Characterisation of Eurasian lynx Lynx lynx den sites and kitten survival

Authors: Boutros, Dominique, Breitenmoser-Würsten, Christine, Zimmermann, Fridolin, Ryser, Andreas, Molinari-Jobin, Anja, et al.

Source: Wildlife Biology, 13(4) : 417-429

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2007)13[417:COELLL]2.0.CO;2

Characterisation of Eurasian lynx *Lynx lynx* den sites and kitten survival

Dominique Boutros, Christine Breitenmoser-Würsten, Fridolin Zimmermann, Andreas Ryser, Anja Molinari-Jobin, Simon Capt, Marcel Güntert & Urs Breitenmoser

Boutros, D., Breitenmoser-Würsten, C., Zimmermann, F., Ryser, A., Molinari-Jobin, A., Capt, S., Güntert, M. & Breitenmoser, U. 2007: Characterisation of Eurasian lynx *Lynx lynx* den sites and kitten survival. - Wildl. Biol. 13: 417-429.

We retrospectively investigated characteristics of den structures and den sites used by female Eurasian lynx *Lynx lynx* in the Jura Mountains and the northwestern Alps of Switzerland. During 1983-2000, we discovered 30 natal and 40 maternal dens belonging to 26 females. Important den structures were closed, i.e. provided good shelter, had few entrances, and measured 1 m^2. Dens were found in rocky places, caves and wooden surroundings. Most dens were located in mixed forests with relatively open vegetation allowing for a visibility of 10-20 m. Contrary to our expectations, natal and maternal dens were equally exposed to human disturbance and were found in terrain which could be dangerous for the kittens. Overall, the two den types barely differed. While concealment did not seem to play a very important part at natal dens and while natal dens were almost never open structures, maternal dens were surrounded by a large number of hiding places and the dens and surroundings were rich in visual contrasts providing good camouflage options. Dens in the Alps and in the Jura Mountains were located in steeper terrain than available on average. The quality of the den sites did not seem to affect the survival of young lynx. Well-suited den sites are so abundant in the Alps and the Jura Mountains that females obviously have no problems finding good den sites.

Key words: Alps, den sites, Jura Mountains, Lynx lynx, survival

Dominique Boutros, Christine Breitenmoser-Würsten, Fridolin Zimmermann, Andreas Ryser & Anja Molinari-Jobin, KORA, Thunstrasse 31, CH-3074 Muri b. Bern, Switzerland - e-mail addresses: dominiqueboutros@hotmail.com (Dominique Boutros); ch.breitenmoser@kora.ch (Christine Breitenmoser-Würsten); f.zimmermann@kora.ch (Fridolin Zimmermann); a.ryser@kora.ch (Andreas Ryser); Molinari-Jobin@freesurf.com (Anja Molinari-Jobin)
Simon Capt, Centre Suisse de Cartographie de la Faune, Terreaux 14, CH-2000 Neuchâtel, Switzerland - e-mail: simon.capt@cscf.unine.ch
Marcel Güntert, Natural History Museum Bern, Bernastrasse 15, CH-3005 Bern, Switzerland - e-mail: marcel.guentert@nmbe.unibe.ch
Urs Breitenmoser, Institute of Veterinary Virology, University of Bern, Länggassstrasse 31, CH-3012 Bern, Switzerland - e-mail: urs.breitenmoser@ivv.unibe.ch

Corresponding author: Dominique Boutros

Received 19 October 2004, accepted 9 March 2006

Associate Editor: Miguel Delibes

Large mammals are commonly characterised by low adult mortality, high life expectancy, and relatively high mortality of juveniles (Clutton-Brock 1991). Like other large carnivores, Eurasian lynx *Lynx lynx* females have rather few offspring and even less survive the first year. Young lynx mortality is highest 3-4 months after birth (Jędrzejewski et al. 1996). Only 50% of young lynx survive the first year (Kaczensky 1991, Breitenmoser et al. 1993). The quality of den sites may be the first critical factor affecting survival, and we expect that a female will choose carefully where to give birth.

There are several publications on denning sites of carnivores, but only few descriptions of lynx den sites have been published. Fernández & Palomares (2000) showed that the physical nature of dens is more important for the breeding Iberian lynx *Lynx pardinus* than habitat features such as prey density and vegetation structure. Preferred breeding structures in old-growth habitat can be a limiting resource for Iberian lynx. The importance of suitable denning sites must thus be recognised and considered in conservation strategies (Fernández & Palomares 2000). Slough (1999) described the characteristics of den sites, maternal dens and denning habitat of Canada lynx *Lynx canadensis*. A considerable number of denning sites have been described for the Eurasian lynx (Matjuschkin 1978, Schmidt 1998), but no quantitative investigation has been made so far on features of microstructure and close surroundings of dens at the population level. During two decades of working with Eurasian lynx in Switzerland, we have gathered information on 70 den sites of radio-tagged female lynx, which we analyse in this paper and relate to the survival of young lynx.

In order to conserve Eurasian lynx it is important to know the environmental requirements of the species, especially with regard to reproduction. For further recovery programmes, suitable habitat with an adequate supply of all relevant resources is a precondition. This includes information on suitable den sites for lynx living in a human-dominated environment. The description of 'suitable habitat', for instance in GIS-based habitat modelling, does generally not consider microstructures such as potential den sites, because such resources are not ascertainable through the geographic or topographic baseline data available.

The objectives of our study were to describe the characteristics of lynx den sites and to test to what extent the den site is crucial for the survival of the kittens, and whether the age (experience) of the mother has an influence on kitten survival. We studied two types of dens: natal dens (place of birth) and maternal dens (all subsequent places kittens are brought to). We considered the following factors as being determinants of den selection: 1) microclimatic (thermal) stability, 2) shelter against weather, 3) protection from predators (Laurenson 1994), and 4) proximity to food sources. Furthermore, we hypothesised a trade-off between the choice of inaccessible (steep) and safe (plane) terrain made by the female lynx. Given the option, the female should choose den sites in steeper and more inaccessible terrain than averagely available. Consequently natal dens should be situated in steeper terrain to avoid human disturbance (Magoun & Copeland 1998). But as the kittens develop and start to move around outside the den, the risk that they might fall down the slope increases (Ewer 1985), and therefore females might choose maternal dens in more even terrain.

