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Factors affecting lynx predation on sheep in the French Jura

P. STAHL, J.M. VANDEL, S. RUETTE, L. COAT, Y. COAT and L. BALESTRA
Office National de la Chasse et de la Faune Sauvage, Montfort, 01 330 Birieux, France

Summary

1. In regions where sheep are kept in fenced pastures and do not graze unattended in carnivore habitats, sheep losses vary greatly between sites and livestock farms. To assess the factors that may predispose farms to lynx predation in the French Jura, we compared sheep availability and environmental characteristics between pastures with and without attacks in a 1800-km^2 study area. Nine lynx were radio-tracked in the same area for a total of 21 lynx years to estimate individual killing rates on sheep and to identify possible habitual livestock killers.

2. Depending on individual and year, lynx predation rate on sheep within lynx home ranges varied between 0 and 12·4 attacks 100 days^{-1}. Predation rate on sheep was not related to sheep abundance nor sheep dispersion in lynx home ranges. Two individuals became habitual sheep killers during, respectively, their third and fourth year of monitoring. Other lynx that had access to the same flocks were only occasional sheep killers. No obvious causal factor (e.g. sex, reproductive status, physical debilitation) explained the differential individual propensity for lynx to kill livestock.

3. We found no difference in sheep availability between pastures with and without attacks, but strong differences in their environmental characteristics. In only 5·1% of 98 pastures > 250 m from a forest were sheep attacked by lynx. In 228 pastures adjacent or connected to forests by cover, 39·1% sustained attacks on sheep by lynx ($P < 0·01$). For these latter pastures, logistic regression showed a positive effect of their proximity to major forested areas ($P < 0·01$), absence of human dwellings ($P < 0·01$), local abundance of roe deer ($P = 0·01$) and the presence of attacked pastures in their vicinity ($P = 0·03$).

4. These results suggests that lynx damage locally can be explained by a predictable set of habitat features that expose sheep on some pastures to risk, and by an unpredictable event, i.e. an individual developing regular predation on sheep.

5. In grazing systems like the Jura, where unattended sheep are distributed patchily and individual problem lynx may appear, removing lynx or lowering density without differentiating individuals will be insufficient to limit conflicts. Selective removals could temporarily reduce predation but the site effect implies that durable management can arise only through improved shepherding. This might include guard dogs in the few local sites at risk and providing shelter for sheep at night when attacks are on the increase.

Key-words: carnivore–livestock conflicts, predation, husbandry, kill rate, landscape, *Lynx lynx*, management.

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Introduction

One of the main difficulties when devising large carnivore conservation plans is the management of carnivore predation on livestock (Boitani 2000; Breitenmoser *et al*. 2000; Swenson *et al*. 2000). In regions where sheep, goats or cattle are not allowed to wander freely in carnivore habitats, i.e. are kept in herds or in fenced pastures, the overall percentage loss is generally low (Kaczensky 1996). Nevertheless, a detailed analysis of the livestock losses invariably shows marked variability between sites or livestock farms. Some farmers have recurring predation problems, whereas other nearby farms experience losses only occasionally or not at all (Suminski 1982; Nass, Lynch & Theade 1984; Fritts *et al*. 1992; Cozza, Fico & Battistini 1996; Stahl *et al*. 2001a).

Correspondence: Philippe Stahl, Office National de la Chasse et de la Faune Sauvage, Montfort, 01 330 Birieux, France (fax +33 4 74 98 14 11; e-mail p.stahl@oncfs.gouv.fr).

Among the factors that might explain this spatial heterogeneity, poor husbandry is often invoked (Ciucci & Boitani 1998). Site effects due to environmental factors or relative availability of wild and domestic prey have also been suspected. In particular, predation on livestock tends to be higher in rough and brushy areas or in remote parts of the farms, but lower in grassy areas (Nass, Lynch & Theade 1984; Fritts *et al*. 1992; Mech *et al*. 2000). Predation on livestock may also be greater when the availability or diversity of wild prey is low (Mech, Fritts & Paul 1988; Meriggi & Lovari 1996; Stoddart, Griffiths & Knowlton 2001), although a positive relationship 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). Additionally, evidence is growing that within a carnivore population only a small proportion of the individuals are responsible for most livestock predation, for example males whose wide-ranging movements lead to high encounter rates with livestock (e.g. Suminski 1982; Rabinowitz 1986; Stander 1990; Torres *et al*. 1996; Linnell *et al*. 2000), breeding adults provisioning young (Till & Knowlton 1983; Conner *et al*. 1998; Landa *et al*. 1999; Sacks *et al*. 1999) or debilitated individuals unable to hunt wild prey (Rabinowitz 1986; Hoogesteijn, Hoogesteijn & Mondolfi 1993).

The purpose of this study was to examine which factors are associated with high local predation on sheep by the Eurasian lynx *Lynx lynx* L. in the French Jura. In this region, lynx predation on sheep is highly clustered, and 33–69% of the attacks have taken place on less than 5% of the total area where attacks have occurred (Stahl *et al*. 2001a). As no measures were taken to protect flocks against predators when lynx expanded into this region, this pattern could not been explained by the differential use of livestock protection techniques. The absence of attacks on numerous flocks, the high clustering of attacks and the abrupt cessation of attacks after the legal selective removal of some individuals suggested that only a few individuals were habitual sheep predators. On the other hand, the reappearance of attacks in the same sites after years with no losses suggested a 'site' effect (Stahl *et al*. 2001a,b).

The two questions were addressed. (i) Does a special set of habitat features predispose some farms or sites to lynx predation? (ii) Do particular lynx develop a livestock-killing behaviour on a more habitual basis than others? To assess factors that may predispose farms to lynx predation on sheep, we described sheep availability and environmental characteristics of pastures with and without attacks in the main lynx–sheep range. Lynx were radio-tracked in the same area to estimate individual killing rates on sheep and to identify possible habitual livestock killers.

Study area

The 1800-km^2 study area was situated in the south-east of the French Jura, eastern France. The landscape was typical of the Jura sheep-herding range. Altitude varied between 400 and 900 m a.s.l. Forests covered 43% of the study area and agricultural land covered 47%, 75% of which was meadow (de Ministère l'agriculture 1988a,b). In the study area, about 8500 sheep were raised, and 11 000–12 000 lambs were produced each year. Flock size averaged 50 ewes (range 5–460). From early spring to late autumn, sheep were kept in pastures of 1–100 ha, surrounded with electric fences or 1·2-m high wire netting. These fences were only designed to constrain sheep movements and not to exclude large carnivores. Rams or cattle grazed only rarely with sheep. Within the pastures, sheep were never guarded and wandered freely by day and night. In winter, sheep were housed. No livestock guard dogs are used in this region. Roe deer *Capreolus capreolus* L. are the most numerous wild ungulates, and make up the staple diet of lynx in this region (Jobin, Molinari & Breitenmoser 2000). The red deer *Cervus elaphus* L. is absent. The chamois *Rupricapra rupricapra* L. is abundant in the High Jura but is rare in the study area. Although we did not attempt to estimate lynx density in the study area, home range size and spatial organization were known to be similar to the High Jura, where adult lynx density was estimated at 1·0 individual 100 km^{-2} (Breitenmoser *et al*. 1993; Office national de la chasse et de la faune sauvage, unpublished data).

