Recovery of Reduced Fox Populations in Rabies Control

By

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With 3 figures and 2 tables

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Introduction

In Central Europe, where the red fox (Vulpes vulpes) maintains the chain of rabies infection, wildlife rabies has been controlled locally with varying success by reducing the number of foxes (3, 5, 6, 7, 8, 11). However, one of the major obstacles in the assessment and prediction of the efficacy of different control measures has been the lack of knowledge of the rate at which reduced fox populations tend to restore their original density. In order to overcome these difficulties WHO and FAO have been co-ordinating ecological and epidemiological studies in various parts of Europe (10).

Population data obtained in these studies have been used to establish a model of the annual population turnover (1). This model may reflect actual conditions of balanced fox populations in large parts of Central Europe and it permits the assessment of single fox control operations. However, in long-term rabies control programmes it is essential to consider other ecological factors in addition to those included in this simple model of a balanced population. Most important is the recovery rate of reduced fox populations which is the expression of the combined effect of a number of such additional ecological factors. Because of the rapid turnover of fox populations the recovery rate can be of such a magnitude that it compensates for or even exceeds the effect of the control measures.

There are only a few sources of field data which allow for rather rough and indirect estimates of recovery from various levels to which fox populations may have been reduced. Population recovery is influenced by hunting pressure, incidence of diseases, the age and sex composition of remaining

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1) These studies have been carried out within the framework of the WHO/FAO co-ordinated Research Programme on Wildlife Rabies in Europe.
4) Referat Veterinärwesen, Regierungspräsidium Südwestfalen-Hohenzollern, 74 Tübingen 1, Nauklerstrasse 47
populations, and other factors. Any calculation of recovery rates must therefore be considered with reservations. Nevertheless an attempt is made in this report to provide some clues which may be used to predict and assess the efficacy of fox control operations.

Sources of data and methods

Study Areas and Densities of Fox Populations: The ecological and epidemiological data used in this paper are from areas in Europe for which the density of the springtime fox population is estimated to be between 0.9 and 1.2 mature individuals/km², if rabies is not present and special fox control measures are not applied. This density figure has been derived from litter counts, sex ratios and productivity observed in areas in the Netherlands, Denmark and the Federal Republic of Germany (1). The results are rather uniform and they are consistent with the indirect measure of density obtained from the number of foxes shot per year and km². This “hunting indicator of the population density” (HIPD) of foxes has been found to centre around 1.2 in wide areas of Denmark, the Federal Republic of Germany and Switzerland (5, 6, 7, 9).

The HIPD seems to provide values of acceptable reliability when based on data from areas of not less than 2000 km² (5). Although it may not be valid to compare the HIPD of different areas, it does provide a useful measure of apparent change in the density of fox populations within broadly defined areas. However, the HIPD value not only reflects the actual population density, but also the hunting intensity. Where hunting pressures tend to remain constant, the HIPD may be used with confidence as an index of population density. In rabies infected areas various factors may account for a reduction in hunting intensity or hunting success. Important in this respect are slackening of interest in fox hunting as the availability of foxes decreases, and the lack of knowledge or inaccessibility of alternative denning places when known burrows are no longer used by foxes after gassing campaigns (8, 10).

To counteract these factors bounties are frequently paid for fox control and hunters are asked to collaborate in rabies control. These measures have only a moderate or transient effect in most European areas as the hunting intensity remains in fact rather constant (3, 5, 6, 8, 10). The evaluation of the HIPD in rabies-free areas of Denmark suggests that the fox population was reduced by no more than 25% even after some years application of hunting intensifying measures (6).

Epidemiological observations: The cyclic changes in the number of rabies cases observed in endemic areas suggest that fox populations are able to attain their original density within three years after they have been reduced by rabies. In different areas of Europe where fox populations were not controlled by gassing of burrows, the number of rabies cases decreased and increased sharply at intervals of three years (2, 10). Such three year intervals are observed in areas of about 1000 km²; otherwise they are often obscured in the statistics of larger areas due to the time phase differences between local epidemic cycles.