Study area

Our investigation of lynx den site was conducted in two populations, one situated in the Swiss and French Jura Mountains and one in the northwestern Swiss Alps (Fig. 1). The Jura Mountains are a secondary chain of limestone mountains forming the northwestern border between Switzerland and France. Elevations range from 372 m a.s.l. (Lake of Geneva) to 1,718 m a.s.l. (Crêt de la Neige). The timber line is reached nowhere. Deciduous forests along the slopes and coniferous forests on the ridges cover 53% of the mountain range. The human population reaches a density of 120/km^2 in most parts of the Jura Mountains. The highlands are intensively used for recreation. The second main study area lies in the northwestern part of the Swiss Alps. Altitude ranges from 400 m a.s.l. (valley bottoms) to 4,000 m a.s.l. (Bernese Alps). Up to approximately 1,000 m a.s.l. forests are dominated by fir *Abies alba* and beech *Fagus silvatica*, often richly interspersed with Norway spruce *Picea abies*, followed by forests dominated by fir and spruce up to the timberline at 1,700-1,800 m a.s.l. Human population density amounts to 57 inhabitants/km^2. Apart from lynx, other predators are red foxes *Vulpes*

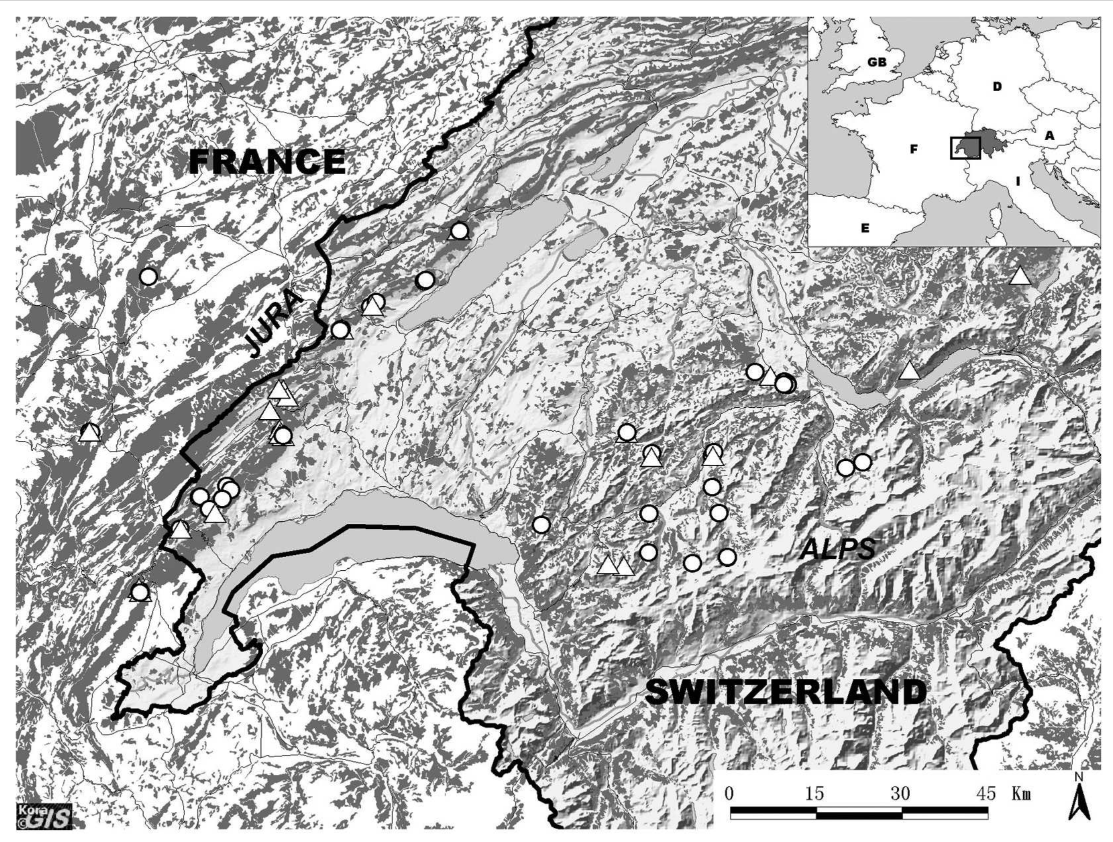

Figure 1. Location of lynx den sites in the Jura Mountains (38) and the northwestern Alps (28) during 1983-2000. The circles represent dens revisited in 2000 and triangles indicate the dens considered but not revisited (only macrostructure analyses). Relief is only shown for Switzerland.

vulpes which is the third most important prey species of lynx in Switzerland (Molinari-Jobin et al. 2007), wild cats *Felis silvestris* (in the Jura Mountains only) and golden eagles *Aquila chrysaetos* (breeding in the Alps only) and a variety of smaller birds of prey and owls. Moreover, badgers *Meles meles*, wild boars *Sus scrofa* and possibly feral cats and stray dogs could represent a danger to young lynx (Kaczensky 1991).

Methods

Since 1983, we have discovered 70 dens belonging to 26 radio-tagged females. Repeated locations of a female at the same spot during the denning season (stationary phase) indicated a possible den site. If subsequently the presence of kittens was confirmed, the place was recorded as a reproductive den. During the first years of our study, the females were just located, but the den site was never approached as long as the family was there. Consequently, for these dens we know the den site (macrostructure), but not the dens themselves (microstructure). Since 1992, the natal dens (in some cases the first maternal dens) have been visited 3-5 weeks after birth and the litters have been inspected in order to collect demographic data (e.g. litter size, sex ratio and health status of kittens). Lynx kittens were ear-tagged, and information on the den site was recorded.

We noted a frequent change of den sites within one reproductive cycle. Females normally moved their kittens to another site after a few weeks, and so used one primary (natal) and 1-2 secondary (maternal) dens for each litter, regardless of whether we visited the den or not. Daily locations of the radio-tagged females allowed us to discover the natal dens (the place where the female settled down for parturition). All subsequently used dens (to which the female carried the cubs) are defined as maternal dens. During summer 2000, we investigated 70 dens (68 former and two of the year). As not all den sites or dens were accessible, and as some old dens were destroyed, we were left with an uneven sample size for den sites (macrostructure) and dens (microstructure). In some cases, the den site and the entrance, but not the interior, was accessible, so the sample size differs from parameter to parameter (Table 1). Of the 30 den sites in the northwestern Alps and the 40 in the Jura Mountains, 44 dens, 23 in the Alps and 21 in the Jura were revisited, whereas 26 dens could not be inspected because they either did not exist any more or could not be found (see Fig. 1). In total, 30 natal and 40 maternal den sites were analysed regarding their geographic and topographic location, and 14 natal and 30 maternal dens were revisited (see Table 1). To revisit the dens, we used GPS location and pictures of the dens and their environment.

