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Characterisation and Assessment of Suitability of Eurasian Lynx (*Lynx lynx*) Den Sites

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Content

Abstract

I retrospectively investigated characteristics of den structures and den sites used by female Eurasian lynx (*Lynx lynx*) in the Jura Mountains and the north-western Alps of Switzerland. Between 1983 and 2000, 30 natal and 40 maternal dens from 26 females were located within the field work of the Swiss Lynx Project. Important den structures were closed, i.e. provided good shelter, had few entrances, and measured one m^2. Most dens were located in mixed forests with relatively open vegetation allowing for a visibility of 10-20 m. Contrary to my expectations, natal, as well as maternal dens were equally exposed to human disturbance and lay in more or less dangerous terrain. Overall, the two den types barely differed. While kittens were better hidden in natal dens and natal dens almost never had an open structure, maternal dens were surrounded by a larger number of hiding places. Furthermore, I noticed numerous differences between the 40 den sites of the Jura Mts. and the 30 den sites of the NW-Alps: dens in the Jura were situated lower and in flatter terrain; besides, they were located more distant from settlements and forest borders and closer to roads than den sites in the Alps. The age of the mother had no direct influence on cub survival. However, the age (experience) of the female was correlated with the microclimatic stability of a den site and its shelter against the weather. These were the principle factors important for the survival of young lynx in the first year of their life.

1. Introduction

The ability to produce surviving offspring is a component of the individual fitness of an animal. As with any mammal, parental care is very important in Eurasian lynx for successful reproduction and consequently for the fitness. The principal benefits of parental care to the care-giver lie in their effects on survival, growth and eventual breeding success of its progeny (Clutton-Brock 1991). In species where internal fertilisation occurs, parental care is usually provided by the female, because the male has no guarantee that the eggs have been fertilised by his sperm, making it not in his interest to help caring for the offspring (McFarland 1985, Alcock 1993). Moreover, it seems that, as a consequence of lactating, the mother rears the cubs on her own. Although birth in large mammals is rather a rare event and despite of felids having relatively many offspring compared to other large mammals, only few survive the first year. Large mammals are commonly characterised by low adult mortality (high life expectancy) and relatively high mortality of juveniles (Clutton-Brock 1991). In consequence the female's increased input, above all the rearing, during the first year is very important.

After a gestation time of approximately 68-72 days (Matjuschkin 1978, Kitchener 1991) female lynx at the end of May, beginning of June give birth to 1-4 kittens (Kitchener 1991, Kaczensky 1991, Breitenmoser et al. 1993). They are born in a semi-altricial state. Their eyes are closed, and they have poor motor condition and thermoregulatory control (Deag et al. 1988, Kitchener 1991). Therefore, kittens to a large degree depend on a number of environmental factors, such as for instance the behaviour of the mother (Jensen et al. 1980). After two weeks, their eyes open and they begin to develop thermoregulatory control (Kitchener 1991). As their motor actions and senses develop, the cubs which are approximately 26 days old begin to explore the area surrounding the lair (Kitchener 1991). Once the young emerge from the safety of the nest they are in a very vulnerable stage. Not yet familiar with the locality, they are in danger of straying away and getting lost. Or if the den site is situated dangerously, there would be considerable danger of youngsters falling and being injured. Furthermore, they are still relatively small and weak and therefore are certainly in danger of attack by predators (Ewer 1985). To sum up, the rearing of the lynx implies three stages: The period of lactation, which is recognised to be energetically the most costly component of reproduction in mammals (Laurenson 1995). The mixed nutrition period during which the young begin to eat solid food but still continue to take milk as well (Ewer 1985). And finally, the weaning period, in which the young learn how to find their own food and after which they become fully independent of their parent (Ewer 1985). For a successful breeding, lynx require a diversity of forest conditions. These forest mosaics must include early successional forests, which are necessary for hunting; but also need to include easily accessible mature forests, which are used for denning (Koehler and Britell 1990). Forests must be large enough in order to provide cover for successful hunting, as well as for changing of the den sites (Breitenmoser and Breitenmoser-Würsten 1998). A fix home range allows lynx the exclusive use of well known resources such as cover, den sites and sufficient prey so as to assure a prosperous breeding (Breitenmoser and Breitenmoser-Würsten 1998). Because lynx are territorial, however, females do not have equal access to all resources available. Females attain sexual maturity at an age of 21 month (Guggisberg 1975, Matjuschkin 1978).

Despite the fact that lynx, compared to other large mammals, can conceive relatively many offspring, only few young lynx survive the first months, young lynx mortality being highest between 3 to 4 months after birth (Jedrzejewski et al. 1996). Only 50 % survive the first year (Breitenmoser et al. 1993, Kaczensky 1991). Consequently, suitable structures and sites for denning are essential resources for lynx (Slough 1999, Fernandez and Palomares 1999, Kitchener 1991).

Although there are several publications on denning sites of carnivores, only few descriptions of den sites of lynxes have been published. Fernández and Palomares (1999) showed that the physical nature of dens is more important for the breeding Iberian lynx (*Lynx pardinus*) than habitat features (like prey densities or structure of vegetation). Preferred breeding structures, such as the preserving of old-growth habitat for the endangered Iberian lynx, can be limiting resources. And therefore, the importance of suitable denning sites must be recognised and considered in conservation strategies (Fernández & Palomares 1999). Slough (1999) described the characteristics of den sites, maternal dens and denning habitat of Canadian 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 the close environment of dens on the population level.

In Switzerland, the Eurasian lynx was exterminated during the 19th century. The reason for this was direct persecution by man and the lynx' high sensibility to destruction of the habitat (deforestation). After 1971, the lynx was re-introduced into the Jura Mts. and the Alps. In the beginning, the two populations spread quite fast. However, since the mid 1980s, the expansion of both populations came to a halt, although not all favourable habitat was populated yet (Breitenmoser 1998). Since 1983, lynx were studied by radio telemetry in different areas of the Alps (Breitenmoser and Haller 1993, Haller 1992) and from 1988 in the Jura Mts. (Breitenmoser et al. 1993). In order to sustain (or to manage) the actual population in Switzerland, it is important to know the environmental requirements of Eurasian lynx, especially with regard to reproduction. Moreover, if lynx are to be re-introduced into a new area (e.g. translocation to eastern Switzerland), high quality territories with appropriated den sites are a precondition. But how does an appropriate den site for lynx living in Switzerland look like?

The objectives of this study were to describe the characteristics of lynx den sites and to test if the den site, and its eventual selection by the mother (experience), are crucial for the survival of the cub. I studied two types of dens: natal and maternal dens. I considered several factors as being determinants of den selection: microclimatic stability, shelter against weather, protection from predators, proximity to food and water sources, security from humans and safety of terrain. I predicted that den sites provide: (i) microclimatic stability, by controlling eventual high ambient temperatures and consequently protect young from thermal maxima (Bleich et al.1996). But on the other hand, there should be as few entrances as possible, in order to avoid draught (Jensen et al. 1980). Thus, the soil of the den site should be dry and of permeable substrate (e.g. humus) so that the kittens will not fall ill. (ii) shelter against weather: Dens should be covered almost entirely by vegetation and/ or the den site itself should have a closed structure to prevent kittens from getting wet or being exposed to direct solar radiation. The latter could be, as far as possible, prevented by choosing the aspect of the lair so that the den site is turned away from the sun. (iii) protection from predators (Laurenson 1994): Den sites should be secure and well-camouflaged. Vegetation should be dense enough to hide the lair from potential avian or mammal predators. On the other hand, the mother should recognise danger early, i.e. have a good overall view. (iiii) proximity to food and water sources: lairs should be situated near prey residences and water bodies. Furthermore, I hypothesised a trade-off between the choice of inaccessible (steep) and safe terrain (plane) made by the female lynx. If the female has the option, she should locate maternal sites in more even terrain than the natal ones, in regard to the risk of kittens to fall down the slope when they start to roam around (Ewer 1985) and consequently natal dens should be situated in steeper terrain to avoid human disturbance (Magoun and Copeland 1998).

2. Study area and methods

2.1. Study area

Investigation of lynx den site was conducted on two populations, one situated in the Swiss and French Jura Mountains and one in the North-West-Alps of Switzerland (Fig. 1).

The Jura Mts. are a secondary chain of limestone mountains with a surface of 4405 km^2 forming the north-western border of Switzerland with France. The closer study area in the Swiss part was limited to the Jura Vaudois and Neuchâtelois, plus a small part of the bordering French Jura (departments of Ain and Doubs). Elevations range from 372 m (Lake of Geneva) to 1679 m (Mont Tendre Mountain). The natural forest limit is reached nowhere. Deciduous forests along the slopes and coniferous forests on the ridges cover 53 % of the highlands. The human population reaches a density of 120/ km^2 in most parts of the Jura Mts.. The highlands are intensively used as recreation area.

The second main study area (2500 km^2) lies in the north western part of the Swiss Alps, including parts of the canton of Bern (Bernese Oberland), of Fribourg, of Valais and of Obwalden. Altitude ranges between 400 m (valley bottoms) and 4000 m (Bernese Alps). Up to approximately 1000 m we find fir-beech forests (*Abieto-Fagetum*), often richly interspersed with spruce trees, which next dominate in fir-spruce forests (*Abieto-Piceetum*) up to the timberline of 1700-1800 m. Population density amounts to 57 inhabitants/ km^2. Thirty-year mean precipitation for April, Mai, June and July in the Jura Mts. was 58, 77, 92 and 76, and in the

NW-Alps 99, 120, 152 and 138 (data provided by MeteoSwiss).

Chamois (*Rupicapra rupicapra*) and roe deer (*Capreolus capreolus*), the main prey of the lynx, are abundant in both study areas. 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. Apart from lynx, other predators are red foxes (*Vulpes vulpes*) (which at the same time is a prey species), wild cats (*Felis sivestris*) and golden eagles (*Aquila chrysaetos*). Moreover, badgers (*Meles meles*), wild boars (*Sus scrofa*) and straying dogs could represent a danger for young lynx (Kaczensky 1991).

