Acta Theriologica 51 (1): 99–106, 2006.
PL ISSN 0001–7051

Feeding ecology of wolves *Canis lupus* returning to Germany

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Ansorge H., Kluth G. and Hahne S. 2006. Feeding ecology of wolves *Canis lupus* returning to Germany. Acta Theriologica 51: 99–106.

Following several years of occasional occurrence, several wolves *Canis lupus* Linnaeus, 1758 have established a resident population in northeastern Saxony (Eastern Germany). From 2001 to 2003, we collected and analysed 192 scats of *C. lupus*. Results of our study are expressed as the frequency of occurrence of prey species and the percentage of biomass consumed using coefficients of digestibility as well as two variants of an equation for prey mass per collectable scat. Diet composition of the wolves was restricted to a few food items, mostly wild ungulates. These remains were found in 97% of the scats, representing 99% of the biomass consumed by the wolves. Roe deer *Capreolus capreolus* was the most frequent and most important prey, constituting nearly of one half the biomass. Red deer *Cervus elaphus* was recorded in one-third of the samples, followed by wild boar *Sus scrofa*, mouflon *Ovis ammon musimon* and brown hare *Lepus europaeus*. Compared with game occurrence, roe deer was clearly preferred over the other species. A difference between winter and summer diets was mainly due to the high occurrence of young wild boar in summer. The general diet pattern of the wolf in Saxony corresponds with that found in the naturally occurring populations in Europe.

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Key words: wolf diet, roe deer, prey preference, seasonal difference

Introduction

Within its entire distribution area, the wolf *Canis lupus* Linnaeus, 1758 feeds mainly on various large wild ungulates (Okarma 1997, Jędrzejewska and Jędrzejewski 1998). Several studies in eastern and northern Europe have shown this pattern in long established as well as in returned wolf populations (Śmietana and Klimek 1993, Olsson *et al.* 1997, Gade-Jørgensen and Stagegaard 2000, Jędrzejewski *et al.* 2000). However, marginal and isolated populations in the southern and western parts of Europe show different diets, including carrion, waste and domestic animals (Cuesta *et al*. 1991, Meriggi *et al*. 1996, Vos 2000, Pezzo *et al.* 2003, Capitani *et al*. 2004). The diet of the wolf population in Poland, which is thought to be the source of wolves immigrating to Germany, has been intensively studied. In the lowland forests of northeastern Poland as well as in the mountain

areas of the southeast, wolves feed mainly on red deer *Cervus elaphus* (Jędrzejewski *et al.* 2000, Śmietana and Klimek 1993), and to a lesser extent on roe deer *Capreolus capreolus* and wild boar *Sus scrofa*. However, no thorough study exists concerning the food habits of wolves having recently returned to formerly populated parts of central Europe, especially to Germany.

This lack of precise information has induced a wide range of opinions and speculations concerning the recovery strategies of wolves in central Europe, particularly since several levels of the "wolf – man" field of tension are strongly connected with the food habits of the wolf. Precise diet analyses of wolves from these areas would be very helpful, especially in regard to public opinion and game management.

Since World War II, the immigration of wolves from Poland into eastern Germany occurred rarely but regularly. During the GDR regime, 13 wolves were legally hunted, most of them (8) during the 1980s. Since having been placed under legal protection in the reunified Germany in 1990, another 5 have been shot, 2 were killed by automobiles and 1 was captured alive. All of these incidents occurred in the easternmost states of Brandenburg (7) and Mecklenburg-Vorpommern (1), which border Poland. Without exception, migrating wolves were involved, residency or reproductive status was not proven (Kluth *et al.* 2002).

The situation changed in 2001 when, in northeastern Saxony (bordering Poland to the east and Brandenburg to the north), first substantiated existence of resident, reproducing wolves was found. The wolves probably originated from the adjacent heath lands and forests of Poland, where an adult female was shot in 1994 (Kluth *et al.* 2002). After a few years of occasional occurrence, a pair formed in the Muskau Heath in 1998 and a first successful reproduction was deduced from several observations of 6 wolves in autumn of 2000. Our study of the food of wolves in eastern Germany demonstrates how these canids can cope well with the conditions in the other parts of central Europe. This should promote public relations and acceptance of wolves in the recolonised areas.