The radio-telemetry projects provided the necessary information on the females and their offspring, such as age, reproductive status, chronology of den use, kitten survival and home ranges (Breitenmoser & Haller 1986, Breitenmoser et al. 1993, Breitenmoser-Würsten et al. 2001, Breitenmoser-Würsten et al. 2007). Kitten survival was judged according to field observations until the end of September and until March of the following year (end of the weaning period), respectively.

In order to assess the physical attributes that could influence microclimatic stability, the kittens' shelter against weather and protection from predators in the den, the following parameters were recorded by means of a standardised protocol: type of den site (i.e. closed structure), lengths and di-

Table 1. Natal and maternal den sites investigated in the Jura Mountains and the northwestern Alps during 1983-2000, including date of birth and age of the mothers. In some cases microstructure parameters could not be investigated and thus only macrostructure analyses were done. The female F24 had two litters in 1993, one in May (*) and one in August (**).

				No of natal dens for		No of maternal dens for		
Lynx	Year of birth	Age of the mother	Litter years	All analyses	Macrostructure analysis only	All analyses	Macrostructure analysis only	Total
Jura Mountains								
F11	1984	4/ 5/ 6	1988, 1989, 1990	1	1	3	-	5
F14	1976	13/ 14	1989, 1990	-	1	-	3	4
F15	1986	5/ 6	1991, 1992	-	1	1	1	3
F18	1985	6/ 8/ 9/ 10/ 11	1991, 1993, 1994, 1995, 1996	4	1	3[b]	-	8
F21	1990	2/ 3/ 6/ 7	1992, 1993, 1996, 1997	1	1	2	1	5
F20	1990	3	1993	-	-	1	-	1
F22	1991	2	1993	-	1	1	1[b]	3
F23	1991	2	1993	-	-	-	1	1
F24	1985	8/ 8/ 9/ 10/ 11	1993*, 1993**,1994, 1995, 1996	-	2	4	1	7
F29	1993	3/ 4	1996, 1997	-	1	1	1	3
Northwestern Alps								
F01	1979	4	1983	-	1	-	-	1
F03	1983	2	1985	-	1	-	-	1
F07	1984	2	1986	-	1	-	-	1
F43	1993	4	1997	-	1	-	-	1
F39	1995	2	1997	-	-	1	-	1
F33	1995	2/ 3	1997, 1998	1	-	1	-	2
F37	1994	3/ 4/ 5	1997, 1998, 1999	-	-	3[a]	1	4
F34	1995	2/ 3/ 4/ 5	1997, 1998, 1999, 2000	2	-	3	-	5
F38	1995	2/ 3/ 5	1997, 1998, 2000	2	-	1	-	3
F32	1994	3/ 5	1997, 1999	2[a]	-	-	-	2
F45	1996	2	1998	-	-	1	-	1
F42	1996	2/ 3	1998, 1999	2	-	-	-	2
F51	1996	2/ 3	1998, 1999	-	1	1	-	2
F52	1996	2/ 3	1998, 1999	-	1	1	-	2
F47	1995	4	1999	-	-	1	-	1
F53	1997	2	1999	-	-	1	-	1
Total: 26			54	15	15	30	10	70

[a] One den site was totally identical with another den site of the same female.
[b] One den site was located identically with another den site of the same female.

ameters, number of entries, soil consistency, nesting material, camouflage, cover degree inside and outside, forest type and structure, aspect, visibility (metres of free sight from den entrance to next closed stand) up- and down-hill as well as to both sides (average right and left side), and terrace existence. Detailed information on the parameters is given in Appendix I.

For the evaluation of the strategic location we recorded slope of den site area, altitude, shortest distance to road, forest border and settlement, accessibility for humans (to define the potential of disturbance), number of hiding places, food availability (distance to the forest border was used to test if lynx locate their dens close to potential food sources, since lynx females often kill ungulates near the lower forest edges; Breitenmoser & Haller 1987), and division into natal and maternal dens.

The distances to the different landscape elements, as well as the missing data of the 26 den sites which could not be revisited, such as slope and altitude, were calculated using topographic maps 1:25,000 in the Geographic Information System (GIS) Arc View (ESRI 1996a,b,c). In order to compare geographic and topographic aspects used with the features available in the study areas, we first calculated the females' home ranges (95% minimum convex polygon method) from the coordinates of daily radio-fixes in each breeding year. Home ranges were then merged for each of the reference areas Jura (32 dens) and Alps (25 dens). These areas were divided into grid squares of one hectare. Geographic and land-use data (GEOSTAT base data set, Swiss Federal Statistic Office) accurate to the hectare for these reference areas provided the reference data set. Data analysis included Mann-Whitney U-tests for inter-group comparisons (Asymptotic significance level set at $P < 0.05$ for two-tailed statistics) and Spearman rank test for correlations. Furthermore, we applied Sequential Bonferroni corrections (Quinn & Keough 2002) to the selected significance level in order to reduce the inflation of the true alpha level derived from multiple hypothesis-testing in our study.

To avoid pseudo-replication, two dens, which were used by two females in two consecutive years, were considered only once for the analyses of microstructure and parameters describing the immediate surroundings. Two more sites were considered only once for the analyses of the topographic and strategic situation, because the females had used immediately neighbouring dens in consecutive years. Furthermore, for some den sites, we knew the location (because the female was repeatedly located at this place), but not the actual site (because the female had moved the litter before we could visit it). This leaves us with a basic sample size (see Table 1) of 42 for the microstructure and 66 for the macrostructure analyses. To test whether females had chosen consecutive dens according to individual preferences for specific den sites or habitat structures, we compared the different dens of the single females among themselves before running the subsequent analyses. We did not detect any particular preferences, except for the above-mentioned four pairs of identical dens/sites, which were exclud-

Figure 2. Natal den in a rock cleft (showing a kitten of female F34 in 2000). This is a rather typical situation since 65% of the dens were made of rock. Photo by D. Boutros.