Methods

LYNX PREDATION RATES ON SHEEP

Nine lynx were captured and radio-collared in the study area between 1995 and 1999, representing a total of 21 lynx years. Other individuals were also present but were not caught. Lynx were trapped with foot snares set around fresh carcasses of wild ungulates killed by lynx. To avoid interfering with lynx predatory behaviour, traps were never set around sheep carcasses. We attempted to locate lynx in the morning or early evening. When a lynx was located near a flock, we relocated it the following night to check and record its presence inside sheep pastures. A total of 3745 locations was obtained. Home ranges were calculated by the minimum convex polygon method (minimal area method; Mohr 1947), after excluding a few outliers (maximum = 6), and using only radio-locations obtained from March to November (n = 2971). Sheep were often housed before or after this period and more than 90% of the attacks were recorded during these months. According to the French standardized monitoring system (Vandel & Stahl 1998; Stahl *et al*. 2001a), an exhaustive census of livestock attacks in the study area was taken during the course of the study by trained experts. In the following analyses only confirmed and probable lynx attacks on sheep were used.

A total of 170 attacks, i.e. one or several sheep killed by lynx in one night in a pasture, was recorded

in the lynx home ranges. Radio-tracked lynx were implicated in 65 attacks (38·2%). In 17 cases, the lynx was observed attacking or eating the sheep, or a photograph was taken with an automatic camera. In 48 cases, the identity of the lynx was suspected because of its close proximity to the kill during the night or morning of the kill, but no direct sighting was made.

In 38 of 170 attacks (22·4%), none of the radio-tracked lynx could be implicated because of their confirmed presence in another part of their home range (> 4 km) the day before and after the kill. The lynx either stayed in the same distant place or moved in the opposite direction relative to the kill. In the first case, it is likely that the lynx also stayed at night in this distant site because short daily distances are associated with the consumption of a prey (Herrenschmidt, Léger & Terrier 1986) and lynx frequently stay in the immediate vicinity of their kill (Pedersen *et al*. 1999).

In 67 of 170 attacks (39·4%), it was not possible to prove whether a particular lynx was responsible for the kill or not, because of intermediate distances (1–4 km) from the kill or absence of radio-tracking data. In those cases, the lynx responsible for the kill remained undetermined, although certain radio-tracked lynx could be eliminated. Taking this uncertainty into account, the following formula was used to estimate the total number of attacks, n_i, that could be assigned to a radio-tracked lynx in its home-range:

$$n_i = a_i + c_i\,[a_i/(a_i + na_i)]$$

a_i being the number of attacks a lynx was responsible for in its home range during year i (March–November), na_i the number of attacks the lynx was not responsible for, and c_i the number of attacks for which it was not known whether or not the lynx was responsible. Predation rates on sheep were calculated as the number of attacks n_i per 100 days.

AVAILABILITY OF SHEEP IN LYNX HOME RANGES

Sheep farm locations and flock size were obtained from the agricultural services, complemented by local enquiries for very small flocks (< 10 sheep) that were not registered. A total of 143 sheep farms were inside lynx home ranges for at least 1 year. The size of the flocks and activity of the farmers during the course of the study were checked yearly. Different indices of sheep availability within lynx home ranges were derived from these data: the total number of ewes raised in the home range (n), the total number of flocks, the overall sheep density (n/home range size), and a sheep dispersion index that was the variance to mean ratio (Chessel 1978) of the number of sheep in a 1-km^2 grid superimposed over lynx home ranges. Non-parametric tests (Man-Whitney U-test and Kendall's coefficient of rank correlation) were performed to examine whether predation rates were related to these four indices of sheep availability.

INFORMATION ON PASTURES

Field investigations and farmer interviews were conducted on 105 out of the 143 sheep farms located in the lynx home ranges (80–90% of the total sheep raised in lynx home ranges). Eleven additional farms located just outside lynx home range borders were also described to increase the sample size. Field investigations and farmer interviews were conducted only once from 1995 to 1999. Nevertheless, according to the farmers' opinions, sheep husbandry and the use of pastures followed the same pattern from year to year.

Pastures were characterized with 11 variables considered to represent potential risk factors (Table 1). Seven categorical variables described habitat characteristics: size of the pasture, type of connection between pasture and nearby forest, presence of a forested or rocky slope near the pasture, presence and type of human dwellings ≤ 1000 m from the pasture fence, presence of shrub in the pasture, presence of a permanent free access shelter for sheep in pastures, and local roe deer abundance. Presence of paved roads or rivers adjacent to pastures was also recorded, but they were rare and were not taken into account in the analysis. The local roe deer abundance was derived from the mean number of roe deer killed per 100 ha of forested and farm land in the district (about 1000 ha). In the French Jura, roe deer are killed according to quotas that are calculated every year in proportion to the estimated number of roe deer present in each district. These estimates are made by the game wardens based on professional experience. As there were no major divergent management goals for the roe deer population between districts during this period, we believe that this index was valid for comparative purposes. Nevertheless, because of the uncertainty in population size estimates, we considered only two levels of abundance: low (≤ 2 roe deer killed 100 ha^{-1}) and high (> 2 roe deer killed 100 ha^{-1}). To study the type of connection between pastures and forests, we combined a field estimate of the distance between the fence of the pasture and the nearest forested cover, and a map of the major forested area. This map was drawn to identify large continuous forested areas > 2000 ha. Pastures were then classified as (i) isolated from forest, when there was no cover > 250 m around the fence of the pasture; (ii) connected to forest, when wooded areas adjacent to the pasture fence belonged to extensions of a major forested area; and (iii) adjacent to forest, when bordered along at least one of their edges by a major forested area or by a small ≤ 250-m long extension of the forest. Forested or rocky slopes were > 40% and > 200-m long slopes. They were classified as 'present' when situated in the forest bordering the pasture and ≤ 250 m from the fence, otherwise 'absent'. Human

Table 1. Environmental and sheep availability variables used to characterize pastures ($n = 326$) in the univariate analyses and logistic regression

