Society Bulletin*, **16**, 269–272.

Meriggi, A. & Lovari, S. (1996) A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology*, **33**, 1561–1571.

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.

de Ministère l'agriculture (1988a) *Recensement agricole 1988, Tableaux Prosper, Cantons et régions agricoles, Ain*. Ministère de l'agriculture et de la forêt, Paris, France.

de Ministère l'agriculture (1988b) *Recensement agricole 1988, Tableaux Prosper, Cantons et régions agricoles, Jura*. Ministère de l'agriculture et de la forêt, Paris, France.

de Ministère l'agriculture (1988c) *Recensement agricole 1988, Tableaux Prosper, Cantons et régions agricoles, Doubs*. Ministère de l'agriculture et de la forêt, Paris, France.

Mizutani, F. (1993) Home range of leopards and their impact on livestock on Kenyan ranches. *Mammals as Predators* (eds N. Dunstone & M.L. Gorman), pp. 425–439. Proceedings of the 65th Symposium. Zoological Society of London, Oxford, UK.

Nass, R.D., Lynch, G. & Theade, J. (1984) Circumstances associated with predation rates on sheep and goats. *Journal of Range Management*, **37**, 423–426.

Neale, J.C.C., Sacks, B.N., Jaeger, M. & McCullough, D.R. (1998) A comparison of bobcat and coyote predation on lambs in north-coastal California. *Journal of Wildlife Management*, **62**, 700–706.

Nédélec, L. (1995) *L'ours et le Berger dans les Pyrénées, le Prix de la Cohabitation*. Documents scientifiques No. 30. Parc national des Pyrénées, Tarbes, France.

Nowell, K. & Jackson, P. (1996) *Wild Cats. Status Survey and Conservation Action Plan*. IUCN, Gland Switzerland.

Okarma, H., Jedrzejewski, W., Schmidt, K., Kowalczyk, R. & Jedrezejwska, B. (1997) Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. *Acta Theriologica*, **42**, 203–224.

Palma, L., Beja, P. & Rodrigues, M. (1999) The use of sighting data to analyse Iberian lynx habitat and distribution. *Journal of Applied Ecology*, **36**, 812–824.

Pearson, E.W. & Caroline, M. (1981) Predator control in relation to livestock losses in central Texas. *Journal of Range Management*, **34**, 435–441.

Pedersen, V.A., Linnell, J.D.C., Andersen, R., Andrén, H., Lindén, M. & Segerström, P. (1999) Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. *Wildlife Biology*, **5**, 203–211.

Rabinowitz, A.R. (1986) Jaguar predation on domestic livestock in Belize. *Wildlife Society Bulletin*, **14**, 170–174.

Reinhardt, I. & Halle, S. (1999) Time of activity of a female free-ranging lynx (*Lynx lynx*) with young kittens in Slovenia. *Zeitschrift für Säugetierkunde*, **64**, 65–75.

Robel, R.J., Dayton, A.D., Henderson, R.R., Meduna, R.L. & Spaeth, C.W. (1981) Relationships between husbandry methods and sheep losses to canine predators. *Journal of Wildlife Management*, **45**, 894–911.

Roberts, D.H. (1986) Determination of predators responsible for killing small livestock. *Journal of Wildlife Research*, **16**, 150–152.

Sacks, B.J., Jaeger, M.M., Neale, J.C.C. & McCullough, D.R. (1999) Territoriality and breeding status of coyotes relative to sheep predation. *Journal of Wildlife Management*, **63**, 593–605.

Sagør, J.T., Swenson, J.E. & Røskaft, E. (1997) Compatibility of brown bear *Ursus arctos* and free-ranging sheep in Norway. *Biological Conservation*, **81**, 91–95.

Schmidt, K. (1998) Maternal behaviour and juvenile dispersal in the Eurasian lynx. *Acta Theriologica*, **43**, 391–408.

Schmidt, K., Jedrzejewski, W. & Okarma, H. (1997) Spatial organisation and social relations in the Eurasian Lynx population in Bialowieza Primeval Forest, Poland. *Acta Theriologica*, **42**, 289–312.

Stahl, P. & Vandel, J.M. (1998) Distribution of the lynx in the French Alps. *Hystrix*, **10**, 3–15.

Stahl, P. & Vandel, J.M. (1999) Mortalité et captures de lynx (*Lynx lynx*) en France (1974–98). *Mammalia*, **63**, 49–59.

Stahl, P., Vandel, J.W., Herrenschmidt, V. & Migot, P. (2001) The effect of removing lynx in reducing attacks on sheep in the French Jura Mountains. *Biological Conservation* (in press).

Stander, P. (1990) A suggested management strategy for stock-raiding lions in Namibia. *South African Journal of Wildlife Research*, **20**, 37–43.

Stuart, C.T. (1988) The incidence of surplus killing by *Panthera pardus* and *Felis caracal* in Cape Province, South Africa. *Mammalia*, **50**, 556–558.

Suminski, H.R. (1982) Mountain lion predation on domestic livestock in Nevada. *Proceedings Tenth Vertebrate Pest Conference* (ed. R.E. Marsh), pp. 62–66. University of California, Davis, CA.

Sunde, P. & Kvam, T. (1997) Diet patterns of Eurasian Lynx, *Lynx lynx*: what causes sexually determined prey size segregation? *Acta Theriologica*, **42**, 189–201.

Sunde, P., Overskaug, K. & Kvam, T. (1998) Culling of lynx *Lynx lynx* related to livestock predation in a heterogeneous landscape. *Wildlife Biology*, **4**, 169–175.

Sunde, P., Snorre, Ø. & Kvam, T. (1998) Tolerance to humans of resting lynx *Lynx lynx* in a hunted population. *Wildlife Biology*, **4**, 177–183.

Swenson, J.E., Gersti, N., Dahle, B. & Zedrosser, A. (2000) *Action plan for the conservation of the brown bear in Europe* (Ursus arctos). Nature and Environment, No. 114, Council of Europe, Strasbourg.

Vandel, J.M. & Stahl, P. (1998a) Colonisation du massif jurassien par le lynx (*Lynx lynx*) et impact sur le cheptel domestique. *Gibier Faune Sauvage, Game Wildlife*, **15** (Hors Série, Tome 3), 1161–1169.

Vandel, J.M. & Stahl, P. (1998b) Lynx (*Lynx lynx*) population monitoring in France: comments on a method of data collection applied over a 6-year period. *The Re-Introduction of the Lynx into the Alps*, pp. 97–104. Environmental Encounters No. 38. Council of Europe, Strasbourg, France.

Warren, J.T. & Mysterud, I. (1990) Domestic sheep mortality on a forested Norwegian range. *Transactions of the 19th IUGB Congress, Trondheim, 1989* (ed. S. Myrberget), pp. 605–612. Norwegian Institute for Nature Research, Trondheim.

Weber, J.M. & Weissbrodt, M. (1999) Feeding habits of the Eurasian lynx in the Swiss Jura Mountains determined by faecal analysis. *Acta Theriologica*, **44**, 333–336.

Yom-Tov, Y., Ashkenazi, S. & Viner, O. (1995) Cattle predation by the golden jackal *Canis aureus* in the Golan heights, Israel. *Biological Conservation*, **73**, 19–22.

Received 20 April 2000; revision received 7 February 2001