Conservation of the lynx Lynx lynx in the Swiss Jura Mountains

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ORIGINAL ARTICLES

Conservation of the lynx *Lynx lynx* in the Swiss Jura Mountains

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Lynx *Lynx lynx* returned to a semi-natural, human dominated landscape in the Jura Mountains in France and Switzerland after reintroductions in the early 1970s. Controversy has resulted from lynx attacking sheep and preying on game species such as roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra*. We review the history of the lynx, the transition of the landscape and fauna in the Jura Mountains, and recent findings from long-term field studies on the species. Possible threats to the survival of the population are assessed. The ecological conditions for the existence of the lynx in the Jura Mountains have improved since the species was eradicated in the 19th century. Both habitat and prey base are suitable for maintaining the population. Immediate threats include traffic accidents and illegal killings. Long-term threats include small population size and genetic impoverishment as a result of the post-reintroduction bottleneck. We recommend conservation and management that involve local people and cooperation at national and international scales. Fragmentation of the habitat and the management system should be avoided, and landscape linkages from the Jura Mountains to adjacent mountain ranges should be established to promote a lynx metapopulation.

Key words: anthropogenic threats, conservation, history, Jura Mountains, Lynx lynx

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The preservation of large carnivores in human-dominated landscapes will be one of the big challenges in nature conservation in the 21st century. On one hand, large carnivore populations need much space, usually considerably more than what protected areas offer, and must therefore be allowed to expand into landscapes used by humans, where, on the other hand, they are not always welcome. Suitable terrestrial carnivore habitat in the cultivated landscape is fragmented by widespread anthropogenic infrastructure. Predation on wild and domestic animals brings carnivores into direct conflict with human hunters and livestock breeders. Even where large carnivores enjoy legal protection, as in most European countries, traffic accidents and retaliation killings are often the two prominent causes of mortality (wolf *Canis lupus*: Boitani 2000; brown bear *Ursus arctos*: Swenson et al. 2000; Eurasian lynx *Lynx lynx*: Breitenmoser et al. 2000). Large carnivores act as umbrella or flagship species (Simberloff 1998), and their presence (or the effort needed to maintain their presence) is an indicator not only of the quality of the environment (habitat and prey base), but also of human tolerance. The conservation of a large carnivore in a cultural landscape is complex, involving not only ecological knowledge, but also the understanding of human dimensions and the implementation of appropriate legislation, management and monitoring.

The restoration and conservation of the Eurasian lynx in the Jura Mountains of Switzerland and France is a case study of returning a large predator to a modern cultivated landscape. The lynx was reintroduced into the Jura Mountains in the first half of the 1970s before expanding over the southwestern part of the mountain range (Breitenmoser & Baettig 1992, Breitenmoser et al. 1998, Capt 2007). The releases were done in secret, and there was no follow-up programme. The history of the scientific survey of the Jura lynx population started in the late 1980s. Retrospective collection of data in France and Switzerland began in 1986 (Herrenschmidt & Leger 1987a, Breitenmoser & Baettig 1992). Since then, monitoring systems have been established in both countries (Vandel & Stahl 1998b, Vandel 2001, Capt et al. 1998), but comprehensive status reports were published only for the French part (Herrenschmidt & Leger 1987b, Vandel & Stahl 1998b, Stahl & Vandel 1999). Radio-telemetry studies were conducted in the Swiss Jura Mountains during 1988-1998, and in the French part during 1995-1998, resulting in a number of theses and publications on lynx land tenure, demography, social organisation (Kaczensky 1991, Dötterer 1992, Breitenmoser et al. 1993), behaviour and habitat use (Bernhart 1990, Weigl 1993, Wölfl 1993, Wölfl & Wölfl 1996, Molinari & Jobin 2001, Zimmermann & Breitenmoser 2001), and predation on wildlife (Liberek 1992, Jobin et al. 2000, Molinari-Jobin et al. 2002) and livestock (Capt et al. 1993, Vandel & Stahl 1998a, Stahl et al. 2001a,b).

A comprehensive review of ecology, population status and conservation needs of lynx in the Jura Mountains is lacking. In this paper, we compile results from monitoring and field studies including development and status of the population (Capt 2007), spatial behaviour (Breitenmoser-Würsten et al. 2007b), demography (Breitenmoser-Würsten et al. 2007a), predation aspects (Molinari-Jobin et al. 2007), and the suitability of the Jura Mountains as lynx habitat (Zimmermann & Breitenmoser 2007). These papers form the scientific framework for the 'technocratic' conservation of the lynx in the Jura Mountains. However, a 'holistic' conservation strategy considering the socio-cultural, economic and political context implies more than ecological knowledge. In this first paper of the series, we provide some background information on the Jura Mountains and its ecological and cultural history and review the present knowledge under the aspect of potential threats and recommendations for a comprehensive conservation strategy. We regard the present status, not only of the lynx population, but also of its living space, the result of an evolving situation. Consequently, the assessment of the past and the present allows us to anticipate future challenges and opportunities. Hence, we ask the following questions:

1) What are the contemporary ecological and anthropogenic conditions for the existence of the lynx in the Jura Mountains?
2) How did these conditions change since the eradication of the lynx in the 18th and 19th centuries?
3) What are the potential or identified threats to the population, the limits of human tolerance, and what are the apparent needs for its future conservation?

