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# Population dynamics of the red fox (*Vulpes vulpes*) after the disappearance of rabies in county Garmisch-Partenkirchen, Germany, 1987–1992

Ad Vos

*Vos, A., Impfstoffwerk Dessau–Tornau GmbH, P.O.Box 214, 06855 Roßlau, Germany*

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Data on 977 foxes harvested between November 1987 and March 1992 from the alpine county Garmisch-Partenkirchen, Germany, concerning reproduction, sex-ratio and age-structure were combined with some results of a mark-recapture study and the hunting statistics in this area and used to construct a new fox-density population model on the basis of the juvenile fox population. This to investigate the effects of the disappearance of rabies on the population dynamics in spring 1985 after succesful application of oral vaccination.The average adult fox density in spring, during 1987–1991, was estimated at 0.74 foxes/km$^2$. The adult spring fox density was three times higher in the northern heterogeneous part of the county (1.77 foxes/km$^2$) than in the southern alpine regions (0.59 foxes/km$^2$). Annual losses, including fox hunting, could not prevent an increase of the fox density between 1987 and 1992. In 1992, seven years after the last fox rabies case, the increased fox density apparently still has not reached its carrying-capacity. The foxes here live in a very stable environment with a high food-supply and number of denning sites, partly of anthropogenic origin.

## 1. Introduction

The present european rabies epizootic reached the alpine county ("Landkreis") Garmich-Partenkirchen, Germany, in 1965. For the next twenty years this area was, with the exception of the period 1970–1971, infected. The rabies-incidence was characterized by high oscillations with repeated peaks of rabies-occurence, often 10 or more cases per 100 km$^2$ and per year (Jackson & Schneider 1984). Since the application of oral vaccination against rabies in Garmisch-Partenkirchen in spring 1985, no rabide fox (*Vulpes vulpes*) has been found here till the end of a field-study, March 1992 (Vos, 1993).

Rabies is acting as a severe source of density dependent mortality. Data from areas in Switzerland indicate that rabies can kill over 50% of a local fox population during the height of an epidemic (Wandeler et al. 1974). What will be the effects of the extrinsically induced disappearance of rabies through oral vaccination on the population dynamics of a fox population?

For a detailed description of the dynamics of the fox population data concerning temporal changes in density are essential. Methods of estimating animal abundance have increased tremendously in the past 40 years. However, the problem of obtaining accurate estimates of the density of the red fox remains largely unsolved. Certain methods like radio-telemetry or counting breeding-sites in spring can be used to estimate fox population density. These methods are however very time-consuming and therefore only suitable for relatively small areas. Other methods provide only an index of abundance; for example bait-acceptance (Gürtler & Zimen 1982) or the Hunting Indicator of Population Density (Bögel et al. 1974). Therefore, a new model to estimate fox numbers in Garmisch-Partenkirchen was constructed in a field-study and used to provide estimates of fox density after succesful application of oral vaccination.

## 2. Study-area

The alpine county Garmisch-Partenkirchen (1012 km$^2$) in Bavaria, where this study was conducted from 1987 to 1992, contained various types of landscape; from marshland to mountain-ranges up to 2964 m above sea level. The county of Garmisch-Partenkirchen (study-area) was bounded on the south by the Austrian Alps. Forty six percent of the area was covered with forest, and 21.5% was used for agricultural purposes (grassland). The northern part (altitude 600–850 m) was covered with a mixture of woods and grassland. The central and southern part consisted of mountain ranges, interspersed with valleys and afforested mountain slopes. Above the tree-line the landscape was steep and rugged.

## 3. Material and methods

Data on age-structure, productivity and sex ratio were obtained from carcasses ($n$ = 1494) provided by hunters and used in a model to estimate fox numbers. These fox carcasses, killed or found dead in the study-area, were collected all year through from November 1987 till March 1992. Information from tagged foxes (capture-recapture-method) and the official annual fox hunting bag were also used. Foxes killed through hunting activities ($n$ = 977), shot or trapped, are henceforth referred to as "harvested". The age of foxes ($n$ = 1371) was estimated by radiography of canine teeth and/or by counting cementum annuli in teeth (Vos 1993).

The productivity of the fox population depends on two factors; litter-size and the proportion of vixens reproducing. The litter-size in this study was estimated by counting placental scars and the number of barren vixens determined through the absence of these scars. For more detailed descriptions of estimating productivity by means of placental scar counts in this study, see Vos (1993).

To compare the estimates of the breeding-site density a systematic search for these was conducted every spring in two selected hunting areas in Garmisch-Partenkirchen; the hunting-area Schwaiganger in the northern part of the county and hunting-area Klais in the alpine southern region.

