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Population structure of the otter, *Lutra lutra*. Parameters and model for a Central European region

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Abstract

A sample of 225 dead otters – mostly road-kills – was collected from 1980 to 1995 in Upper Lusatia („Oberlausitz", Germany). All otter carcasses were examined for signs of reproduction and were aged according to incremental cementum lines. The data obtained were combined with field observations of cubs to endeavour the modelling of real population parameters.

In the Upper Lusatia region the mean litter size of the otter (2.7) and the proportion of early losses of cubs (24%) appeared to be at a normal level compared to different data from the European area. The proportion of adult non-breeding females amounted to 40%. Among otter carcasses the males predominated especially in younger age classes. In Upper Lusatia, otters live to a very old age, up to 16 years, and the sample shows a high fraction of older animals.

By using the obtained parameters a population model for the otter in the Upper Lusatia region was developed. The age pyramid of this model is relatively stretched with a female-biased sex ratio among the adults, thus compensating for the low proportion of breeding females.

Mortality is very high during the first year, but very few otters die in middle ages of life. Except for juveniles the survivalship curve shows a convex trend typical for long-lived large mammals.

Introduction

The Eurasian otter, *Lutra lutra* (Linné, 1758), belongs to the most endangered mammalian species of Europe. In western and central parts of its European area of distribution the population splittings have been followed by considerable decrease or extinction (Reuther 1992). Therefore, many investigations were directed to the problems of conservation biology of this species in the last twenty years. Nevertheless, there is still little knowledge on the population ecology of the otter.

Very useful data, analyses, and conclusions were published by Heggberget (1988), Kruuk and Conroy (1991), Heggberget and Christensen (1994) and Rosoux and Tournebize (1995) based on samples of otter carcasses. In addition, Sidorovich (1991) gave interesting results using direct observations to assess the population structure and dynamics of the otter in Byelorussia.

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However, most of these studies concerning population ecology of the otter were carried out in northern and eastern European regions. There is still a lack of information on the structure, natality, and mortality of Central European populations living in destroyed habitats and fragmented areas. Only the analyses of the material collected by the Zoological Institute of Halle have resulted in initial insight into the population structure of the otter in eastern Germany (Stubbe 1989; Uthleb et al. 1992). However they are also based on otter carcasses and reflect only the sample of dead otters discovered.

The aim of the present study in the Upper Lusatia region was to establish the modelling of population parameters by combining sample data and records from field observations. This model should adequately mirror the living population to support the species conservation program for the otter in Saxony.

Material and methods

Sample and observation area

The „Oberlausitz" region – Upper Lusatia – in Saxony (Germany) is inhabited by one of the most numerous otter populations; further west otters do not occur. The area of about 5 000 km^2 in the southeast of eastern Germany encompasses different landscapes ranging from a lowland plain rich in ponds and forests to hilly countryside and wooded highlands. There is a centre of otter reproduction in the „Upper Lusatian Pond District" where a multitude of fish farms guarantee excellent feeding conditions for the otter. Surrounded mostly by reeds, old trees, and bushes these carp ponds are connected by extensive ditches with natural bank structures. In the other landscapes of Upper Lusatia without large numbers of fish ponds, the otter lives at lower density suggesting regular migration from the Pond District (Ansorge 1994).

Sample material

A total of 225 otter carcasses was collected from 1980 to 1995. Most of them were found in the Pond District. The main cause of death was road traffic (64% of the discovered otters) having increased up to 85% in the last few years. Otters were delivered at all times of the year with a distinct peak in autumn caused by draining of the ponds.

Reproduction and age analysis

Otter carcasses were dissected and sex was determined by inspection of internal reproductive organs. Data on female reproduction were obtained by counting numbers of follicles, embryos, placental scars and luteal corpora (Heggberget and Christensen 1994). Date of birth of cubs was determined by estimating developmental stages of embryos and registration of fresh placental scars.

More than 40 observations by a few skilled otter watchers were used to determine the number of cubs accompanying the female.

Litter size as estimated by counting embryos and placental scars was compared to the litter size as obtained by counting living cubs per female using a G-test (Weber 1980).