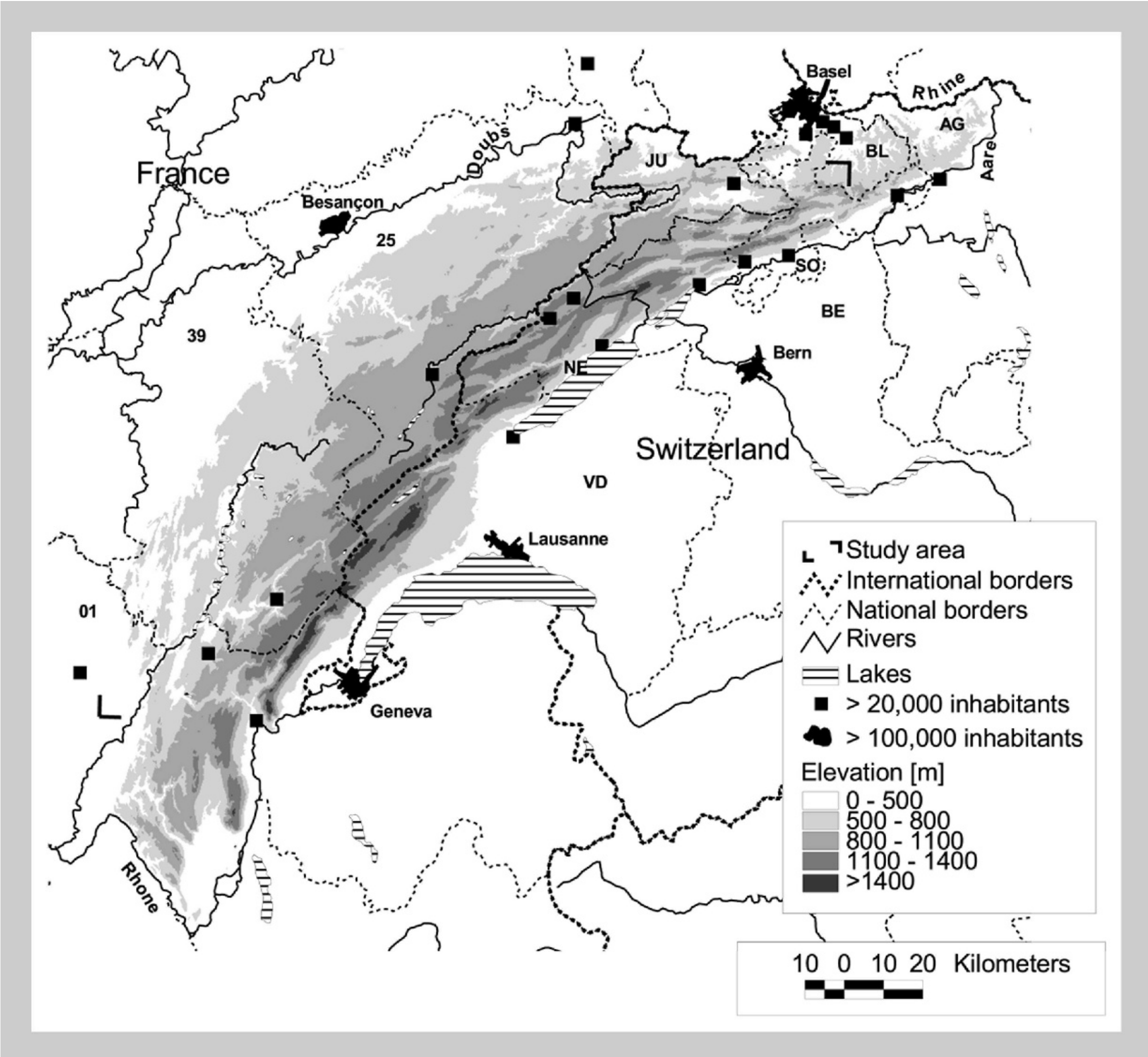

Figure 1. Jura Mountains in France and Switzerland. The shape of the range is indicated by the 500 m elevation isoclines. The centre of the field work was the Jura Mountains of the canton of Vaud (VD) and the neighbouring areas of the canton of Neuchâtel (NE) and the departments of Ain (01) and Jura (39). The study area in which radio-telemetry was performed is indicated by the two corners (position of the southwestern corner is 46°06'N/5°15'E and the position of the northeastern corner is 47°25'N/7°44'E). Labels and abbreviations of French departments and Swiss cantons are given in Table 1.

Material and methods

Study area

The Jura Mountains stretch from the junction of the rivers Aare and Rhine in the northeast to the junction of the Guiers with the Rhone River in the southwest (Fig. 1). It is situated between the plateau of the Haute-Saône in France in the north and the Swiss Plateau in the south. The high ridges of this secondary mountain chain are 1,200-1,500 m a.s.l., the highest peak is the Crêt de la Neige at 1,718 m a.s.l. The rock is Mesozoic calcium from the ancient Tethys Sea. The formation of the parallel mountain chains of the Jura took place during the late phase of the formation of the Alps, in the late Tertiary period (Miocene to Pliocene, 13-5 million years BP). The result of the folding process was a mountainous karst landscape in the south, table mountains in the northeast, and high plateaus in the northwest (see Blant 2001 for details). Although the mountain chain, which is exposed to western winds from the Atlantic ocean, experience 1,300-2,000 mm precipitation annually (Blant 2001), water is scarce because the karst region supports surface waters only along valley bottoms.

The Jura Mountains (Blant 2001) are more than what a traveller sees along the border between France and Switzerland. For lynx, we defined the outlines of the Jura Mountains according to geographic and habitat features, such as lakes and rivers as natural boundaries, or the sharp transition from the wooded slopes to the open agricultural plateau at the foothills in Switzerland. Where an absence of natural barriers occurs (i.e. in the northwestern periphery) we use the 500 m contour line (see Fig. 1) separating the mountain forests from the open agricultural landscape of the plains. Close to the foothills of the Jura Mountains, we find the large cities of Lyon, Geneva, Lausanne, Neuchâtel, Basel and Besançon. This area includes, completely or in part, 10 administrative units, three French departments and seven Swiss cantons (abbreviations are given in Table 1). The focus area for the field work summarised in this paper were the Jura Mountains in the canton of Vaud (VD), but dispersing lynx roamed over much of the mountains (see Fig. 1).

Data sources and analyses

Estimation of (relative) areas and population density for the administrative units (see Table 1) were determined with the Geographic Information System (GIS) Arc-View (ESRI, Redlands CA, USA), using CORINE land use data (European Topic Centre on Land Cover, Environment Satellite Data Centre, Kiruna, Sweden) for the entire Jura Mountains and GEOSTAT data (Federal Office of Statistics, data release 1992) for the Swiss part. As a consequence of differences in the resolution (250 × 250 m grid for the CORINE, and 100 × 100 m for the GEOSTAT data), the geographic projection, and the classification of original categories, the results varied according to the data source. As a rule, we computed areas from vector rather than grid data and used the highest available resolution.