Study area

The present study region and permanent area of the wolf occurrence comprises about 400 km^2 in the Muskau Heath in northeastern Saxony (Eastern Germany). Adjacent areas were visited only occasionally by the wolves. The main part of the study area is a military training area of about 145 km^2, including 100 km^2 of forest. Here, the wolves are safe from permanent human disturbance, spaciously evading the temporary shooting practices. The Muskau Heath is exactly the area where, in ca. 1800, the wolves still lived while extirpated from the rest of Saxony (Winkelmann 1996).

Furthermore, former opencast coal mines of large dimensions belong to the wolves´ present home range. There are few human settlements or roads in the study area, and disturbances are rare. The military training area as well as the coal mines are characterized by a mosaic of closed forests and open landscape, which is preferred by the wolves for hunting the abundant game populations present. The population densities of the game species in this area were estimated by the State Forest Department, representing the spring population densities at the study area and during the study period: roe deer 5.2/100 ha, wild boar 2.9/100 ha and red deer 2.5/100 ha.

According to our monitoring results, the wolves in the Muskau Heath raised between 2 and 5 pups each year during the study period. In the beginning of 2002, the 4 pups from 2000 apparently left their natal territory and settled in the western portion of the study area, where they conducted 2 successful attacks on sheep in spring. Later the group split up and only 1–2 wolves became resident in that area. In contrast, the pups born in the Muskau Heath in 2001 apparently left the natal area without giving an indication to their whereabouts since then.

Material and methods

A total of 192 scats were collected throughout all seasons of the years 2001 to 2003. Most of them were collected as part of the wolf monitoring program, which is conducted on behalf of the Saxonian State Ministry of Environment and Agriculture by experienced and field-trained personnel. This survey has been conducted on a regular basis since 2001. It includes searching for and documenting tracks, scats and kills in the central portion of the wolves` territory inside the military training area.

To avoid misidentification of fox and wolf scats, small scats were usually discarded and only collected if found next to a corresponding wolf-pup track or if they contained large pieces of bone unusual for fox scats. In the military area, dogs are not present. Outside the area feral dogs, which would regularly feed on wildlife, are not a problem. Before being included in the analysis, all scats were again judged for their probability of being wolf scats when measurements were taken and their contents underwent a first scan in the lab.

To evaluate seasonal differences in the food habits of wolves while considering the relatively small sample size,

the scats were subdivided into two seasonal subsamples. The winter sample includes scats collected from November to April whereas summer scats were found between May and October.

The faeces were treated by a technical process as described in Jędrzejewska and Jędrzejewski (1998) and according to the standard methods of Lockie (1959) and Goszczyński (1974). The samples were soaked and washed in a sieve of 0.5-mm mesh width to clean the faeces contents from mud and debris. After drying the samples, the inorganic non-food items, such as sand or gravel, were sorted and the rest of the undigested prey remains weighed.

The fragments of mammal hairs – the most extensive component found in the samples – were identified by microscopic analysis using the keys of Teerink (1991) and Meyer *et al.* (2002) as well as comparison with a reference collection of hairs and microscopic slides. Nevertheless, some hair of the deer species could not be identified (Jędrzejewski *et al.* 2000). These difficulties were surmounted by determining the fragments of bones and, rarely, hooves and teeth. Furthermore, these components provided information on the age of the prey. Parts of the skull and postcrania, deciduous teeth, hooves and hair allow the young roe deer, wild boar and red deer to be determined. Nevertheless it was not possible to distinguish nearly full-grown animals in their first year from older ungulates by the scat remains. Therefore, the number of young animals represents a minimum.

Mammal, bird and fish bones were identified by comparison with museum collections and, additionally, the use of the guide and atlas for fish bones (Conroy *et al.* 1993, Knollseisen 1996). All remains of insects or plants were classified to higher taxonomic groups, and occasionally to the species level.

