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Reproductive performance of the Red fox, *Vulpes vulpes*, in Garmisch-Partenkirchen, Germany, 1987–1992

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Abstract

The reproductive performance of the red fox *Vulpes vulpes* was studied after the disappearance of rabies between 1987 and 1992 in the county of Garmisch-Partenkirchen. The uteri of 452 adult vixens from the study area, and another 603 vixens from rabies-endemic and rabies-free areas in Bavaria were examined. No significant difference in embryonic litter size was found between 74 rabid and 34 non-rabid vixens in 1987. Furthermore, no difference in mean litter size was found between a rabies-endemic area and the rabies-free study area, Garmisch-Partenkirchen. Litter size and the proportion of barren vixens did not show any significant yearly variation during 1988–1991 in the study area. No difference in litter size (number of placental scars) between the various age classes was found. However, the differences in productivity between the different age-classes were significant, due to a higher proportion of barren yearlings. Although the fox-density increased continually during this field study, apparently the density is still below its carrying capacity. Therefore, no density-dependent effect on the productivity of the red fox population in Garmisch-Partenkirchen could be shown.

Introduction

When a population is reduced below its carrying capacity, an increased productivity may compensate for these losses. MacDonald (1987) described this possibility for the red fox (*Vulpes vulpes*), larger litters being typical for areas with heavy mortality. Could, therefore, a decrease in the productivity be expected in areas where the fox density has increased as a result of the disappearance of rabies? This would be of interest in areas where this important mortality factor of the fox population has disappeared after application of oral vaccination. Data from areas in Switzerland indicate that rabies can kill over 50 % of a local fox population during the height of the epidemic (Wandeler et al. 1974a).

The productivity of a fox population depends on two factors: litter size and the proportion of adult vixens reproducing (Lloyd et al. 1976; MacDonald and Voigt 1985). This study describes the reproductive performance of the fox in the alpine county ("Landkreis") Garmisch-Partenkirchen, Germany. The present European rabies epizootic reached Garmisch-Partenkirchen in the autumn of 1965. For the next twenty years, with the exception of 1970–1971, the county was infected. The rabies-incidence in this area was classified as type four; high oscillations with repeated peaks of rabies-occurrence, often 10 or more cases per 100 km^2 and per year (Jackson and Schneider 1984). Since the application of oral vaccination against rabies in the spring of 1985, no rabid fox has been found here up to the end of this field study in March 1992. The fox density in Garmisch-Partenkirchen increased continually during this study, although it seems that it had not yet reached its carrying-capacity during this period, 1987–1992 (Vos 1993).

Study area

The study area, the county of Garmisch-Partenkirchen (1012 km^2) in Bavaria is bounded on the south by the Austrian Alps. Approximately 46 % of the county is covered with forest, and 21.5 % is used for agricultural purposes (mainly pastures). The northern part (altitude 600–850 m) of Garmisch-Partenkirchen consists of hilly landscape, covered with a mixture of woods and grassland. The central and southern parts are characterized by mountain-ranges, up to 2964 m, interspersed with valleys and mountainslopes covered with forest. Above tree-line, steep and ragged landscape dominates, with a few scattered alpine meadows.

Material and methods

The data presented here came from a study on fox population dynamics after the disappearance of rabies in Garmisch-Partenkirchen. Uteri were obtained from carcasses of adult vixens (n = 452) killed or found dead in the study area between November 1987 and March 1992. The vixens were collected throughout the year. Litter size was determined from counts of implanted embryos and, after parturition, by placental scar counts, as described by Vos (1993). Since the placental scars persist, they were also used to determine whether or not a vixen had been reproductively active during the last breeding season. The term "barren" includes all adult vixens that failed to reproduce; i. e., those that did not ovulate or failed to implant or lost the entire set of implanted embryos before parturition. To examine the relationship between rabies and the reproductive performance of foxes, vixens (n = 603) from rabies-endemic and rabies-free areas in Bavaria were examined. These vixens consisted of animals delivered for rabies diagnosis collected annually from February to April 1987 through 1991. The age of the vixens was estimated by radiography of canine teeth and/or by counting cementum annuli in the first premolars or canines (Vos 1993).

Results

In spring 1987, in Bavaria, the average number of implanted embryos of rabid vixens ($\bar{x}$ = 5.57, n = 74) did not differ significantly from non-rabid vixens ($\bar{x}$ = 6.26, n = 34) (Kolmogoroff and Smirnoff Test, D = 0.28, n. s.). Also, no significant difference could be observed between the average number of implanted embryos in vixens from a rabies-infected area, the district ("Regierungsbezirk") of Schwaben ($\bar{x}$ = 5.68, n = 29), and those from the rabies-free county of Garmisch-Partenkirchen since 1985 ($\bar{x}$ = 5.75, n = 16) (Student's t-Test, t = 0.16, df = 15). Apparently rabies has no direct influence on litter size. The frequency distribution of the number of placental scars in vixens from Garmisch-Partenkirchen between 1988 and 1991 is presented in table 1. No significant differences in the average number of placental scars (Student's t-Test) and the frequency distribution (Kolmogoroff and Smirnoff Test) could be observed among years.

