Abstract: We monitored European lynx (*Lynx lynx*) in a reintroduced population in the Swiss Alps from 1983 to 1988. We predicted that recolonizing lynx initially would reach a higher population density (and would kill more ungulates) than they would sustain once the population was established. We compared the home ranges and distribution of kills of 8 lynx in the established center of the population with those of 6 lynx at the expanding front of the population. Home ranges overlapped between males and females and were exclusive within the sexes in both areas, but at the front, home-range sizes were 3 times smaller. The distributions of kills were more concentrated, and distances between consecutive kills were shorter at the front. Kill rates did not differ (*P* = 0.411), but the proportion of carcasses consumed was 10% higher at the center than at the front (*P* = 0.037). We suggest that the smaller lynx home ranges at the front indicated a denser predator population and that the spatial concentration of kills there was due to a higher prey availability. Ungulates seemed to be more abundant and clustered, and lacked anti-predator behavior in areas where their natural predators had been missing for a longer period. We interpreted the decrease of the lynx population in the center of the population as a numerical response of the predator to a readaptation (numerical and behavioral response) by the prey.
PATTERNS OF PREDATION BY REINTRODUCED EUROPEAN LYNX IN THE SWISS ALPS

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The European lynx was reintroduced to Switzerland in 1971 (Breitenmoser 1983, Breitenmoser and Baettig 1992, Haller 1992) after it had been eradicated in the previous century (Schauberg 1969, Elberle 1972). This reintroduction has provided a rare experiment in the dynamics of an indigenous predator spreading throughout its traditional natural distribution. The first introduction was made at the northern edge of the Swiss Alps; from there, the population expanded over the northern and western Alps (Breitenmoser 1983, Haller 1992). As it spread, the lynx preyed upon smaller ungulates such as roe deer (Capreolus capreolus), chamois (Rupicapra rupicapra), and occasionally domestic sheep (Breitenmoser and Haller 1987, Haller 1992). When lynx first arrived in an area, hunters and farmers complained of excessive lynx predation on both wildlife and livestock. Later, behind the expanding front of the population, there were fewer complaints. Either people became more accepting of the lynx, leaving predation less noticeable, or predatory decreased, reflecting a decline in lynx density. There was some evidence for the second interpretation. Game wardens recorded a decrease both in lynx sightings and in kills found (after a temporary increase in predation, first on ungulates and later on domestic sheep) following the arrival of the lynx in different regions of the northern Alps (Haller and Breitenmoser 1986: Fig. 14).

This observation led us to propose hypotheses on how predators expand into new areas. We hypothesized that there were 2 phases of expansion. During the first phase, we postulated a high number of predators would feed on a dense population of naive prey that were easy to kill. We then speculated that this high predation would result in decreased prey availability, and induce a second phase where the predators would hunt over a larger area and consequently have larger home ranges. We also suspected that before expanding their home ranges, they would incorporate domestic species into their diets due to the reduced availability of their usual wild prey.

After working in the center of the lynx population distribution, where the predator had been present since the early 1970's (Haller and Breitenmoser 1986, Breitenmoser and Haller 1987), we selected a second area on the front of population expansion (Haller 1992) to test our assumption. From our hypothesis, we derived 3 predictions about the behavior and the predation rates of the lynx. In the center, home ranges and daily movements of lynx should be larger, distribution of kills should be more uniform (i.e., distances between kills should be larger), and kill rates should be lower and the proportions of each kill consumed should be greater, in comparison to the same features at the edge of the range. With these predictions, we implied a correlation between prey availability, lynx home-
range size, and lynx density. We discuss possible processes leading to differences in home-range size and point to some management conflicts that occur when a large predator is reintroduced into a human-altered area.

The study was funded by the Swiss National Science Foundation (Grant No. 3100-00893/30), the Federal Office of Forestry, the Swiss League for Protection of Nature, the WWF Switzerland, and the canton of Berne. We thank Ch. Breitenmoser-Würsten for help throughout the study, F. Bernhart for assistance with fieldwork, and A. R. E. Sinclair, Ch. Rohner, and M. O’Donoghue for discussions and review of the manuscript.