Variables	Categories	Number of pastures
Number of lynx attacks	0	231
	≥ 1	95
Pasture size	≤ 2 ha	166
	> 2 ha	160
Pasture–forest connection	Pasture isolated from forest	98
	Pasture adjacent to forest	99
	Pasture connected to forest	129
Forested or rocky slope within ≤ 250 m	Presence	93
	Absence	233
Human dwelling within ≤ 1000 m	Absence or isolated house	145
	Village	181
Shrub cover inside pasture	≤ 5% of the total area	211
	> 5% of the total area	115
Permanent free access shelter for sheep	Absence	234
	Presence	92
Roe deer abundance	Low (≤ 2 roe deer killed 100 ha^{-1})	160
	High (> 2 roe deer killed 100 ha^{-1})	166
Mean length of time sheep were pasturing	≤ 1 month	150
	> 1 month	176
Mean number of pasturing sheep	≤ 50	196
	> 50	130
Number of ewes within ≤ 2 km	≤ 150	171
	> 150	155
Other pastures with attacks within ≤ 2 km	Presence	172
	Absence	154

settlement presence was recorded at a maximum 1-km distance from the fence, and when present classified as an isolated house or a village. Bush was defined as dense 0·50–2-m high vegetation and recorded as ≤ 5% or > 5% of the pasture area.

For each pasture and year, three variables described the availability of sheep: the length of time ewes or lambs occupied the pasture, the mean number of pasturing ewes and lambs, and the local abundance of sheep expressed as the total number of ewes raised in farms located ≤ 2 km from the pasture. The annual length of time sheep were allowed to graze in each pasture was supplied by farmers. When sheep were moved between different pastures, the length of time the flock stayed in each pasture was estimated in proportion to their surface area. When estimating the average number of pasturing sheep, the number of lambs was recalculated every month to take into account the input and output due to lambing, selling and movements. As flock sizes remained constant from year to year for the majority of flocks and because of constant farming practices, the number of sheep grazing each pasture was averaged for the whole study period. The number of grazing sheep and the pasture occupancy period was set to zero when sheep were housed at night. Because we were cautious about the exact numerical value of the data obtained from farmers and subsequent extrapolations, these variables were treated as categorical variables. In addition, most flocks were either very small in our study area (breeders who raised sheep for home consumption or local sales) or large (full-time producers) and sheep variables had few intermediate values. Categorical cut-offs were chosen so that each category had an approximately similar number of pastures (Table 1). Finally, the presence of pastures with attacks within ≤ 2 km was considered an additional 'risk factor'. This factor expressed spatial autocorrelation of the attack risk between nearby pastures.

MODELLING THE PREDATION RISK

The effect of each of the variables on the probability of lynx attack for each pasture was first considered separately by univariate analyses, using Fisher's exact tests. To illustrate relative risks (RR), the ratio of the attack rate (percentage of pastures with attacks vs. pastures at risk) for two categories of a variable was also calculated. We then built a multifactorial model of predation risk for pastures with a logistic regression. The model for the probability of attack (A) was:

$$\text{Logit}\,(A) = \beta_0 + \sum \beta_i X_i,$$

where β_0 = constant, and β_i = coefficient associated with level i of the risk factor X; β_i was fixed to zero for the reference category.

All the significant variables ($P < 0{\cdot}05$) in univariate analysis were taken into account. Variables with intermediate levels of significance ($P < 0{\cdot}20$) in univariate analysis were also considered to take a possible confounding effect into account better (Greenland 1989). We built all possible models by combining the factors and their interactions, although only second-order interactions were considered because higher-order terms are difficult to interpret. Each model was noted with its number of parameters and its deviance, which

Table 2. Distribution of lynx attacks among flocks in the study area from 1 January 1995 to 31 December 1999 and during the time lynx were radio-tracked

	1995–99				Radio-tracking periods			
	Number of flocks		Number of lynx attacks		Number of flocks		Number of lynx attacks	
Number of attacks per flock	*n*	%	*n*	%	*n*	%	*n*	%
0 attack	87	60·8	0	0·0	101	70·6	0	0·0
1–2 attacks	30	21·0	20	5·8	26	18·2	33	19·4
3–9 attacks	16	11·2	80	23·3	11	7·7	55	32·4
≥ 10 attacks	10	7·0	243	70·8	5	3·5	82	48·2
	143	100·0	343	100·0	143	100·0	170	100·0

Table 3. Lynx predation rate on sheep (number of attacks per 100 days). a_i = number of attacks a lynx was responsible for in its home range during the radio-tracking period of year i; na_i = number of attacks the lynx was not responsible for; c_i = number of attacks for which it was not known whether the lynx was responsible or (not)

					Lynx attacks on sheep			
Lynx	Year	Radio-tracking period (day/month)	Locations	Home range (ha)	a_i	na_i	c_i	Predation rate
M1	1995	07/03–30/11	269	33 770	3	11	4	1·4
	1996	01/03–30/11	290	35 450	4	7	3	1·9
	1997	01/03–22/10	238	37 430	3	11	3	1·6
M2	1995	06/04–08/10	177	15 700	0	2	1	0·0
M3	1995*	09/03–31/05	87	7 820	0	1	0	0·0
	1995†	10/06–30/11	156	12 520	1	9	1	0·6
	1996	01/03–30/11	161	28 420	5	8	19	4·5
	1997	01/03–30/11	217	12 680	19	6	13	10·5
F4	1995	30/03–30/11	223	10 620	0	6	1	0·0
	1996	01/03–30/11	194	26 280	0	5	0	0·0
F5	1995	30/08–30/11	103	9 780	5	2	1	6·2
	1996	01/03–15/10	160	13 000	1	1	3	1·1
F6	1995	01/03–05/11‡	144[c]	11 525‡	0	0	3	0·0
F7	1996	09/04–30/11	213	16 510	2	3	1	1·0
	1997	01/03–30/11	180	15 830	7	4	3	3·3
	1998	01/03–19/08	60	14 580	7	0	6	7·6
	1999	01/03–08/07	100	10 840	8	0	8	12·4
F8	1996	23/10–30/11	24	16 280	0	0	1	0·0
	1997	01/03–30/11	74	15 360	0	0	0	0·0
	1998	01/03–07/08	16	7 600	0	0	1	0·0
M9	1996	29/04–21/09	29	17 550	0	0	1	0·0

*Before dispersal.
†After dispersal.
‡Winter home range (1 December 1994 to 21 February 1995) and site where the lynx was killed (5 November 1995).

was a measure of the goodness-of-fit of the model. We used a backward stepwise procedure for model simplification, by first dropping non-significant second-order interactions and then main effects from the full model. For each model, we calculated Akaike's information criterion (AIC; Burhnam & Anderson 1992) and selected the model with the lowest AIC values. When differences in AIC between two models were < 1, we selected the most parsimonious model. Logistic regressions were performed with program GLIM (Francis, Green & Payne 1993).