Ecological and anthropogenic conditions for the existence of the lynx in the Jura Mountains

Habitat elements

The Jura Mountains stretch over 300 km from the southwest to the northeast, 30-60 km from the southeast to the northwest, and cover almost 14,000 km^2 (see Fig. 1 and Table 1). Forest is the most prominent landscape feature of the Jura Mountains and a natural timberline is lacking. Half of the entire surface is covered by forest, and none of the 10 administrative units listed in Table 1 has < 40% woodland cover. Forest types range from mixed deciduous forest with relict Mediterranean elements on the foothills of the south slopes to the

Table 1. Characteristics of the cultivated landscape of the French departments and Swiss cantons comprising the Jura Mountains. Data sources are CORINE land use data (G_{250}) for France and the entire Jura Mountains, and GEOSTAT data (G_{100}) for Switzerland. Population density data are not available from the CORINE data set, but the population density (inhabitants/km^2) computed from the G_{100} data set is highly correlated ($r^2 = 0.949$, $P < 0.001$) with the relative area of settlements from the G_{250} for the Swiss cantons, and is a good indicator for the human presence.

			Area inside the Jura		Population	Relative (%) area of			
						Settlements			
Unit	Sign	Language	Km^2	% of unit	density	G_{250}[a]	G_{100}	Forest	Pastures
French departments			8923	65.2	-	2.4	-	50.6	27.8
Ain	01	F	2483	43.0	-	4.0	-	59.8	13.0
Jura	39	F	3068	60.4	-	1.7	-	54.6	20.7
Doubs	25	F	3372	64.5	-	1.9	-	41.3	37.5
Swiss cantons			4768	34.8	188	4.1	5.9	45.4	12.6
Vaud	VD	F	1054	33.0	60	0.9	3.2	49.4	14.0
Neuchâtel	NE	F	690	100.0[b]	213	3.4	5.6	44.0	16.5
Jura	JU	F	765	92.7	80	1.5	3.9	44.2	15.9
Berne	BE	F/G	679	11.3	199	3.5	5.6	48.4	17.6
Solothurn	SO	G	615	78.6	237	5.6	7.7	47.5	9.9
Basel-Landschaft	BL	G	518	100.0	491	13.3	12.2	42.0	5.8
Aargau	AG	G	447	23.4	198	5.7	7.6	41.0	3.1
Jura Mountains			13691		-	3.0	-	49.3	21.8

[a] Due to the large grid size, the G_{250} overestimates high and underestimates low values, but the relative ranking of the units is correct.
[b] Only lake of Neuchâtel outside the Jura Mountains.

boreal coniferous forest on the ridges and in the cold depressions on the mountain plateaus. Characteristic tree species are oaks *Quercus* sp. at the climatically favourable bases of the hills, beech *Fagus sylvatica* and other deciduous trees on the slopes, and fir *Abies alba* on the ridges and the high plateaus. Spruce *Picea abies* was historically restricted to a few extreme sites, but is widespread and locally dominant today. Permanent pastures used for grazing cattle in summer cover 22% of the Jura Mountains (see Table 1). A harsh climate and infertile soils limit high elevation land use to forestry and pastoralism (Wachter 1995). All other arable land (e.g. crops, meadows, vineyards and orchards) make up from 10% (NE) to 25% (AG) of the administrative units, and settlements cover 3% (range: 1.7-12.2%) of the mountain range (see Table 1).

Wild prey

The main prey of the lynx in the Jura Mountains is the roe deer *Capreolus capreolus*. Roe deer made up 69% of all kills found, followed by the chamois *Rupicapra rupicapra* (22%), red fox *Vulpes vulpes* and brown hare *Lepus europaeus* (Jobin et al. 2000, Molinari-Jobin et al. 2007). The roe deer is abundant throughout the Jura Mountains. Chamois frequent the highest chain of the mountain range (mainly the Swiss part) and exhibits a clustered distribution (e.g. along the rocky slopes of ravines). Reliable and comparable estimates of the population densities are lacking for both species. Molinari-Jobin et al. (2002) have estimated a density of 6-9 roe deer/km^2 and of 1-2 chamois/km^2 for the study area in the Jura VD. This is probably a medium to low density compared to other roe deer habitat of the mountain range, but an above-average density of chamois for the entire Jura Mountains. Although potential prey species are diverse (see review in Molinari-Jobin et al. 2007), other species are only occasionally killed and are not a significant part of the lynx diet. The abundance of the main prey does not appear to be limiting in the Jura Mountains.

Depredation

Domestic prey in the Jura Mountains were usually sheep *Ovis aries* (Vandel & Stahl 1998a, Angst et al. 2000, Stahl et al. 2001a, Molinari-Jobin et al. 2007). Sheep are mainly available in the lower parts of the Jura Mountains along the northern rim, where they are kept in fenced parks. Most of the attacks occurred in the French department of Ain (01 in Fig. 1), fewer in the department of Jura (39), and considerably fewer in the Swiss part, primarily the canton of Jura (JU). In France, a total of 1,132 attacks (with an average of 1.6 sheep killed or wounded in an attack) were recorded during 1984-1998, with a peak of 188 attacks in 1989 (Stahl et al. 2001a). On the Swiss side, 153 sheep were identified as lynx kills during 1981-2001, with a peak of 43 in 2001 (KORA, unpubl. data). The higher parts of the Jura Mountains were not affected by lynx attacks on livestock. Sheep flocks are rare, and the pastures are predominantly used by cattle during summer. Although livestock is of no importance for the sustenance of the lynx population, the killing of sheep by lynx affects human tolerance (Molinari-Jobin et al. 2007), and has repeatedly led to legal removal of problem animals (Stahl et al. 2001b, Angst et al. 2002) and to illegal retaliation killings (Ceza et al. 2001).