To separate young and adult otters, age estimation was based on the general obliteration of sutures, the development of the postorbital constriction, the sagittal crest, the bone deposition around canine alveoles and the surface structure of the brain-pun as well as the baculum development and the formation of femur epiphysis (van Bree et al. 1966; Stubbe 1969; Heggberget 1984; Skaren 1987; Uthleb et al. 1992).

The adult otters (i. e. older than 2 years) were aged by the configuration of incremental cementum lines of the upper canine or adjacent teeth. Longitudinal sections by an efficient method of low speed cutting (Driscoll et al. 1985; Ansorge 1995) produce the number of annual lines which are then used to establish definite age classes (Heggberget 1984).

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Results and discussion

Sample structure

The sex-age composition of the sample material illustrated in figure 1 shows a relatively stretched age pyramid. Only 28% of the animals died during first year of life. Most animals of the population sample (58%) were adults between 3 and 10 years of age and only few otters (3.1%) reached an age of between 10 and 16 years. The mean age class of all otters found dead was 4.2.

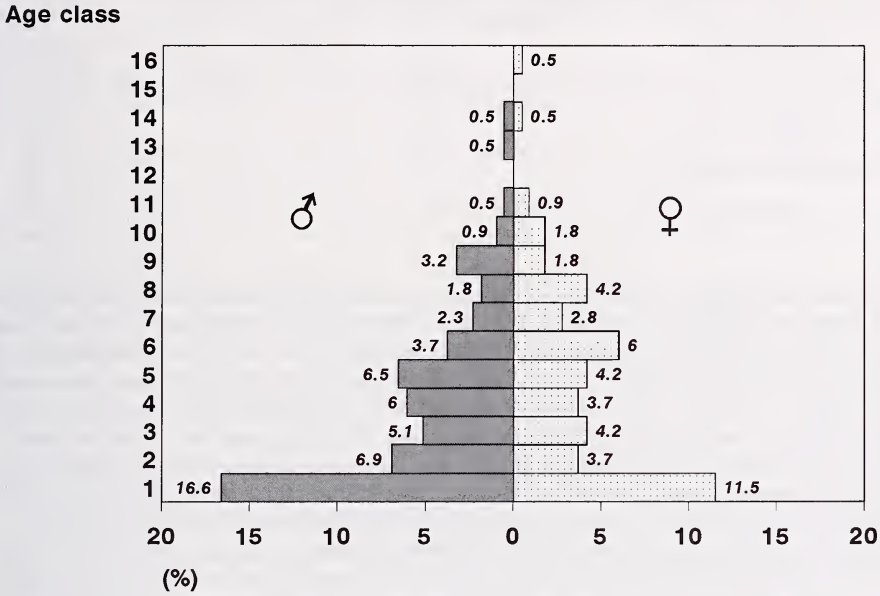

Fig. 1. Sex and age structure of the otter sample (n = 117, percentage of each age class in italics).

The sex ratio of the whole sample amounted to 56% males and 44% females (1.2 : 1). Especially in age classes 1–5 the males predominated with 60% (1.5 : 1). In animals older than 5 years there was a clear female-biased sex ratio with only 42% males (0.7 : 1). However, there was an equal balance of 1.02 males to 1 female amongst all adult otters including animals older than two years.

Reproductive performance

Our observations indicate that females have one litter per year and otter cubs are born throughout the year. In the total sample of 99 female otters (including 61 adults) only 14 specimens between 5 and 10 years old showed countable reproduction signs (Tab. 1). Litter size ranged from 1 to 4 with an average of 2.7 counted by both embryos and placental scars (Tab. 2).

On three occasions, different stages of luteal corpora could be verified (3, 2, 2 corpora lutea). However, with the latter result, there appears to be little use in estimating prenatal mortality. The significant difference ($G = 27.6$, $df = 1$, $p < 0.01$) between the mean litter size counted by embryos or placental scars and the number of living cubs indicates losses of about 24% during the first two months after birth.