2.2. Den location

Over the past 18 years, some 70 dens of 26 radio-tagged females have been discovered by KORA/ Swiss lynx project. Repeated locations of a female at the same site during the denning season (stationary phase) identified a possible den site. If the female was later seen with kittens or if tracks of kittens were seen at the site, the place was confirmed as a reproductive den. At the beginning, the dens were just located, but in recent years the dens have been inspected in order to collect data on demographic parameters (litter size, sex ratio, health status of kittens). On this occasion, the lynx kittens have been marked with a little ear tag. Additionally, a frequent shifting between den sites had been noticed within one reproductive cycle. I categorised dens as either natal (used during parturition) or maternal (used subsequent to the natal den and before weaning) (Magoun and Copeland 1998). During summer 2000, the dens were systematically searched with the GPS and with the help of pictures. Each time, I was thereby accompanied by a person who had been there before. Of the 70 dens, 44 were found again, whereas 26 dens could not be inspected because they either did not exist any more or could not been found (Fig. 1).

2.3. Sampling procedure

After visiting the den sites, I noticed that in 2 cases a den was completely identical with another den of the same female, and in 2 other cases a den was located identically as another den site. Consequently, for the evaluation of the physical nature of a den site (micro-structure and aspects of the immediate surroundings) I disposed of a sample of 42 dens, i.e. the re-visited dens. And for the evaluation of the habitat features and the strategic location, I included all 66 den sites. Comparison of natal and maternal den sites, as well as the comparison of the two regions, were made for all variables.

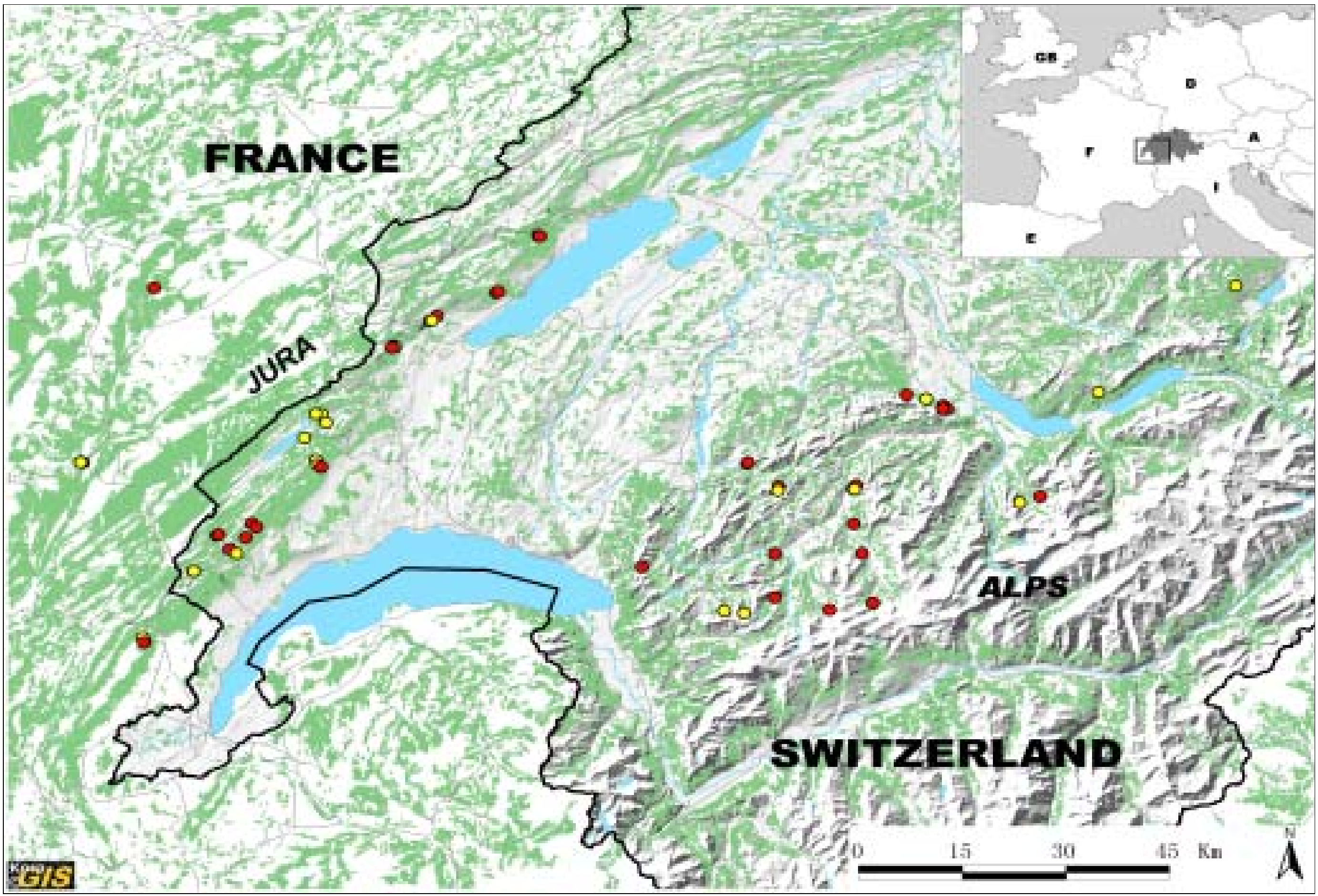

Fig. 1. Map of the study area in the Jura Mts. and the NW-Alps with the localisation of all 70 investigated den sites. Of these, 44 den sites were visited (red) and 26 were not visited (yellow).

2.3.1. Available data from previous studies

First of all, I collected all the available data from previous studies, among others from marking and monitoring forms and from databases of KORA: Co-ordinates of den sites for their localisation and co-ordinates of daily female residence in order to construct their home ranges and build three reference areas; former pictures of the dens for their identification; survival rate and causes of mortality of the kittens, whereby I divided the survival rate into survival until summer (end of summer), winter (October-March) and next spring; moreover, age of the mother, while females younger than four years were considered inexperienced, as they, at the earliest, reproduce at the age of two years; and finally, the division into natal and maternal dens.

In the NW-Alps sixteen European lynx females were radio-tagged and they bred successfully between 1983 and 2000, and in the Jura Mts. from 1988 to 1997 ten females bred successfully. During the investigation in the year 2000, I was able to find again 23 out of the 30 used den sites of the NW-Alps, and 21 out of the 40 used den sites of the Jura Mts.. In total, 30 natal and 40 maternal den sites were analysed, and 29 natal and 37 maternal dens were inspected (Table 1).

As already mentioned, in two cases two den sites were completely identical and in other two cases two

Table 1. Number of natal and maternal den sites from 1983 - 2000 in the Jura Mts. and the NW-Alps, that were inspected and investigated. Date of birth and age of the mothers.

Lynx	Year of birth	Age of mother	Breeding years	*n* natal dens	*n* maternal dens	inspected/ investigated
Jura Mts.						
F11	1984	4/ 5/ 6	1988, 1989, 1990	2	3	4/ 5
F14	1976	13/ 14	1989, 1990	1	3	0/ 4
F15	1986	5/ 6	1991, 1992	1	2	1/ 3
F18	1985	6/ 8/ 9/ 10/ 11	1991, 1993, 1994, 1995, 1996	5	3 [b]	7/ 8
F21	1990	2/ 3/ 6/ 7	1992, 1993, 1996, 1997	2	3	2/ 5
F20	1990	3	1993	0	1	1/ 1
F22	1991	2	1993	1	2 [b]	1/ 3
F23	1991	2	1993	0	1	0/ 1
F24	1985	8/ 8/ 9/ 10/ 11	1993*, 1993**,1994, 1995, 1996	2	5	4/ 7
F29	1993	3/ 4	1996, 1997	1	2	1/ 3
NW-Alps						
F01	1979	4	1983	1	0	0/ 1
F03	1983	2	1985	1	0	0/ 1
F07	1984	2	1986	1	0	0/ 1
F43	1993	4	1997	1	0	0/ 1
F39	1995	2	1997	0	1	1/ 1
F33	1995	2/ 3	1997, 1998	1	1	2/ 2
F37	1994	3/ 4/ 5	1997, 1998, 1999	0	4 [a]	3/ 4
F34	1995	2/ 3/ 4/ 5	1997, 1998, 1999, 2000	2	3	5/ 5
F38	1995	2/ 3/ 5	1997, 1998, 2000	2	1	3/ 3
F32	1994	3/ 5	1997, 1999	2 [a]	0	2/ 2
F45	1996	2	1998	0	1	1/ 1
F42	1996	2/ 3	1998, 1999	2	0	2/ 2
F51	1996	2/ 3	1998, 1999	1	1	1/ 2
F52	1996	2/ 3	1998, 1999	1	1	1/ 2
F47	1995	4	1999	0	1	1/ 1
F53	1997	2	1999	0	1	1/ 1
Total: 26			*54*	*30*	*40*	*44/ 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
The female F24 had two litters in 1993, one in May (*) and one in August (**).

dens were located identically, but the den sites themselves differed (Table 1). Consequently, the data set for some investigation reduced from 70 to 66 and for the rest of the analysis from 44 to 42.

2.3.2. Field methods and evaluations by GIS

In order to assess the microclimatic stability in the den (a) the structure variables of dens were recorded; (b) all lengths and diameters were measured with measuring tape and the number of entries to the dens were counted; (c) the difference of temperature from inside to outside was calculated; (d) the soil consistency and humidity, and the nesting material were estimated; and finally (e) the forest type was characterised.

Afterwards, seven variables measuring cub protection against weather were measured, estimated or characterised. This variables were: (a) cover degree inside and outside; (b) type of den site (i.e. closed structure); (c) forest and understory structure, which described the protection in front of the den; (d) again, soil humidity; and (e) aspect, which was compared with the available aspect of the reference area.

Furthermore, protection from predators was defined by following variables: (a) visibility from the den slope up, slope down and to both sides (average from right and left side), i.e. meters of free sight from the den entrance to the next tree, and presence of a terrace, in order to record if the mother had a resting place in front of the den with a good overall view; (b) camouflage, colour and light (comparison inside-outside), to test whether lairs were dark and of brown colour like the fur of the kittens; (c) forest and herb structure, to analyse their impact on accessibility for avian and terrestrial predators, and on the concealing of the lair; (d) and finally, structure of den site and cover degree.

For the evaluation of the strategic location I recorded: (a) slope of den site area; (b) altitude; (c) shortest distance to road, forest border and settlement; and noise level and accessibility for humans, in order to define the potential human presence; (e) number of hiding places, terrace occurrence, and division into natal and maternal dens. Other variables characterising the strategic location were food and water availability: the distance to the forest border was used to test if lynx locate their dens close to potential food sources, since lynx kill ungulates often near forest edges (A. Jobin, pers. comm.). For the investigation of water availability, the distance to the next water body was measured. Although, the distance to the water body is supposed to become a critical factor with water shortage (few precipitation).