Besides diet composition, i.e. the range of prey items, results are expressed as the frequency of occurrence and as the percentage of biomass consumed. The frequency of occurrence of the different food types was calculated by the relation of the number of scats containing a certain food item to the total number of scats analysed. To calculate prey biomass, we used three methods according to Goszczyński (1974), Weaver (1993) and Ruehe *et al.* (2003). After estimating the relative volume of each food item in every scat, the respective biomass consumed by the wolf was calculated (Goszczyński 1974, 1976). This method is based on specific coefficients of digestibility for different prey sizes. In addition to the coefficients given in the review of Jędrzejewska and Jędrzejewski (1998), the present study uses a coefficient of digestibility, CD = 50, for rather small piglets and fawns. Moreover, a further method for the estimation of biomass used in studies of wolf diets (eg Gade-Jørgensen and Stagegaard 2000) was employed with our data. This calculation for prey biomass per collectable scat (Weaver 1993) is based on a linear regression model and also takes the different prey sizes into account. Furthermore, a third model for calculating prey biomass was used in order to avoid misleading interpretations (Ciucci *et al.* 1996) and to assess the influence of the different calculation methods. According to Weaver (1993), this equation was developed and proposed by Ruehe *et al.* (2003) for European conditions. Mean body weights of prey species were estimated based on animals hunted from the study area as well as collection material and are as follows: red deer *Cervus elaphus* 65 kg (calve 25 kg), wild boar *Sus scrofa* 45 kg (piglet 10 kg), moufflon *Ovis ammon musimon* 35 kg, roe deer *Capreolus capreolus* 15 kg (fawn 4 kg), brown hare *Lepus europaeus* 4 kg, water vole *Arvicola terrestris* 80 g and field vole *Microtus arvalis* 25 g. The weights of calves, piglets and fawns were estimated considering the mean size of young animals of the species found in the wolf scats. Information on ungulate occurrence from the study area and for the study period was obtained from the estimated population densities of the official game census of the State Forest Department (personal communication). It was based on a questionnaire as well as on the hunting bag evaluated by the professional wildlife service.

Seasonal differences in the main prey species in the wolf diet as well as in the relation of game density and number of wolf prey were tested using a χ^2-test at a significance level of $p = 0.05$ (Weber 1980). The selection of prey species by the wolves was calculated with Ivlev's selectivity index

$$D = \frac{r \quad p}{r \quad p \quad 2rp}$$

(Jacobs 1974, Jędrzejewski *et al.* 2000), based on the mean of the biomass relations in the scats obtained by the three different methods (r) and the biomass of ungulate species in the study area (p).

Results

The scat contents of the wolves occurring in northeastern Saxony were restricted to a few food items (Table 1). In total 83% of the faeces contained remains of only one food object , whereas two different food items deliberately consumed by the wolves were recorded in 16% of the studied material. Simultaneous presence of three food items were found twice (1%) and only once (0.5%) did remains of five different real food items occur.

Almost all faeces of the sample contained remains of wild ungulates, representing the absolute dominant food category. All three biomass calculations showed the same high proportion of ungulates, amounting to more than 96% of the biomass consumed. Within these game species, the most frequent food item of all was roe deer, which was found in one-half of the faeces collected. This was followed by red deer and wild boar, whereas mouflon was more rarely found in the wolves' scats. Roe deer and red deer also made up the largest part of the whole biomass consumed, being of approximately equal importance. The proportion of wild boar consumed was clearly smaller. Only the model of Ruehe *et al.*

Table 1. Wolf diet in Saxony as determined by faecal analysis from all seasons (n = 192).

Food type	Number of faeces	Occurrence (%)	Biomass (%) (Goszczyński 1974)	Biomass (%) (Weaver 1993)	Biomass (%) (Ruehe *et al*. 2003)
Cervus elaphus	61	31.8	34.7	36.9	56.7
Calves (included above)	5	2.6	3.5	2.6	2.2
Capreolus capreolus	95	49.5	44.3	37.4	21.6
Fawns (included above)	13	6.8	3.5	5.0	1.2
Sus scrofa	48	25	13.4	18.2	16.0
Piglets (included above)	23	12	5.7	8.4	3.7
Ovis ammon musimon	8	4.2	5	4.8	5.0
Artiodactyla	186	96.9	97.4	97.2	99.3
Lepus europaeus	10	5.2	2.6	2.8	0.8
Young (included above)	2	1	0.3	0.5	< 0.1
Microtus arvalis	4	2.6	< 0.1	0.1	< 0.1
Arvicola terrestris	1	0.5	< 0.1	< 0.1	< 0.1
Gallus gallus f. familiaris	2	1	< 0.1		
Cyprinidae indet.	1	0.5	< 0.1		

(2003) for prey mass resulted in a distinct bias towards the red deer, making up more than one-half of the biomass consumed. Young and not fully-grown animals were determined for each of the three ungulate species most abundant in the wolves' prey. However, the data of Table 1 represents only the minimum number of fawns, calves or piglets, because not all remaining individuals of these species could be definitely determined to be adults.