Data from areas in Switzerland indicate that rabies can kill 50—60% of a local fox population during the height of the epidemic (10). In part of North Baden, Federal Republic of Germany, rabies and intensified hunting reduced the HIPD of foxes to about 40% of their original levels from 1957 to 1963. In Hessen, the HIPD of foxes decreased to about 50% when rabies spread into this Land. These data suggest that rabies and the small additional

Zusammenfassung

In 2 Versuchsreihen mit insgesamt 8 trächtigen Sauen wurde die Wirkung von Mebendazol und Levamisol auf die galaktogene Strongyloidesinfektion untersucht. Hierbei wurde folgendes festgestellt:

1. Durch Mebendazol, in der Gesamtdosis von 72 mg/kg (Versuch 1) und 104 mg/kg (Versuch 2), im Verlauf der letzten 12 bzw. 14 Tage vor der Geburt oral verabreicht, nimmt die Zahl der in der Milch enthaltenen Larven ab.


3. Während der 10tägigen Verabreichungszeit von täglich 2 mal 7 mg/kg Levamisol ist dieses Präparat in der Konzentration von 6—7 ppm in der Milch enthalten. Diese Konzentration schädigt die in der Muttermilch enthaltenen Larven. Die Infektion eines mit solcher Milch ernährten Ferkels war wesentlich geringer als die des Kontrolltieres.


5. Eine alleinige galaktogene Infektion bleibt bei den Ferkeln mindestens 8 Wochen nach dem Absetzen bestehen.

Summary

Chemoprophylaxis of galactogenic Strongyloides infection in the pig

Studies on two groups comprising a total of 8 pregnant sows on the effect of Mebendazol and Levamisol on galactogenic Strongyloides infection gave the following results:
(1). Relevant data were available from areas in Denmark, England, Federal Republic of Germany, the Netherlands and Switzerland.

According to this model which is based on an average of 1 mature fox/km² in springtime, as noted above, the maximum population, including the new generation, would amount to 3 foxes/km² in early summer so that 66 % must be removed before the following breeding season, to again reach a level of 1 mature fox/km². The annual loss of 2 foxes/km² may further be subdivided, as the number of animals shot/km² has been shown to be approximately 1.2 in large European areas of about that population density (Table 1).

### Table 1
Annual turnover of fox population estimated per square kilometer
(rabies-free area without special measures for fox control)

<table>
<thead>
<tr>
<th>Density before birth of new generation</th>
<th>Density after birth of new generation</th>
<th>Losses due to hunting</th>
<th>Losses due to disease and accidents</th>
<th>Total losses</th>
<th>Density before birth of new generation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3</td>
<td>1.2</td>
<td>0.8</td>
<td>2.0</td>
<td>1</td>
</tr>
</tbody>
</table>

* determined
** because the maximum population will have to be reduced by 9/10 (determined figure) during the year to reach the initial level of 1 fox/km². The total losses therefore amount to 2 foxes/km².
*** determined by bag records (foxes shot in reporting districts, cantons and larger areas).

**Mean recovery rates:** Mean annual recovery rates from reduced population levels have been calculated according to the following formula:

Mean annual recovery rate in % = \[ \frac{1}{\text{reduction period}} \] %

whereby

\[
\text{Multiplication factor of annual increase} = \left( \frac{\text{final population level}}{\text{reduced population level}} \right) - 1
\]

Fox populations in Europe breed once a year and only a few generations have to be considered within the recovery period. Therefore, for fox populations, the above formula applies rather than an exponential growth based on the natural logarithm, as is often used for more complex growth cycles (4).