The average litter size based on the number of embryos was higher than the average litter size based on the number of placental scars in vixens from Garmisch-Partenkirchen. This difference was a result of the period in which the samples were taken. Vixens with implanted embryos were delivered only during early-pregnancy stages; only prenatal losses during implantation and these early pregnancy stages could be considered. How

Table 1. **Number of placental scars in vixens in Garmisch-Partenkirchen, 1987–1991**
($\bar{x}$ – mean number of placental scars, SD – standard deviation)

	Number of placental scars									
Year	1	2	3	4	5	6	7	8	$\bar{x}$	SD
1988	1	1	3	3	8	6	1	1	4.8	1.59
1989	–	1	6	10	6	9	1	–	4.6	1.25
1990	–	1	3	8	11	4	4	–	4.8	1.27
1991	–	–	3	4	11	2	–	–	4.9	1.10
Total	1	3	15	25	36	23	8	1	4.8	1.29

ever, by the evaluation of the placental scars, all visible losses between implantation and birth were taken into account. In early summer, on average 4.6 cubs were observed at the den sites (n = 14). The difference between the number of embryos of early pregnancy stages and the number of cubs observed at the den sites, indicated a loss of around 20 %. Litter size of foxes from different areas is shown in table 2.

The productivity of the fox is not only determined by litter size, also the proportion of reproductively active vixens plays an important role. No differences in the proportion of barren vixens could be observed for Garmisch-Partenkirchen between the years 1988–1991 (χ^2-Test, χ^2 = 4.27, df = 3, n. s.). The yearly productivity of the vixens (i. e. including barren animals) in Garmisch-Partenkirchen was estimated on the basis of the mean number of placental scars and the proportion of barren vixens (Tab. 3). For productivity, no differences among years could be shown (analysis of variance, F = 0.72, df[3,135], n. s.). 15.3 % of the examined adult vixens (n = 170) were barren. Of these 26 barren vixens, 69.2 % were yearlings, 19.2 % were 2-year olds and two vixens were over four years of age. The proportion of barren yearlings was significantly higher compared to the other age classes (χ^2-Test, χ^2 = 6.5, df = 1, $P < 0.05$).

In table 4 the mean litter size (placental scar counts) and the proportion of barren vixens are presented for the different age classes. No age-dependent effect on litter size could be shown (analysis of variance, F = 1.79, df[3.98], n. s.). Also no age-dependent litter size (number of embryos) could be found for vixens in the Bavarian sample (analysis of variance, F = 0.65, df[2,83], n. s.). However, the productivity of yearlings in Garmisch-Partenkirchen was significantly lower than of vixens 3-years of age and older (Duncan-Test, $P < 0.05$). The 2-year-old vixens showed the highest mean litter size. As a result of

Table 2. **Litter size of foxes in different study areas**

Study-area		PS	E	YF	Author
rabies-free	CH	5.2	5.2	4.7	Wandeler et al. (1974)
rabies infec.	CH	5.1	5.1		Wandeler et al. (1974)
Oberlausitz	D	6.7	6.3		Ansorge (1990)
Midwest	USA	7.1	6.8	4.1–4.3	Storm et al. (1976)
London	GB	4.8			Harris and Smith (1987)
Bristol	GB	4.7			Harris and Smith (1987)
	D	6.3			Stubbe (1980)
N-Dakota	USA	2.8–5.0			Allen (1984)
	CH	5.4		4.7	Lloyd et al. (1976)
Bavaria	D	6.2			Lloyd et al. (1976)
	NL	6.0			Lloyd et al. (1976)
Wales	GB	5.5			Lloyd et al. (1976)
Wriezen	D			5.3–6.2	Goretzki et al. (1981)
Garmisch-P.	D	4.8	5.8	4.6	Vos (1993)

PS = placental scars; E = Embryos; YF = cubs at den. In some samples data of PS and E are combined.

Table 3. **Yearly productivity of vixens in Garmisch-Partenkirchen, based on the number of placental scars and the proportion of barren vixens**

	1988	1989	1990	1991
Litter size	4.8	4.6	4.8	4.9
Barren vixens (%)	25.0	7.3	19.1	10.0
Productivity	3.6	4.3	3.9	4.4

Table 4. **Productivity of vixens**
Mean number of placental scars (litter size) and the proportion of barren vixens for different age classes in Garmisch-Partenkirchen

Age class (year)	Litter-size	Barren vixens (%)	Productivity
1–2	4.5	24.0	3.4
2–3	5.3	17.9	4.3
3–4	4.7	0.0	4.7
≥ 4	4.9	6.8	4.6

the relativly high proportion of barren vixens, the productivity of this age class was below that of older vixens.

