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FOXES AND RABIES IN LORRAINE: A BEHAVIOURAL-ECOLOGY APPROACH

LA VOLPE E LA RABBIA IN LORENA: ASPETTI DI ECOLOGIA COMPORTAMENTALE DELLE VOLPI

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ABSTRACT

Some aspects of the behavioural ecology of rabid foxes were studied in areas invaded by rabies since the year 1973. The principal aim was to understand how fox populations can survive, despite a high level of mortality due to the virus. The individual and seasonal activity-areas of eleven foxes ranged from about 200 ha to 400 ha. All the situations encountered during the study of neighbouring foxes showed a lack of, or only a small, sharing of neighbouring part of activity-areas. These foxes tend to shift their activity areas quite permanently. Of six rabid foxes, no one strolled beyond the farther border of their immediate neighbours. The data suggest that transmission is effected by aggressive contacts between rabid and healthy foxes, rather than by a more passive transmission (e.g. grooming). Post-mortem examinations of 1,259 foxes from eastern France suggest that rabies reaches the yearling foxes less frequently than adults. Despite rabies out break the fox population level in spring is roughly the same (e.g.: the decrease from one year to the next, if it occurs, is usually less important than intra-annual decrease).

Key **words:** Rabies, Behavioural ecology, *Vulpes vulpes*, France.

RIASSUNTO

Nel presente studio sono esposti alcuni aspetti di ecologia comportamentale della Volpe in un'area interessata dalla rabbia dal 1973. Lo scopo principale è quello di capire come la popolazione volpina sopravviva nonostante sia sottoposta ad una elevata mortalità dovuta alla rabbia. 11 volpi erano catturate, marcate con radiocollari e rilasciate; di queste, 3 erano infettate in laboratorio con virus rabido prima del rilascio e altre 3 contraevano la rabbia naturalmente dopo la liberazione. Le aree vitali individuali e stagionali delle 11 volpi catturate variavano da 200-400 ha e non erano sovrapposte, o mostravano una minima sovrapposizione, con le aree limitrofe di altre volpi. Per queste ultime le aree vitali cambiavano molto frequentemente. Nessuna delle 6 volpi rabide sconfinava nelle aree vitali limitrofe di altri individui. I dati ottenuti suggeriscono che la trasmissione della rabbia dipende dai contatti aggressivi tra volpi rabide e sane e non dalla semplice trasmissione passiva (es. pulizia della pelliccia). Dall'esame di 1.259 volpi uccise nella Francia orientale, si riscontra che la rabbia colpisce più frequentemente gli individui adulti che non i giovani (da 5 a 13 mesi di età). Nonostante la presenza della rabbia, la consistenza primaverile della popolazione volpina si mantiene pressochè allo stesso livello negli anni. Il decremento della popolazione da un anno a quello successivo, se capita, è generalmente meno consistente di quello che si osserva nello stesso anno.

Parole chiave: Rabbia, Ecologia del comportamento, *Vulpes vulpes*, Francia.

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INTRODUCTION

This communication is a synthesis of some results obtained during several years of studying fox-rabies relationships in Lorraine (north east of France). A more detailed account of the observations may be found in already published articles (see references list). Our aim was to study fox behaviour as a key factor in the understanding of rabies epidemiology in Lorraine. The data obtained by us provide the basis of a new hypothesis about rabies transmission with implication for improving its control.

MATERIAL AND METHODS

Detailed accounts of the materials and methods used can be found in our papers listed here in the references. Briefly, the behavioural ecology of healthy and rabid foxes was studied with radiotracking techniques (149 MHz frequency). Eleven foxes were trapped over an area of 2,500 ha, then fitted with a radio collar and released; three foxes were inoculated with rabies virus (pooled salivary glands of naturally infected foxes) before being released.

Population structures were assessed by studying the heads of dead foxes collected throughout eastern France. Age, sex and rabies were diagnosed. The age of foxes was determined according to the cementum line technique on a decalcified canine tooth (Artois and Salmon, 1981). When the sex was unknown or dubious, it was assessed by looking for sexual chromatin on brain impression slides (Salmon and Blancou, 1980).

Data on the population density of foxes in the study area were obtained from 1979 onwards by spotlight counting at night in winter (Artois, 1981). Bounties statistics from rabies enzootic areas were compared to the occurrence of rabies.

RESULTS

USE OF SPACE BY INDIVIDUAL AND INTER-INDIVIDUAL SHARING OF THE SPACE

Individual and seasonal areas of activity of 11 radiotracked foxes in Lorraine (Artois and Aubert, 1990) ranged from 150 ha to 792 ha (grid method). The size of these areas correlated with the number of radio-locations ($s = 1.59n + 126.32$ where s: surface ha and n: number of locations with $r = 0.80$ and $P = 0.001$). This phenomenon is not due to a inappropriate technique (see below) but requires a correction of evaluated areas in order to permit comparisons. After such a correction, the individual activity-areas ranged from about 200 ha to 400 ha, except one occurrence of 728 ha.

No significant differences appeared between male and female areas on the basis of covariance analysis (Dagnélie, 1975). Similarly, no significant seasonal periodicity in the size of activity-areas was observed, although large variations occurred between individuals and between seasons.