Thus a population reduced to a 20 % level (80 % reduction) can attain its original density within four years if it increases every year by 49.5 % over the population of the preceding year, since:

\[
100 \left[ \frac{100}{20} \right]^\frac{1}{4} - 1 = 100 (1.495 - 1) = 49.5
\]

This rate of population increase can only be considered as a mean because the survival rate of foxes should be higher than the mean at the beginning of the recovery when the population is still very low. Accordingly, the survival rate should be lower than the mean when the population turnover approaches equilibrium.

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5) percent increase over the population of the preceding year
6) population as percent of the original non-reduced population; this may also be applied for part of the period required for complete recovery
7) years required for the increase from the reduced to the final population level.
Estimates of recovery rates

The evaluation of data on the recovery of reduced fox populations can only provide figures within certain margins of error. However, relatively high estimates should be chosen within these margins, in order to avoid failures when the estimates are applied to field projects of fox control.

Field observations: Epidemiological observations in endemic areas indicate that fox populations reduced by rabies to 40—50% of their original density (9, 10) can recover within three years (2, 10). The ecological observations i.e. the increase of the HIPD, after discontinuation of gassing operations are consistent with this observation.

Apart from inconsistencies observed in areas too small to provide reliable data, surprisingly parallel curves depicting the increase of the HIPD have been found in different areas (Fig. 1). It is reasonable to assume that the actual density of the fox population does not return to the original level at a rate higher than the HIPD. Otherwise the intensity of hunting, on which the HIPD largely depends, should decrease as the fox population increases and vice versa. This seems to be unlikely as experience in rabies control indicates a decrease of hunting intensity as the population density decreases.

Taking this into account the results shown in Figure 1 suggest that fox populations require about four years to recover from the 20—30% level, three years from the 40% level, two years from the 60% level and one year from the 80% level. The maximum increase of the HIPD observed in two large areas was 71%. The actual increase of the fox population therefore could not have exceeded this rate in any one of the four years required for recovery from a reduction to 20—30% of the original population.

On the other hand, the maximum rate of recovery should be significantly higher than the mean rate of 41.5%, calculated for a recovery within four years from the 25% level (Fig. 2). We must therefore assume that the maximum annual increase of fox populations lies between 45% and 70% under conditions prevailing after fox control operations and elimination of rabies.

An annual population increase of this magnitude could be due to an increase in productivity and/or a decrease in mortality. There is some evidence from field studies that the recovery of reduced fox populations is mainly caused by an increase of the survival rate, i.e. the reduction of proportional losses due to hunting, diseases and accidents. The litter size does not show any significant change, when fox populations are reduced by rabies and control measures (8) and the common pregnancy rate of 90% (1) leaves a very small margin for an increase in the productivity of a fox population. Also the risk of accidents should vary little so that losses due to hunting and diseases remain the most important factors responsible for changes in fox populations.

The model describing standard conditions of the population turnover (Table 1) allows for a 70% increase of the population if the hunting rate is reduced by 1/3, and total losses due to diseases and accidents are reduced by about 40% (since: 3 foxes — 0.8 shot — 0.48 killed by diseases and accidents = 1.7 foxes instead of 1.0).

Such changes in mortality factors may actually occur. It is, however, difficult to assume a greater reduction of these mortality rates. This limitation would be consistent with results suggesting a maximum increase of fox population in the order to 45—70%. Therefore we consider a maximum increase of 70% to be possible, theoretical increases between 70% and 90% to be improbable, and values of > 90% as impossible. A recovery rate of 90% would imply a decrease of hunting rates by 50% and a reduction of losses due to "diseases and accidents" by 40%, according to the population turnover
Fig. 2. Computation of period required for complete recovery of fox populations at various recovery rates following reduction to different levels of the original populations

Table 2
Analysis of hypothetical gradients of

<table>
<thead>
<tr>
<th>Population level before recovery</th>
<th>Population increase in first recovery year</th>
<th>Recovery rate</th>
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<tr>
<td></td>
<td>Population level attained</td>
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1) Values determined graphically and read from figure 2.
2) In percent of original non-reduced population.
shown in Table 1. Moreover, it would imply an increase of the HIPD far beyond values observed in the field.