STUDY AREA

Our study was conducted in the western part of the Swiss Alps (Fig. 1; the center of the study area is at 7°40’E, 46°40’N). The center of the lynx population comprised the northern part of the study area (canton of Berne); whereas the front covered the south (canton of Valais). Lynx were present in the canton of Berne after 1972 (Breitenmoser 1983), and in Valais by around 1980 (with first observations as early as 1976, Haller 1992). The 2 cantons are separated by the Bernese Alps, rising to an elevation of 4,000 m. The valley bottoms vary from 400 to 800 m elevation. Forests extend along the steep slopes up to the timberline at 1,800–2,200 m. Lower ridges and slopes have previously been deforested and now provide summer pastures for cattle and sheep. Only 28% of the study area is covered by forest.

Chamois and roe deer are abundant throughout the study area, but the latter are rarer in Valais than in Berne. Red deer (Cervus elaphus), ibex (Capra ibex), brown and white hare (Lepus capensis and L. timidus), marmot (Marmota marmota), and black grouse (Tetrao tetrix) are common but irregularly distributed. From late spring to autumn, domestic sheep graze unguarded on the mountain meadows. Apart from lynx, the only other predators that occasionally kill ungulates are red foxes (Vulpes vulpes) and golden eagles (Aquila chrysaetos). Wolves (Canis lupus) and brown bears (Ursus arctos) were exterminated in the 18th and 19th centuries. Small sanctuaries with high ungulate densities are scattered over the Alps. In our study area, every lynx home range in the canton of Berne included at least a part of a sanctuary, and in the canton of Valais, the center of the home ranges of 2 lynx, M4 (= Maux) and F9 (= Fau), were situated in 1 sanctuary.

METHODS

We captured lynx with foot snares close to fresh kills, or in large double-door live traps on narrow paths. Lynx were immobilized with 0.8–1.5 ml of Ketamin/Xylacain mixture (88 mg Bayer “Rompun” dissolved in 4 ml Parke-Davis “Ketanest”), and fitted with radio collars (200 g; K. Wagener, Cologne, Germany). An incisor was removed to determine the age of the animals. Radio-marked lynx were subsequently relocated from the ground. Rough topography and large differences in elevation prevented us from using standard triangulation methods. Instead, locations were normally obtained by walking in to the animals. If close approach was impossible, locations exceeding an estimated accuracy of 1 x 1 km were excluded from analysis. Fixes were recorded according to the official Swiss coordinate system. Only 1 location/day and individual was used for all analysis.

We used the programs Ranges IV (Kenward 1980) and SEAS (Cary 1989) to compute the areas of activity and the incremental areas, using 2 home-range models: minimum area method (convex polygon, Mohr 1947, Voigt and Timline 1980), and a more restrictive convex polygon model that we named restricted convex polygon. In the latter model, the range was computed as the convex polygon of the extreme locations, but excursions (mainly by males during the mating season) were excluded. In addition, we excluded areas >10 km² inside the polygon but inaccessible to a lynx due to high mountain ridges, rivers, or lakes (Haller and Breitenmoser 1986). Minimum daily movements were calculated as the straight-line distances between locations on 2 consecutive days. Activity centers were defined as the arithmetic mean of the x- and y-coordinates of all locations of an individual.

To find kills, we monitored the movements of individual lynx daily. Lynx usually fed for several days on a kill, hiding during the day and returning to the carcass each night. We found the kill sites through radio tracking, by following lynx tracks in the snow, or scanning an area where a lynx previously had been located with a dog. We found 91% of the ungulates killed during the winter months. As confirmed through fecal analysis (Breitenmoser and Haller 1987).
smaller animals were only occasionally killed, so they were excluded from statistical analysis. To estimate kill rate and consumption rate, lynx were monitored more intensively than the others. The size of each lynx in the center (M2 and F2) and at the front (M4 and F9). These lynx (labeled as M2, F2, M4, and F9, respectively) died 71% of all kills found. Consumption of kills was classified visually in increments of 25% of the consumable portion (Breitenmoser and Haller 1987). Kills made within 10 days by the same animal were considered consecutive kills. To compare nonnormally distributed data from the 2 areas of Berner and Valais, the Wilcoxon U-test was used, and the Kruskal-Wallis (H-test statistic) analysis of variance was used to compare several individuals. We tested for normality by means of the Kolmogorov-Smirnov goodness-of-fit statistic.