Figure 3. Maternal den site of female F21 in 1992 placed in the root stock of an overthrown tree; a rather atypical den site, lying in flat terrain (15°), providing little shelter and being easily accessible. Nevertheless it represents a maternal den site fairly well, since there were several hiding places around it. Photo by U. Breitenmoser.

ed once. However, the fact that a female chose the same den site again may indicate that this was a particularly ideal site. Furthermore, we examined whether daughters chose similar denning sites as their mothers, but did not find any concordance.

Results

We had information about macrostructure for a total of 66 dens and information about microstructure for 42 dens which was used for analysis.

Physical characteristics and shelter

Natal dens, as well as maternal dens, were mainly situated in rocky sites; 26 dens were in rock (Fig. 2), 13 dens were in wooden material (Fig. 3), and two were made of dirt, i.e. they were subterrestrial caves. Compared to maternal dens, we found no natal dens under rootstocks, hanging branches, piles of dead branches and in the undergrowth. However, we could not record a significant difference between the structures of natal and maternal dens (Table 2). Of all natal and maternal dens, 71% (29 out of 41; one den listed in Table 2 was not assessable) had a closed structure (completely covered by rock or vegetation).

The main chamber of the den had an area of 0.03-8.0 m^2, with an average of 0.97 m^2. While natal den area ranged within 0.24-3.12 m^2, maternal dens had areas of 0.03-8.0 m^2, i.e. their area varied more widely. Of the dens, 50% (21/42) had one entrance. As expected, in 72% (28/39; three dens were not assessable) of natal and maternal dens the soil inside the den was permeable and made of humus. Besides, 64% (25/39; three dens were not assessable) of the dens were generally furnished with nesting material. This means that the floor was covered

Table 2. Structures of natal and maternal dens used by female lynx in the northwestern Alps and the Jura Mountains.

		Northwestern Alps		Jura Mountains		Total	
Type	Description	Natal	Maternal	Natal	Maternal	N	%
Block heap	Among boulders	2	2	2	4	10	24.4
Rock recess	Rock shelter with topsoil ground	1	2	-	3	6	14.6
Rock den	Rock cave	1	-	3	3	7	17.1
Roots of tree	Roots of a standing tree	2	2	-	-	4	9.8
Root stock	Root stock of an overthrown tree	-	1	-	3	4	9.8
Rock cleft	Crevice in the rock	1	2	-	-	3	7.3
Hanging branches	Under low hanging branches	-	2	-	1	3	7.3
Subterrestrial cave	Underground cave	1	1	-	-	2	4.9
Dead branches	Pile of dead branches	-	-	-	1	1	2.4
Undergrowth	in the undergrowth, thicket of bushes	-	1	-	-	1	2.4
Total		8	13	5[a]	15	41	100.0

[a] One natal den site in the Jura Mountains was not assessable.

with leaves, branches and pebbles. Of all natal and maternal den sites, 71% (29/41; one den was not assessable) were situated in mixed forest types, which for the majority were dominated by coniferous trees. No natal dens were located in deciduous forest.

Cover degree in front of the den varied widely, and often there was almost no vegetation cover. In 71% (30/42) of den sites, protection from precipitation in front of the den was not complete. However, in 62% (26/42) of cases, kittens were better protected inside than outside the den, i.e. the den had a higher degree of cover than the surroundings. In 83% (35/42) of cases, protection from sun and rain inside the den was complete. Regarding the aspects of the den sites, east (23%; 15/66) and southeast (21%; 14/66) facing aspects were chosen for almost half of the dens. But had the female really made an active choice or had she just located the den according to occurrence? The small sample size for each of the two reference areas allowed no exact statistic evaluation in the GIS, but we can still draw some conclusions. In the Jura Mountains, southeast was the main available aspect (30.8%), and the majority of the dens were facing southeast (34.4%; 11/32) or east (34.4%; 11/32). In the Alps, the distribution of available aspects was quite balanced, and so were the den sites used. But, they did not face east and southeast at all. Open forest structure surrounded 46% of dens (19/41; one den was not assessable). Maternal den sites were mainly situated in open (43%; 12/28), but also in closed forests. Natal dens, however, were only found in open (54%; 7/13) and half-closed forests (46%; 6/13). Additionally, forest structure significantly correlated with the difference of cover degree, i.e. the more open the forest, the more closed the cover degree inside the den compared to the outside (Spearman rank test: $r = 0.38$, $N = 41$, $P < 0.05$).

Topographic features, visibility and access

In 70% (28/40; two dens were not assessable) of dens, the interior was rich in visual contrasts and therefore provided good camouflage. However, while high (6/13) and low contrast (7/13) was balanced in natal dens (46% high; 54% low), in 82% of the maternal dens contrast was high (23/28). This indicates a significant difference regarding the camouflage in natal and maternal dens ($Z = -2.255$, $P = 0.024$). As kittens in maternal dens are frequently in motion inside and outside the den, concealment and camouflage may be more important for this type of den. While we counted several hiding places around 81% (21/26; two dens were not assessable) of maternal den sites, there were only few hiding places around 67% (8/12; two dens were not assessable) of natal dens. Accordingly, maternal den sites had significantly more hiding places in their vicinity than did natal dens ($Z = -3.040$, $P = 0.002$). In 50% (21/42) of cases, both natal and maternal dens sites could easily be reached by humans. There was an inverse correlation between accessibility to humans and terrain steepness ($r = -0.51$, $N = 42$, $P < 0.01$). We expected that to recognise potential danger early, the mother would rely on a terrace in front of the den with a good overall view. Such a terrace or resting place was found at 62% (26/42) of den sites. Even 71% (10/14) of natal den sites had such a viewpoint.

Up-hill visibility from natal and maternal den sites was on average 5 m and thus much lower than the visibility to both sides and down-hill. The average visibility to both sides of 15 m did not differ between natal (16 m) and maternal dens (14 m). The mean down-hill visibility of 20 m differed slightly, but not significantly, between natal (23 m) and maternal dens (19 m). Over all, visibility did not differ between dens in the Alps and dens in the Jura Mountains. However, down-hill visibility from dens in the Jura Mountains was significantly better than it was from dens in the Alps ($Z = -2.421$, $P = 0.015$).