### 3.1. Description of the model

The fox density was estimated by means of the juvenile fox population (<1 year). Of the total number of fox cubs born, some have been killed through hunting activities or died from other causes (e.g. traffic, diseases), others however survived their first year. Only the number of juveniles harvested could be estimated directly.The yearly number of juveniles harvested in the study-area was determined from the proportion of juveniles in a sample of foxes harvested and handed in by hunters ($P_j$) and the total number of all foxes harvested ($J_t$); the annual hunting-bag. The numbers of juveniles that died from other causes or survived their first year was unknown. For the purpose of this study the number of juvenile foxes that were not harvested during their first year was termed "missing-value" (a)

This value was estimated from the number of cubs tagged at the breeding-site and later harvested during their first year. Assuming that all tagged foxes harvested were reported, the "missing-value" (a) is given by

$$a = 1 - (z/M) \qquad \text{Eq. 1}$$

where M = number of cubs tagged at breeding-site, and z = number of tagged cubs (M) that were harvested and reported during their first year.

Using the "missing-value" and the number of juveniles harvested the absolute number of cubs born ($N_j$) can be written as

$$N_j = (P_j * J_t) / (1 - a) \qquad \text{Eq. 2}$$

where $P_j$ = proportion of juvenile foxes in the sample of foxes harvested, $J_t$ = official annual hunting bag (number of foxes harvested), and a = proportion [estimation] of juvenile foxes not harvested.

Accepting assumption on productivity and sex ratio, the number of adult foxes in spring ($N_a$) is given by

$$N_a = (N_j * (1 + s)) / ((1 - q) * r) \qquad \text{Eq. 3}$$

where $N_j$ = number of cubs born, s = sex ratio (male:female) of the adult fox population, r = litter-size: average number of placental scars of the reproductive-active vixens, and q = proportion of barren adult vixens.

The number of breeding sites (B) can be written as

$$B = N_j / r \qquad \text{Eq. 4}$$

Table 1. The number of placental scars of the vixens in Garmisch-Partenkirchen, 1988–1991. ($\bar{x}$ = mean number of placental scars).

| Year | Number of placental scars 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | $\bar{x}$±*SD* | *n* |
|---|---|---|---|---|---|---|---|---|---|---|
| 1988 | 1 | 1 | 3 | 3 | 8 | 6 | 1 | 1 | 4.79±1.59 | 24 |
| 1989 | | 1 | 6 | 10 | 6 | 9 | 1 | | 4.58±1.25 | 33 |
| 1990 | | 1 | 3 | 8 | 11 | 4 | 4 | | 4.84±1.27 | 31 |
| 1991 | | | 3 | 4 | 11 | 4 | 2 | | 4.92±1.10 | 24 |
| Total | 1 | 3 | 15 | 25 | 36 | 23 | 8 | 1 | 4.77±1.29 | 112 |

## 4. Results

The official registrated annual fox hunting bag consist of the number of foxes harvested between April 1st and March 31st next year. Most cubs are born around April 1st (Lloyd 1980, Ansorge 1990). For the application of this model it was of great advantage that the generation-cycle of the red fox coincides with the official fox hunting-year, as described above.

In the sample of foxes harvested and handed in by hunters ($n$ = 977) 56% were juveniles. Between April 1987 and March 1992 an average of 701 foxes were harvested during a hunting year. Only 26% ($n$ = 15) of the 58 cubs tagged at the breeding-site, were harvested and reported during their first year, which results in a "missing-value" of 0.74. The annual productivity was therefore 1518 animals.

The sex ratio of a sample of the dead fox population does not necessarily reflect the ratio of the living population, due to sex dependent mortality rates. Although no data was available concerning the sex ratio of the adult living fox population, the gathered data suggested that in Garmisch-Partenkirchen the adult sex ratio was close to unity (Vos 1993). The average litter-size of 112 reproductive-active vixens was 4.77 (Table 1) and 15.3% of 170 adult vixens examined were barren. The productivity, based on litter-size and the proportion of barren vixens, did not show any significant yearly variation during 1988–1991 in Garmisch-Partenkirchen (*F*-Test, $F$ = 0.72, $df$ (3,135), *NS*). Thus the number of adult foxes in spring was estimated as 752 foxes, or 0.74 foxes per km$^2$. The density of the breeding-sites was estimated at 0.31 litters per km$^2$. The fox- and breeding-site density was three times greater in the north (forest interspersed with meadows) compared to the markedly different habitat of the mountainous south of the study-area (Table 2). These estimates of the breeding-site density were similar to the results obtained by direct counts of breeding-sites in the two selected hunting-areas; Schwaiganger – 0.69 breeding-sites/km$^2$ and Klais – 0.25 breeding-sites/km$^2$.

Table 2. Average adult fox density in spring and breeding-site density in the north and south of Garmisch-Partenkirchen between 1988 and 1991.

| | Litter-size | Proportion of barren vixens | Foxes/km$^2$ | Breeding-sites/km$^2$ |
|---|---|---|---|---|
| North | 5.02 | 0.12 | 1.77 | 0.78 |
| South | 4.49 | 0.15 | 0.59 | 0.25 |

For most of the parameters, sufficient data were available to estimate the annual fox density between 1988 and 1991. However, the number of foxes tagged at breeding-sites was too small to estimate a seperate "missing-value" for individual years. Therefore, the average "missing-value" (a = 0.74) was used to estimate the annual fox density during the field-study (Table 3). Between 1988 and 1990 the adult spring fox-population increased considerably (38%). From these estimates and the official fox hunting-bag it was shown that 40–50% of the annual mortality was caused by hunting.