The distances to the different landscape elements, as well as the missing data of the 26 den sites which could not be inspected, such as slope and altitude, were calculated using topographic maps in ARC VIEW (GIS, 1:25’000). Many of the differences between Jura and Alps, such as the distances from the den site to settlement, road, forest border and water body, are likely a consequence of a different landscape. In the run-up to my study, I should have quantified the absolute availability of landscape parameters in the two study areas and investigated whether the used den site locations were not simply determined by the given circumstances of the residence area. But within the scope of the restricted time of my work I had to do without it. However, I will analyse it specifically in a further study.

The following previously mentioned information were qualitatively imprecise: temperature, soil humidity and light. Retrospectively it was impossible to properly measure these parameters. However, the relative difference of temperature and light in all probability stayed the same.

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

2.4. Data analysis

As already mentioned (2.3.), two dens and four den sites were identical. To avoid pseudoreplication without discarding valuable data, I removed, depending on the evaluation, the 2 res. 4 dens. Due to small sample size and non-normally distributed data, I performed all analyses using non-parametric statistics. All variables were first tested for normality, using both graphical and statistical methods. Inter-group comparisons between natal and maternal dens, and between dens of the Jura Mts. and of the NW-Alps were analysed with Mann-Whitney U-Tests, with the significance level set at $p<0.05$ for two-tailed statistics. Correlations between the different variables were calculated with Spearman rank test. A probability of less then 0.05 was accepted as statistical justification for rejecting the null hypothesis. To explore which parameters were associated with the different features and the strategic location of the den sites, I used Correspondence Analysis (CA). All tests were run with SPSS software, except the CA which was performed using XLSTAT.

3. Results

3.1. Features of den sites

42 re-visited dens of 20 different females were inspected and measured, 21 in the Jura Mts. and 21 in the NW-Alps, altogether, 13 natal and 29 maternal dens (Table 1).

3.1.1. Microclimatic stability

Twenty-seven dens were in rock; 10 of these were located between boulders. Each time 7 den sites were rock recesses and rock lairs. And three dens were located in rock clefts. Other thirteen den sites were of wooden material; always four in the roots of standing trees and in the root stocks of overthrown trees. Further 3 dens were located under the low hanging branches of trees, and one under a pile of dead branches and one in the undergrowth. And finally two den sites were made of earth, i.e. were earth lairs (Fig. 2) (for examples see pictures in Appendix I).

Natal dens as well as maternal dens were mainly situated in rocky sites. Block heaps (n = 4) and rock lairs (n = 4) were the most common natal den structures, and again block heaps (n = 6) and rock recesses (n = 6) were mostly used as maternal dens. There were no natal dens under root stocks, hanging branches, piles of dead branches and in the undergrowth. However, I could not record a significant difference among the structures of natal and maternal dens (Fig. 2). 29 out of 41 of these dens had a closed structure.

The main chamber of the den had an area of 0.03 to 8 m^2, with an average of 0.97 m^2. While natal den area ranged from 0.24 to 3.12 m^2, maternal dens had an area of 0.03-8.0 m^2, i.e. their area varied more widely. However, mean area did not differ significantly.

21 out of 42 dens had one entrance to the lair. But the number of entries neither to natal nor to maternal den sites was correlated with the difference of temperature inside and outside the den. More than half of the den sites were cooler inside than outside (26 out of 35).

As expected, the soil of the lair in natal and maternal dens was mainly permeable (28 out of 39), dry (20 out of 36) and made of humus (28 out of 39). Besides, it was generally furnished with nesting material (25 out of 40). This means that in addition to leaves, the floor was covered with branches and stones.

Natal, as well as maternal den sites were most of the time situated in mixed forest types (n = 29), which for the majority were dominated by coniferous trees (Fig. 3). It is to be noticed that no natal den was located in deciduous forests.

Via CA I found out that the crucial factors for microclimatic stability were size and type of den site. They were responsible for 42 % of the variation. Additionally, forest type (18 % of variation) and the number of entries (16 % of variation) also had a certain influence.

3.1.2. Shelter against weather

The cover degree in front of the den varied widely and often there was almost no cover by vegetation. Correspondingly, in 30 den sites the protection from precipitation in front of the lair was not guaranteed completely. However, in two third (n = 26) of the cases the kittens were covered better inside than outside, i.e. the lair had a higher cover degree (Fig. 4).

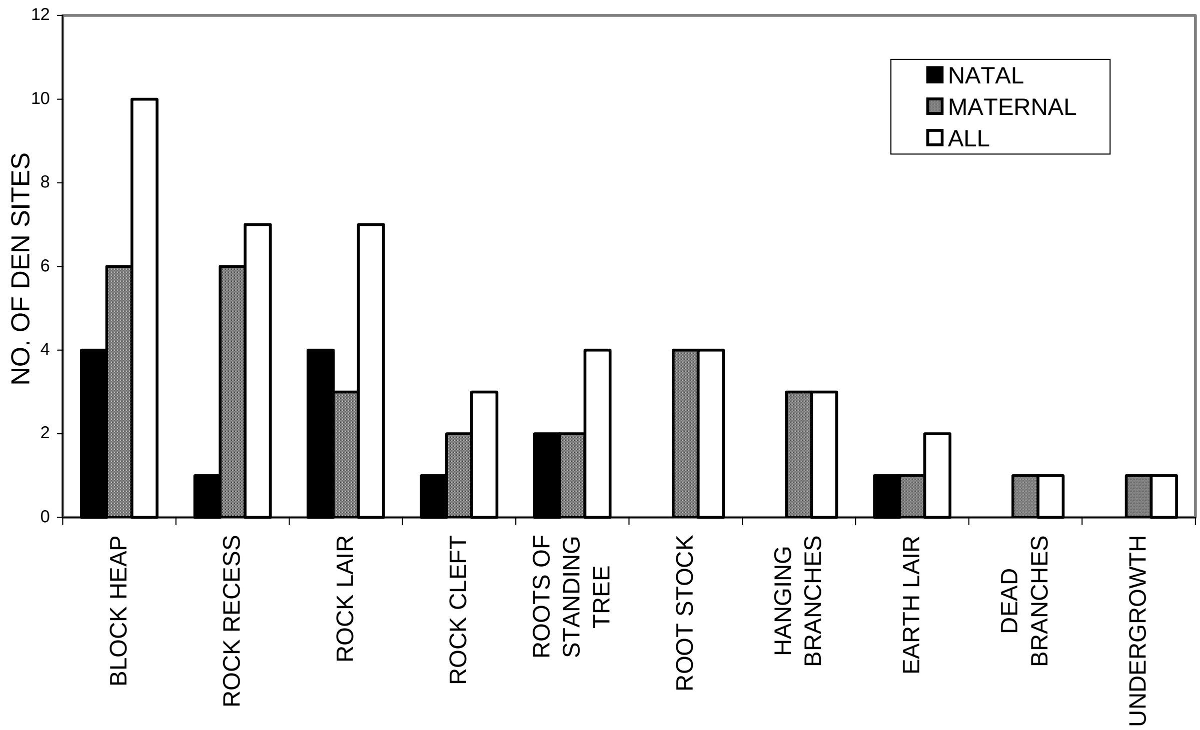

Fig. 2. Structure of natal and maternal dens used by female Lynx.

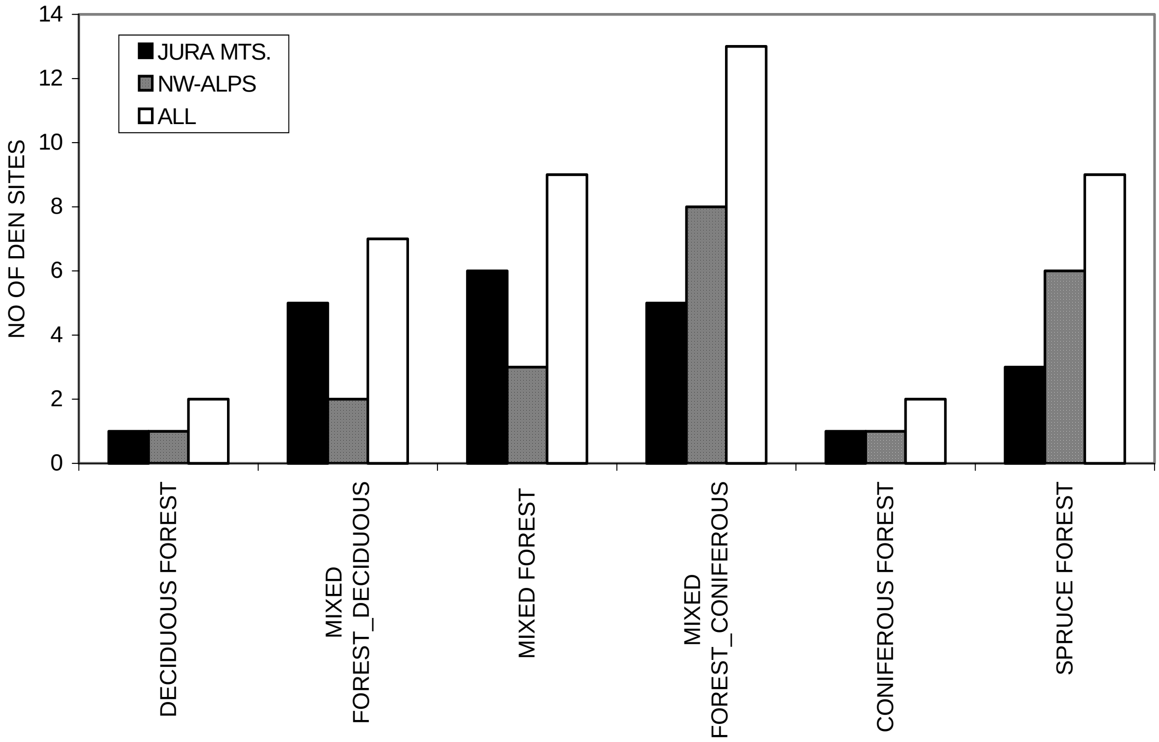

Fig. 3. Number of den sites of the Jura Mts. and the NW-Alps that were located in the six different forest types.