Human population, political and cultural units

The percentage of built-up area is an indicator of human population density, which is considerably high. In Switzerland, it ranges from 60 inhabitants/km^2 (Jura VD) up to 491 inhabitants/km^2 (BL). Roughly extrapolated over the French part from the relative area of settlements (G_{250} in Table 1), the human density over the entire Jura Mountains is 130-140 inhabitants/km^2. It is an important characteristic that is relevant to the conservation of the lynx because much of the natural landscape adjoins areas with high human population densities. Current pattern of human settlement in an otherwise remote and rural area reflects the early importance of local industry, first the small-scale production of lime, iron and glass, fuelled by charcoal, and later the watch and ancillary industry (Blant 2001, Bergier 1990).

The Jura Mountains are easily identified on an aerial photo, but have never been a cultural or political unit. The international border separates the three French departments from the seven Swiss cantons (see Fig. 1). As a consequence of the centralistic French system, the three French administrative units have a similar political structure, but the Ain (01) department belongs to the region Rhône-Alpes, whereas the departments Jura (39) and Doubs (25) are part of the region Franche-Compté. Within both regions (and of course within France as a whole), the Jura Mountains are an economic fringe area. This is also true for the Swiss cantons of Vaud, Bern and Aargau (VD, BE and AG in Fig. 1), where the Jura region is only a small part of the canton. The other four cantons lie entirely (NE, JU and BL) or mostly (SO) within the Jura Mountains. The lack of unity has not only political, but also cultural foundations: almost 90% of the Jura Mountains belong to the French-speaking area, but the most populated parts (the cantons of SO, BL and AG) belong to the German-speaking area (see Table 1).

Hunting system and protected areas

The hunting system in the French Jura Mountains is community-based; local residents hunt within the limits of their municipality, supervised by regional wildlife officers of the Office National de la Chasse et de la Faune Sauvage (ONCFS). The French-speaking Swiss cantons of VD, NE, JU and BE use a licence hunting system (a hunter gets a limited quota of game for the entire area of the canton within a restricted period) controlled by state game wardens. The Germanic cantons of SO, BL and AG have a lease-based system with private hunting parties managing wildlife in an enclosed area.

Blant (2001) presented an extensive overview on protected sites in the Jura Mountains. There are 41 nature reserves with limited access, but they are all very small. Two regional parks exist, and two more have been designed. They are important for the maintenance of the regional biodiversity and provide good (protected) habitat and healthy prey populations for the lynx, but are open for regulated pastoralism, limited timber exploitation, hunting and recreation. Considering the huge space required by a viable lynx population, they are rather insignificant at the population level.

History of the landscape and the large mammal fauna of the Jura Mountains

The modern vegetation of the Jura Mountains developed at the end of the last ice age some 12,000 years ago. Under the climatic influence of moisture from the Atlantic Ocean, forests became the dominant type of vegetation (the name 'Jura' is derived from the Celtic term for forest; Blant 2001.) This process was never free from human influence. Humans have exploited the Jura Mountains first as hunter-gatherers, then as nomadic herders and finally as sedentary and semi-nomadic farmers. The foothill oak forests have been used to produce charcoal for smelting, and water-powered industries have existed on the rivers in the narrow gorges since the Middle Ages.

Early human activities promoted species diversity through the creation of new cultural habitats with plants and animals from open (not forested) ecosystems; the maximum diversity in Europe was probably reached around 1800 (Blant 2001). Regardless, human exploitation of the ecosystem started much earlier. The general pattern was that overexploitation of forests and silvopastoral livestock husbandry, along with unrestricted hunting, destroyed the habitat and the prey base of large carnivores. The predators, still present after the destruction of wild ungulate populations, were then forced to prey on livestock. This, in turn, boosted their persecution and extinction. There is no quantitative data available for the Jura Mountains, but local descriptions suggest that this pattern of nature destruction was the same elsewhere, although it happened some 100 years earlier than in the Alps (Breitenmoser 1998).

Destruction of forest

N.E. Tscharner, sheriff of the Lower Aargau (the Jura part of today's canton of Aargau) reported in the year 1768 that the forests of his district could no longer satisfy local demands for timber and firewood (Wullschleger 1974). Tscharner identified several reasons for the destruction of the woods: lack of silvicultural knowledge, short rotations of logging, larceny as a result of general poverty, and the neglect to protect tree regeneration from cattle (silvopastoralism was usual). Other reasons for heavy 18th and 19th century logging were the increasing need for firewood and charcoal (Rieben 1957), the floating of logs from the Jura Mountains to the shipyards at the mouth of the Rhone river, and the need of the growing cities for firewood (Bergier 1990). The Russian writer Dostojewski wrote in 1868 that there was still enough forest in the mountains, but because the Swiss "live like the savages", there "will be no forest left within 25 years" (Hauser 1974). Landolt (1863) estimated the woodland of the cantons of Solothurn, Basel-Landschaft and Neuchâtel to be 30, 35 and 25% of the total area, which is considerably less than today (see Table 1). Landolt (1863) stressed the disastrous status of the forest in the Alps, observing that "the Jura makes no exception, as the densely settled high valleys would be in a critical situation if nature would not

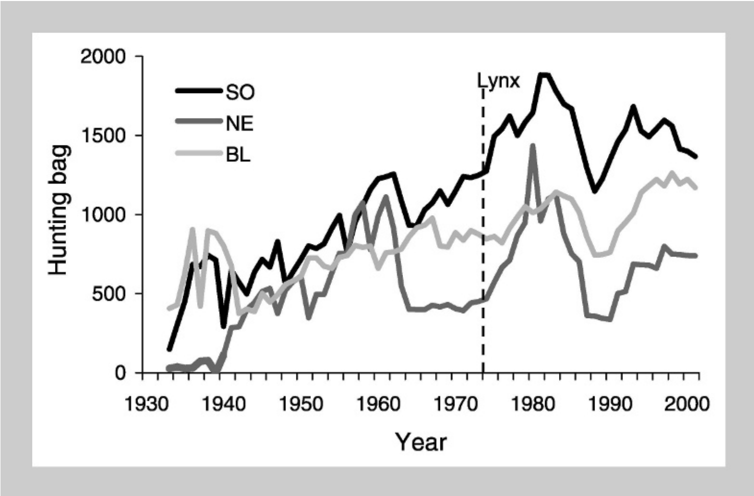

Figure 2. Roe deer hunting bag of the cantons of Basel-Landschaft (BL), Solothurn (SO, Jura part only) and Neuchâtel (NE) from 1933 (beginning of the Swiss hunting statistics) till 2000. Only these three administrative units within the Jura Mountains provide long-term bag statistics. The curves illustrate the recolonisation of the Jura Mountains starting from the north (BL) and the lasting increase of the roe deer population until the 1980s. The vertical broken line marks the start of the reintroduction of the lynx in the year 1974 in NE.