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Table 1. Age of otter females with reproduction signs from the Upper Lusatia region

age class	5	6	7	8	9	10
total number of females	8	12	6	8	4	4
females with reproduction signs number	1	2	1	5	3	2
%	13	17	17	63	75	50

Table 2. Otter reproduction data of the Upper Lusatia region

number of litters	litter size					
	1	2	3	4	∅	n
counted by embryos	–	2	1	1	2.8	4
counted by placental scars	1	3	4	2	2.7	10
cubs observed	12	20	15	1	2.1	48

From their research on Shetland otters, Kruuk et al. (1991) ascertained a strong correlation between numbers of cubs observed and available prey abundance. This could hint at the social regulation of population density reported from other medium-sized carnivores (e. g. Tullar et al. 1976; Harris 1981). However, Sidorovich (1991) noticed significantly higher fecundity in harvested otter populations of Byelorussia than in protected areas. Compared with the few studies on litter size of otters based on counts of embryos and placental scars, the reproductive parameters from the Upper Lusatia region range at the top of known variation (see Sidorovich 1991; Heggberget and Christensen 1994). The number of 2.7 cubs per litter was only reached in Byelorussia (Sidorovich 1991).

In contrast, the mean number of cubs following a female in Upper Lusatia was 2.1 per litter. This is considerably lower than in other field studies carried out in inland areas (Reuther 1980; Barus and Zejda 1981; Wlodek et al. 1989; Sidorovich 1991). However, Uthleb et al. (1992) reported similarly low mean numbers for otters from all over eastern Germany. Otters of northern coastal areas, such as Norway and the Shetlands, breed even smaller litters (Heggberget and Christensen 1994; Kruuk et al. 1991). The latter authors suggest that food shortage is the main cause of the low reproduction success.

The situation in the Upper Lusatia is more difficult to explain. The high numbers of embryos and placental scars correspond to the very good feeding conditions at most times for the otter foraging mainly in the carp ponds. The high mortality of about 24% of cubs during the first months could be caused by disturbances due to diverse human activities.

In the present study the percentage of non-breeding adult females is calculated by the proportion of gravid females in the total sample of adult females (4/61 see Table 2). However, the proportion of non-breeding adult females was calculated by taking into account that otter embryos are visible only during about 40 days prior to birth (see Stubbe 1993). Thus, the chance of detecting embryos in a gravid female in a given year is 40/365. Consequently, the proportion of gravid vixens is higher than the actually observed percentage, namely 60%.

This low pregnancy rate could be affected by different causes such as PCB contamination (Weber et al. 1991) or density control by reduced fecundity. However, no data concerning these questions are available. In the centre of the Upper Lusatian Pond District otters live in a relatively high density of 1.0–1.3 adults per 10 km^2 (Ansorge 1994). Unfortunately, no other data on the proportion of breeding females are available from compar-

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able habitats. Only Sidorovich (1991) reported percentages from 27% to 75% of non-breeding females due to over-hunting and very low otter density in Byelorussia.

However, the average number of 1.3 cubs older than two months per adult female seems to be relatively low in the Upper Lusatia. The reason could be the high local otter density and high cub mortality. Basically the higher number of older females results in the considerably high reproduction rate of the whole population.

Construction of the population model

Our model is based on the data of reproduction and the age and sex structure of the otter carcasses. Using these basic data the following assumptions could be made for the construction of the model.

1. A stable otter population without emigrating and immigrating animals is required.
2. All data obtained since 1980 are considered as having been determined at the same time.
3. The probability for adult otters to die by road-kill does not change across age classes (see Kruuk and Conroy 1991).
4. The sex ratio of new born cubs is nearly balanced (Heggberget 1988; Sidorovich 1991).

There is however, a critical point in these basic postulates for the population model. The model accepts a stable population without any emigration or immigration. As an unknown part of especially subadults in their second year of life probably leave the increasing population searching for new home ranges. In this case, the real mortality is likely to be lower than estimated. Unfortunately, almost nothing is known about the migration of otters in the Upper Lusatia region.

In the Upper Lusatia region 24% of the cubs die during the first weeks of life probably in balanced sex ratio. The sex-specific mortalities of older juveniles and adults should be represented by the discovered dead otters. However, the greater number of males dying in lower age classes causes a higher percentage of older females in the living population (83.5% females in age class 3–16). This knowledge and the information about the annual percentage of breeding females (60%) and the mean litter size at birth (2.7) permit to estimate the number of newborn cubs per year. The juveniles in age class 1 at the beginning of the first year of life amount to 51.4% of the total population. The portion of the older age classes was directly determined by their percentage in the sample collected since 1980. The age structure given in figure 1 shows some deviations from the general expectation of decreasing otter numbers with increasing age. Therefore, these irregularities were offset by using a curvilinear regression after Sokal and Rohlf (1995) excluding the juvenile population part (Fig. 2). The sex ratio of a specific age class was determined by deducting the sex-specific losses of the previous age class from its stock. Age class 1 is assumed to start with an equal sex ratio (Heggberget 1988; Sidorovich 1991). For calculating the sexes of age class 2 only the dead otters which had been discovered could be used. For earlier losses, an equal sex ratio had to also be assumed.