Results

LYNX PREDATION ON SHEEP

Lynx attacks were not evenly distributed among flocks in the study area. About 61% of the 143 flocks included in lynx home ranges during at least 1 year were never attacked by lynx between January 1995 and December 1999, and only 7% suffered ≥ 10 attacks (maximum 29). The 10 most frequently attacked flocks suffered 71% of the total number of attacks. The same irregular distribution was recorded for flocks attacked during the time lynx were radio-tracked, with 48% of the attacks on five flocks (3·5%), suggesting that our study period gave a reasonable picture of the uneven lynx predation on sheep (Table 2).

A total of 170 lynx attacks was recorded in lynx home ranges for a total of 246 sheep killed or wounded. The average number of sheep killed or wounded per attack was 1·5 (maximum = 6). A total of 109 attacks was assigned to a radio-tracked lynx for a total of 164 sheep killed, with an average of 1·6 sheep killed or wounded per attack (Table 3). Lynx predation rate on sheep within lynx home ranges varied from 0 to 12·4

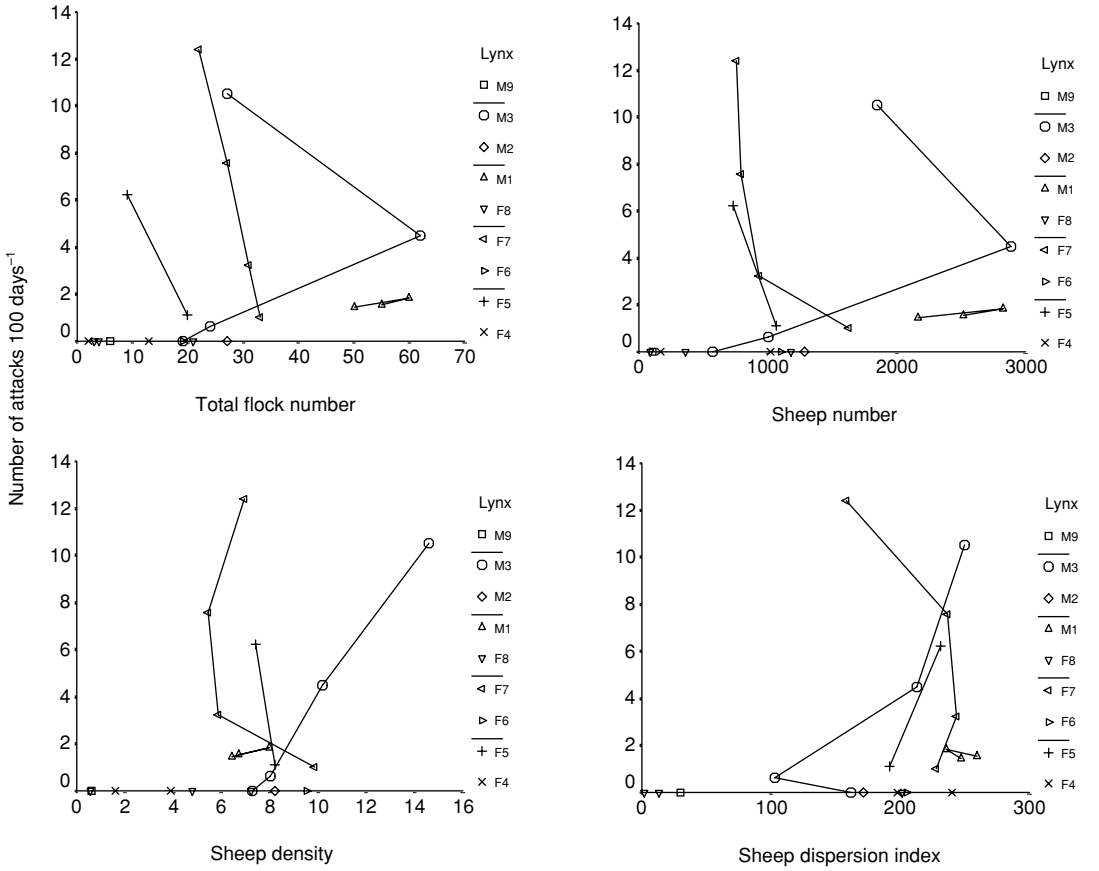

Fig. 1. Relationship between lynx predation rate on sheep and several indices of sheep availability in the corresponding lynx home range. Lynx identifiers refer to Table 3. For the same individual, predation rates of consecutive years are linked by a line.

attacks 100 days^{-1} (Table 3**)**. Lynx that did not attack sheep (predation rate = 0) had fewer sheep available in their home ranges (Man-Whitney *U*-test; $n = 9$; total sheep: $P = 0{\cdot}03$; sheep density: $P = 0{\cdot}05$; number of flocks: $P < 0{\cdot}01$; sheep dispersion index: $P = 0{\cdot}02$), suggesting a threshold in availability of sheep for developing predation on this prey. However, for lynx having attacked sheep at least once (predation rate > 0), predation rates were not related to the total number of sheep raised in their home ranges (Kendall's coefficient rank correlation; $n = 12$; $P = 0{\cdot}29$) nor to the number of flocks ($P = 0{\cdot}37$), sheep density ($P = 0{\cdot}29$) or sheep dispersion index ($P = 0{\cdot}25$). The same was true if only flocks that had been attacked by lynx at least once between 1995 and 1999 were considered ($P > 0{\cdot}10$ in all cases). This absence of significant effect was clearly shown by the annual variability in predation rates for lynx radio-tracked during several years in the same area (Fig. 1).

Three detailed cases emphasized the inter- and intra-individual variability of lynx predation rates.

Case study 1

Male M3 was caught in early March 1995, when 10 months old. Only two attacks had been recorded during the preceding 1994 spring–summer–autumn period in its predispersal home range. This suggested that this male had not been raised by a habitual sheep-killing female. From March to June, M3 did not attack sheep in its predispersal home range. After dispersal in June 1995 this young male settled in another area, about 20 km to the south-east. In 1996, M3's predation rate on sheep increased to 4·7 attacks 100 days^{-1}. In 1997, M3 occupied a smaller home range, which had a 76% overlap with the 1996 home range (Fig. 2**)**. Its predation rate more than doubled to 10·2 attacks 100 days^{-1}. This dramatic increase was associated with an increase in sheep consumption (Table 4). In late summer and autumn, this male regularly shifted from one flock to another, visiting four neighbouring flocks. It was legally removed in early March 1998, when it returned to a sheep kill in a building adjacent to a farm after having jumped over a 1·8-m high wall to enter the building. Lynx attacks in that area stopped and remained low in 1999 despite the presence of other signs of lynx presence. The adult female F6 had been radio-tracked in the winter of 1994–95 in the same area (Fig. 2). Its radio-collar failed in late winter 1995 but this female stayed in this area, where it raised young before being illegally killed in autumn 1995. In its home range, which encompassed 50% of the flocks attacked by M3 in 1995–97, only three attacks were recorded in the course of the year 1995. It is unlikely that F6 was responsible of any of these kills because these attacks occurred in late June and early July when F6 had just bred.