have richly endowed them with moors'' (peat was used for fuel). Although banned by federal law in the early 20th century, forest grazing remained widespread in the Jura Mountains. Rieben (1957) ultimately demanded that the woodlands in the Swiss Jura Mountains be fenced off to allow natural forest regeneration and erosion control. No data on the regeneration of woodland are readily available for the Jura Mountains. We can, however, assume that the regeneration of the forest area was similar to the Swiss average, which has been estimated to be almost 80% since the middle of the 19th century (Breitenmoser & Breitenmoser-Würsten 2001).

Decline and recovery of wild ungulates

Wild ungulates also declined during the 18th and 19th centuries. Although there is a complete lack of quantitative information, historians (summarised by Baumann 1949, Schmidt 1976 and Kurt 1977) agree that in the 19th century, wild ungulates were virtually extinct in Switzerland, with the exception of some small chamois populations in the Alps. Roe deer, the main prey of lynx, were believed to have disappeared form Switzerland by the beginning of the 19th century. Some roe deer may have survived in the northern part of the Jura Mountains or may have occasionally immigrated from neighbouring Germany and France (Baumann 1949). Schmidt (1976) mentioned an increasing number of observations reported in hunters' magazines after 1880. From the bridgehead along the Rhine River east of Basel, the roe deer recolonised the Jura Mountains as far south as Geneva till 1930 (Kurt 1977). The progression of the roe deer south along the Jura Mountains is reflected in hunting success (Fig. 2). When the federal statistics started in 1933, there was already a considerable roe deer harvest in the canton of Basel-Landschaft (BL) and it was increasing in Solothurn (SO). Harvest began in Neuchâtel (NE), the southern most of the three cantons (see Fig. 1), after 1940.

The chamois, the most important alternative prey for lynx, existed in the Jura Mountains at least up to the Middle Ages. Salzmann (1975) and Blant (2001) question whether it was ever completely absent, but there was clearly no vital population. The species recolonised the Jura Mountains in the first half of the 20th century, as a result of spontaneous immigrations from the Alps and reintroductions at several places along the mountain chain. The red deer *Cervus elaphus* was eradicated in the Jura Mountains during the 19th century (Blant 2001), but returned to the southern part of the range after releases in France and Switzerland in the 1970s and 1980s. The brown hare *Lepus europaeus*, the only lagomorph species widespread in the mountain range, declined during the second half of the 20th century (Blant 2001). The decline was so dramatic that hunting was discontinued in most parts of the Swiss Jura Mountains (Blant 2001).

Eradication of large carnivores and reintroduction of lynx

The indigenous large carnivores of the Jurassic arc all disappeared in the middle of the 19th century (Blant 2001). Eiberle (1972) believed that both brown bear and wolf resisted eradication in the Jura

Mountains longer than the lynx. Schauenberg (1969), Eiberle (1972) and Herrenschmidt & Leger (1987a) reviewed the historic record of lynx for the Jura Mountains. The last evidence reported on either side of the national border included a lynx killed in 1830 near Lignerolle (VD, Switzerland) and another lynx killed near Pontarlier (39, France). A capture in 1885 at the rim of the French Jura Mountains is doubtful (Schauenberg 1969). The sites of the last observations are in the south-central part of the mountain chain, the most elevated and remote part. In the north of the Jura Mountains, the lynx disappeared much earlier. According to Eiberle (1972), direct persecution was the main reason for its annihilation. However, the historic record is misleading because it consists almost exclusively of records of shootings and bounties paid. The massive alteration of the habitat and the destruction of the wild prey base must have stressed the large carnivore populations. That brown bear and wolf (more typical victims of human persecution than the lynx) survived longer could probably be explained by the lynx's higher vulnerability to anthropogenic alteration of habitat and prey base (Breitenmoser 1997).

Lynx were reintroduced into the Swiss Jura Mountains in the 1970s. The releases and the development of the population were described in detail by Breitenmoser & Baettig (1992), its status by Breitenmoser et al. (1998) and Capt (2007). Compared to historic conditions during the extinction phase, several prerequisites important for the existence of lynx have changed during the 20th century. First, forests have recovered and expanded throughout the Jura Mountains. This was also a consequence of the exodus of people. Both the French and the Swiss Jura Mountains have experienced a net loss in the human population during the past century. Second, roe deer and chamois have recovered throughout the mountain range to a level likely exceeding historic abundance. Third, as a result of increasing conservation awareness, human attitudes towards large carnivores has changed since the 1950s (Roth 1986). The lynx was granted legal protection by the national legislation in Switzerland in 1962 (Breitenmoser et al. 1998), and in France in 1977 (Stahl & Vandel 1998).

Conflicts and threats in a cultivated landscape

Although the Jura Mountains provide better living conditions for a large carnivore regarding habitat quality, prey availability and resident human population than during the times when the lynx was eradicated, the lynx did not inherit a wilderness. Human density has decreased in the mountain range itself, but increased greatly in its vicinity. Modern traffic infrastructure and recreational use of the mountains gave rise to new threats, adding to old conflicts that may not have disappeared entire-

Table 2. Assessment of identified and potential threats to the lynx population in the Jura Mountains, and conservation actions recommended. Each of the six authors judged the threats independently according to the following scale: 1 = not a risk for the lynx population at present or in the near future; 3 = identified cause of individual losses, but not a threat to the population on its own; 5 = a potential risk at the population level; 2 and 4 are intermediate levels. M (Range) gives the mean and range (minimum-maximum) of the evaluation (N = 6). For the recommended actions see text.