**Possible mean recovery rates:** Figure 2 shows the years required for complete recovery at different rates and starting from different levels of reduced populations. This nomogram can be applied to any animal population for which mean rates of annual population increase are calculated according to the formula described under “methods”. Field observations permit the rejection from the nomogram of certain assumptions as being “improbable” or “impossible”. Within the remaining field of the nomogram, the curve representing true recovery values must lie. Different hypothetical curves drawn in the “acceptable” field of the nomogram can be analysed and compared to field observations. It is the purpose of the following analysis to define in the nomogram a curve representing the best possible estimate of true but unknown values.

Field observations strongly suggest that actual recovery rates of fox populations fall outside rectangles A, B, and C in the nomogram (Fig. 2).

Rectangle A is defined by an intersection indicating that four years are required by a population to recover from a 35% level at a mean recovery rate of 30%. This may still be acceptable. However, at a mean rate of 25% almost five years would be required starting from the 35% population level and even more than six years starting from the 20% level. These figures within rectangle A deviate too much from field observations and can therefore be rejected.

Values within rectangle B can be rejected as these concern mean recovery rates above 70%. A mean recovery rate of 75% implies that a population requires only 2—3 years to recover from the 20—30% level and little over three years from the 15% level. As pointed out before, fox populations have been found to recover from the 20—30% level within four years. The actual mean recovery rates may therefore be significantly lower, even than those excluded by rectangle B.

Rectangle C can be excluded from further consideration, as there is no evidence that recovery can be completed within little more than two years starting from a 40% level. The mean recovery rate would be about 49%

### Table 2

<table>
<thead>
<tr>
<th>Complete recovery</th>
<th>Mean recovery rate</th>
<th>Years required</th>
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*Increase in % over the population at the beginning of first recovery year. Values determined according to procedure shown in figure 3.*
in this case. However, this mean rate applies rather to a recovery from the 20% level within four years as suggested by field studies (Fig. 1).

In the remaining field of the nomogram various curves have been drawn of which No. II is most likely to reflect actual conditions (Fig. 2 and Table 2). Recovery from 25%, 40% and 60% levels within 4, 3 and 2 years respectively is consistent with field observations (Fig. 1). Curve I, though possible, seems to represent relatively low estimates as five years would be required for a fox population to recover from the 25% level. This does not match the ecological findings. Curves III and IV deviate too much from the perpendicular so that in the upper part of the nomogram the annual increase exceeds acceptable values. Curve IV can be rejected because it includes an increase of the population by about 100% within one year from the 20% level to the 40% level. Also curve III includes a relatively high increase by about 80% within one year from the 19.5% level to 35.5% level. However, the modification of the gradient of curve III by drawing the line III(a) almost parallel to curve II, results in lower recovery rates, the maximum increase being close to 70% during the first recovery year. A similar modification of line IV leads to non-acceptable values.

Since we consider population increases up to about 70% in a single recovery year as possible we may accept curve III(a) as the highest possible estimate of recovery rates to be considered in fox control operations. However, we are reluctant to select this curve since it would imply that fox populations are able to recover from a 35% level in three years and from the 30% level in little more than three years. There is little evidence from field observations that this recovery does actually occur. We therefore prefer curve II for further consideration, as this matches better with epidemiological and ecological observations.

![Diagram showing increase of population during first recovery year](image)
The difference between curve II and III(a) is shown in Table 2, where mean recovery rates are listed as determined graphically from Figure 2. This evaluation and the following calculation of population growth in initial recovery years shows that the difference between curves II and III(a) is of minor importance.

**Probable recovery rates at various reduced population levels:** For the assessment of fox control operations, it is essential to know the counteracting recovery rate during the first year of population recovery. This rate should be higher than the mean rate determined for the whole recovery period.