Medium- and small-sized prey items were seldom used by the wolves, amounting to only a small percent of the total biomass consumed. However, faeces without any remains of ungulates contained brown hare in every case. Voles were always recorded as single individuals in the wolf scats, being eaten only rarely. There was only one case of feeding on anthropogenic waste in the sample material, which concerned roast-chicken leftovers as well as a chicken egg and a cyprinid vertebra bone. No other domestic animal was found in the wolf scats.

There was no record of fruits in the faeces. All types of plants in the wolf scats such as grass or leaves do not represent true food items. The latter is also true in the case of the various kinds of insects found in the wolf faeces. These could be divided into parasites of prey ungulates, necrophagous beetles, insects eaten by chance and secondarily invading coprophagous insects.

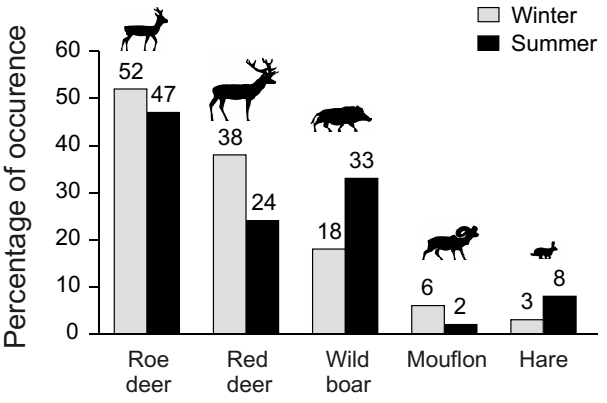

Fig. 1. Seasonal differences in the occurrence of main prey species from one wolf pack from Saxony between 2001 and 2003 (winter n = 102, summer n = 90).

Within the wolf diet throughout the year, there was a statistically significant difference between the winter and summer seasons in the

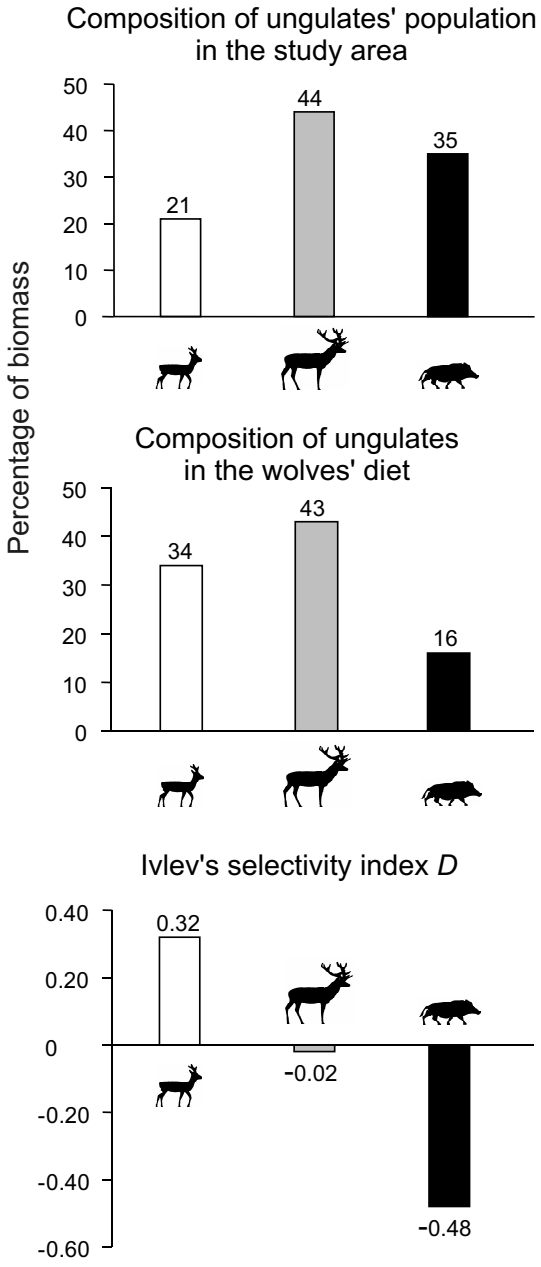

Fig. 2. Prey selection by one wolf pack from Saxony between 2001 and 2003.