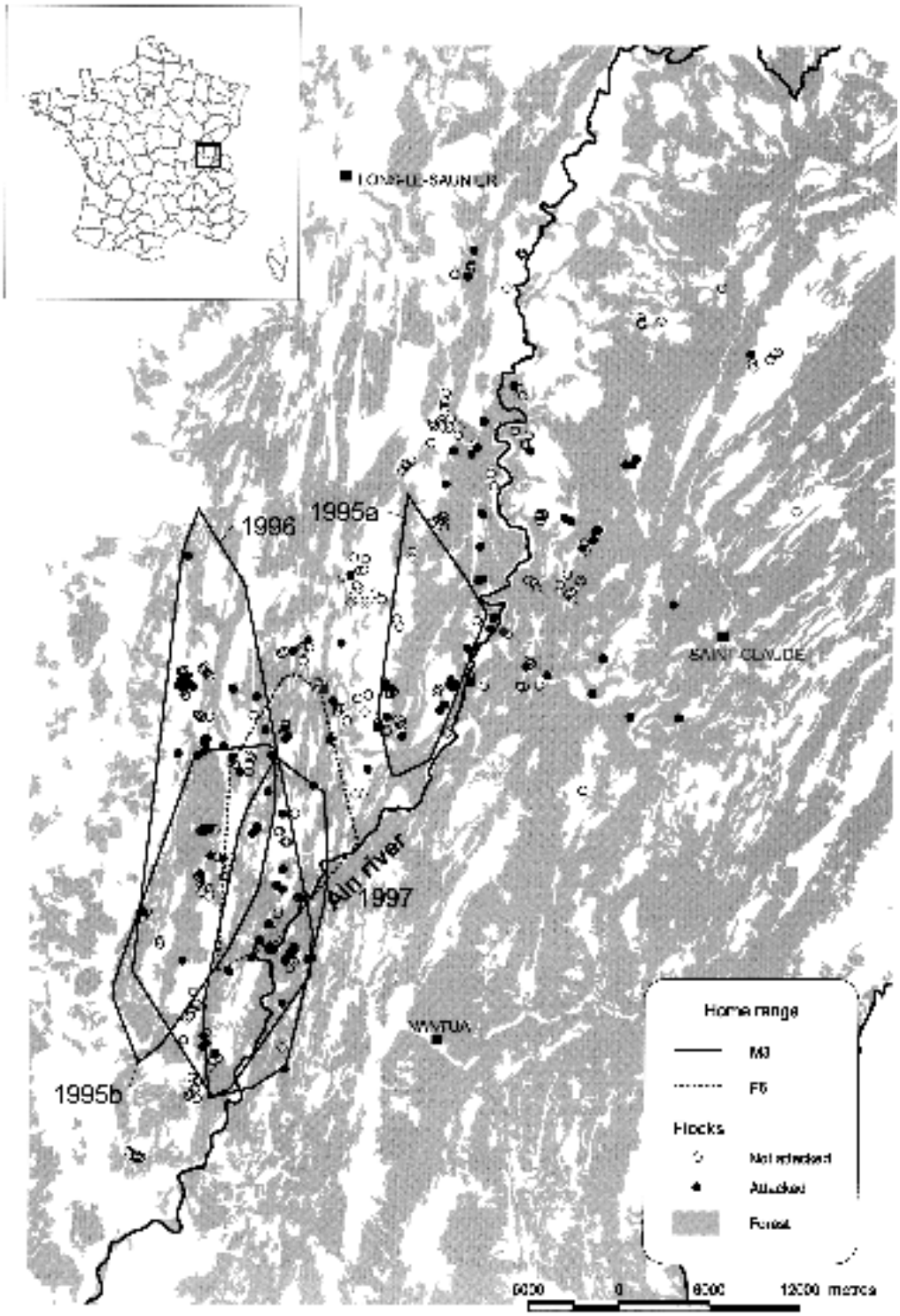

Fig. 2. Home ranges of male M3 (1995–97) and female F6 (1995), and the distribution of flocks that were attacked by lynx in their home ranges.

Case study 2

Female F7 was caught in March 1996 and radio-tracked over 4 years. She occupied a very stable home range, with a 73–100% inter-annual overlap (Fig. 3). Female F7 raised young in 1997, 1998 and 1999. The mean annual predation rate on sheep within her home range increased progressively from 1 to 12·4 attacks 100 days^{-1} between 1996 and 1999 (Table 3). In 1999, most of the attacks were on two neighbouring small flocks of 30–50 ewes. Sheep consumption was always high for this female (Table 4); she was regularly observed or photographed feeding her young on sheep. The home range of adult male M2 had a 74–79% overlap with that of female F7. This male was monitored over 6 months from March to October 1995 before

Table 4. Sheep consumption by males M1 and M3 and females F5 and F7

		M1		M3		F5		F7	
		1995–97	1995–96	1997	Total	1995–96	1996–97	1998–99	Total
Number of attacks		10	6	19	25	6	9	15	24
Sheep killed		17	8	25	33	5	14	22	36
Sheep wounded		2	4	2	6	2	2	0	2
Sheep consumed		7	1	15	16	4	8	14	22
Attacks with ≥ 1 sheep killed	*n*	10	5	18	23	5	8	15	23
	%	100	83·3	94·7	92·0	83·3	88·9	100	95·8
Attacks with ≥ 1 sheep consumed	*n*	6	1	13	14	4	8	13	21
	%	60	20	72·2	60·9	80	100	86·7	91·3

Table 5. Proportion of pastures attacked by lynx in each category of the variables. *P*-value indicates difference in the proportion of pastures attacked by lynx between categories of a variable (Fisher's exact test). Pastures considered 'isolated' from forest (i.e. without any cover within 250 m around the fence, $n = 98$) were not included in this table