**RESULTS**

**Home Ranges and Daily Movements**

We monitored 11 individual lynx and obtained a total of 2,435 locations (Table 1). Male lynx ranges almost completely covered those of females, but within the sexes, individuals separated in space or time. Lynx of the same sex with overlapping home ranges (Fig. 1) were monitored during different periods (Table 1). Lynx showed seasonal differences in home-range size as a consequence of the mating season (excursions of males) or breeding (restricted movements of females), but the pattern was the same in the center (Haller and Breitenmoser 1986) as at the front (Haller 1992). Home ranges were larger in the center of the population compared with those at the front of the population. However, the size of the individual home ranges depended on the home-range model applied (Table 2). Lynx used the lower parts of several valleys and avoided the higher alpine habitat (see distribution of the locations in Fig. 1). Therefore, the subjective model (restricted convex polygon, Fig. 2) gave a more realistic estimate of the true area used by an individual. For the minimum area method, home ranges were on average 3.2 times larger, and for the restricted convex polygon method, 3.0 times larger in the center than at the front (Table 2, Figs. 1 and 2). Because males typically had larger home ranges than females (Table 2), we corrected for the sex-specific difference by dividing the size of each home range by the mean home-range size of its sex. For both models, these standardized home ranges were larger in the center than at the front (U = 23, P = 0.010 for the minimum area method, and U = 24, P = 0.006 for the restricted convex polygon model) for 6 resident lynx in the center and 4 at the front (Table 2). The cumulative home ranges of lynx at the front of the population in Valais also increased at a much slower rate than those in the center (Fig. 3).

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**Table 1. Lynx populations (M = male, F = female) monitored at the center and expanding front of reintroduction, Swiss Alps, 1983-88.**

<table>
<thead>
<tr>
<th>Lynx</th>
<th>Period monitored</th>
<th>Age&lt;sup&gt;a&lt;/sup&gt; (Y-M)</th>
<th>Social status&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Mass (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Center (Bern)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M1</td>
<td>Mar 1986-May 1984</td>
<td>4-09</td>
<td>ar</td>
<td>23.5</td>
</tr>
<tr>
<td>F1</td>
<td>Mar 1986-Nov 1983</td>
<td>3-09</td>
<td>ar</td>
<td>17.0</td>
</tr>
<tr>
<td>M2</td>
<td>Mar 1984-May 1985</td>
<td>14-09</td>
<td>ar</td>
<td>24.5</td>
</tr>
<tr>
<td>F2</td>
<td>Feb 1984-Mar 1985</td>
<td>2-10</td>
<td>ar</td>
<td>17.0</td>
</tr>
<tr>
<td>F3</td>
<td>Feb 1984-Apr 1985</td>
<td>0-10</td>
<td>ar</td>
<td>17.0</td>
</tr>
<tr>
<td>F4</td>
<td>Apr 1984-Oct 1984</td>
<td>0-11</td>
<td>55</td>
<td>17.5</td>
</tr>
<tr>
<td>F7</td>
<td>Oct 1985-Mar 1986</td>
<td>1-04</td>
<td>ar</td>
<td>17.5</td>
</tr>
<tr>
<td>F8</td>
<td>Jan 1987-Mar 1988</td>
<td>0-07</td>
<td>ar</td>
<td>17.5</td>
</tr>
</tbody>
</table>

Front (Valais)