Threat	M (Range)	Rank	Actions recommended
Resource depression			
1. Habitat deterioration	1.0 (1-1)	9	None
2. Fragmentation	2.0 (1-4)	5	Fauna passages; habitat corridors
3. Prey decline	1.2 (1-2)	8	Monitoring ungulate populations; sustainable management roe deer and chamois population
Anthropogenic losses			
4. Population control/hunting	1.5 (1-2)	7	Monitoring lynx population; sustainable interventions; inter-regional consultation and coordination
5. Poaching/illegal killing	4.5 (4-5)	1	Law enforcement; conflict management; preventive measures, compensation, removal of stock raiders (depredation); translocations, legal sustainable hunting (impact game)
6. Anthropogenic accidents (traffic)	3.2 (3-4)	2	None
Natural factors/population viability			
7. Disease	1.8 (1-3)	6	Surveillance; selective intervention if needed
8. Demographic viability	2.5 (2-3)	4	Monitoring of population parameters (e.g. reproduction); restocking if needed
9. Genetic viability/inbreeding	3.0 (2-5)	3	Genetic monitoring; merge populations; translocations if needed

ly. In this section, we assess the different threats to the lynx population in the Jura Mountains (Table 2). For some risks, we cite empirical data (e.g. demographic data; see Breitenmoser-Würsten et al. 2007a) or use models (e.g. population size and habitat quality; see Zimmermann & Breitenmoser 2007). For others we rely on the experience and personal judgement of the authors. Our combined opinion regarding the importance of the threats is summarised in Table 2.

Resource depression

Habitat and prey are the two most important resources a lynx needs to survive. The typical habitat of the Eurasian lynx in Europe is woodland. Forests provide cover for hunting, resting and breeding, and connectivity over enough area to sustain the spatial structure of the population (Breitenmoser-Würsten et al. 2007b). Specific features such as den sites, are not limited (Boutros et al. 2007). The structure and the tree species composition has recently improved towards more natural forests, and there is no reason to believe that this tendency will discontinue. We consider habitat quality *per se* to be of little concern at present and in the near future, compared to fragmentation of the habitat (see Table 2). Small-scale fragmentation, resulting in a patchy mosaic of forest and pastures, is a benefit to prey and does not hinder lynx movements. Larger gaps in the forest (typically correlated with dense human infrastructure), however, cause breaks in the land tenure system and limit potential population size (Zimmermann & Breitenmoser 2007). Road and railways are not barriers to lynx movement in the Jura Mountains, as long as they are not associated with broad strips of open landscape. Highways formed boundaries between lynx home ranges or separated subpopulations with limited exchange of individuals in the Alps (Breitenmoser-Würsten et al. 2001), but we have no indication for this from the Jura Mountains. A depression of the prey base strong enough to jeopardise the lynx population is not likely to happen in the Jura Mountains. We have observed a numerical and functional response of lynx to changes in roe deer density in the Alps (KORA, unpubl. data), but prey availability was not limiting the lynx population in the Jura Mountains (Molinari-Jobin et al. 2007). Derived from the trends in the hunting statistics, the roe deer population has increased during the period of lynx fieldwork both in the French (Stahl et al. 2001a) and in the Swiss (Molinari-Jobin et al. 2002) Jura Mountains. The chamois is an important alternative prey, which is readily available in the central part of the range. We judge the risk of a significant prey depression in the Jura Mountains minor at present and in the near future (see Table 2).

Human disturbance and anthropogenic losses

Humans can have a direct negative impact on lynx by altering lynx behaviour through forest exploitation, recreation and other disturbance, accidental killing (e.g. traffic accidents), and deliberate killing of lynx through poaching and retaliation. We have not quantified the importance of disturbance, but anecdotal observations during radio-tracking revealed that lynx did not respond to human presence or nearby activities. Some lynx became tolerant of our presence during fieldwork, demonstrating individual potential to adapt to disturbance. There is one case known from our study area in June 1987 where a female lynx abandoned a litter after an intervention of woodsmen at the den. On the other hand, research tagging of lynx kittens at the den site (Breitenmoser-Würsten et al. 2007a) was benign. Although most lynx dens were remote, females sometimes gave birth near areas of high human activity (Boutros et al. 2007), e.g. 50 m from a logging place.

Lynx were generally tolerant of human presence and activity within the prime habitat of the home-range cores. Nevertheless, direct and indirect disturbance losses were the most important of all known mortalities (Schmidt-Posthaus et al. 2002, Breitenmoser-Würsten et al. 2007a). In the Jura Mountains, 36% of lynx mortality was caused by traffic accidents, 6% by other human related accidents, 11% by legal killings or removals, and 19% by illegal killings. Road kills are most likely to be reported and are overrepresented in the sample. Traversing roads and railways were common within individual home ranges. Even a second-class highway traversing the study area in the Swiss Jura Mountains was regularly crossed by lynx living on either side. The radio-tagged female, F_{MARA}, crossed this highway regularly for many years, but was killed on this road at 14 years of age. The second, most important cause of human related mortality is illegal killing. Although most information was available from the study area (Breitenmoser-Würsten et al. 2007a), the distribution of known cases indicate that illegal killings occur throughout the Jura Mountains. Illegal killing was ranked first in our assessment of threats (see Table 2) and is mainly a consequence of the hunters' resistance against the return of the competitor. This is expressed in most statements of hunters and even of sheep breeders (e.g. Boegli 1992 and Grosjean 1992, respectively), but there is an underlying general sociocultural conflict between urban advocates of the lynx and rural society, which is hard to grasp. Considering a fair number of unrecorded cases of illegal killings (based on radio-tagged lynx alone, Breitenmoser-Würsten et al. (2007a) estimated that illegal killing could be as much as half of the mortality) it is obvious that anthropogenic mortality shapes the dynamic of the lynx population in the Jura Mountains. After illegal killing, we have ranked traffic accidents highest among the threats to the lynx (see Table 2). Officially authorised removal of animals has not been a major source of losses to the Jura Mountains lynx. In France, nine lynx have been removed as stock raiders so far (Stahl et al. 2001b), and one has been removed in Switzerland (Breitenmoser-Würsten et al. 2007a). However, population control measures are only sustainable as long as they are compensatory to other losses. The most obvious effect of the high anthropogenic losses was the low mean age of resident lynx, indicating a fast turnover of the population (Breitenmoser-Würsten et al. 2007a).