Variables	Categories	Number of pastures	% pastures attacked by lynx	*P*-value
Pasture size	≤ 2 ha	102	28·4	0·003
	> 2 ha	126	48·4	
Pasture–forest connection	Pasture adjacent to forest	99	52·5	0·001
	Pasture connected to forest	129	29·5	
Forested or rocky slope within ≤ 250 m	Presence	88	42·7	0·06
	Absence	140	36·8	
Human dwelling within ≤ 1000 m	Absence or isolated house	123	50·4	< 0·001
	Village	105	26·7	
Shrub cover inside pasture	≤ 5% of the total area	127	30·7	0·003
	> 5% of the total area	101	50·5	
Permanent free access shelter for sheep	Absence	168	42·9	0·09
	Presence	60	30	
Roe deer abundance	Low	92	31·5	0·05
	High	136	44·9	
Mean length of time sheep were pasturing	≤ 1 month	107	37·4	0·59
	> 1 month	121	41·3	
Mean number of pasturing sheep	≤ 50	133	36·1	0·22
	> 50	95	44·2	
Number of ewes raised within ≤ 2 km	≤ 150	124	35·0	0·14
	> 150	104	44·8	
Other pastures with attacks within ≤ 2 km	Presence	125	34·4	0·10
	Absence	103	45·6	

dying from nephritis after a dramatic loss of weight (11·6 kg vs. 19 kg in March). This male never attacked sheep despite the presence of 27 flocks in its home range, 15 of which were attacked by other lynx between 1995 and 1999. The adult male M1 was caught in March 1995 and monitored over 3 years. Depending on the year, its home range overlapped 84–100% with the home ranges of female F7 and 87% with the home range of male M2. Despite the presence of numerous sheep pastures and flocks in its large home range (Fig. 3), its predation rate remained moderate, at 1·4–2·0 attacks 100 days^{-1} with a low frequency of sheep consumption and no clustering of attacks on a few flocks (Table 4).

Case study 3

Adult female F5 was caught in late August 1995 and raised no young. In the few weeks before sheep were housed, this female was responsible for five attacks in an isolated pasture where 150 sheep were raised, corresponding to an overall predation rate of 6·2 attacks 100 days^{-1}. The following year, female F5 raised two young and rarely attacked sheep. Adult female F4 had two young in 1995 and occupied a home range adjacent to F5's home range (Fig. 4), with very few sheep ($n = 167$). In 1996, this female had no young, expanded its range in the sheep range (1024 sheep, 13 flocks), including the flock regularly attacked by female F5 in 1995, but was never found to be responsible for attacks on sheep.

MODELLING PREDATION RISK IN PASTURES

Of the 326 sheep pastures belonging to 116 farms, 95 were attacked by lynx (29·1%). The number of attacks per pasture varied from 1 to 22 over the 1995–99 period. Of 98 pastures that were isolated from the

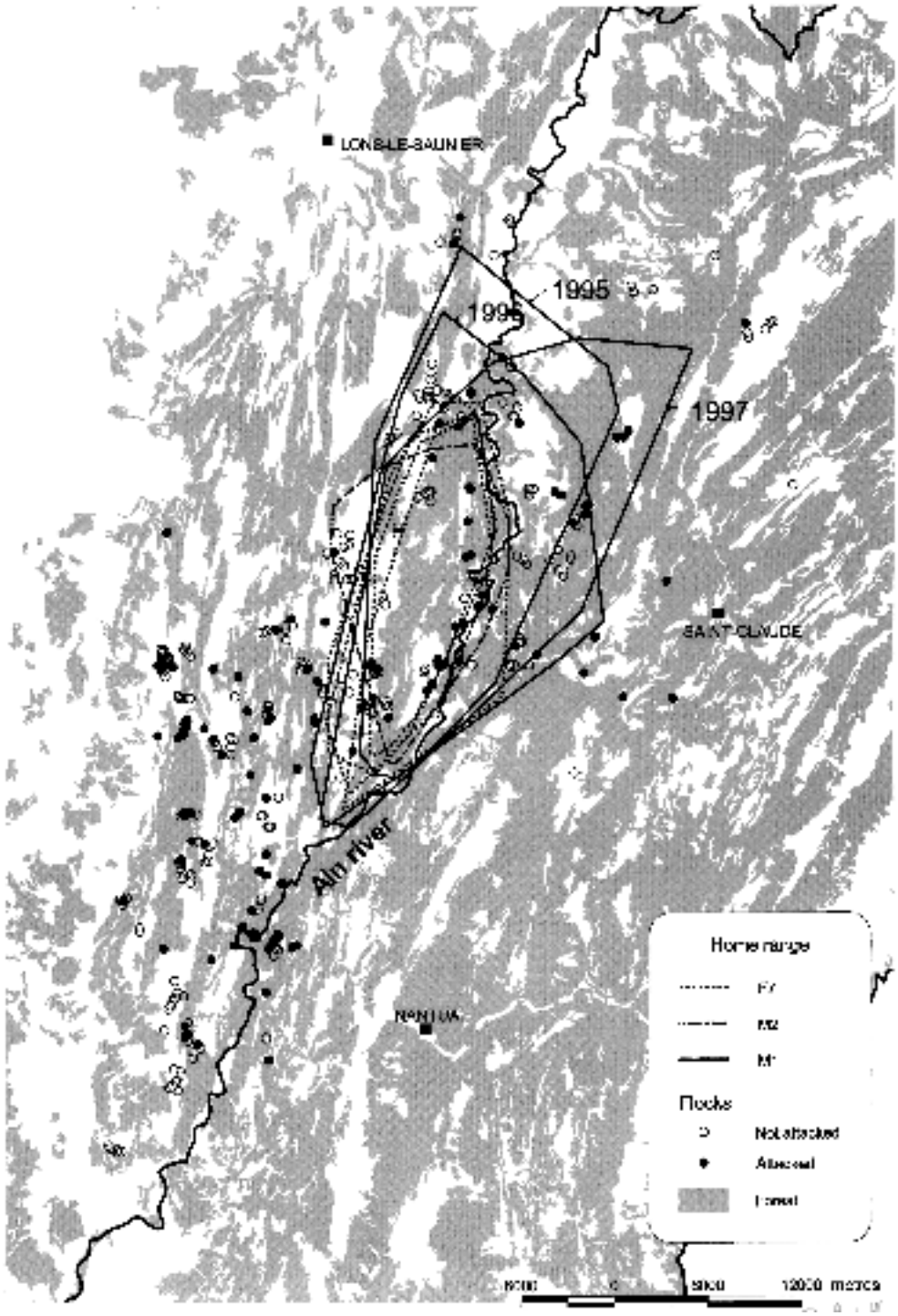

Fig. 3. Home ranges of males M1 (1995–97) and M2 (1995) and female F7 (1996–99), and the distribution of flocks that were attacked by lynx in their home ranges. Female F7 occupied a very stable home range during the whole period and years are not indicated in the figure.

major forested areas, i.e. without any shrub < 250 m from their fence (260–4250 m from forests), only five (5·1%) were attacked by lynx. Of the 228 pastures adjacent or connected to forests, 90 (39·5%) were attacked by lynx ($\chi^2 = 39{\cdot}2$, d.f. = 1, $P < 0{\cdot}001$). To study potential risk factors associated with pastures adjacent to or connected to forested areas, pastures isolated from forests were excluded from further analysis.