The steepness of the terrain at den sites was recorded in 10 classes of 5° each. Of the 66 dens considered, 21% (14/66) were located on slopes of 41-45°, 20% (13/66) on slopes of 36-40°, and 18% (12/66) on slopes of 26-30°. There was no significant difference between the slopes of natal and maternal dens, and between those in the Alps (median class = 41-45°) and those in the Jura Mountains (median class = 26-30°). This is remarkable as the terrain in the Alps is significantly steeper than in the Jura Mountains ($\chi^2 = 60721$, df = 4, $P < 0.01$). To find out if den sites were chosen specifically in regard to slope, we compared used with available terrain. For this, data were pooled into five classes instead of 10. A test for small sample size (Byers et al.1984), revealed that the females in both regions found dens in significantly steeper terrain than averagely available (Jura: $\chi^2 = 369$, df = 4, $P < 0.01$; the Alps: $\chi^2 = 59$, df = 4, $P < 0.01$). In the Jura reference area, which included 32 dens, slopes of 26-35° (45%) and 36-45° (32%) were the most used, even though the majority of available slopes were 0-15° (72.2%). In the northwestern Alps, 25 dens were mainly situated on slopes of 36-45° (60%), while the majority of available slopes were 16-25° (33%) and 26-35° (28%).

Dens were located according to the altitude level of the study sites, at 1,395 m a.s.l. (1,060-1,910 m) in the northwestern Alps, and at 1,095 m a.s.l. (610-1,410 m) in the Jura Mountains. In both regions, natal dens (610-1,780 m a.s.l.) were averagely located about 100 m higher than maternal dens (720-1,910 m a.s.l.). This difference was, however, not significant.

Maternal dens were situated slightly, but not significantly, closer to roads (206 m) than were natal dens (305 m). In the Jura Mountains, however, dens lay significantly closer to roads than in the Alps ($Z = -3.912$, $P < 0.001$). This could be explained by the correlation between distance to road and altitude ($r = 0.53$, $N = 66$, $P < 0.01$). As dens in the Alps were located higher than those in the Jura Mountains, they were at the same time more distant from roads.

Maternal dens were insignificantly closer to permanently inhabited settlements (540 m) than were natal dens (557 m). Both types of dens were located nearer to settlements in the northwestern Alps than they were in the Jura Mountains ($Z = -2.005$, $P = 0.045$; according to Bonferroni corrections the P-value is not significant). Vicinity to settlements was overall correlated to flatter slopes ($r = 0.29$, $N = 66$, $P < 0.05$); hence in the generally less steep Jura Mountains, females had to choose slopes further away from settlements to find adequate sites. Natal dens tended, but not significantly so, to be situated closer to forest borders than did maternal dens ($Z = -1.774$, $P = 0.076$). On the other hand, we recorded den sites in the Alps that were significantly closer to the forest border than those in the Jura Mountains ($Z = -4.070$, $P < 0.001$), a consequence of the more fragmented forests at the higher altitudes of the Alps. This also explains our observation that distance to forest border was negatively correlated with elevation of den site ($r = -0.61$, $N = 66$, $P < 0.01$).

Survival of young lynx and age of the mother

The 54 litters listed in Table 1 comprised a minimum of 103 kittens, but for many litters the record is not so complete that it allows an assessment of the survival in relation to the quality and situation of the den sites. In several cases, we did not know the number of kittens born or we lost radio-telemetric contact with the female during or shortly after the denning phase. For 23 out of 26 litters in the Jura Mountains (Breitenmoser-Würsten et al. 2007) and for 19 out of 28 litters in the Alps (unpubl. data), we have a rather complete record, if we consider the number of kittens counted during the first visit at the den to be the original litter size. The 19 litters in the Alps included 44 young lynx, of which 18 (41%) survived until independency in the following March. In the Jura Mountains, we counted 45 kittens in the 23 litters (assuming two kittens for the first litter of F24 in 1993; see Table 1); 18 (40%) survived to the next spring. The over-all survival rate was not different for the two areas ($\chi^2 = 0.271$, $P = 0.603$). By the end of September, seven of the 45 kittens (16%) had disappeared in the Jura Mountains, and 7-13 of the 44 kittens in the Alps were missing (16-30%; even the maximum possible loss of 13 is not significantly different from losses in the Jura Mountains: $\chi^2 = 2.499$, $P = 0.114$). These figures indicate that the heavy toll of the first year was paid after and not during the denning phase.

For 15 mothers, the age was precisely known, and for the other 11 females it was estimated at the first capture. We assumed that the first acknowledged litter was also the first litter of the female, i.e. that she was then two years old. Of the investigated dens, 46% belonged to two (14/54) or three (11/54) year old 'inexperienced' females (see Table 1). The age of the mother correlated only with the cover degree inside the den ($r = 0.31$, $N = 42$, $P < 0.05$); the older the mother, the better the cover degree inside. There was no correlation between age of the mother and survival of the kittens until September.

Discussion

One limitation of our study was that we had to measure microstructure parameters retrospectively. Although we also measured parameters like temperature and light, we did finally decide not to consider them for this reason. Vegetation certainly had changed in some places, but not so extremely that we could no longer recognise the site using old pictures. Some very early den sites still looked exactly the same. In conclusion, with the help of the old pictures we were able to recreate most conditions. Nevertheless, this is one of the reasons why we were left with a changing sample size for microstructure analyses.

Physical nature of den sites

For the microclimatic stability of a den site, the structure and size of the den site is decisive. Our results showed that dens in the Alps and in the Jura Mountains were made of rock and had a surface of approximately 1 m^2. Few entrances, permeable soil of humus furnished with nesting material protected kittens from draught and disease. Besides, the forests in which the dens were located did not only conceal the dens, but also moderated the microclimate. Ambient temperature, soil substrate and nesting material varied according to forest type. All these factors are important for growing lynx kittens, especially in the first weeks of their life when they are almost unable to regulate their body temperature (Jensen et al. 1980). Although we did decide, because of the retrospective character of our study, not to consider the temperature measurements we made, the fact that almost ⅔ of the dens were cooler inside than outside indicates that the dens protect the litters from thermal extremes. The preference for cooling rock dens when temperatures are getting warmer in summer supports our prediction that dens moderate high, but also low ambient temperatures during the day, as Fernández & Palomares (2000) demonstrated for Iberian lynx dens.