<table>
<thead>
<tr>
<th>Lynx</th>
<th>Period monitored</th>
<th>Age&lt;sup&gt;a&lt;/sup&gt; (Y-M)</th>
<th>Social status&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Mass (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F5</td>
<td>Mar 1985-Mar 1987</td>
<td>6-10</td>
<td>ar</td>
<td>17.5</td>
</tr>
<tr>
<td>F9</td>
<td>Mar 1985-Jun 1986</td>
<td>5-10</td>
<td>ar</td>
<td>17.5</td>
</tr>
<tr>
<td>M4</td>
<td>Mar 1986-Aug 1988</td>
<td>6-11</td>
<td>ar</td>
<td>17.5</td>
</tr>
<tr>
<td>F10</td>
<td>Jan 1988-Dec 1988</td>
<td>6-09</td>
<td>ar</td>
<td>19.0</td>
</tr>
</tbody>
</table>

<sup>a</sup> Age at capture (Y = Year, M = Month)

<sup>b</sup> a = adult, r = resident, d = dispersing, ? = status unknown

*Followed over 2 different periods October 1985-July 1986 (40 locations) and September 1987-March 1988 (66 locations).
The larger home ranges in the center did not correspond to greater \((U = 256.290; P = 0.206)\) daily movements (Table 2). The mean minimum daily movement in the canton of Berne was 2.18 km \((n = 1,183)\); whereas in the canton of Valais it was 1.90 km \((n = 422)\). In general, lynx at the front of the population moved almost as much in their small home ranges as did lynx within large home ranges in the center of the distribution. For the 4 more intensively monitored individuals, however, the differences between the minimum daily movements were significant \((U = 29.45, 3 \text{ df}, P < 0.001)\). \(M_{\text{center}}\) and \(F_{\text{center}}\) (M2 and F2, Berne) moved farther between consecutive locations than \(M_{\text{front}}\) and \(F_{\text{front}}\) (M4 and F9, Valais, Table 2).

**Kill Distribution and Distance Between Consecutive Kills**

We found 179 kills of 10 prey species (Table 3). Ungulates, mainly roe deer and chamois, comprised 93% of the prey. Of the 167 ungulates reported (Table 3), 118 (71%) were kills of \(F_{\text{center}}\), \(M_{\text{center}}\), \(M_{\text{front}}\) and \(F_{\text{front}}\). The kills of \(M_{\text{front}}\) and

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**Table 2. Home ranges and daily movements of lynx at the center and expanding front of reintroduction, Swiss Alps, 1983-86.**

<table>
<thead>
<tr>
<th>Lynx</th>
<th>Social status</th>
<th>No. locations</th>
<th>Convex polygons</th>
<th>Reconstructed convex polygons</th>
<th>Minimum daily movement (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>No.</td>
<td>%</td>
<td>No.</td>
</tr>
<tr>
<td><strong>Center (Berne)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M1</td>
<td>r</td>
<td>227</td>
<td>170</td>
<td>76</td>
<td>170</td>
</tr>
<tr>
<td>M2</td>
<td>r</td>
<td>263</td>
<td>275</td>
<td>99</td>
<td>275</td>
</tr>
<tr>
<td>F3</td>
<td>r</td>
<td>295</td>
<td>234</td>
<td>79</td>
<td>234</td>
</tr>
<tr>
<td>F4</td>
<td>?</td>
<td>45</td>
<td>245</td>
<td>10</td>
<td>245</td>
</tr>
<tr>
<td>F7</td>
<td>r</td>
<td>106</td>
<td>423</td>
<td>39</td>
<td>423</td>
</tr>
<tr>
<td>F8</td>
<td>r</td>
<td>175</td>
<td>195</td>
<td>11</td>
<td>195</td>
</tr>
<tr>
<td><strong>Front (Valais)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F5</td>
<td>r</td>
<td>120</td>
<td>56</td>
<td>46</td>
<td>56</td>
</tr>
<tr>
<td>F6</td>
<td>d</td>
<td>15</td>
<td>140</td>
<td>94</td>
<td>140</td>
</tr>
<tr>
<td>M4</td>
<td>r</td>
<td>283</td>
<td>103</td>
<td>36</td>
<td>103</td>
</tr>
<tr>
<td>F9</td>
<td>r</td>
<td>233</td>
<td>120</td>
<td>51</td>
<td>120</td>
</tr>
<tr>
<td>M5</td>
<td>d</td>
<td>40</td>
<td>375</td>
<td>93</td>
<td>375</td>
</tr>
<tr>
<td>F10</td>
<td>r</td>
<td>54</td>
<td>44</td>
<td>39</td>
<td>44</td>
</tr>
</tbody>
</table>

\(r = \text{resident}, d = \text{dispersing}, ? = \text{status unknown}\).
Fig. 2. Examples of the spatial distribution of ungulates killed in lynx home ranges (restricted convex polygon; arrows indicate excursions) in the established center (A, Berne), and at the expanding front (B, Valais) of the population in the Swiss Alps, 1983–
88. Circles = kills of male lynx, stars = kills of female lynx.