Univariate analyses showed a significant effect (Fisher's exact test; $P < 0{\cdot}05$) of six environmental factors (Table 5). Predation risk was higher in large pastures (relative risk, RR, compared with small pastures = 1·70), adjacent to forest (RR compared with connected to forest = 1·78), with no human presence or only one isolated house < 1000 m from the fence (RR compared with presence of a village = 1·89), with > 5% shrub cover (RR compared with ≤ 5% shrub cover = 1·64), situated near a steep and rocky forested slope

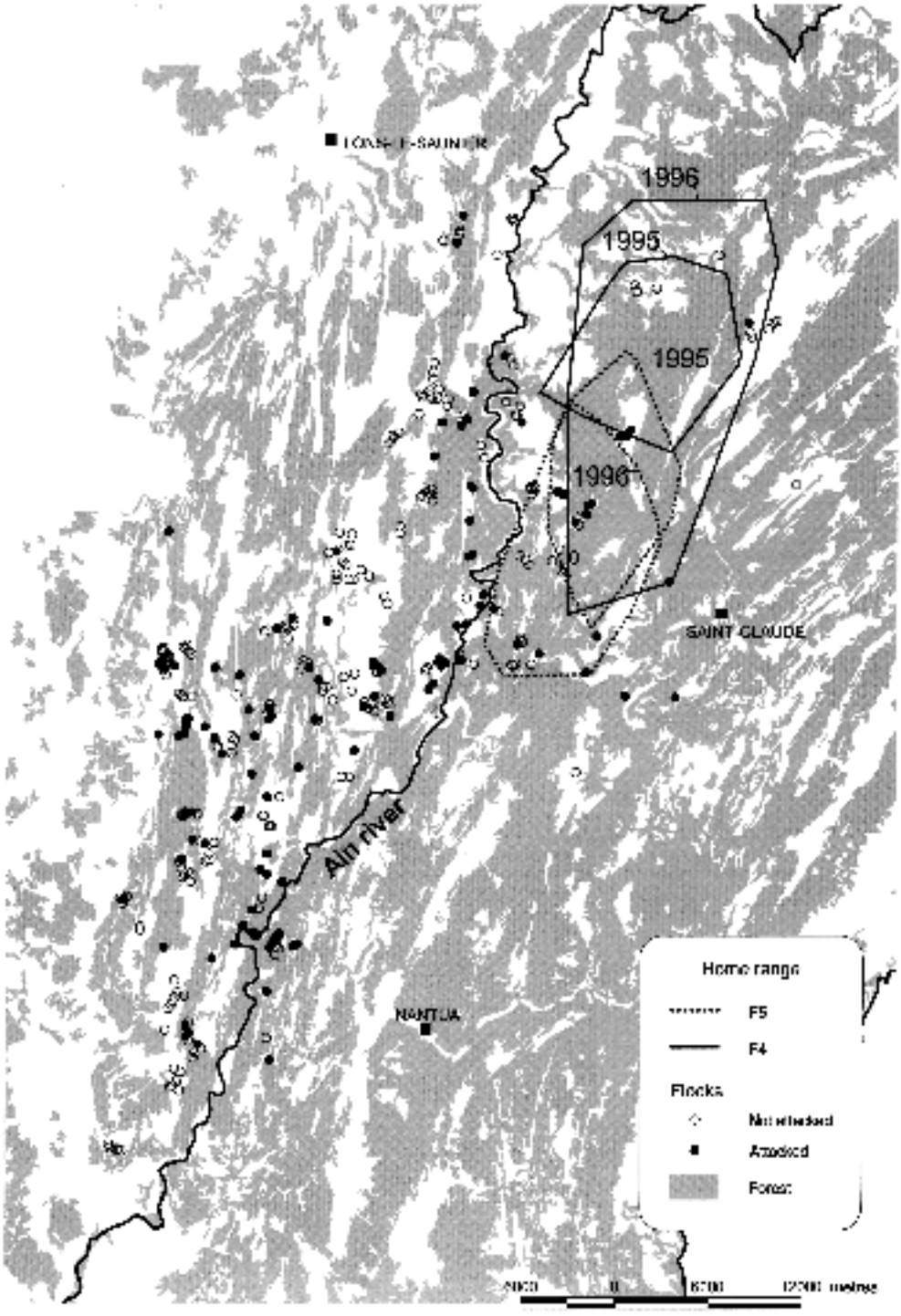

Fig. 4. Home ranges of females F4 (1995–96) and F5 (1995–96), and the distribution of flocks that were attacked by lynx in their home ranges.

(RR compared with absence of slope = 1·43) and in roe deer-rich areas (RR compared with low abundance = 1·43). The two factors expressing sheep availability within a pasture were not related to predation risk ($P > 0{\cdot}20$).

The six factors having a significant effect on predation risk were considered in the logistic regression, except the factor 'presence of a forested or rocky slope' which was highly correlated with the factor 'pasture–forest connection' ($P < 0{\cdot}001$). Two other factors that had intermediate levels of significance in the univariate analysis were considered in modelling: presence of pastures with attacks ≤ 2 km from the fence ($P = 0{\cdot}10$) and local abundance of sheep ($P = 0{\cdot}14$). The presence of permanent shelter for sheep ($P = 0{\cdot}09$; Table 5) was not considered because many combinations with other categories were not represented in our sample.

None of the two-way interactions between the seven factors considered remained in the model. The final minimum adequate model included additive effects of

the pasture–forest connection ('connected to forest' compared with 'adjacent to forest': $\beta = -0{\cdot}786$, SE = 0·298, $P = 0{\cdot}008$), human presence (presence of a village/absence or isolated house: $\beta = -1{\cdot}103$, SE = 0·315, $P < 0{\cdot}001$), roe deer abundance (high abundance/low abundance: $\beta = 0{\cdot}763$, SE = 0·312, $P = 0{\cdot}014$) and presence of pastures with attacks within ≤2 km from the fence (presence/absence: $\beta = 0{\cdot}658$, SE = 0·297, $P = 0{\cdot}027$). The constant was –0·295 (SE = 0·309).

Discussion

Assessing factors that may predispose livestock to large carnivore predation is difficult because of the interdependence between livestock husbandry, environmental factors and the behavioural ecology of predators. Linnell *et al*. (1996, 1999) made a distinction between grazing systems in which livestock is entirely free-ranging and unattended within natural carnivore habitat, and agricultural systems where livestock is kept in open fields, constantly herded or confined at night. In the former system, where sheep or cattle are distributed at random in natural carnivore habitats, most individual carnivores have similar opportunities to encounter and kill livestock, and 'problem individuals' are unlikely to appear (Linnell *et al*. 1999; 2000). In the second agricultural system, where sheep, goats or cattle are constantly herded, Linnell *et al*. (1999) hypothesized that predation on livestock requires the development of a specialized behaviour on the part of the predator. In that situation, true 'problem individuals' are expected to occur because individuals must learn how to access this protected food source.