## 5. Discussion

Several methods to estimate fox numbers have been described (Lloyd 1980), some were unusual like the fox-sightings of mail-carriers used as an index of fox-density by Allen & Sargeant (1975). An index can be useful but does not allow an estimate of the absolute number of foxes, such as counts of breeding-sites for example. However, this last method is very time-consuming and inaccurate in inaccessible areas for it is difficult to locate all breeding-sites, e.g. dense forest or steep mountain-slopes. Another method of estimating fox abundance is through home-range size obtained by radio-telemetry. However, also this method is not without difficulties; e.g. Capt & Stalder 1991.

This model described in the present study also permits an estimate of fox-density, but has to deal with certain shortcomings. Some parameters were based on a sample of dead foxes, like litter-size, number of barren vixens and sex-ratio. As a result of the sex- and age-dependent mortality-rates, these data do not necessarily represent the living fox population (Kappeler 1985).

The "missing-value", was used on the assumption that all taged juveniles harvested were reported which unfortunately could not be verified. The collaboration with the hunters in Garmisch-Partenkirchen was excellent and therefore, the above mentioned premiss was accepted. The possible loss of ear-tags could result in an over estimation of the "missing-value" and consequently the population density. Hubert et al. (1976), using different types of ear-tags, showed that only 1.3% of the foxes lost both ear-tags within a year. Hence, the effect of loss of ear-tags on the "missing-value" was insignificant. The relatively small number of cubs tagged at the breeding-site ($n = 58$) did not allow an estimate of the "missing-value" on a yearly basis. The hunting-pressure is also reflected by this value; a decrease in hunting-pressure results in an increase of the "missing-value", irrespective of the fox-density. When the mortality of a fox population increases as a result of an increased hunting pressure the average age of the harvested fox population decreases (Lloyd 1980, Macdonald 1987). Therefore, in the hunting-season, April 1st 1991 – March 31th 1992, a decrease in hunting-pressure was observed; the average age of foxes harvested increased, although no decrease in productivity in spring 1991 was observed (Vos 1993). The fox-density in spring 1991 was estimated by applying the average "missing-value". Hence, the adult spring fox-density determined for 1991 (0.79 fox/km$^2$), according to the model, was below the actual density. This inaccuracy could be reduced by increasing the number of cubs tagged, this would permit a "missing-value" for the individual years.With a "missing-value" for the individual years possible fluctuations in hunting pressure could be taken into consideration and therefore, give a more accurate estimate of the fox density.

The model was also used to estimate fox density in the different habitats of Garmisch-Partenkirchen. In the north of the county, the estimated adult fox density (1.77 fox/km$^2$) approaches the figures estimated for urban fox populations in England and the fox population in the Dutch coastal regions (Page 1981, Voight & Macdonald 1984, Mulder 1988). In accordance with the social-structure of these fox populations some observations were made in the northern parts of the study area that indicate the presence of fox-families. In the northern heterogeneous part the adult spring fox density was three times higher than in the southern alpine regions of the county. Here, the carrying capacity of landscapes

Table 3. Parameters used and the fox- and breeding-site density in Garmisch-Partenkirchen between 1988 and 1991 (s = 1 [sex ratio of the adult fox population] and a = 0.74 [proportion of juvenile foxes not harvested]).

| | Juveniles harvested (%) | Hunting-bag | Litter-size | Barren vixens (%) | Foxes/km$^2$ | Breeding-sites/km$^2$ |
|---|---|---|---|---|---|---|
| 1988 | 56.1 | 531 | 4.79 | 25.0 | 0.63 | 0.24 |
| 1989 | 59.6 | 616 | 4.58 | 7.3 | 0.66 | 0.30 |
| 1990 | 57.9 | 775 | 4.84 | 19.1 | 0.87 | 0.35 |
| 1991 | 51.4 | 883 | 4.92 | 10.0 | 0.79 | 0.35 |

such as large uninterrupted forestcomplexes, steep mountain-slopes and areas without vegetation can only support a relatively small number of foxes.

According to Bögel et al. (1974) complete recovery after a serious rabies-outbreak may require 1–7 years, depending on the level to which the population was reduced before recovery began. The recovery-rate is furthermore influenced by e.g. hunting pressure, migration, age- and sex-composition of the remaining population. However, the growth-rate of a fox population is not unlimited, density dependent factors ultimately regulate fox numers. Not only diseases like rabies, but also a decrease in reproductive performance, can influence the growth-rate a fox population. Decreasing reproductive performance could indicate that the population approaches the carrying capacity. However, no significant yearly difference between 1988 and 1991 was observed in the two major factors determining the productivity of the fox population; litter-size and the proportion of barren vixens. Therefore, seven years after the last case of fox-rabies in this area, the fox population is apparently not at or near the carrying-capacity. The abundant food and shelter-possibilities, partially supplied by man, in the study-area enabled the observed population increase.

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