Dens must shelter kittens from the weather, from getting wet or being exposed to direct sun radiation. Most dens had closed structures. As the vertical cover from vegetation in front of the den was often low, the den interior shielded the kittens entirely from precipitation and sun. The aspects of the slopes (and thus exposure to direct sun) which the females chose for their dens did not deviate from the absolute availability of aspects within the females' home ranges. However, dens in the Jura Mountains predominantly faced east and southeast (the main exposure of the southern slope of the mountain chain; see Fig. 1), exposing them to the morning sun. On the other hand, dens in the Alps mainly faced north, northeast and west, and so were placed on cooler and wetter slopes. Probably females are restricted in their choice as favoured areas are already used by humans. In the Alps, southern and eastern orientated slopes were largely turned into pastures, while in the Jura Mountains they are still densely forested.

Another demand on dens is to provide protection from avian and mammalian predators. Protection is given directly through the limited access to the den and indirectly through the vegetation cover. When kittens are born, they are a drab sand colour and show relatively little patterning (Turner 1997). After nine weeks, their fur changes to a reddish summer fur, which is more or less strongly spotted (Festetics 1980). At the time kittens start to move around, concealment and camouflage become essential (Kitchener 1991). In our study, maternal dens showed a high contrast providing good camouflage. This is also the time when the mother starts to leave the kittens alone for several hours while hunting and feeding, exposing them more to predation (Kitchener 1991). So we expected a dense horizontal and vertical cover to protect the litter from mammalian and avian predation and to provide additional escape cover, as Laurenson (1994) found out for cheetahs *Acinonyx jubatus*. As expected, forest structure is decisive for the choice of cover, i.e., if the den site itself did not have enough protective structures, the forest patch chosen would be more closed. The fact that there are many hiding places around maternal dens also supports the importance of protection. Some of the caves and clefts used as maternal dens had such a narrow entrance that no animal larger than a lynx kitten could enter it. Obviously, the mother could not join the kittens in these dens, but she called them out when returning to the site.

Losses to predators are mainly minimised through the vigilance of the mothers, detecting approaching predators and taking evasive actions (Caro 1987). In order to recognise potential danger early, the mother requires a good overall view. Most Eurasian lynx dens in our study had a terrace, serving as a resting place and a lookout. The up-hill visibility was lowest. The steeper the slope, the better the shelter, but at the price of reduced visibility up-hill. Free sight down-hill increased with steepness and open forest. Lynx, with their very acute eyesight (Guggisberg 1975), recognise danger at long distance by sight. In our study areas, there are presently no potential aggressors besides humans or large dogs, which could fight off an adult female lynx. For unguarded kittens, however, several avian predators, red foxes, wildcats and even small mustelids are potential dangers.

Location of den sites and human presence

In the cultivated landscapes of the Jura Mountains or the Alps, where people can easily appear anywhere, we anticipated that female lynx would prefer den sites in steep terrain to avoid humans. We hypothesised a trade-off between the choice of steep slopes inaccessible to man and flatter terrain less dangerous for the kittens, when they begin to explore the area surrounding the den (Kitchener 1991). However, we found no significant difference between the slopes of early natal and subsequent maternal dens. Nevertheless, all dens, both in the Alps and in the Jura Mountains, were located in considerably steeper terrain than available. Even if a terrain of a macrostructural point of view seems steep, it always has flatter sections. So we could argue that Eurasian lynx choose terrain that is hardly accessible for humans. Moreover, we recorded several hiding places around maternal dens, while around natal dens there were only few. So kittens can spread out and hide in case of the mother growling when sensing danger, until they hear the 'all clear' (Ewer 1985, Kitchener 1991). When we approached the litters to tag the kittens, we observed that the females generally withdrew from the site, whereas the young hid on the spot. Dens did not differ regarding their distances to settlements, nor in their vicinity to roads.

Shift from natal to maternal den sites

Distances between primary and subsequently used lynx dens never exceeded 500 m. The females shift the kittens regularly, but generally within short distances (Breitenmoser & Haller 1986). Frequent changing of dens may be protective, reducing the risk that the den will be detected by potential predators (Guggisberg 1975, Ewer 1985, Piechocki 1989, Kitchener 1991) or disturbed by humans (Matjuschkin 1978). Other reasons for changing dens are flooding (Hellgren & Vaughan 1989), changes in temperature (Magoun & Copeland 1998), pollution through food remains, ectoparasites (Kitchener 1991) or local prey depletion (Kaczensky 1991). Additional motivations for den relocation could be growing kittens and thus increasing activity of the kittens (Ewer 1985) or an increasing need for space if the den is too narrow as shown with natal dens in the Iberian lynx (Fernandez et al. 2002). Our investigations did not pinpoint any specific reason, but may provide several anecdotal observations. Human disturbance at the den seems to be an obvious reason for changing dens. Other motivations could be location of maternal dens in less dangerous and steep terrain, and prey depletion in the vicinity of the previous den. Maternal den structures were more diverse and also more open. Ruggiero et al. (1998) reported the same for martens *Martes americana*, whose maternal structures were more diverse than their natal structures. This suggests that females are very selective regarding structural attributes when choosing natal dens, but cannot make such a careful choice when they need to find an alternative den site in a hurry.

Survival of young lynx and age of the mother

Mortality of young felids is believed to be highest 3-4 month after birth (Jędrzejewski et al. 1996), when kittens emerge from the dens (Laurenson 1994), and increases again later when the independent young lynx search for their own territories (Breitenmoser & Breitenmoser-Würsten 1998). In our studies, we found that 53 of 89 (60%) lynx kittens died before the next spring, but only 14-20 disappeared before the end of September. However, there is no reliable data on early losses during the denning phase, neither from zoos nor from the wild. Even if kittens are found and tagged in field studies, this is normally done at the age of 3-5 weeks. Earlier losses would go undetected, and subsequent losses are often only discovered in fall or winter. From our field study with radio-tagged females, we know of only two total losses of litters (excluding two losses due to a fatal accident of the mothers), and one partial loss (a young lynx with bite wounds). The limited information about losses during the denning phase did not indicate any correlation between the survival of kittens and the features of den sites. The causes of death in the Jura Mountains or the northwestern Alps (Schmidt-Posthaus et al.2002, Breitenmoser-Würsten et al. 2001, Breitenmoser-Würsten et al. 2007), could not be related to the quality of the dens. For the known cases of death, we can say that 58% were human-related (traffic accident or illegal killings), 19% were orphans, and in 15% the cause of death remained unknown.