The Jura offered a third and intermediate situation where sheep are fenced in, unevenly distributed but not herded or protected from carnivore predation. Husbandry practices are similar among producers, and most sheep wander freely at night in their pastures. In this situation, which is very common in Europe, we have shown that only a minority of lynx became habitual livestock killers. The two most obvious livestock killers were a male and an adult female, which progressively increased their predation rate on sheep, leading to habitual killings of sheep during, respectively, their third and fourth year of monitoring. These high predation rates were not primarily related to sheep abundance. Contrary to other individuals, these two lynx repeatedly attacked the same neighbouring flocks, which led to a clustering of the attacks in a small area. Once developed, reversing this behaviour seems to be difficult. In the flock regularly attacked by the female, temporary protection by an experienced adult guard dog was very effective, but predation shifted to unprotected neighbouring flocks and was resumed on the first flock after the dog's departure (Vandel *et al*. 2001). Similar shifting of predation was documented for Norwegian wolverines *Gulo gulo* L. (Landa *et al*. 1998). The male also resumed killing livestock in early spring, as soon as sheep were available after winter confinement.

No obvious causal factor could explain the development of a sheep-killing behaviour in these individuals and not in other ones. In large felids it has been suggested that the majority of livestock predation incidents are caused by males (Suminski 1982; Stander 1990; Linnell *et al*. 1999), either because of a higher encounter rate due to their larger home ranges and long-distance movements (Stander 1990), or because of intrinsic male behaviour (Linnell *et al*. 2000). In the Jura, no evidence supports the view of a male-biased sex ratio among lynx that regularly kill sheep (Stahl *et al*. 2001b), and in this study two adult males whose home ranges largely overlapped the sheep-killing female's home range had a low predation rate. The two habitual livestock killers frequently killed and fed on wild ungulates and were not old or injured, as suggested for snow leopard *Uncia uncia* Schreber or jaguar *Panthera onca* L. livestock killers (Rabinowitz 1986; Fox & Chundawat 1988; Hoogesteijn, Hoogesteijn & Mondolfi 1993). Another male in bad condition never attacked sheep in the same area. We did not know where the female was born, but the male had not been raised by a sheep-attacking female as very few attacks had been recorded in its predispersal home range. These case studies suggest that no simple set of rules is likely to give a very good predictor of habitual sheep-killing behaviour in the lynx. The causal paths involved in the ontogeny of sheep-killing behaviour are probably complex and perhaps variable. Because the two individuals progressively increased their predation rate on sheep, a learning process could be involved in their specialization. Anecdotal evidence suggested that killing fenced-in sheep is not so easy for a lynx because of the sudden and rapid movements of the whole flock when the lynx approaches (L. Coat, unpublished data). A progressive increase in preference or ability to kill sheep with continuing exposure to this food source was suggested for coyotes *Canis latrans* Say (Sacks *et al*. 1999) and could exist for lynx. Individualistic differences could also exist (Linnell *et al*. 1999). Differences in predation rates among individuals having similar access to livestock have been shown in coyote (Till & Knowlton 1983; Sacks *et al*. 1999) and bear *Ursus arctos* L. (Anderson *et al*. 1997). The potential for individuality is probably as high in lynx as in other long-lived carnivores. However, more case studies are needed to clarify the respective influence of a learning process, individuality and the environmental factors on the ontogeny of livestock-killing behaviour in the lynx.

Although frequent damage in nearby flocks was clearly related to the presence of a regular livestock killer, not all pastures were at similar risk. Some environmental factors were associated with lynx attacks. The risk was much lower for pastures isolated from forests and without any cover in their immediate vicinity. For pastures adjacent or connected to forest by cover, the proximity to major forested areas, the absence of human dwellings and local abundance of wild ungulates positively influenced the risk of attacks. The last

risk factor was the proximity of pastures where attacks take place. This may show the presence of a lynx that has focused in the area and is expanding its search in nearby food patches.

Numerous studies support our finding that the remoteness of the area, local abundance of prey, topographical features or the presence of scrub and woodland cover as opposed to open terrain are important risk factors (Shaw *et al*. 1988; Warren & Mysterud 1990; Sunde, Snorre & Kvam 1998; Mech *et al*. 2000). In human-dominated landscapes, habitat suitability for the bigger cats is primarily determined by the amount of cover and prey (Sunquist & Sunquist 1989; Palma, Beja & Rodrigues 1999), with habitat providing cover and food used more than expected (Van Dyke *et al*. 1986). Habitat features identified as risk factors in this study could all influence the amount of time lynx spend in an area, either resting or hunting wild ungulates, and this in turn could increase their encounter rates with sheep. The lack of independence between radio-tracking and identification of lynx attacks did not allow us to test this hypothesis, but it was qualitatively supported by the frequent observations of lynx resting during the day in dense cover and rocky slopes near pastures. Finally, in the Jura grazing system, frequent lynx damage in some localities could be explained by a predictable set of habitat features that place pastures at risk, and an unpredictable event, i.e. the presence of an individual which developed a habitual predation behaviour on sheep in these special environmental circumstances.

From a management perspective, the high spatial heterogeneity of lynx damage on sheep (Stahl *et al*. 2001a) and the high variability of predation rates among individuals in this study strongly argue against methods acting at the lynx-population level to minimize the losses, such as hunting or non-selective removal. In a Jura-type grazing system, the removal of non-habitual livestock killers would be totally ineffective. Because of lynx territorial behaviour (Breitenmoser *et al*. 1993; Schmidt, Jedrzejewski & Okarma 1997), non-selective removal could even have a detrimental effect if a lynx that did not kill sheep was removed. On the other hand, the site effect implies that selective removals will only temporarily reduce the problem of concentrated lynx damage (Stahl *et al*. 2001b), and the only proactive way to obtain a durable effect is to improve shepherding techniques. Because habitat features are probably the ultimate factors that predispose a location to a high level of predation by lynx, subsidizing farmers to graze their sheep in pastures distant from large forested areas could be effective in reducing the amount of losses and claims for lynx removal. Nevertheless, this is often not practical in mixed farm-forested areas and could have negative ecological consequences as, in many regions, sheep and goats are grazed in areas that are unsuitable for other purposes and contribute to the mosaic of open habitat. In a Jura-type grazing system, using guard dogs in the few local sites that are at risk and subsidizing the sheltering of sheep at night, when attacks tend to increase, would be the best measures to promote.

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