Kill Rates and Exploitation of Carcasses

Kill rates did not differ (P = 0.411) between the 2 regions of the study area. The mean time interval between consecutive kills was 5.0 days (n = 45) in Berne, and 5.1 days (n = 35) in Valais. Mean values for individual lynx were 6.8 (n = 14), 4.1 (n = 23), 6.0 (n = 20) and 3.9 (n = 15) days for Mcenter, Fcenter, Mfront, and Ffront, respectively. The difference (H = 9.272, 3 df, P = 0.028) among individuals was sex related. Neither the 2 males (P = 0.595) nor the 2 females (P = 0.609) showed different kill rates. Females had to kill more when they were raising
Fig. 3. Cumulative area of home ranges (convex polygon) of resident lynx in the Swiss Alps, 1983-88. Above the dotted line are animals in the established center (Berne), and below are those at the expanding front (Valais) of the lynx population.

The mean consumption of carcasses was 10% higher in the canton of Berne (n = 51) than in Valais (n = 52, P = 0.007). Family groups were responsible for this difference. Although M_Mont. and F_Mont. ate slightly more of a kill than F_Young and M_Mont., respectively (Table 4), the difference between the 2 areas was not significant (P = 0.142) when we excluded all kills used by females with young (χ = 75%, n = 38 for Berne; χ = 74%, n = 28 for Valais). The lowest consumption rate was by F_Youth, which ate an average of 59% (n = 24) of each kill. We observed surplus killing (killing of a prey without eating anything from the kill, Kruuk 1972) occasionally in Berne (7 times) and in Valais (3 times), and wastage (eating only part of a prey) was frequent. Lynx consumed half or less of the carcasses of 38.8% (Berne, n = 90) and 33.8% (Valais, n = 77) of the ungulates killed. At the front, lynx sometimes had several kills at the same time. For example, F_Young killed 4 chamois in 1 day in March 1987 when she was still with her juvenile (M5, Table 1). In subsequent days, the 2 lynx consumed only 25% of 3 carcasses and left 1 untouched.

DISCUSSION

The major difference between lynx at the expanding front of the population relative to those at the established center was their smaller home ranges, more concentrated kill distributions, and shorter distances between consecutive kills. These results are consistent with our predictions. Kill rates and use of carcasses did not differ between lynx in the 2 locations. Anecdotal observations indicate that surplus killing was more frequent at an earlier stage of lynx recolonization in Valais (Haller 1992) (Breitenmoser an along the expans impact on the pr
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Table 4. Characteristics of lynx

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Wynx</th>
</tr>
</thead>
<tbody>
<tr>
<td>M_Mont. (M)</td>
<td>10</td>
</tr>
<tr>
<td>F_Young (F)</td>
<td>6</td>
</tr>
<tr>
<td>M_Mont. (M)</td>
<td>2</td>
</tr>
<tr>
<td>F_Young (F)</td>
<td>4</td>
</tr>
</tbody>
</table>