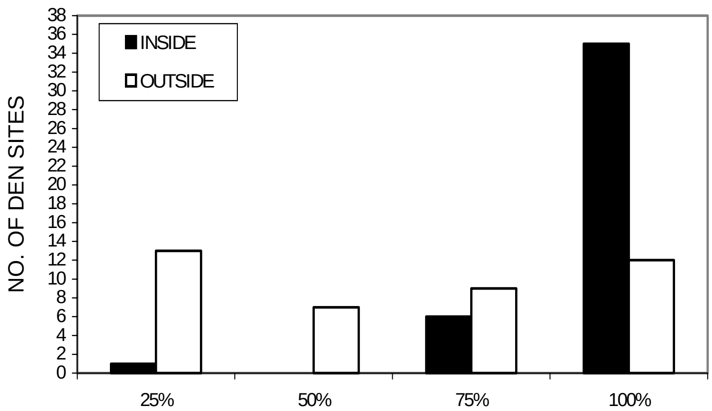

Fig. 4. Cover degree inside and outside den sites.

Considering the aspects of all den sites I noticed, that east (n = 15) and south-east (n = 14) aspects were chosen for almost half of the dens. But had the female really made a choice or had she just located the den according to the occurrence? In order to compare the used aspects with the available aspects of the study area, I first calculated the home ranges of the females which were based on the co-ordinates of the daily female radio-tracking of each breeding year. Only tracking forms with the preciseness of 2-4 were considered. I determined home ranges with the 95% minimum convex polygon method (GIS) calculated over all years that a female had kittens. Afterwards, the home ranges were summarised and divided into three different zones (reference areas 1, 2 and 3) (Fig. 5). If I had joined the home ranges of the Jura to one singular area, a large amount of unused space would have been included. These three reference areas were then, by means of a grid, divided into squares of one hectare. Then the aspect of each square was calculated and the average aspect of all squares together was computed for each reference area (Table 2).

The small sample size allowed no exact statistic evaluation, but still made it possible to draw some conclusions. In reference area 1, which included 12 den sites, south-east was the main available aspect (30 %) and the majority of the dens, too, were situated south-eastward (42 %). In reference area 2, with 20 den sites, 32 % of aspects given by environment were south-east. In this area also six dens faced south-east (30 %), but the greater part faced east (45 %). Finally in reference area 3, including 25 dens, the distribution of available aspects was quite balanced. And although these den sites, too, had several aspects, they did not point east and south-east at all (Table 2).

The majority of dens was surrounded by an open forest structure (n = 17). Maternal den sites were mainly situated in open forest (n = 12), but some also

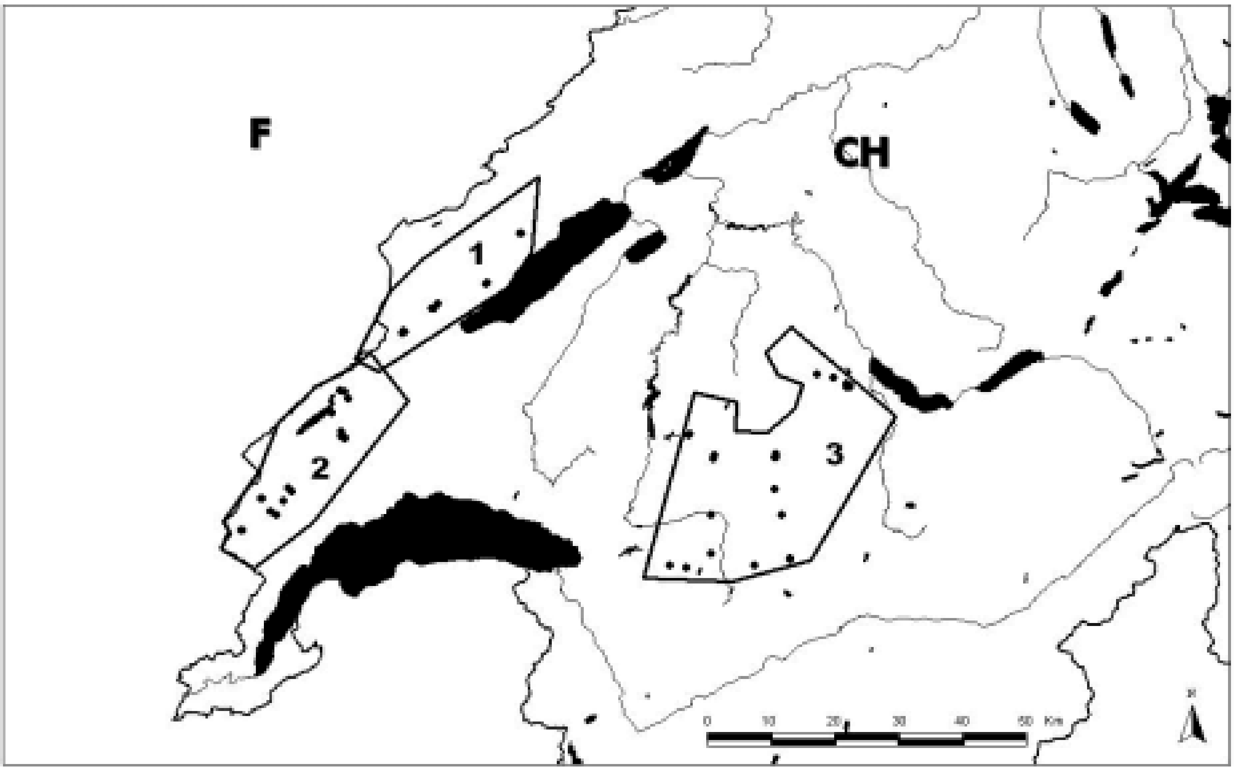

Fig. 5. Map with the three reference areas for the investigation of the aspect.

Table 2. Used and available aspect in the three reference areas.

Reference area 1

	USED	AVAILABLE
FLAT	(0) 0%	13%
NN	(1) 8.2%	9%
NE	(0) 0%	4%
EE	(2) 16.6%	8%
SE	(5) 42%	30%
SS	(2) 16.6%	16%
SW	(0) 0%	3%
WW	(0) 0%	4%
NW	(2) 16.6%	13%
TOTAL	(12) 100%	100%

Reference area 2

	USED	AVAILABLE
FLAT	(0) 0%	14%
NN	(1) 5%	6%
NE	(1) 5%	5%
EE	(9) 45%	13%
SE	(6) 30%	32%
SS	(1) 5%	9%
SW	(0) 0%	3%
WW	(0) 0%	5%
NW	(2) 10%	13%
TOTAL	(20) 100%	100%

Reference area 3

	USED	AVAILABLE
FLAT	(0) 0%	7%
NN	(6) 24%	13%
NE	(6) 24%	11%
EE	(0) 0%	12%
SE	(0) 0%	12%
SS	(1) 4%	9%
SW	(3) 12%	8%
WW	(5) 20%	13%
NW	(4) 16%	14%
TOTAL	(25) 100%	100%

in closed forests. Natal dens, however, were never located in closed forests, but only in open (n = 7) and half closed forests (n = 6). Additionally, the 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 with outside ($r = 0.38$, $n = 42$, $p < 0.05$). By way of contrast, the understory layer did not contribute to the shelter given by vegetation. Understory level around natal dens was medium (n = 7) to low (n = 6), whereas around maternal dens in 11 out of 29 cases the understory was high.

As mentioned in 3.1.1., the ground of the lairs was mainly dry. Additionally, soil humidity was correlated with the cover degree of the den site inside ($r = 0.507$, $n = 36$, $p<0.01$). Consequently, the dampness of the ground indicated to what extend the litter was protected from precipitation, i.e. the better the cover degree inside, the dryer the soil and the more protective the lair against rain.

By means of CA, I noticed that the main factors having an impact on shelter against weather, were the aspect and the den type. They explained 48 % of the variance. Soil humidity (24 % of variance) and forest structure (10 % of variance), however, also had an influence. So, as previously mentioned, cover degree, correlating with the structure of the forest and the soil humidity, also had an impact on shelter.

3.1.3. Protection from predators

The interior of the lairs generally was highly contrasted, i.e. provided good camouflage (n = 29). However, while the camouflage seemed not to be important in natal dens (high n = 6; low n = 7), in more than two third of maternal dens the contrast was high (n = 23). The difference of camouflage between natal and maternal dens was therefore significant (U-Test, $p< 0.05$). As kittens in maternal dens are frequently in motion, the concealment within the environment is very important. Colour itself, on the other hand, seemed not to be of much importance; most of the dens were brown (16 out of 24). While maternal dens mainly had the same light inside and in front of the den (13 out of 25), natal dens mostly were darker inside (n = 8). However, the difference between natal and maternal dens was not significant, but there was a tendency (U-Test, $p = 0.056$). Furthermore, the difference of light was correlated with the forest structure. The more open the forest, the darker the light inside the den compared to outside ($r = 0.38$, $n = 39$, $p< 0.05$).

I predicted that in order to recognise potential danger early, the mother would rely on a terrace in front of the den with a good overall view. More than half of the den sites had such a resting place (n = 26). Especially natal den sites, where even three quarters had a terrace (n = 10).

With an average of 5 m the visibility from natal and maternal dens up-hill was quite smaller than the visibility to the other sides. The mean visibility of 20 m down-hill, slightly but not significantly differed between natal (23 m) to maternal dens (19 m). The downward sight a female had was correlated with the structure of the forest. The more open a forest, the more distant the view ($r = 0.54$, $n = 38$, $p< 0.01$). The visibility to both sides, with an average of 15 m, did not significantly differ from natal (16 m) to maternal den sites (14 m). Nevertheless, the visibility slope down, from dens situated in the Jura Mts., was significantly better than from dens in the NW-Alps (U-Test, $p< 0.05$). Moreover, the visibility up-hill was negatively correlated with the slope, i.e. the flatter the terrain, the better the visibility slope up ($r = -0.34$, $p< 0.05$). Otherwise, with regard to visibility, I could not find a difference between the dens from Jura Mts. and NW-Alps (Fig. 6).