Natural factors and population viability

Natural or intrinsic threats include disease, predation and loss of demographic and/or genetic viability. Occurrence of disease in lynx from the Jura Mountains (Schmidt-Posthaus et al. 2002, Breitenmoser-Würsten et al. 2007a), include three cases of rabies in France (Stahl & Vandel 1999). In the Alps, lynx suffered losses from sarcoptic mange (Ryser-Degiorgis et al. 2002), but the solitarily living lynx is generally not very vulnerable to epizootic diseases (Ryser-Degiorgis 2001). Rabies and sarcoptic mange were most likely transferred from red foxes, the vector species of these diseases and an occasional prey of lynx (Molinari-Jobin et al. 2007). Predation is no risk for the lynx in the Jura Mountains at present. Top predators are rare victims of predation; Matjuschkin (1978) listed some anecdotal observations of mainly young lynx being killed by other predators. If it were to recolonise the Jura Mountains, the wolf would be a competitor to (more than a predator of) lynx and, hence, depress the total carrying capacity of the mountain range for the felid carnivore.

A healthy lynx population requires a minimum density and the typical land tenure system to secure a sufficient recruitment (Breitenmoser et al. 1993, Breitenmoser-Würsten et al. 2007b). The loss of demographic viability can be a consequence of low abundance or an unbalanced sex ratio as a result of a high or sex-biased mortality, and a high degree of fragmentation that impedes the migration of individuals between disjunct subpopulations. Assessing demographic viability requires a wealth of information and data, and establishing whether any free-living population is demographically viable can be hard. The same is true for genetic viability, although we now have instruments to measure the degree of inbreeding and genetic drift. In a reintroduced population (a typical bottleneck-situation) such as the lynx in the Jura Mountains, the risk of genetic drift and loss of genetic variability is high (Frankham et al. 2002). The possible consequences can be anatomic malformation, reduced fertility and weakened immunoresistance. Preliminary results from the assessment of the genetic status of the Jura lynx population compared to the founder population from the Slovak Carpathian Mountains indicate slightly reduced heterozygosity and loss of rare alleles (G. Obexer-Ruff & C. Breitenmoser-Würsten, pers. comm.). We have no indication that reduced genetic variability has impacted the population, but as long as the Jura lynx population remains isolated (Zimmermann & Breitenmoser 2007), the genetic status of the population should be carefully monitored (see Table 2).

Conservation concepts and management

The review of the ecology and the status of the lynx in the Jura Mountains, and the identification of threats, allow prioritising of conservation measures. The implementation of such measures requires a legal framework, a conservation strategy, and a broad consensus among all interest groups involved.

Conservation priorities

According to our assessment and ranking of threats (see Table 2), habitat loss, prey decline and disease pose minimal risks to the population. Habitat fragmentation, traffic accidents and loss of demographic or genetic viability, however, are problematic when combined with other risks. Illegal killing is the only threat that we believe to be effective at the population level on its own. Many of the threats are potentially interlinked; if the population is stressed from one, the mortality due to another risk factor may increase. Such positive feedback mechanisms can cause an extinction vortex even if the single threats involved do not seem to cause significant mortality. At that point, deterministic (anthropogenic mortality, prey decline, habitat deterioration and fragmentation) and stochastic (genetic drift, random demographic fluctuations, catastrophes and diseases) factors interact (Lacy 1997). In this paper, we will discuss possible measures and actions to secure 1) the ecological foundation (habitat and prey), 2) population viability (fragmentation, demographic and genetic viability), and 3) coexistence with humans.

Ecological conditions

The basic ecological conditions for the lynx in the Jura Mountains are excellent if the habitat is maintained and harvest of ungulates is sustainable. The forests have expanded and are today more natural than they were some decades ago. There is no reason to believe that this tendency will end, and we do not see any need for specific conservation actions regarding habitat management. The prey base has increased and is now at least stable. Lynx have had a considerable impact on local roe deer populations in the Alps (Haller 1992, Breitenmoser et al. 1993, and KORA, unpubl. data), but not in the Jura Mountains. The chamois is more vulnerable to lynx predation than the roe deer (Jobin et al. 2000, Molinari-Jobin et al. 2002), and depression of local chamois populations may be more likely. Predation should be taken into consideration when the harvest quotas of ungulates are established. Nevertheless, the impact of lynx on its prey populations is of more concern in the conflict with hunters than it is in resource depression.

Population viability

The viability of a population depends on available living space (Zimmermann & Breitenmoser 2002), demography and stochastic events. For lynx to survive in the Jura Mountains, we must counteract fragmentation, secure a demographically healthy population, and increase the genetic variability if needed. Within the Jura Mountains, fragmentation is relatively low (Holzgang et al. 2001, Zimmermann & Breitenmoser 2007). Passages across major traffic lanes have already been built or are planned at several points in the Swiss Jura Mountains (Holzgang et al. 2001, Oggier et al. 2001). To connect the Jura Mountains with neighbouring mountain ranges, habitat in the most likely corridors for migrating wildlife (Zimmermann & Breitenmoser 2007) should be improved. The importance of the first chain of the Jura Mountains as a corridor between the Alps in the south and the Vosges Mountains and the Black Forest in the north have been recognised, and international corridors including fauna passages have been proposed (Holzgang et al. 2001).