The annual recovery rate can be estimated by analysing the curves drawn in the nomogram (Fig. 2). Along the curves the difference in population levels is measured for one year periods according to the procedure described in Figure 3. Starting from various population levels, the levels attained one year later are listed and the percentage increase calculated (Table 2). Thus from the nomogram with its hypothetical curves all necessary information can be graphically obtained on the annual population increase as well as on the whole recovery period (Table 2).

As discussed before, curves I and III seem to be less realistic than curves II and III(a). Since curve II seems to match best with field observations and with possible changes in the annual population turnover, we propose to use for the assessment of fox control operations the recovery rates and the population increases determined by this curve.

**Discussion**

The application of a nomogram showing mathematical correlations of population growth greatly facilitated the estimation of recovery rates of fox populations. The procedure may be applied to different animal species irrespective of the cause of population reduction. However, different types of nomograms are required according to the reproduction characteristics of the animal species concerned. The formula of population growth used for the nomogram in this paper refers to populations reproducing only once in a given period of time (in foxes in Europe only once a year) with no overlap in generations. A different formula of exponential growth based on the natural logarithm would for example apply to populations of rodents that produce several litters a year with early maturity rates and overlapping generations.

The utility of this method for the estimation of recovery rates depends on the accuracy of field observations and on a reasonable model of population turnover. Such basic data should allow for an estimation of the recovery rate of fox populations within a margin of error not exceeding 5% so that the resulting figures can actually be used in planning and assessing the efficacy of fox control programmes. In practice it has, however, been impossible to obtain information on the accuracy of field procedures for censuses of fox populations. Any estimates of recovery rates must therefore be considered as figures of unknown accuracy and variation. Complete recovery may require 1.5—7 years depending on the level to which the population was reduced before recovery began. Figures such as 3.3, 3.6, or 4.0 years cannot be taken absolutely as the population breeds only once, in spring, and is reduced during the year in a non-linear fashion. Nonetheless, fractions of years must be considered in calculations of recovery rates (Table 2).

Field data obtained so far (e.g. Fig. 1) suggest that curve II in Figure 2 gives the best approximation of the true rates of recovery (Table 2). The difference between rates calculated for the first recovery year from curves II and III(a) (Table 2) is in the range of 7%, thus being relatively close to
each other. In the important range of population levels of 25—50%, the difference is even as small as 5% in terms of values obtained by curve II. Curves I and III lie about 20% away from curve II, however, and curve IV which is plotted in Figure 2 but not listed in Table 2 lies even further towards the range of improbability. These observations further support the application in models of figures obtained from curves II or III(a), preferably from curve II.

As in other ecological systems, absolute prediction cannot be made. Variations of climate, food sources, etc., cannot be foreseen. However, the estimates of recovery rates presented in this report are based on fairly simple assumptions, and on data not difficult to obtain for rather large geographical areas. The estimates can easily be modified should annual turnover figures or increases in the HIPD be shown to be higher or lower in specific areas where fox control is deemed necessary.

It has, however, to be borne in mind that the estimated rates proposed in Table 2 apply to relatively large areas and that conditions may vary considerably in smaller areas of a few hundred square kilometers. Thus population increases due to the immigration of foxes into rabies control areas are not considered in the estimated recovery rates, as this should not play an important role in the areas of the size to which the estimated recovery rates would be applied. The annual immigration of foxes should, however, be taken into consideration in a strip of about 10 km. depth along the border of areas of low fox population density (10).

It seems that the assumptions made in the interpretation of field data are generally valid and that the method described allows reasonable predictions of recovery rates for large areas over a suitable period of time. In view of the lack of precision in the estimates the recovery rates presented in this report must be continuously re-examined when used in the assessment of fox reduction for rabies control. The upper limit of recovery rates which were found to be about 70%, may serve as a key figure in this respect. Further, field observations may show whether recorded recovery rates over 70% do indeed represent overestimates resulting from erroneous density figures.