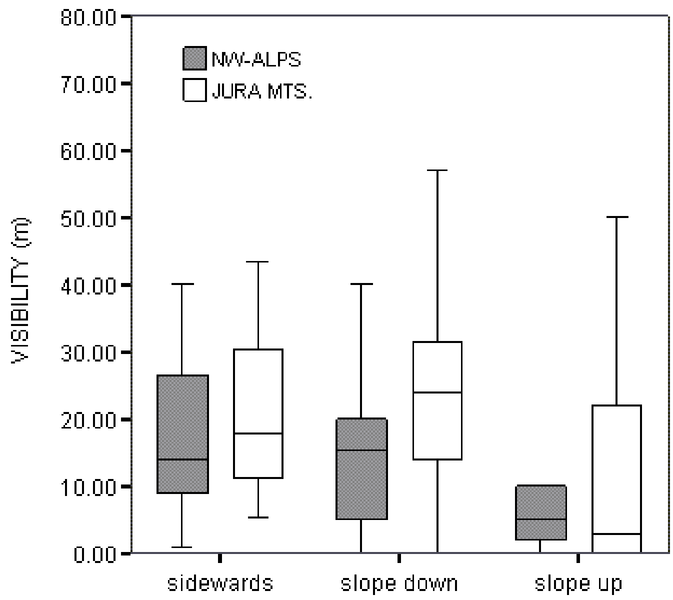

Fig. 6. Visibility from den sites in the Jura Mts. and the NW-Alps to all four directions (slope up, slope down and sidewards). Bars represent the inter-quartile range. The whiskers show the range of values that fall within 1.5 hspreads of the hinges.

In order to hide the lair from potential avian or mammal predators the vegetation should be sufficiently dense. As previously worked out (3.1.2.), not the understory vegetation but rather the forest structure provided a good cover, i.e. the forest was more closed, when the den site itself had not enough protective structures and gave poor shelter.

By way of CA I identified the principle factors influencing the protection from predators, namely the visibility to both sides and slope down, explaining 33 % of the variance, and the visibility slope up (31 % of variance). Consequently, slope (being correlated with the visibility slope up) and forest structure (correlating with the down-hill) to a certain extent were also decisive. And as I will mention later, the accessibility for humans was correlated to the visibility to both sides and therefore had also an indirect impact.

3.2. Location of den sites

66 den sites from 26 females were investigated, 28 in the NW-Alps and 38 in the Jura Mts. Altogether 29 natal and 37 maternal dens (Table 1).

3.2.1. Topographical demands and human influence

The majority of the dens were located at an average slope of 41-45° (n = 14), 36-41° (n = 13) and 26-30° (n = 12). While dens in the NW-Alps (41-45°) lay in significantly steeper terrain than dens in the Jura Mts.(26-30°) (U-Test, $p< 0.05$); I could not notice a significant difference between the slope of natal (Jura 31-35°/36-40°; Alps 41-45°) and maternal dens (Jura 26-30°; Alps 36-40°) (Fig. 7).

Generally, den sites were situated between 610 and 1910 m at an average of 1200 m. As expected, the dens in the NW-Alps (1060-1910 m) were located at a significantly higher elevation (1395 m), than those in the Jura Mts. (610- 1410 m) with an average of 1095 m (U-Test, $p< 0.01$). In both regions, natal dens (610-1780) were located on average 100 m higher than maternal ones (720-1910); the difference between the altitude of natal and maternal dens was not significant though.

Although maternal dens were situated closer to roads (206 m) than natal dens (305 m), the distances did not differ significantly. In the Jura Mts., however, dens lay significantly closer to roads than in the NW-Alps (U-Test, $p< 0.01$) (Fig. 8). 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 NW-Alps were located higher than those in the Jura Mts., they were at the same time more distant from roads. Besides, the vicinity to roads also correlated with the slope, i.e. the flatter the area the nearer the roads ($r = 0.38$, $n = 66$, $p< 0.01$).

The mean distance from natal dens to the next permanently inhabited settlement was 557 m and the one to maternal dens 540 m. Though maternal dens appeared to be closer to settlements, the difference was not significant. However, I recorded a significant difference in the distance to settlements between the dens of the NW-Alps and the Jura Mts. (U-Test, $p< 0.05$); in the NW-Alps dens were located nearer to settlements than in the Jura Mts. (Fig. 8). As with the distance to the road, I noticed a correlation between the vicinity to settlements and the slope ($r = 0.29$, $n = 66$, $p< 0.05$): The flatter the den site area the closer the settlements. The vicinity of settlements was also correlated with the noise level ($r = 0.31$, $n = 40$, $p< 0.05$): The more distant the dens from the settlements, the calmer the den site surroundings. Around most dens the noise level was neither loud nor silent, but medium (n = 21).

Though natal dens were not located significantly nearer to forest borders than maternal dens, a tendency was distinguishable (U-Test, $p = 0.076$). On the other hand, I recorded that den sites in the NW-Alps were significantly closer to the forest border than in the Jura Mts. (U-Test, $p< 0.01$) (Fig. 8).

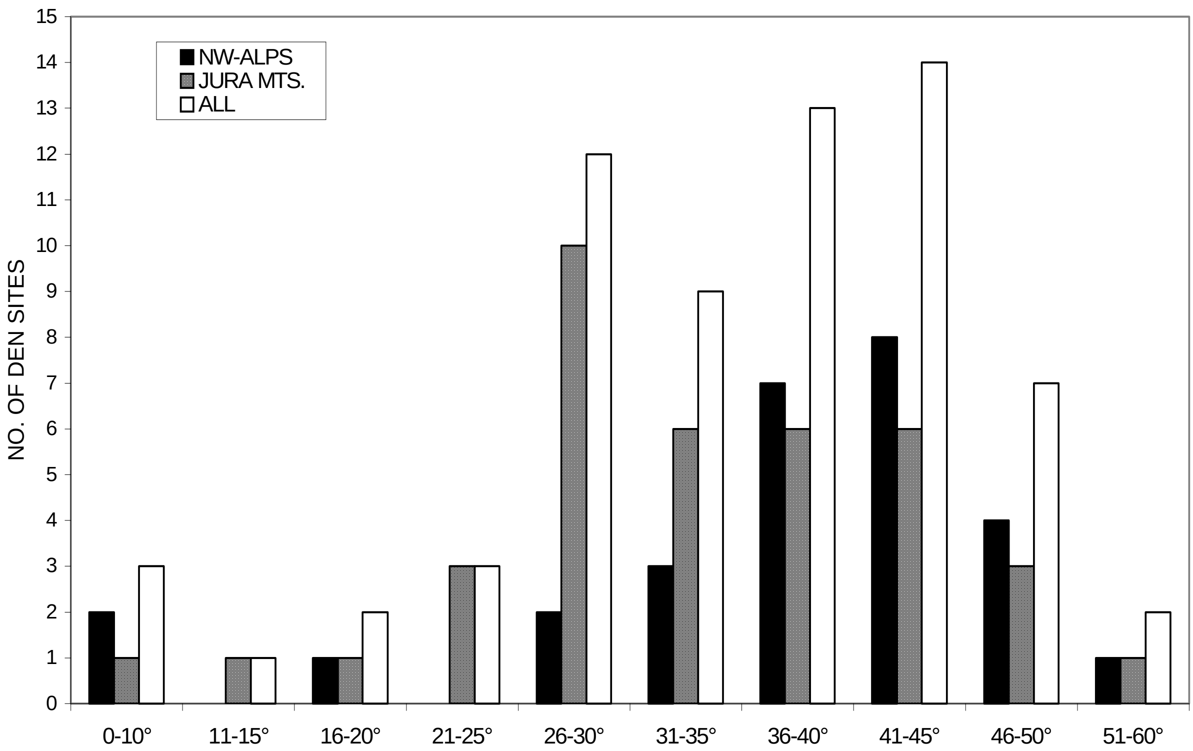

Fig. 7. Slope of den site area in the Jura Mts. and the NW-Alps (in degree).

The proximity to the forest border negatively correlated with the elevation of the den site ($r = -0.61$, $n = 66$, $p < 0.01$), i.e. the higher the location of the den the nearer the forest border. And as dens in the NW-Alps were on higher elevation than those in the Jura Mts., they were also closer to forest borders.

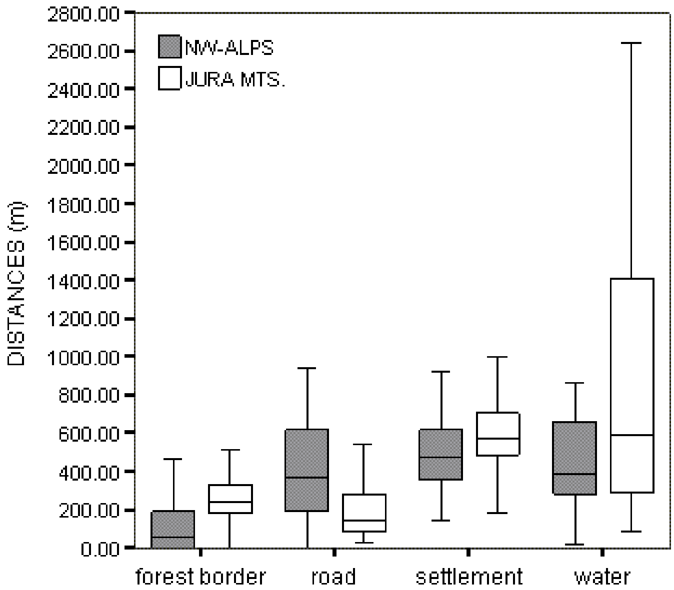

Fig. 8. Distances from den sites in the Jura Mts. and the NW-Alps to the next road, settlements, forest border and water bodies. Bars represent the inter-quartile range. The whiskers show the range of values that fall within 1.5 hspreads of the hinges.

While I counted several hiding places around maternal den sites ($n = 21$), there were only few around natal dens ($n = 8$). Accordingly, a maternal den site had significantly more hiding places in its surroundings than a natal one (U-Test, $p < 0.01$), which is important for quick hiding in case of danger when the kittens roam around.

Half of the den sites, natal as well as maternal dens, could be easily reached by humans ($n = 21$). Thus, the steeper the terrain around the den the more difficult the accessibility for humans ($r = -0.51$, $n = 42$, $p < 0.01$). Moreover, accessibility was correlated with the visibility sideways ($r = 0.40$, $n = 37$, $p < 0.05$), i.e. the easier attainable for human beings the better the sight to the right and to the left.

Through the CA I discovered that the crucial factors for a good strategic location were the distances to the forest border, to the settlements and to the road, and the altitude. They gave an explanation for 79 % of the variance. Also slope and noise level had an indirect impact because they correlated with the crucial factors.

3.2.2. Demands for food and water

As I observed in 3.2.1., the distance to the forest border primarily depended on the region and did not differ between natal and maternal dens. However, a tendency of locating natal dens nearer to the forest border than maternal dens was noticeable. In general the distance from the water source to the natal den was 385 m (range15-2486 m) and to the maternal den 628 m (range 86-2640 m). But although, in both regions, natal dens (Alps 326 m, Jura 521 m) were situated nearer to water bodies than maternal dens (Alps 663 m, Jura 600 m), the difference between natal/ maternal and Alps/ Jura was not significant. However, since the proximity to water did not significantly correlate with the precipitation (values from MeteoSwiss), I concluded that there existed enough possibilities for drinking and that the distance to the water therefore could be neglected (Fig. 9).