Population structure

The complete sex and age structure of the population model formed by these deductions is presented in figure 2. It shows a striking bias in favour of the females older than one year. The sex ratio of the reproductive population amounts to 1 : 3.5 males : females. Despite the high number of non-breeding females, this high percentage of females yields the reproduction rate of somewhat more than 100% for the whole population.

Most investigations on mustelid populations usually show sex ratios biased towards males (see Buskirk and Lindstedt 1989). Sexual dimorphism in home range size and sex-

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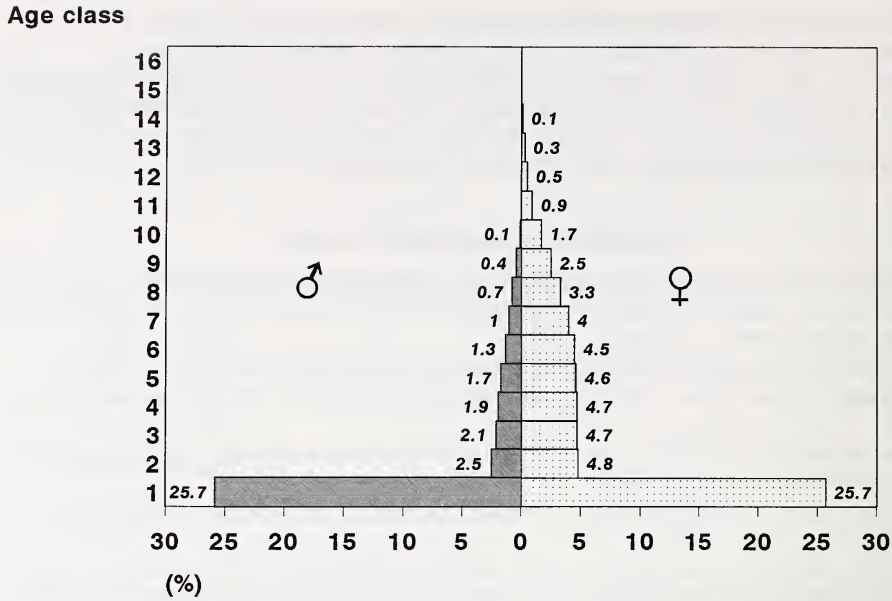

Fig. 2. Model of the population structure (percentage of each age class in italics).

specific behaviour result in a greater presence of male otters in the collected otter carcasses (e. g. Uthleb et al. 1992; Rosoux and Tournebize 1995). Hence, the number of females in the population might predominate over the number of males as demonstrated in a field survey of harvested populations by Sidorovich (1991).

In Upper Lusatia the phenomenon of exploitation has been replaced by road traffic, and local field observations point to the female-biased sex ratio of the model. One good reason for this bias is also given by the switch of the sex ratio in older age classes, because there is a lack of older males in the population and females predominate in the collected sample.

The life expectancy table for the otter in Upper Lusatia is presented in table 3 with pooling the sexes in respective age classes. This table illustrates a very high mortality of about 86% during the first year. This period seems to be the most critical stage in the life cycle of the studied otter population because the mortalities of the following middle age classes remain clearly lower. The juvenile mortality is much higher than in all the other studies, which determined mortality rates only from otters found dead (Sidorovich 1991; Kruuk et al. 1991; Heggberget 1984). Compared with this researche, the present population model from Upper Lusatia starts at birth including the high percentage of early cub losses. Additionally, it should be assumed that cubs are more affected by non-violent death and the chance of these dead cubs to be found is definitely much lower than that of adult carcasses.