Summary

A nomogram is used to express the relationship between percent reduction and mean recovery rates of fox populations as well as the length of recovery periods. Estimates are made of most probable rates of fox population recovery. The estimates are based on epidemiological observations, limits of the annual population turnover, and in particular on hunting figures as an indirect measure of the fox population density in Central Europe. The resulting gradient of the population increase during recovery periods (gradient II in Figure 2 and Table 2) should be considered in the planning and assessment of fox control programmes related to wildlife rabies.

The method described for the estimation of population recovery can be applied to other animal species irrespective of the cause of previous reduction. However, the appropriate formula of population growth must be chosen according to the reproduction characteristics of the species concerned.

Zusammenfassung

Erholung reduzierter Fuchspopulationen in der Tollwutbekämpfung

In einem Nomogramm werden der Grad der Verminderung von Populationen, die Dauer der anschließenden Erholungsphase und der mittlere jährliche Zuwachs zueinander in Beziehung gesetzt. Mit diesem Nomogramm läßt
sich für Fuchspopulationen diejenige jährliche Erholungsrate schätzen, die mit größter Wahrscheinlichkeit den wahren Verhältnissen entspricht. Die Schätzung basiert auf epidemiologischen Beobachtungen, Grenzwerten des Populationsgeschehens und insbesondere auf Abschusszahlen, wie sie als indirektes Maß der Populationsänderung in Zentraleuropa verwendet werden. Der sich aus der Untersuchung ergebende Gradient für die Populationszunahme während der Erholungsphase (Gradient II in Abb. 2 und Tab. 2) sollte bei der Planung und Bewertung von Fuchsbekämpfungsaktionen im Rahmen der Tollwutbekämpfung berücksichtigt werden.


Résumé
Reconstitution d'une population de renards après réduction par
la lutte antirabique

La relation entre le pourcentage de réduction de la population des renards, les taux moyens de reconstitution de cette population et le temps de reconstitution est représentée par un nomogramme. Des estimations des taux les plus probables de la reconstitution de la population vulpine sont établies. Ces estimations sont fondées sur les observations épidémiologiques, sur les taux limites du renouvellement annuel de la population et en particulier sur les chiffres des tableaux de chasse qui donnent indirectement des mesures de la densité de la population en Europe centrale. Le gradient d'accroissement de la population pendant les périodes de reconstitution (gradient II de la figure 2 et du tableau 2) devrait être pris en considération lorsqu'on élabora ou qu'on évalue des programmes de destruction des renards dans le cadre de la lutte contre la rage des animaux sauvages.

La méthode exposée pour l'estimation de la reconstitution de la population est applicable à toute autre espèce animale quelle que soit la cause de la réduction que la population a subie. Mais il faut choisir la formule appropriée de croissance de la population en tenant compte des caractéristiques de reproduction de l'espèce considérée.

Resumen
Recuperación de las poblaciones reducidas de zorros
tras las medidas adoptadas de control antirrábico

En un nomograma se relacionan entre sí el grado disminución de las poblaciones, la duración de la fase inmediata de restablecimiento y el incremento anual medio. Con arreglo a este nomograma se puede calcular para las poblaciones de zorros aquella tasa anual de restablecimiento que corresponde con probabilidad máxima a las circunstancias reales. El cálculo se fundamenta en observaciones epidemiológicas, valores límites del evento de población y, sobre todo, en las cifras de piezas cobradas, tal y como se utilizan en Europa Central como medida indirecta de la densidad de población. El gradiente resultante de la investigación para el aumento de la población durante la fase de recuperación (gradiante II en la fig. 2 y tabla 2) debería tenerse en cuenta en el proyecto y evaluación de acciones de lucha contra los zorros en el marco de una campaña antirrábica.
El procedimiento descrito para calcular la recuperación de las poblaciones se puede aplicar a otras especies animales, siendo independiente de la causa del amenuamiento previo de la población. Sin embargo, al preparar el nomograma se debe elegir una fórmula que corresponda al tipo de crecimiento de población de la especie animal correspondiente.

References

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