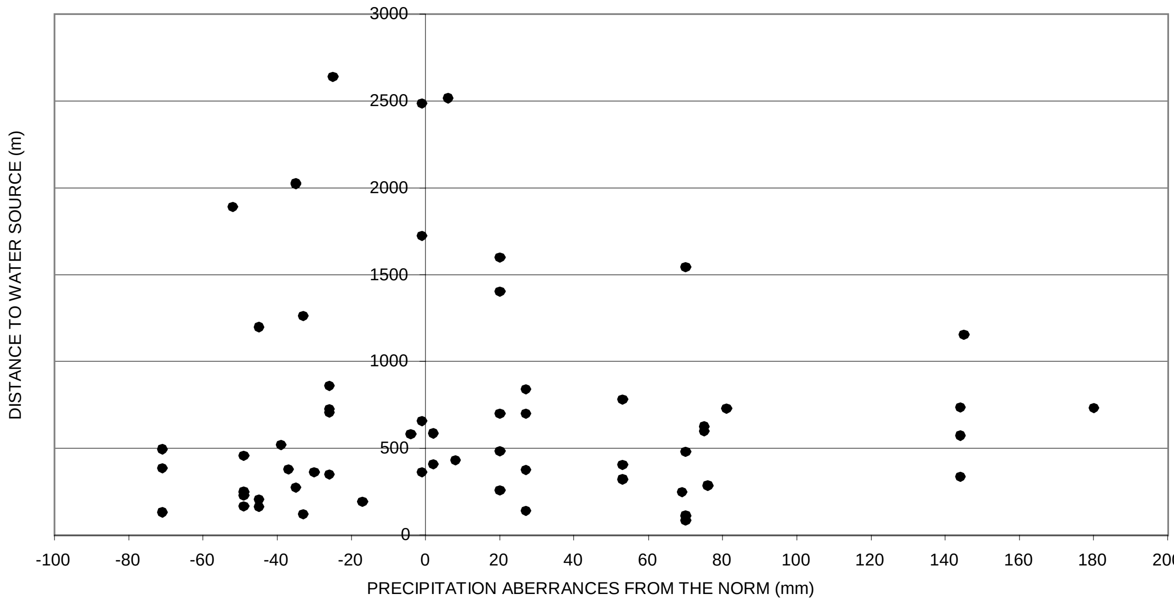

Fig. 9. There was no significant correlation between the distances from the den sites to the water bodies and the precipitation (water shortage).

3.3. Choice of den site/ survival of the cub

To investigate the survival of the kittens I only included their mortality rate over the first year of their lives. I did this for two reasons: On the one hand, because in large mammals juvenile mortality is important. On the other hand, young lynx, when leaving the mother, could no longer be observed since they had no radio collar. That is why the available data on young lynx often are limited to the first year. Besides, it is difficult to record the exact date of death as the cubs were not regularly observed/ monitored (i.e. their mother radio-tagged). The disappearance of a cub would maybe only be discovered some time after its death. Therefore the data of KORA database were roughly divided into survival until summer, winter or next spring.

In general a female lynx gave birth to 2 kittens in the months of May or June. Of the 97 kittens (n = 102), whose destinies were known, 70 kittens were still living in summer and only 46 in winter, i.e. only 47 % survived their first year of life (data base of KORA) (Table 3). Of the 50 known litters (n = 54), 14 litters survived entirely until next spring, from 16 litters only half survived and from 14 litters all kittens died before the following spring. Of the 18 kittens with known date of death dying during the first year, 11 died for unknown reasons, 6 conditional on humans and one through disease. Moreover, I also analysed the reproductive success for each female, i.e. how many of all her kittens survived until the following spring. F37 managed to rear all her 5 kittens, 3 of 4 cubs of F52 and of F38, and 2 of 3 of F51, too, survived. On the other hand, only 1 out of 7 kittens from F21, and 1 of 5 kittens of F14 survived the first year (Table 3). Offspring survival correlated with the difference of cover

Table 3. No. of kittens per female that were still alive in summer, winter or the following spring, i.e. that survived the first year of their lives (data provided by KORA).

Female	**No. of kittens**	**No. of litters**	**No. of kittens alive in**		
			summer	**winter**	**next spring**
F18	11	5	11	10	6
F21	7	4	7	1	1
F53	2	1	2	1	1
F24	9	5	9	8	4
F37	5	3	5	5	5
F51	3	2	3	2	2
F45	1	1	1	1	0
F11	6	3	6	5	3
F32	6	2	6	2	2
F03	2	1	2	1	1
F15	3	2	3	3	1
F14	5	2	5	4	1
F39	1	1	1	1	0
F42	5	2	5	3	2
F20	1	1	1	1	1
F29	3	2	1*	1	1
F07	1	1	?		
F38	4	3	4	3	3
F47	2	1	2	1	1
F23	2	1	2	2	1
F34	11	4	11	8	5
F43	1	1	?		
F52	4	2	4	3	3
F33	3	2	2**	1	1
F22	2	1	2	2	1
F01	2	1	2	1	0
Total	*102*	*54*	*97*	*70*	*46*

* the destiny of the two other kittens is not known
** the destiny of the third kitten is not known

degree ($r = 0.33$, $n = 40$, $p < 0.05$), the cover degree inside ($r = 0.35$, $n = 40$, $p < 0.05$) and the soil humidity ($r = 0.34$, $n = 34$, $p < 0.05$). I therefore concluded that the better the cover degree inside the lair and the better the cover degree inside compared to outside, the more litters survived up to the following spring. And thereof further follows that the chance of survival is higher for young growing up in lairs with dry soil.

A similar problem arose with the calculation of the females' age. Since some females were not radio-tagged from birth, their age could only be determined after examination of one of their teeth (small incisor pulled at capture/ marking). Of the females, which were ear-tagged during their childhood, the age was known. Consequently, for 15 females the age was calculated precisely and for the other 11 females it was estimated. I assumed that the first acknowledged litter also was the primary litter of this female, i.e. that she then was two years old.

Approximately 46 % of the investigated dens were from two (n = 14) or three (n = 11) year old females (Table 1), which I considered to be "inexperienced". Cover degree inside the den also correlated with the age of the mother ($r = 0.31$, $n = 42$, $p < 0.05$): The older the mother the better the cover degree inside. I also found a tendency that the age of the mother correlated with the distance to the forest border ($r = 0.22$, $n = 66$, $p = 0.084$). To my surprise, there was no correlation between the age of the mother and the survival of the litter.

Another difficulty in my analysis was that the 66 investigated dens were from 26 females. Thus, the females had various dens per year and over various years (Table 1). Were this dens hence not dependent from each other, as one female eventually had a preference for specific den or habitat structures? For this reason before running the analysis I compared the different dens of a single female among themselves. I could not notice particular preferences, except for the two dens which were absolutely identical and for the other two dens which were located in the same place. As a consequence, I omitted the double dens of my evaluations. Furthermore, I examined whether daughters choose similar denning sites as their mothers did. But also in this case I could not find a concordance.

When I included the age of the mother and the survival of the litter in the CA mentioned in chapter 3.1.1., 3.1.2., 3.1.3. and 3.2.1. I found out that

a) the main factors explaining microclimatic stability, were age of the mother and den type (33 % of the variance), with other 26 % of the variance given through the size of the den site, i.e. the surface of the main room;
b) the principle factors explaining the shelter against the weather, were once again age of the mother and den type (38 % of the variance). Moreover, aspect (24 % of the variance) and survival of the litter (14 % of the variance) were correlated with it;
c) the age of the mother and the survival of the litter were not among the factors explaining the variance in the protection against predators and the location of the den site.

4. Discussion

The choice of a particular breeding den is related to a combination of factors. On one side, it is influenced by the ability to satisfy the demands of cubs during their development, i.e. award/ grant their security. On the other side, it should also correspond to the needs of lactating females (Fernández and Palomares 1999). I concentrated above all on the security and protection a den should provide to the offspring, using two different approaches for analysis: the physical nature of dens and the habitat features.

4.1. Features of den sites

For the microclimatic stability of a den site, structure and size of den sites are decisive. My results showed that preferred dens were made of rock and had a surface of approximately 1 m^2. Few entrances and a dry, permeable soil of humus, furnished with nesting material, preserved kittens from draught and disease. Lindemann (1955) argued that young lynx in all development stages show a special preference for soft and dry substratum. And since temperature inside was cooler than outside, the litter was also protected from thermal maxima. Besides, the forest in which the den was located, too, had an influence on the microclimate of the den. According to the type of the forest, the ambient temperature, the soil substrate and the nesting material varied. 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). The preference for cooling rock lairs when temperatures are getting warmer in summer, supports my prediction that dens moderate high ambient temperature.

Moreover, den sites should shelter cubs from the weather. A lair should prevent kittens, as far as possible, from getting wet or being exposed to direct sun radiation. That is why dens most of the time had closed structures. Since the vertical cover by vegetation in front of the lair was often insufficient, in return, the lair interior shielded the cubs entirely from precipitation and sun. However, the cover degree depended also on the forest structure. If the forest was closed the lair was even more open. But as dens mainly were located in open forests, the cover degree inside compared to outside was bigger. Does the female have a possibility to influence the protection from heat in front of the den by choosing its aspect so that it is turned away from the sun? My study did not reflect such a preference, the females' choice reflected the absolute availability. But what if the choice of the home range itself was already influenced by the quality of available den sites? However, dens in the Jura faced east and south-east, i.e. were exposed to morning sun and therefore not too susceptible to the main daily heat. But after a cold night the morning sun also warms up quickly. Dens in the Alps mainly pointed north, north-east and west. This can be explained through forest distribution. Southern and eastern orientated slopes mostly are used as meadows or pastures, while there is a stronger forestation on north- and west-slopes. Additionally, the soil humidity could be considered an indicator for the shelter from precipitation. And since, as already mentioned, the ground inside the dens was dry, the cover degree inside had to be good. As a consequence cubs did not risk to fall ill, e.g. to catch a pneumonia secondary to exposure (precipitation, moisture and draught). To sum up, dens rather were closed or covered (vegetation).