The incidence of diseases, heterozygosity and allele frequency must be carefully surveyed. Every lynx found dead and samples from living animals must be included in pathological and genetic screening. Increasing disease frequency might indicate inbreeding depression. The possibility of intervention is limited, but in a critical situation, veterinary treatment of individuals in the field may be justified. To reduce the effect of genetic impoverishment, animals with a low degree of inbreeding (but from the same subspecies or ecotype) should be released. However, to prevent negative stochastic processes and to keep the population viable, lynx colonisation over the entire mountain range and connections to neighbouring populations should be a priority (Zimmermann & Breitenmoser 2007).

Coexistence with humans

Anthropogenic losses are the most important threat, but they are hard to overcome. Corridors and green bridges will not reduce traffic accidents, because lynx are struck on any road or railway, not only at critical spots. Retaliation killing can only be reduced when the conflict with hunters and sheep breeders is solved. The effect of depredation is mitigated in both countries through governmental compensation of approved losses, promotion of preventive measures (fences and guarding animals), and the removal of chronic stock raiders (Capt et al. 1993, Angst et al. 2000, Buwal 2004, Stahl et al. 2001b, 2002, Angst et al. 2002). According to a survey by Steck & Tester (2001), Swiss sheep breeders were mostly satisfied with the compensation scheme. Spatial and temporal distribution of killed lynx compared to cases of depredation, and statements of sheep breeders and hunters indicated that the conflict with the hunters is the primary reason for illegal killings (Ceza et al. 2001, Egli et al. 2001). To reduce illegal killings, better law enforcement is needed (Ceza et al. 2001). However, it is not likely that this conflict (lasting 30 years in Switzerland) can be solved through restrictive measures alone (Breitenmoser & Breitenmoser-Würsten 2001). Conflict management that addresses the underlying sociopolitical conflicts will also be needed. Although hunters and sheep breeders are branded as the sole lynx antagonists, they find support in their rural community. A public opinion poll in Switzerland (Wild-Eck & Zimmerman 2001) revealed that 75% of those asked were in favour of lynx. However, the support was weaker in the Alps, in the French speaking part of Switzerland and in the rural areas compared to the urban centres. Two years later, Hunziker et al. (2001) performed a more specific inquiry regarding the acceptance of carnivores. At that time, a controversy about lynx in the northwestern Alps of Switzerland was at its peak (Breitenmoser et al. 1999) and was daily covered by the mass media. Hunziker et al. (2001) found an increased general acceptance of large carnivores compared to the previous poll, but in the Simmental, the epicentre of the conflict, a majority was now against the presence of lynx. Both, the general increase and the regional decrease in acceptance was likely a consequence of the media campaigns. When, at a national level, people condemned the publicised illegal killing, local people declared their solidarity with the hunters and sheep breeders (Hunziker et al. 2001). This process indicates that such conflicts cannot be solved through legal protection and law enforcement alone. Local people and interest groups must be involved in the discussion and in the decision-making process. This implies negotiation and eventually a compromise regarding the conservation and management of lynx.

Legal framework, management concepts and implementation

International treaties such as the Council of Europe's Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) and the Habitat Directives of the European Union assure the existence of the Jura lynx population. National laws in both countries give the species year-round protection. Treaties and laws, however, are not directly relevant for discussion with local people. At the operational level, conservation action plans are needed. Model plans have recently been produced by the Large Carnivore Initiative for Europe, a loose connection of experts and NGOs involved in carnivore conservation across Europe, on behalf of the Council of Europe/Bern Convention (for the lynx, see Breitenmoser et al. 2000). The Swiss Agency for Environment, Forest and Landscape (SAEFL) introduced a management plan for lynx in 2000 (Buwal 2004), which had previously been through political and public consultation. The management plan prescribes population control if the impact of a local lynx population on its prey population is too strong. Possible interventions could be either translocation of lynx aiming to expand the population, or when further translocations are no longer possible, limited reduction. A recent inquiry on the attitudes of residents in the French Alps towards the wolf (Bath 1998) revealed that people are willing to accept its presence, as long as there were not 'too many'. The same pattern was observed by Egli et al. (2001) in the Swiss Alps. All persons asked stated that they were willing to accept lynx, if they would not exceed a certain number. Of course, opinions regarding tolerable lynx abundance are divided. Further, Egli et al. (2001) found that local people did not trust in lynx numbers produced by scientists. But the mistrust goes beyond numbers. For rural people (and not just for the anti-carnivore hardliners), scientists and managers (from the urban centres) often represent dominant culture and hegemonic knowledge (Skogen 2003). However, a foundation of trust between all partners involved is indispensable for an adaptive process in carnivore conservation. Joint practical work can diminish cultural barriers. Skogen (2003) described a project in Norway where biologists, managers and local hunters joined in lynx census fieldwork. This project did not only improve the lynx monitoring, it had an additional confidence-building effect.

Conclusions

In order to facilitate lynx monitoring in the Swiss Jura Mountains and build mutual trust between interest groups, we have established a 'lynx group' including game wardens, hunters, naturalists and scientists. Such a monitoring group already exists in France ('Réseau Lynx'; see Vandel & Stahl 1998a). Continued monitoring, interregional cooperation and public involvement should eventually result in a broadly accepted management plan for the Jura lynx population. The Swiss Lynx Concept, adopted in 2000 and revised in 2004 (Buwal 2004), marked the transition from a policy of full protection to conservation through management. As a first practical measure, six lynx from the northwestern Swiss Alps and three from the Jura population were translocated to the eastern Swiss Alps. This measure aimed to expand the area occupied by lynx and at the same time reduce local lynx abundance in areas where they were considered 'too many'. An additional aim was to mix the gene pools of the two reintroduced populations.

Translocations and even removal of problem animals are widely accepted management measures. The Swiss Lynx Concept, however, holds out the prospect of culling lynx if they have a considerable impact on local wild prey abundance. Such interventions are still highly controversial, greeted by hunters, but rejected by nature conservation organisations. The compromise in lynx management has not yet been found. But after a long-lasting period of total defamation and persecution and some decades of rehabilitation and full legal protection, we seem to come to an increasingly accepted understanding that the maintenance of large carnivore populations in a multi-use landscape requires an adaptive management with active intervention. To assure that any intervention is sustainable, however, management and conservation plans must be based upon ecological and biological knowledge and sound monitoring.

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