proportion of the main prey species ($\chi^2 = 7.81$, $p < 0.05$). The difference was mainly based on the higher frequency of wild boar and smaller proportion of all other prey during the summer (Fig. 1). This was due to the high occurrence of piglets found in the scats in summer (20%). This resulted in differing proportions of consumed biomass as well, concerning above all wild boar (winter 7%, summer 19%) and red deer (winter 38%, summer 31%), whereby the proportion of the roe deer was quite balanced throughout the year (calculations after Goszczyński 1974). Estimations after Weaver (1993) and Ruehe *et al*. (2003) resulted in similar differences between winter and summer food.

Referring to the biomass proportions in the wolf diet outlined above and compared with the biomass relations of ungulates estimated from the area of the wolf occurrence in Saxony (Fig. 2), there was a highly significant difference between food supply and prey selection ($\chi^2 = 104.86$, $p < 0{,}001$). The selectivity index given in Fig. 2 shows the clear preference for roe deer over other species. While red deer is more selected by the wolves as prey than wild boar in Saxony, it is still slightly selected against.

Discussion

The present study offers beginning insights into the feeding ecology of the wolves found in Germany. It presents the first indication of the prey composition of wolves from this territory since the 17th century. Many anecdotes about damage to livestock by wolves present a picture of the feeding habits of these canids in this former time (Butzeck *et al*. 1988, Winkelmann 1996). The predominant pasturing of domestic animals in meadows and bushland during the main part of the year showed livestock as a stable food base.

Today, the food habits of Saxony wolves characterise them as being distinctly opportunist carnivores. The diet composition is restricted to a few food items only, which are mostly wild ungulates. None of the faeces analysed contained remains of domestic animals, except for one roast chicken bone, although two attacks on domestic sheep were registered during the study period. The wolves in Saxony seem to be experienced and efficient hunters of hoofed mammals, and rarely kill and feed on livestock. This is only partly caused by lesser livestock availability, since many sheep and cattle are still held in the open from spring to autumn. In the present

study area of wolf occurrence, about 6500 sheep graze regularly in several common herds or are maintained by numerous hobby shepherds. It should be taken into account that during summer months almost all sheep are kept behind electric fences 24 hours a day. Additionally, threatened herds in the centre of the wolves' area of activity are protected by a second higher electric fence representing an instrument of the official wolf management programme.

However, the main reason for rare predation on livestock is more likely the high number of wild ungulates, especially in the restricted military training areas. These populations are often much more numerous than the general game density estimated by the state forest department. Our results correspond with the general dietary pattern of wolves from the entire, more natural area of occurrence in Europe, where wild ungulates are the absolute dominant prey of the wolf (Okarma 1997, Jędrzejewska and Jędrzejewski 1998).

All relevant studies agree that wolves hunt hoofed game, and it depends on game density if and to what extent wolves feed on domestic animals or other anthropogenic resources (e.g. Okarma 1997, Jędrzejewska and Jędrzejewski 1998, Gade-Jørgensen and Stagegaard 2000, Jędrzejewski *et al*. 2000, Sidorovich *et al*. 2003, Capitani *et al.* 2004). There are also conclusive examples for regional or temporal changes in the proportions of livestock and wild ungulates in the wolves' prey being strongly correlated with game density (Jędrzejewska and Jędrzejewski 1998, Sidorovich *et al*. 2003, Capitani *et al.* 2004). The high proportion of livestock, garbage and even small mammals and fruits in the diet of some wolf populations in southern and western Europe corresponds to the small supply of wild ungulates in the respective regions (Cuesta *et al.* 1991, Meriggi *et al.* 1996, Vos 2000, Pezzo *et al.* 2003, Capitani *et al.* 2004). Obviously, in Saxony, the density of hoofed mammals is high enough to support the resource needs of the recently recovering wolf packs, thus attacks to livestock as well as feeding on waste occur only very rarely.