An other objective of this study was to investigate the protection from predators. On the one hand, the protection given directly by a den and on the other hand the cover through vegetation. Especially in maternal dens the interior of the lairs provided a good camouflage. When kittens are born, they are of drab sand colour, after 9 weeks their fur changes to a reddish summer fur (Festetics 1980). Moreover, I presume that young lynx, such as cheetahs, show relatively little patterning while adults are more or less strongly spotted (Turner 1997). As expected, the contrast in natal dens was rather uniform, while maternal dens showed a high contrast. Another reason for the importance of a good camouflage in maternal dens is that kittens start to walk around with 26 days (Kitchener 1991). Accordingly, they are frequently in motion and therefor concealment with the environment becomes important. Dense horizontal and vertical cover protects the litter from mammalian and avian predation and provides additional escape cover (Koehler 1990). My results indicated that not understory vegetation structure but only forest structure preserved cubs from aggressors. Besides, encounters with predators can be minimised by mothers being more vigilant, detecting predators more often and taking evasive action (Caro 1987). In order to recognise potential danger early, the mother requires a good overall view. For that reason the dens were equipped with a terrace. This served the mother as resting place and simultaneously as survey point. The visibility slope up was the lowest one. However, it increased the flatter the terrain became. I assume that the visibility up-hill is a trade-off to the shelter. The steeper the slope, the better the shelter, but at the price of a reduced visibility. Often dens were located below small precipice. The visibility slope down and to both sides was similar. Anyway, free sight downwards increased the more open the forest was. I guess that lynx rather recognise danger by sight than by smell, as lynx hunt by eye and as their sight is very acute (Guggisberg 1975). Guggisberg (1975) recorded, that in summer lynx see a snow hare and a roebuck at 350 m and a mouse at 50 m. Moreover, a lynx notices a raptor at 3 km (Matjuschkin 1978). On the other hand, scent plays primarily a role in individual recognition, for identifying territorial markings, in assessment of sexual status, in finding a partner at mating time and in the interactions between mother and young (Ewer 1985, Guggisberg 1975). Additionally, lynx have a very good hearing. They hear a police whistle at a distance of 4.5 km (Vollrath 1981), and can locate noise according to distance and height and differentiate between noises (Haltenorth 1957). However, as small predators must fear lynx as enemy (cats and mustelides were killed by lynx but not eaten), it can be expected that they avoid places with strong lynx presence (Kaczensky 1991).

In conclusion it can be said that the principle factor influencing the protection from predators were the visibility to both sides and the visibility up-hill and down.

4.2. Location of den sites

Furthermore, I hypothesised a trade-off between the choice of inaccessible (steep) and safe terrain (plane) made by the female lynx. While the cubs are very young (natal dens), the female will stay much longer with them (need for thermoregulation, protection from other carnivores; especially at night) than later in the maternal dens (increasing harassment of the mother and increased need for food intake). So, the mother will be much more absent from maternal than from natal dens. After spending 100 % of her time with her young in the first two days after birth, the female spends only 50 % with them at 4-5 weeks of age (Ewer 1985). Besides, female lynx in the stationary phase showed strong spatial restrictions. They only used 4-8 % of their home range for hunting (Kaczensky 1991). Furthermore, when cubs begin to explore the area surrounding the lair (Kitchener 1991) and if maternal dens are located in steep terrain the risk of accident, e.g. to fall down the slope, increases. Additionally, kittens are more exposed to predators (Ewer 1985). In consequence there should be several hiding possibilities around maternal dens. Contrary to expectation there was no significant difference between the slope of natal and maternal dens. On the other hand, I recorded the presence of 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’ (Kitchener 1991, Ewer 1985). Moreover, through the availability of concealed places the female can leave the kittens behind for a short period of time in order to hunt successfully. In cheetahs, 73 % of all hunts failed because of cub activity, cub play, cub seen by the prey or mother or cub seen (Caro 1987). Inaccessible terrain means inaccessible for humans. As anticipated, the accessibility of den site area became more difficult the steeper the terrain got. Natal dens, however, were not more difficult to be reached, i.e. natal and maternal dens were easily accessible. And since the mother stays longer in natal dens, this is not surprising. Accordingly, I could say that primary and subsequently used dens were equally exposed to human disturbance and lay in more or less dangerous terrain. However, I was not able to declare whether human disturbance had a general impact on denning sites. To test this, I should analyse whether females stay longer in specific places when civilisation is further off and less disturbing. Schmidt (1998) observed that a female whose dens were near the state border (low human activity), used them longer than another female who lived in an exploited forest (higher human activity). Or I could examine whether females choose den areas with less human activity than in the rest of the available den areas. Moreover, the influence of civilisation seems to have poor-forestation as a negative consequence (Breitenmoser and Baettig 1992). And it is a matter of fact that 63 % of lynx in Switzerland are killed by man (Kaczensky 1991). However, the popular belief that cubs touched by humans are abandoned or killed by their mother is not supported by Laurenson and Caro (1992). As dens were easily accessibility for humans and the accessibility was correlated with the visibility to the right and the left side, the visibility increased. But did in return the vicinity from natal and maternal dens to humans differ? Neither did they differ significantly in their distances to settlements, nor in their vicinity to roads. I could only notice a tendency that natal dens were located closer to forest borders than maternal ones. Thus the selection of the nearness to the forest border, in my opinion, rather deals with the demands of feeding optimisation than with human avoidance. Most roe deer stay next to forest borders and mostly the remains of lynx prey lie near it (Breitenmoser and Haller 1987). And due to breeding the higher requirements constrain females to den in sites with optimal access to food (Fernández and Palomares 2000). Unlike the statements of Feldman (1993) and Laurenson (1993) that domestic cat and cheetah lairs are gradually moved closer to the food source as the cubs developed towards independence, in my study, natal dens were closer to food sources. During the early days, the females tend to be absent as short a time as possible. But the opportunity to make kills in the vicinity of the den will be exhausted very fast, due to the adaptation (e.g. increased vigilance) of the prey to the presence of the lynx (“Behavioural depression”) (Breitenmoser and Haller 1987). Therefore she must hunt further away, what explains the location of the maternal dens. Anyway, it looked like there was enough prey available in the study area (Hausser 1995). However, it is interesting to see that lynx, compared with other predatory felines, have their offspring late in the year – at the same time when also their prey have young. Supplementary to provisioning with food comes the optimal bringing up of the kittens to independence by learning them to catch prey. Roe deer, as well as chamois prefer south slopes (Hausser 1995). The proximity to water should also be an important factor determining the suitability of lynx den sites since lactating female probably increase their water intake, as cheetahs do (Laurenson 1993). But as Switzerland is a rainy country I presumed that there were enough water sources. Moreover, the water sources represented in GIS are permanently available and should only become important with drought when the many puddles, that are used for water supply by lynx, dry out. My investigations did not show any correlation between precipitation and distance to water bodies. In consequence I assume that even in years lacking rain, there exist sufficient possibilities for a female to obtain water.

4.3. Comparisons between natal and maternal den sites

The change of den site is still more intriguing when the mode of transport is considered, along with the attendant risks of leaving both nests (if she has more than one kitten), the original and the new one, unguarded while moving the young one at a time (Feldman 1993). The distances between primary and subsequently used lynx dens never passed 500 m, i.e. the female seems to shift the cub regularly but within short distances (Breitenmoser and Haller 1986). Relocation of den site has commonly been ascribed to the den becoming polluted with food remains and faeces (Kitchener 1991) and a build-up of ectoparasites (Deag et al. 1987, Ewer 1985, Tuner and Bateson 1998). However, in several felid species, moves have been observed to be so frequent that hygiene can not sufficiently explain the phenomenon; it may be more likely that frequent shifting is protective, reducing the chance that the den be detected by potential predators (Ewer 1985, Kitchener 1991, Guggisberg 1975, Piechocki 1989). Other reasons could be disturbance by humans (Matjuschkin 1978), the nest becoming unsuitable through some accident, such as flooding (Hellgren and Vaughan 1989) or due to changes in temperature (Magoun and Copeland 1998). Another reason for den relocation could be the development of the young, their increasing activity (Ewer 1985) or prey depletion (Kaczensky 1991). According to Magoun and Copeland (1998) maternal dens may not be as secure from predators as natal dens, and female wolverines may be more sensitive to low-level human disturbance at maternal dens. In lynx I could not find such a difference between natal and maternal dens. While on the one hand, natal den structures, except for two dens in the roots of standing trees and one earth lair, were made of rock and mainly closed; on the other hand, maternal dens structures were more diverse and also more open. Ruggiero et al. (1998) reported the same of marten (*Martes americana*), were maternal structures were more diverse than natal dens. This suggests that females are most selective regarding structural attributes when choosing natal dens.

Consequently, I assume that maternal dens are as secure from predators as natal dens are. Above all, as already mentioned, because the features of primary and subsequently used dens were identical, except for camouflage, number of hiding places and den structure.

4.4. Difference between the den sites in the two regions

The den sites in the two study areas differed from each other in several points. Preferred forest types in the Jura Mts. were mixed forests, either dominated by deciduous or coniferous trees. In the NW-Alps the favourite forests were mixed forests, dominated by coniferous, or simply spruce forests. Actually, the forest types used corresponded to the availability in the study areas (see 2.1.). Maybe the visibility slope down in the Jura Mts. was better than in the NW-Alps, because dens in the Jura Mts. lay nearer to roads and were thus more easily accessible by humans. The difference of slope and altitude can be attributed to the fact that the average altitude in the Jura Mts. is inferior to the one in the NW-Alps, and therefore the terrain in the Alps often is steeper. Of course the altitudinal range in which lynx are living is closely related to the amount of forested area (Breitenmoser and Haller 1986). This explains why there were differences in the distances to roads, settlements and forest borders between the two regions. I deduce that there are fewer roads the higher the altitude and the steeper the area. And since this was the case in the Alps, dens were more distant from roads. But why were dens in the Alps situated nearer to settlements? Could a reason for this be that the single settlements in the Alps, contrary to the Jura where settlements are rather clustered, are quite scattered (see 2.1.). Furthermore, the smaller distances to forest borders in the Alps can be interpreted by the fact that Jura Mts. forests consist of larger coherent stands and that in the numerous smaller forest fragments in the Alps the probability of dens to be situated near a forest border is higher, as there exist more borders.