Discussion

Like Wandeler et al. (1974b), no difference in the mean number of implanted embryos could be observed between a highly infected area and the rabies-free study area, Garmisch-Partenkirchen since 1985. After the disappearance of the important density-dependent mortality factor, rabies, the red fox density increased continually in Garmisch-Partenkirchen (Vos 1993). However, even the growth rate of the population of this generalist, the red fox, is not unlimited. The population threshold (carrying-capacity) of a certain area is a result of density-independent factors, e. g. habitat structure. However, the population numbers are regulated by density-dependent events (Wehner and Gehring 1990).

Negative density-dependent processes limit the growth rate of the fox population. The occurrence of these feedback mechanisms could indicate that the fox population approaches the carrying capacity. These mechanisms do not necessarily mean an increased mortality rate; a decrease in reproduction performance could also influence the growth-rate. In Garmisch-Partenkirchen, no yearly difference was observed in the two important reproduction parameters; litter-size and the proportion of barren vixens. The foxes in this county live in a very stable environment with a high food supply. Apparently the increased fox density after the disappearance of rabies has not reached its carrying capacity. Therefore, no decrease or yearly fluctuations in the reproductive performance were observed during this field study. This is in contrast to several other studies, where the fluctuating numbers of barren vixens can be seen as a density-dependent regulation mechanism in areas with limited or strongly fluctuating food supplies (Englund 1980; MacDonald 1980; Schantz 1981). Englund (1980) found in the northern corniferous belts of Sweden not only large annual variation in the number of barren vixens, but also in the number of cubs per litter. In these areas foxes depend for food almost exclusively on the fluctuating rodent populations. The observed spatial and temporal differences in the reproductive performance of foxes in the different areas are to a large extent a result of variations in the social structure of the fox populations. In some habitats foxes live in social groups comprised of one adult male and several adult vixens (MacDonald 1979; Schantz 1981), whilst elsewhere foxes live in territorial pairs (Storm et al. 1976). Observations of the above-mentioned family groups have been made in areas of high population density and stable food availability (MacDonald 1980), but also in areas where fox populations experience strong food-resource fluctuations (Englund 1980; Schantz 1981). The subordinate vixens of these groups reproduce only in years when there are abundant food resources. At low or intermediate levels of food abundance only the dominate alpha vixen reproduces (MacDonald 1983).

Like Ansorge (1990), litter size did not show an age-dependent effect in this study.

Contrary to these results, Allen (1984) found an increase in ovulation rate and embryonic litter size as a function of increasing female age of foxes in North Dakota. However, Harris and Smith (1987) could only observe a decrease in litter size in extremely old vixens in the London area. In accordance with other studies (Harris 1979; Englund 1980) most barren vixens in Garmisch-Partenkirchen were yearlings, hence the productivity of this age class was lower than that of older vixens.

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Zusammenfassung

Die Reproduktion des Rotfuchses (Vulpes vulpes) im Landkreis Garmisch-Partenkirchen, Deutschland, 1987–1992

Untersucht wurde die Reproduktionsleistung des Rotfuchses *Vulpes vulpes* nach dem Verschwinden der Tollwut zwischen 1987 und 1992 im alpinen Landkreis Garmisch-Partenkirchen. Uteri von 452 adulten Fähen aus dem Untersuchungsgebiet und die von 603 Fähen aus ganz Bayern wurden auf Anwesenheit von plazentalen Narben oder Embryonen untersucht. Keine signifikanten Unterschiede in der durchschnittlichen Zahl der Embryonen zwischen 74 tollwutpositiven und 34 tollwutnegativen Fähen konnten festgestellt werden. Kein signifikanter Unterschied in der durchschnittlichen embryonalen Wurfgröße konnte während dieser Untersuchung zwischen den Fähen aus dem tollwutinfizierten Regierungsbezirk Schwaben und dem seit 1985 tollwutfreien Landkreis Garmisch-Partenkirchen nachgewiesen werden. Keine signifikanten jährlichen Differenzen im Anteil nicht-reproduzierender Fähen und der Wurfgröße wurden während 1988 und 1991 gefunden. Auch unterschied sich die Wurfgröße nicht zwischen den verschiedenen Altersklassen. Die Unterschiede in der Produktivität der Altersklassen als Folge des höheren Anteils nicht-reproduzierender 1jähriger Fähen waren jedoch signifikant. Die Ergebnisse dieser Untersuchung deuten darauf hin, daß die Fuchsdichte im Landkreis Garmisch-Partenkirchen sieben Jahre nach dem Verschwinden der Tollwut anscheinend ihren kritischen Grenzwert noch immer nicht erreicht hat.

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