* Means within columns
  | 10 kills were used to identify
  | 20 kills were used to identify
Table 3. Kills by lynx monitored by telemetry at the center and expanding front of reintroduction, Swiss Alps, 1983–88.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total</th>
<th>Berne</th>
<th>M2*</th>
<th>F2*</th>
<th>Valais</th>
<th>M4*</th>
<th>F4*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ungulates</td>
<td>167</td>
<td>90</td>
<td>12</td>
<td>21</td>
<td>20</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>Roe deer</td>
<td>76</td>
<td>56</td>
<td>7</td>
<td>1</td>
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<td>1</td>
<td>1</td>
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<tr>
<td>Chamois</td>
<td>78</td>
<td>30</td>
<td>14</td>
<td>7</td>
<td>48</td>
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<td>16</td>
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<td>Red deer</td>
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<td>1</td>
</tr>
<tr>
<td>Domestic sheep</td>
<td>11</td>
<td>4</td>
<td>1</td>
<td>7</td>
<td>3</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Domestic goat</td>
<td>1</td>
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<td>1</td>
<td>1</td>
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<td>1</td>
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<tr>
<td>Other species</td>
<td>12</td>
<td>9</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Brown hare</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>White hare</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Marmot</td>
<td>2</td>
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<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Red squirrelb</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Black grouse</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

*a M2 = M_{Berne}, F2 = F_{Berne}, M4 = M_{Valais}, and F4 = F_{Valais}.
b Sarcoscopus vagans.

The lynx at the center of the population, 90, and 33.8% of the 4 chamois were still with 3 carcasses, 0 and 30% of the 3 chamois were alive. The lynx at the expanding front, lynx had a higher impact on the prey populations than at the center of the established population.

Invading species can have a fatal impact on native animals or plants through competition or predation (Elton 1969). Little is known about the effect of an advancing front of predators on prey populations. A distant parallel could be seen in the Pleistocene overkill hypothesis. Martin (1984) proposed that a spreading front of human colonizers was responsible for the extinction of a great number of mammals and birds in North America. These invaders, however, were aliens and the resident populations were not adapted to the new assault. Lynx and roe deer in Switzerland, in contrast, had co-evolved, and although the 150-year absence of predation probably altered the prey genetically, they should have the potential to coexist. In fact, the readaptation in the established population happened within only about 10 years.

We believe we observed the late stage of phase 1 (high impact) and the shift to phase 2 (moderate impact) of recolonization in Valais. Two observations support this interpretation: (1) M_{Valais} abruptly tripled his home range after more than 2 years of monitoring (Fig. 3) and (2) M_{Berne} and F_{Berne} switched from killing chamois almost exclusively during the first year of monitoring to preying also on domestic sheep, and later other wildlife species, in the second and third years (Haller 1992).

Was there a difference in lynx density between the expanding front and the established center of the population? Home-range size is an appropriate indicator of lynx density only if territories are exclusive. Although the social behavior of most cats is flexible, adult animals of the same sex tend to occupy exclusive home ranges (Eisenberg 1986). Lynx in the Swiss Alps seem to fit this model. We found complete overlap between male and female home ranges but no evidence of other adult lynx within this area at the same time (Haller and Breitenmoser 1986).

There are no other studies of the Eurasian lynx using telemetry with which our data can be compared. However, data from snow tracking in Sweden (Haglund 1966, Jonsson 1980) and


<table>
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<tr>
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<th>Distance from activity center (km)</th>
<th>Distance to previous kill (km)</th>
<th>Carcase use (%)</th>
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<td></td>
<td>( x )</td>
<td>SE</td>
<td>( n )</td>
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<tr>
<td>( M_{Berne} ) (F2)</td>
<td>10.9</td>
<td>5.1</td>
<td>29</td>
</tr>
<tr>
<td>( F_{Berne} ) (F2)</td>
<td>6.5A</td>
<td>3.5</td>
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<td>( M_{Valais} ) (M3)</td>
<td>2.6A</td>
<td>2.3</td>
<td>29</td>
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<tr>
<td>( F_{Valais} ) (F2)</td>
<td>4.5A</td>
<td>2.5</td>
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*a Mean within column sharing the same letter do not differ \( P > 0.05 \); univariate multiple comparisons with unequal sample sizes.
b 10 kills were used together with 2 young.
c 20 kills were used together with 1 young, and 4 kills together with 2 young.
the U.S.S.R. (Zheltukhin 1984) confirm the exclusive use of home ranges by individuals of the same sex. In the U.S.S.R., lynx territory-size was negatively correlated with population density (Matjuschkin 1979). From empirical data on solitary carnivores, Sandell (1989) has shown a strong negative correlation between population density and female home-range size. Because all our female lynx in the center of the population had larger home ranges than those at the front (Table 2, Fig. 3), we conclude that there was a lower lynx density in the center.