Feldman (1993) argued that the experience of domestic cat females has no influence on kitten mortality. And also Palomares et al. (2005) showed that in Iberian lynx survival of young lynx was not related to the mother's age. Caro (1994), however, assumed that in cheetahs the mothers' age might be important for the survival of kittens as young females are less successful at hunting large prey, have to make more hunting attempts and travel farther away from the den. So, we expected that more experienced females would rear healthier kittens with higher chances of survival, but found no correlation between the age of the mother and the survival of juveniles. The supposition that female lynx choose their den sites near forest boarders (presence of prey) for food optimisation was not confirmed, as prey (and thus food) seems abundant and evenly dispersed in our study area. Nevertheless, the female's age seems to influence den site selection. Anecdotal observations in our study indicated that young mothers chose some natal dens in places easily accessible for humans or, on one occasion, a spot very wet after a thunderstorm. But the only clear correlation was that older females chose dens with a higher cover degree. Besides, it was interesting to see that four females chose exactly the same site in two consecutive years, and that these sites were very hard to access. This indicates that particularly safe sites may be used repeatedly for denning.

Conclusive remarks

Female lynx used a variety of different places as natal or maternal sites, and the fact that maternal dens were always located close to natal dens indicated that females had no problems discovering alternative sites. Considering the variety of dens and the very high diversity of the two study areas, den sites did not seem to be a limiting resource. Different from e.g. Iberian lynx in a flat living space (Fernández & Palomares 2000), den limitation in Eurasian lynx in our mountainous study areas is of no conservation concern. Microstructure is not necessarily related to a certain habitat type. For instance, a grown-over block heap may be found in the forest, but may not be indicated in any map nor visible on any GIS model. The resolution of the presently readily available eco-geographic baseline data to feed a GIS model does not allow for microstructure analyses. A female lynx is obviously able to assess the quality of a den site in regard to protection. From our human perspective, most sites were well chosen (because we had a hard time to find or reach them). In the Alps and in the Jura Mountains, well-suited den sites may be so abundant that females never have a problem finding good sites in strategic places.

We conclude that quality of den sites was not a limiting factor in the survival of young lynx in our study areas, though our data set is not complete in all respects. Finding the den site and litter of lynx or other large carnivores is, even in long-time field studies, a rare incident, and to acquire a convincing sample is almost impossible for one study alone. To achieve this over a long period from different projects, however, requires consistent and careful recording of all observations, a point we missed in the early years of our field studies.

Acknowledgements - for the achievement of this study, the following persons deserve special thanks: Jean-Pierre Airoldi for the statistical advice, Hannes Baur for assistance with the evaluation programs, and Damiano Torriani for the making of the maps. All collaborators involved in the Swiss lynx project/ KORA. We also thank the Federal Department of National Topography. Digital geographic data: Water and Political Frontiers: © BFS GEOSTAT, © Federal Department of National Topography; Place and Forest: Vector 200, © Federal Department of National Topography; Height pattern: DHM25: © Federal Department of National Topography, RIMINI: © BFS GEOSTAT.

References

Breitenmoser, U. & Breitenmoser-Würsten, C. 1998: Der Luchs. - Wildbiologie - Biologie einheimischer Wildtiere, 1/10a, Infodienst Wildbiologie & Ökologie, Zürich, Switzerland, 24 pp. (In German)

Breitenmoser, U. & Haller, H. 1986: Zur Raumorganisation der in den Schweizer Alpen wiederangesiedelten Population des Luchses (Lynx lynx). (In German with an English summary: Spatial organization of the reintroduced population of the lynx (Lynx lynx) in the Swiss Alps). - Zeitschrift für Säugetierkunde 51: 289-311.

Breitenmoser, U. & Haller, H. 1987: Zur Nahrungsökologie des Luchses Lynx lynx in den Schweizerischen Nordalpen. (In German with an English summary: Feeding ecology of the lynx (Lynx lynx) in the Swiss Alps). - Zeitschrift für Säugetierkunde 52: 168-191.

Breitenmoser, U., Kaczensky, P., Dötterer, M., Breitenmoser-Würsten, C., Capt, S., Bernhart, F. & Liberek, M. 1993: Spatial organisation and recruitment of lynx Lynx lynx in a re-introduced population in the Swiss Jura Mountains. - Journal of Zoology (London) 231: 449-464.

Breitenmoser-Würsten, C., Vandel, J-M., Zimmermann, F. & Breitenmoser, U. 2007: Demography of lynx Lynx lynx in the Jura Mountains. - Wildlife Biology 13: 381-392.

Breitenmoser-Würsten, C., Zimmermann, F., Ryser, A., Capt, S., Lass, J. & Breitenmoser, U. 2001: Untersuchungen zur Luchspopulation in den Nordwestalpen der Schweiz 1997-2000. - KORA Bericht Nr. 9, pp. 49-61. (In German).

Byers, C.R., Steinhorst, K. & Krausman, P.R. 1984: Clarification of a technique for analysis of utilisation-availability data. - Journal of Wildlife Management 48: 1050-1059.

Caro, T.M. 1987: Indirect costs of play: cheetah cubs reduce maternal hunting success. - Animal Behaviour 35: 295-297.

Caro, T.M. 1994: Cheetahs of the Serengeti Plains, group living in a asocial species. - University of Chicago Press, Chicago, USA, 43 pp.