Disregarding the juvenile age class, the life expectancy table (Tab. 3) shows a very remarkable trend of survivalship. The respective survivalship curve in figure 3 demonstrates the high initial mortality affecting the juveniles. However, physiological longevity is reached by many otters in Upper Lusatia and the shape of the curve for otters two years old or over shows a slightly convex trend. This means that once otters have survived the first year of life they will probably live to middle or older age. This trend is typical indeed for moderately exploited populations of long-living large mammals (Odum 1971).

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Table 3. Life expectancy table (according to Odum 1971) for the otter in the Upper Lusatia region.

Age class (x)	Number (l_x)	Number dying (d_x)	Mortality rate (q_x)	Life expectancy (e_x)
1	1 000	858	858	1.4
2	142	10	70	6.1
3	132	4	30	5.5
4	128	5	39	4.7
5	123	10	81	3.9
6	113	16	142	3.2
7	97	19	196	2.6
8	78	22	282	2.1
9	56	21	375	1.8
10	35	17	486	1.5
11	18	8	444	1.5
12	10	4	400	1.3
13	6	4	666	0.8
14	2	2	1 000	0.5

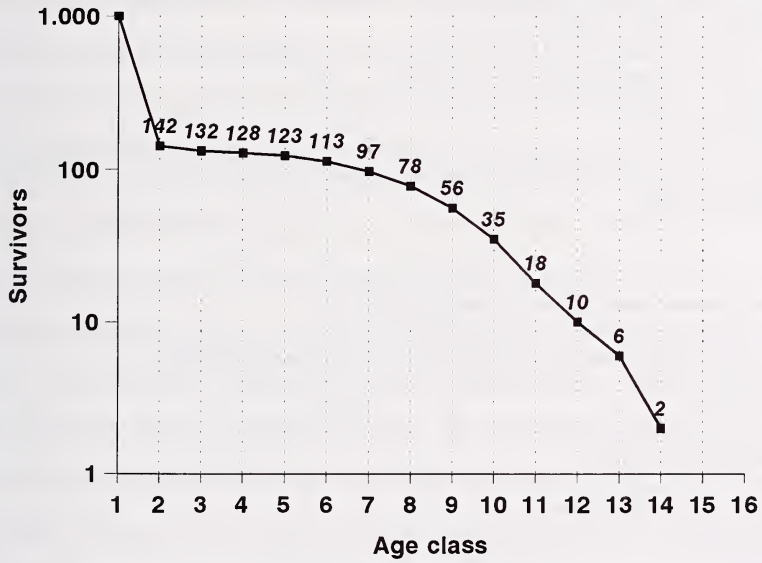

Fig. 3. Survivalship curve of the otter in the Upper Lusatia region.

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Zusammenfassung

Die Populationsstruktur des Fischotters Lutra lutra – Kenngrößen und Modell aus Mitteleuropa

Die Untersuchung beruht auf 225 toten Fischottern, die seit 1980 in der Oberlausitz meist als Verkehrsopfer aufgefunden wurden. Von allen Weibchen wurden die Anzahl vorhandener Embryonen, Uterus-

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narben und Gelbkörper registriert. Das Lebensalter der Otter wurde mit Längsschnitten des Zahnzements festgestellt. Durch verläßliche Beobachtungen wurde die Wurfgröße nach lebenden Jungtieren im Freiland ermittelt.

In der Oberlausitz liegen die mittlere Wurfgröße (2,7 nach Embryonen und Uterusnarben) und die postnatalen Verluste (24%) auf dem bisher bekannten Niveau. Der Anteil der nicht reproduzierenden erwachsenen Fähen beträgt 40%.

Bei den Totfunden überwiegen die Männchen besonders in den jüngeren Altersklassen. Die Fischotter erreichen in der Oberlausitz ein recht hohes Alter. Der Anteil älterer Tiere ist unter den Todfunden recht erheblich.

Aus den ermittelten Daten wird ein Populationsmodell für die Fischotter der Oberlausitz entwikkelt. Die Alterspyramide dieses Modells ist recht gestreckt mit starkem Übergewicht der Weibchen in den adulten Altersklassen.

Die Mortalität ist nur im ersten Lebensjahr sehr hoch. Wenige Otter sterben im mittleren Lebensabschnitt. Die Überlebenskurve erwachsener Otter zeigt den convexen Verlauf langlebiger Großsäuger.

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