4.5. Survival of young lynx and age of the mother

Mortality of young lynx is highest between 3-4 month after birth (Jedrzejewski et al 1996), just after cubs emerge from the lair (Laurenson 1994) and mortality increases again later, when they are in search of an own beat (Breitenmoser and Breitenmoser-Würsten 1998). In my study I recorded that 27 kittens died between summer and winter, and later 24 between winter and the following spring. Accordingly, mortality rate for the first year was 53 percent. The survival was correlated with the cover degree and soil humidity of a lair. The better closed and therefore the dryer a lair the more kittens survived. For this reason, I assume shelter to be a decisive factor for the survival of the litter. As already mentioned (3.3.), the time when collaborators of KORA noticed the loss of a cub was often imprecise. An other important problem to point out is that litter size was most often recorded when the kittens were marked for the first time and it may well be that some kittens had already died. For example, kittens that are physically deficient and whose deformities or abnormal behaviour is noticeable, are eaten by the mother (Haltenorth 1957). Sokolov (1994) described cases of intraspecific aggression among small lynx kittens, leading to the death of weakly developed kittens. Causes of death can, additionally to those already mentioned (3.3.), be: young and inexperienced lynx being injured by prey; the decline of prey abundance can affect lynx (Matjuschkin 1978); kittens can die of starvation in consequence of the mother being killed (Robinette et al. 1960) or abandoning them (Caro 1994); or they can die of diseases caused by inbreeding, cat epidemic or ileus (Kaczensky 1991).

Astonishingly, the age of the mother seemed to have no influence on the survival of cubs. But as the cover degree was correlated with the age of the mother as well as with the survival of the kittens, the experience of the mother seemed, at least, to have an indirect effect on the microclimatic stability of a den site and the shelter against the weather. Consequently, I do not agree with Feldman (1993) who argued that there is no influence, of the mother having kittens for the first time ore not (primiparous or multiparous), on kitten mortality or the number of dens a mother uses for her litter. However, I cannot prove with my data that thereat is an advantage for the kittens to have an experienced mother. According to Caro (1994), the age of a mother may be important as young females are less successful at hunting large prey, have to make more hunting attempts and travel farther away from the den. Although I omitted the identical dens of my analyses (3.3.), it was interesting to see that a female chose exactly the same site during two successive years. This indicates that particular sites may be used repeatedly for denning.

To sum up, the principle features important for the physical nature of a den site are its closed structure, i.e. a good cover on top and few entries, and its area. Important habitat features are mixed forest and vegetation that is rather open to grant the female a visibility of 10-20 m. In the Jura Mts. the next settlement lay at 575 m, the next road at 146 m and the next forest border at 244 m. In the NW-Alps the distance to the settlements was 472 m, to the roads 370 m and to the forest border 58 m. There was no trade-off between the choice of steep and inaccessible natal den site area, and safe and accessible area of maternal dens. Both den types were equally exposed to potential human disturbance and lay in more or less dangerous terrain. In conclusion, I agree with Fernández and Palomares (1991) that the physical nature of dens is more important for breeding lynx than habitat feature, like distance to prey and water or structure of vegetation.

4.6. Methodological criticism and conclusive remarks

A difficulty was to measure parameters retrospectively. Had vegetation not changed since the time the den was used? How could I measure temperature, soil humidity and light? As already mentioned, for evaluations of temperature and light, I only considered the relative difference from inside to outside, and they were insofar independent from year, season and daytime, as my measurements also took place in summer. Soil humidity provided me with information on cover degree, and as most dens were sufficiently closed the dependence of soil dampness from seasonal rainfall could be neglected. Vegetation certainly had changed in some places, but not so extremely that I could no longer recognise it by means of old pictures. Some very early den sites still looked exactly the same. For future studies I would suggest to measure temperature at various times of the day, such as Stains (1996) did with racoon dens, in order to analyse how den temperatures, compared with ambient temperatures, behave during the day. Moreover, it would be interesting to see, whether the size of the entrance to the den has an influence on temperature.

As already mentioned (2.3.2.), a next thing to do is to investigate the two regions separately, i.e. whether the used den sites correspond to the landscape. In the case that the measured parameters do not correspond, I would, consequently, assume that the females make a specific choice. To analyse then whether the choices made by the females in the Alps differ from those in the Jura, one could compare these differing parameters.

Other questions which arise are: What is the availability of the parameters which are decisive for a good den site and consequently for successful rearing of offspring in reality? Do they represent a limited resource? And if they do, are there possibilities to preserve such dens or to introduce suitable, artificial structures? The availability of suitable den sites in relation to human activities is important for the conservation of a lynx population in a human-dominated landscape. A lack of suitable den sites in an area could potentially reduce lynx recruitment (Slough 1999).

What is the position of the lair within the females' home range with regard to her conspecifics, e.g. her female neighbours? Also factors like distance to the neighbours' territory affect the selection of habitat (Fernández and Palomares 1999). A tendency to locate den sites near the centre of the territory might represent an effort to minimise interference with conspecifics (adjacent home range) (Mech 1970) and to protect her progeny. The fact that maternal dens were always close to natal dens indicated that dens are readily available. Furthermore, if they are located more or less near the centre of a female's home range, I would assume that she can make a strategic choice (select from a wide supply) and must not " take what is around".

Another aspect that should be taken into consideration is the impact of the fathers' behaviour. Although males do not play an active role in rearing of the cubs, they may perform a useful role when the occasion arises (Eaton 1971). Besides, the overlap of male and female home range leads us, too, to the supposition that male lynx may be involved (Matjuschkin 1978). Breitenmoser et al.(1993) speculated that during the denning season male lynx show an increased presence in a belt around the core zone of the mothers' home range, in order to protect the young and the resources from other lynx, yet that they avoid the core area of the mother not to jeopardise her hunting success.

5. References

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Pictures of typical den structures made of rock, wood and earth.

BLOCK HEAP AIDA 96 II (picture D. Boutros, 2000)

ROCK LAIR KIRA 88 II (picture U. Breitenmoser, 1988)

ROCK CLEFT SABA 00 (picture D. Boutros, 2000)

ROCK RECESS NADA 93 (picture S. Capt, 1993)

ROOTS OF A STANDING TREE HERA 99 (picture F. Zimmermann, 1999)

ROOT STOCK KIRA 90 II (picture P. Kaczensky, 1990)

PILE OF DEAD BRANCHES WINA 93 II (picture U. Breitenmoser, 1993)

UNDER LOW HANGING BRANCHES RENA 99 (picture D. Boutros, 2000)

EARTH LAIR KORA 97/ 99 (picture D. Boutros, 2000)

19.7.00

Field protocol

Protocol no.: ________ (e.g. F11/94/001)

Date: ______ / Time: ____ to ____ Filled out by: ________

Name of mother / no.: ________ / ____

Den date: □ sure ______ □ approximate ______ □ not known

Den size (/ date of measurement): ______ / ______ □ not known

	1	2	3	4	5
Eartag no.					
Sex					
Weight (g)					

□ primary site □ secondary site □ not known

Site / Location / Meadowname: ________

Altitude (M. ü. M.): ________

Geographical Position (coordinates) / GPS: ______ / ______

Aspect: a) on site: ______ b) map / GIS: ______

Slope: a) on site: ______ b) map / GIS: ______

1. Small structure of den site

a) Type of den site / spatial shelter — Number of entries / exits: ____

- □ rock cleft - Felsspalte
- □ rock lair (narrow entrance) - Felshöhle (enger Eingang)
- □ rock plate - Felsplatte
- □ rock recess (on herbal material) - Felsnische (auf pflanzl. Material)
- □ block heap (big stones) - Blockhalde (grobe Steine)
- □ in the roots of a standing tree - im Wurzelwerk von stehendem Baum
- □ root stock/root plate of an overthrown tree - Wurzelstock/Wurzelteller von umgeworfenem Baum
- □ under a sloped lying tree - unter schräg liegendem Baum
- □ earth lair - Erdbau
- □ pile of dead branches - Reisighaufen
- □ low hanging branches - tief hängende Äste
- □ undergrowth/scrub - Gestrüpp

discription: ____________________

b) Size of den site (cm):

- Entrance: width: ______ height: ______ depth: ______
- Main room: width: ______ height: ______ depth: ______

c) Pictures: - den site: no. ___ terrace: no. ___
- pictures from den site away: in all 4 directions (parallel and vertical to the slope) and one upwards

up: no. ___ down: no. ___ right: no. ___ left: no. ____ upwards: no. ___

- □ standard photo (28 lens, Camera at 1 m = height of lynx)
- □ non-standard: ____________________

d) Protection against weather (cover degree by vegetation; from above):

□ until 25 % □ 50 % □ 75 % □ until fully closed

e) Visibility (horizontal; how much % free sight on 20 m):
Free sight on how many m ?

- slope up: __________
- slope down: __________
- left: __________
- right: __________

description: ____________________

f) Nest material/underground (e.g. cushioned by arid plant particles):

____

____

g) Soil consistency of den site: □ naked rock □ humus / soil □ permeable □ non-permeable

h) Humidity: □ arid □ humid □ wet

i) Temperature: time of measure: __________

- in den site (lair): __________
- in front of den site: __________

j) Light: time of measure: __________

- in den site: □ bright □ medium □ dark
- in front of den site: □ bright □ medium □ dark

k) Camouflage, cryptical background:

- □ high-contrast (flecked): ____________________
- □ low-contrast (uniform): ____________________

colour: ____________________

l) Evaluation of den site:

advantages: ____________________

____

disadvantages: ____________________

____

2. Vicinty of den site

a) Shape of terrain (sketch of finerelief; knoll; trough, etc.):

____

b) Terrace (size; description and sketch): length: ______ width: ______

____

____

____

c) Accessibility to den site and terrace (description):

____

____

____

d) Vegetation (description; hight of vegetation: gras, herb, etc.; sun protection, shade throw of trees):

____

____

____

____

e) Noise level (e.g. waterfall): □ silent □ medium □ loud

description of noise source: ______________________________

f) Particularities (e.g. power lines, close to vulpine lair, etc.):

____

____

____

____

g) Distance:

	horizontal	vertical	Type of animal, water, etc.
Pasture area			
Settlement			
Water			
Rock			
Forest border			
Road/path			

Bisher erschienene KORA Berichte

KORA Bericht Nr. 1	Landry, J.M., 1997. La bête du Val Ferret.
KORA Bericht Nr. 2	Landry, J.M., 1998. L'utilisation du chien de protection dans les Alpes suisses: une première analyse.
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KORA Bericht Nr. 12 *e*	Boutros Dominique, 2002. Characterisation and Assessment of Suitability of Eurasian Lynx (*Lynx lynx*) Den Sites.

Bezugsquelle
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