Clutton-Brock, T.H. 1991: The evolution of parental care. - Princeton University Press, Princeton, New Jersey, USA, pp. 85-88.
Esri (Environmental System Research Institute) 1996a: Using ArcView GIS: User manual. - Environmental Systems Research Institute, Redlands, California.
Esri (Environmental System Research Institute) 1996b: Using ArcView Spatial Analyst. - Environmental Systems Research Institute, Redlands, California.
Esri (Environmental System Research Institute) 1996c: Using Avenue. - Environmental Systems Research Institute, Redlands, California.
Ewer, R.F. 1985: The carnivores. - Cornell University Press, Comstock Publishing Associates, Ithaca and London, pp. 329-355.
Feldman, H.N. 1993: Maternal care and differences in the use of nests in the domestic cat. - Animal Behaviour 45: 13-23.
Fernández, N. & Palomares, F. 2000: The selection of breeding dens by endangered Iberian lynx (Lynx pardinus): implications for its conservation. - Biological Conservation 94: 51-61.
Fernández, N., Palomares, F. & Delibes, M. 2002: The use of breeding dens and kitten development in the Iberian lynx (Lynx pardinus). - Journal of Zoology 258: 1-5.
Festetics, A. 1980: Der Luchs in Europa. - Kilda-Verlag, Greven, Germany, pp. 199-200. (In German).
Guggisberg, C.A.W. 1975: Wild cats of the world. - Taplinger Publishing Company, New York, USA, pp. 56-57.
Hellgren, E.C. & Vaughan, M.R. 1989: Denning ecology of black bears in a south-eastern wetland. - Journal of Wildlife Management 53: 347-353.
Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Bunevich, A.N. & Milkowski, L. 1996: Population dynamics (1869-1994), demography, and home ranges of the lynx in Białowieża Primeval forest (Poland and Belarus). - Ecography 19: 122-138.
Jensen, R.A., Davis, J.L. & Shnerson, A. 1980: Early experience facilitates the development of temperature regulation in the cat. - Developmental Psychobiology 13: 1-6.
Kaczensky, P. 1991: Untersuchungen zur Raumnutzung weiblicher Luchse (Lynx lynx), sowie zur Abwanderung und Mortalität ihrer Jungen im Schweizer Jura. - Diploma thesis, Lehrstuhl für Wildbiologie und Jagdkunde, Forstwissenschaftlichen Fakultät an der Universität München, Germany, pp. 14-63. (In German).
Kitchener, A. 1991: The natural history of the wild cats. - Christopher Helm, A&C Black, London, Great Britain, pp. 187-200.
Laurenson, M.K. 1994: High juvenile mortality in cheetahs and its consequences for maternal care. - Journal of Zoology (London) 234: 387-408.
Magoun, A.J. & Copeland, J.P. 1998: Characteristics of wolverine reproductive den sites. - Journal of Wildlife Management 62: 1313-1320.
Matjuschkin, E.N. 1978: Der Luchs, Lynx lynx. - A. Ziemsen Verlag, Die neue Brehm-Bücherei, Wittenberg Lutherstadt, Germany, pp. 99-104. (In German).
Molinari-Jobin, A., Zimmermann, F., Ryser, A., Molinari, P., Haller, H., Breitenmoser-Würsten, C., Capt, S., Eyholzer, R. & Breitenmoser, U. 2007: Variation in diet, prey selectivity and home range size of Eurasian lynx Lynx lynx in Switzerland. - Wildlife Biology 13: 393-405.
Palomares, F., Revilla, E., Calzada, J., Fernández, N. & Delibes, M. 2005: Reproduction and pre-dispersal survival of Iberian lynx in a subpopulation of the Doñana National Park. - Biological Conservation 122: 53-59.
Piechocki, R. 1989: Die Wildkatze. - A. Ziemsen Verlag, Die neue Brehm-Bücherei, Wittenberg Lutherstadt, Germany, pp. 173-179. (In German).
Quinn, G.P. & Keough, M.J. 2002: Experimental design and data analysis for Biologists. - Cambridge University Press, Cambridge, London, 50 pp.
Ruggiero, L.F., Pearson, D.E. & Henry, S.E. 1998: Characteristics of American marten den sites in Wyoming. - Journal of Wildlife Management 62: 663-673.
Schmidt, K. 1998: Maternal behaviour and juvenile dispersal in the Eurasian lynx. - Acta Theriologica 43: 391-408.
Schmidt-Posthaus, H., Breitenmoser-Würsten, C., Posthaus, H., Bacciarini, L.N. & Breitenmoser, U. 2002: Causes of mortality in reintroduced Eurasian lynx in Switzerland. - Journal of Wildlife Diseases 38: 84-92.
Slough, B.G. 1999: Characteristics of Canada lynx, Lynx canadensis, maternal dens and denning habitat. - Canadian Field-Naturalist 113: 605-608.
Turner, A. 1997: The big cats and their fossil relatives. - Columbia University Press, New York, USA, pp. 94-95.

Appendix I

Details of all measured parameters and number of assessable natal and maternal dens in the northwestern Alps and the Jura Mountains (except den structures, see Table 2).

		Assessable				
		NW-Alps		Jura Mountains		
Parameter	Explanation	Natal	Maternal	Natal	Maternal	Total
Microstructure:						
Closed structure	Completely covered by e.g. rock or vegetation (yes/no)	8	13	5	15	41
Main room area	Average length multiplied with average width of the main room; measured using measuring tape	7	13	5	13	38
Number of entries	1 = one, 2 = two, 3 = three, 4 = several	8	13	6	15	42
Soil consistency	1 = non-permeable/naked rock, 2 = permeable/humus, 3 = non-permeable/humus, 4 = permeable/naked rock	8	13	5	13	39
Nesting material	1 = humus or rock, 2 = in addition leaves, branches and pebbles	8	13	5	13	39
Camouflage	1 = high contrast, 2 = low contrast (inside the den)	8	13	5	14	40
Cover degree inside	1 = 25%, 2 = 50%, 3 = 75%, 4 = 100%	8	13	6	15	42
Cover degree outside	Cover degree from above given by vegetation	8	13	6	15	42
Forest type	DF = deciduous forest, MF = mixed forest dominated by deciduous or coniferous forest, or equally mixed, CF = coniferous forest, SF = spruce forest	8	13	5	15	41
Forest structure	1 = closed (thick timber forest), 2 = half open (loose arrangement of trees), 3 = open (clearing with single trees)	8	13	5	15	41
Aspect	Measured using compass; (N, NE, E, SE, S, SW, W, NW)	14	14	15	23	66
Visibility slope up	Measured by distance measurer, metres of free sight from the	7	11	5	14	37
Visibility slope down	den entrance to the next close stands (measured 1 m above	7	11	5	14	37
Visibility slope sideward	ground level)	7	11	5	14	37
Terrace existence	(Yes/no)	8	13	6	15	42
Macrostructure:						
Slope of den site area	See details in Results	14	14	15	23	66
Altitude	Measured using an altimeter; (m)	14			23	66
Distance to road	Roads that are passable by car; (m)	14	14	15	23	66
Distance to forest border	A forest border was considered as such if the adjacent grassland was bigger than 1 ha; (m)	14	14	15	23	66
Distance to settlement	All-year inhabited houses located below 1200 m a.s.l.; (m)	14	14	15	23	66
Accessibility for humans	1 = easy, 2 = medium, 3 = difficult (for humans)	8	13	6	15	42
Number of hiding places	1 = several, 2 = hardly any; any structure that may serve as a sheltered place for the cubs	8	13	4	12	37