We interpret the decreasing lynx density and the changing pattern of predation from phase 1 to phase 2 of recolonization as a numerical response of the predator to reduced prey availability. The dense chamois population in the central area of the home ranges of Mvae and Fve (37 km²) declined from about 800 individuals to 300 in the first 6 years of lynx presence, and the small population of roe deer was exterminated (Haller 1992). Although there also were some indications of a temporary decrease in local roe deer and chamois populations in Berne during the same period of recolonization (H. Brüthardt, Game Dep. Canton of Berne, pers. commun.), we do not have equivalent data to compare changes of the prey populations in the 2 areas. In recent years, the ungulate populations in the central area seemed to remain stable, and lynx took about 6-9% of a local roe deer population and 2-3% of the chamois population, respectively (Breitenmoser and Haller 1987). Unfortunately, no data on demographics of the prey population are available for the early stage of the recolonization of the central area.

We speculate that in addition to the numerical response of prey (decrease in numbers), the prey responded behaviorally to the return of the predator. Hunters and game wardens in the center of the lynx population judged that ungulates became “very wild” after the return of lynx. Roe deer and chamois may have redeveloped anti-predator behavior, which made them less vulnerable to the lynx. Charnov et al. (1976) have termed this effect “behavioral depression.” The detected presence of a predator may increase the alertness of the prey and temporarily depress prey availability. The difference in home-range size and kill distribution between the center and the front may not only have been a consequence of different prey density. If ungulates exhibited anti-predator behavior again and became less vulnerable through behavioral depression, lynx had to roam over a larger area to hunt successfully. Behavioral depression of a prey after 1 predator stayed in an area would also reduce prey availability for any conspecific hunting in the same spot soon after. Mvae and Fve hunted in the same parts of their overlapping home ranges (Fig. 2B), but Mvre and Fvre often hunted in different areas (Fig. 2A, Breitenmoser and Haller 1987) and avoided each other (Haller and Breitenmoser 1986).

Alternatively, differences in lynx density could be a consequence of different habitat quality. Forest is the most important habitat for lynx (Matjuschkin 1975). There is no difference in forest cover between the 2 regions of Berne and Valais (28% vs. 29.5% respectively), but there may be differences in other critical habitat characteristics that we were not able to measure.

MANAGEMENT AND RESEARCH IMPLICATIONS

Reintroductions of carnivores are most often seen as a conservation tool. Additionally, they should be used as experiments on predator-prey relationships to test changes in distribution, abundance, and behavioral reactions of the prey. To test our hypotheses in further reintroduction programs, it would be important to study not only density and distribution but also social and behavioral features (e.g., group size or alertness) of the local prey population before predators are released. It would be more promising to observe the changes in 1 area over a longer period than to follow an expanding front that is spatially and temporally variable. When lynx were reintroduced in the Swiss Alps, the released predators and their prey were not monitored, and we missed the interesting first phase of the colonization in the center.

No one expected an important impact on ungulate populations and livestock when lynx were reintroduced to Switzerland. In autochthonous lynx populations in eastern Europe, no conflicts from lynx predation have been reported (Heller 1971, Breitenmoser and Breitenmoser-Würsten 1990). The effect of felids on prey populations in natural ecosystems is generally small, but it can be severe where prey species have not evolved adequate anti-predator defense, or in cases where man has interfered (Kruuk 1986). Large predators have been absent in most parts of central and western Europe for at least a century. During this period, wildlife management was aimed at increasing, and later stabi-
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locations, supplemental feeding, and sanctuaries. Sheep breeders also lost the tradition of pro-
tecting their herds against natural predators.