Whereas wild ungulates form the food base of most wolf populations in Europe, different species are affected in each case, according to the prey's occurrence and density. Red deer are the most hunted prey in large parts of the wolves area (Jędrzejewska and Jędrzejewski 1998), while in Finland moose *Alces alces* or, in Italy, wild boar assume this role (Gade-Jørgensen and Stagegaard 2000, Capitani *et al.* 2004). In Saxony, roe deer are the most abundant hoofed mammal, with densities estimated up to more than 10/100 ha (personal communication by the State Forest Department). In the study area, roe deer are the most frequent ungulate species as well, but are distinctly less widely distributed than usual. This is due to the smaller portion of agricultural areas and the larger extent of pine forests and sandy open lands. Nevertheless, the estimation of game abundance in general includes methodical and practical problems. Therefore, the official density data of the State Forest Department could underestimate the real situation. But, in this case, it should apply to all hoofed game species in a similar way.

Moreover, in our study roe deer represent the most frequent food item in wolf scats. In a European frame, this represents one of the highest use of roe deer compared with other studies. Only in parts of northern Italy do roe deer occur in similarly high frequencies in the diet of wolves (Mattioli *et al.* 1995, 2004). However, in these regions, roe deer presents very high densities while other cervids are quite rare. One further study from Poland showing high proportions of roe deer (Gębczyńska and Raczyński 2004) suffers from small sample sizes.

The wolf populations of other newly colonized areas in Europe show similar food habits. Feeding on wild ungulates is the "certain common feature" (Okarma 1995). Under conditions of habitat destruction or reduced abundance of hoofed game, expanding wolf populations can show different feeding patterns. In newly colonized areas of the northern Apennines, wolves feed mainly on livestock, fruits and wild boar (Meriggi *et al.* 1996), whereas in other areas of northern Italy with recent expansions of wolf, the main prey consists of roe deer as in Saxony (Capitani *et al*. 2004).

In light of the objections mentioned above, the high occurrence of roe deer in wolf scats from

Saxony presents a remarkable fact in the feeding habits of the wolf in European framework. It will be interesting to follow developments following the stabilization of the wolf population in Saxony.

However, roe deer seem to be selectively preferred in the study area. They represent the most frequent and most important prey of wolves. It is less profitable to hunt the larger red deer if the more abundant roe deer is easier to obtain. On the other hand, red deer are a more attractive and favourable prey for wolves than the wild boar. This can explain the seasonal difference in the food composition of the wolves in Saxony. The proportion of wild boar in the food of wolves increased in summer only because of the high occurrence of piglets represented a very easily attainable prey. This again is a good sign for wolves in Saxony, where hunters are strongly recommended to hunt wild boar as an agricultural pest. Even though the recent development in the wolves' return is accompanied by an overall positive reaction from the general public and the media, an array of arguments clearly oppose their return. In this context, the present results are important for management and raising public awareness. Even in environments highly modified by human activities wolves can show quite natural feeding traits with minimal conflict if the food base is comparable to more natural areas.

Feeding studies on carnivores, and especially faecal analysis, suffer from difficulties in estimating the proportions of the true biomass consumed. Helpful discussions have ameliorate, but not solved the problem (eg Floyd *et al*. 1978, Weaver 1993, Ciucci *et al*. 1996, Jędrzejewska and Jędrzejewski 1998, Ruehe *et al*. 2003, Ciucci *et al*. 2004). In our study, two well-tested methods were applied for calculating consumed biomass (Goszczyński 1974, Weaver 1993). The results are presented together with a third modification (Ruehe *et al*. 2003). The differences between methods are evident (Table 1), but difficult to evaluate. Goszczyński's coefficients take the different digestibilities of small, medium and large types of prey very well into account, but all species of wild ungulates receive the same factor. In contrast, Weaver's equation allows a graduated differentiation by the mass of large prey. Its limitation of being restricted to mammals is hardly relevant for the present study. Surprisingly, the same method applied experimentally to European wolves and prey species by Ruehe *et al*. (2003) resulted in greater deviations from others, with unique values for the larger species. The general findings here of each of the three methods were similar. However, to facilitate further comparisons, they are all presented and utilized carefully. In the case of the selectivity index of prey species, the mean number of the three respective biomasses calculated from the three methods were used. Nevertheless, the differences in the biomass estimations were noticeable, but not substantial.

Acknowledgements: We are very grateful to all assistants who participated in the study, from collecting scats to determining intricate food remains. Sincere thanks go to D. Russell and J. F. Merritt for English revision. Parts of the study were supported by the Saxon State Ministry for Environment and Agriculture and by the research program Collegium Pontes 2004.

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Received 13 August 2004, accepted 14 June 2005.

Associate Editor was Andrzej Zalewski.