Since the release of lynx in the Swiss Alps, several reintroduction programs have been started in other European countries (Breitenmoser and Breitenmoser-Würsten 1990). In most of them, extensive predation on wildlife and livestock has provoked conflicts between conservationists on one side and hunters and farmers on the other. In Slovenia, lynx completely eradicated 2 colonies of moufflon (Ovis ammon) in hunting enclosures (Cop 1989). In Austria, lynx preyed heavily on red deer concentrated around feeding stations (Gossow and Honsig-Erlenburg 1986). In France, lynx caused severe losses of ungpered domestic sheep (Herrenschmidt and Vandell 1986).

Our study suggests that such situations reflect a temporary phase after the reintroduction of lynx and that the readaptation of both prey and predator will result in a more balanced long-
term state. Today, in the center of the lynx population in the Swiss Alps, the impact of lynx on roe deer and chamois populations appears to be minor (Breitenmoser and Haller 1987), and the losses of livestock to lynx have decreased (Haller and Breitenmoser 1986). However, some management practices (e.g., artificial feeding) adopted in areas without large predators may result in unnatural concentrations of wildlife and are likely to cause excessive predation after the reintroduction of a carnivore. In addition, livestock is often left unattended in potential predator habitats. Such practices may have to be altered if areas are to accommodate reintroduction of large predators.

LITERATURE CITED


EVIDENCE OF TULAREMIA REGULATING A SEMI-ISOLATED COTTONTAIL RABBIT POPULATION

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Abstract: We studied a semi-isolated cottontail rabbit (Sylvilagus floridanus) population in southern Illinois from 1982 to 1986 to determine patterns of population change following a tularemia epizootic in 1980 and to evaluate the role of enzootic disease in population regulation. The population reached a density of >14 rabbits/ha in the best habitats 7 years after the 1980 epizootic, but dropped in summer 1985 and harvest at autumn reduced the population base. Condition indices and necropsy did not indicate food as a limiting factor at the observed peak density. Prior to 1988, serosurveys to detect IgG/IgM antibodies to Francisella tularensis provided the only evidence of enzootic tularemia in the population, but clinical cases were detected beginning April 1986. During spring 1988–winter 1990, 32.4% of 57 radio-marked animals died from tularemia. Concurrently, IgM seroprevalence rates increased, and some regression models revealed that IgM seroprevalence predicted seasonal survival. A deterministic model based on seasonal and annual survival data, estimates of recruitment, and known harvest removal mimicked population trends evident from roadkills and mark-recapture population estimates. Simulations without enzootic tularemia produced populations larger than those with tularemia, irrespective of drought and harvest effects. Our findings illustrate the risk wildlife populations may face from disease and the need to monitor health of intensively managed or isolated wildlife populations.

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Understanding the regulation of animal populations has challenged wildlife biologists and ecologists, for such insight offers theoretical and applied benefits. Hassell (1982,16) noted that "The impact of infectious diseases upon host population dynamics has been relatively neglected by ecologists. The emphasis over the last 50 years or so has been much more on the extent to which competition and predation affect population dynamics...." Although theoretical studies indicate that pathogens (parasites) could regulate host populations (Anderson and May 1979, May and Anderson 1979), regulation is difficult to demonstrate in the field where experimental controls are rarely feasible, other factors also affect host populations, and effects of parasites on host population dynamics often are cryptic.

The cottontail rabbit is a useful model to examine mechanisms that may regulate local population size. On a broad scale, habitat quantity and quality affect abundance of cottontails. Edwards et al. (1981) viewed land-use as the principal factor determining the minimum population level in Illinois and hypothesized local abundance to be regulated by a combination of dispersal and mortality. In contrast, Jacobson et al. (1978) could not relate low densities of rabbits in Virginia to advanced a disease (tularemia) to account.

Tularemia, Francisella tularensis a contamination that has populations. Jelks with the except the most frequent Drastic die-off.

Cahan et al. 1982 has been documented in cottos (Jacobson et al. tularemia in cottos, 1958, Burg, 1989), in which indication that tularemia (Yeater et al. 1981). However, the tularemia may have to....

We conducted experiments at our study site from 1982 through 1988 to detect a disease following trends in the tularemia, an endemic relative to tularemia, relative important to the population. Our study was focused on two components of the disease: Federal Aid for Tularemia, Conservation organizations and at Wayne Pit staff and study during this study and J. L. R.