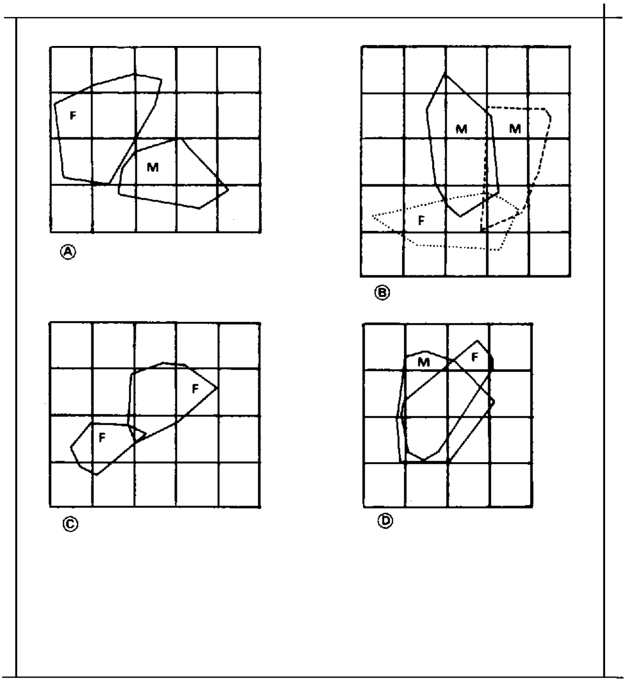


Fig. 1 — Study of the sharing of space by neighbouring foxes. A) no contact between one male (M) and one female (F). B) partial overlapping of the same female's area by two neighbouring males. C) sharing of a small part of the same area by one male and one female. D) sharing of a large part of the same area by one male and one female.

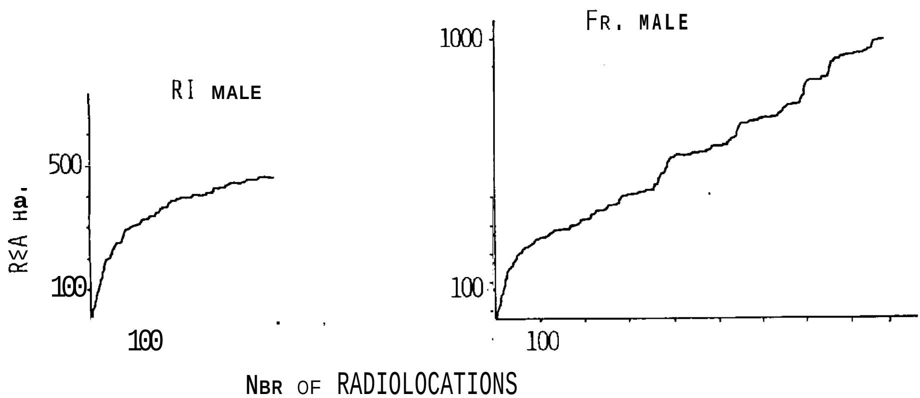


Fig. 2 — Relation between visited area and the number of radio-location of two foxes. The visited area is the cumulative number of squares of the grid (side = 100 meters) visited at least once.

All the situations encountered during the study of interactions between foxes (four different situations involving two or three individuals each) showed a lack of, or minimal, sharing of contiguous parts of activity-area when foxes were of the same sex. On the other hand, sharing of **a** small but significant part of the activity area could occur between males and females, at least in some seasons (Fig. **1).A** brief stay was recorded once for two neighbouring dog-foxes (one location well inside the neighbour's activity-area); when space was shared by several individuals they were seldom seen in close proximity.

These results suggest a relatively solitary behaviour. This might be related to the tendency for foxes to increase the size of, or to move, their activity-area with time, since area increases with the number of radio-locations (Fig. 2). This phenomenon is poorly defined or non-existent for some individuals (e.g. fox R1) but is particularly obvious for others (e.g. fox Fr.). For individuals conforming to the first case, the home-range remained rather constant after 30 *to* 100 fixes. Ables (1969) considers this constancy usual for foxes. For those conforming to the second case, which we believe to be frequent, the activity-area is constantly shifting into neighbouring areas and is almost never fixed to a definite "boundary".

INFLUENCE OF RABIES ON FOX MOVEMENTS

Three foxes were inoculated with rabies virus and three others became rabid following unknown natural contacts with a rabid animal as they were being monitored by radio-tracking (Artois and Aubert, 1985). For all three inoculated foxes it was possible to compare their activity patterns before and after the onset of rabies symptoms. During the phase of abnormal behaviour all three were occasionally found several hundred metres beyond their previous range, but all three died on the edges of their ranges (Fig. **3).**

A naturally infected female, Pascaline, behaved in this way also but subsequently moved away and was recovered dead 2 km outside her range. Nathalie (female) was found at 1.5 km and Clement (male) at 2.2 km from their core activity-area. Erratic movements were not characteristic of **a** rabid fox, but when it did occur, no difference in habitat use was observed, between day and night (for instance in Annonciade, an inoculated female). Of the six rabid foxes, none passed beyond the farthest borders of their immediate neighbours, when known, or not farther than two average range away from the activity center of the moving rabid fox.

It is not known whether rabies is more often transmitted by a healthy fox deliberately making aggressive contacts with a rabid fox, (perhaps because the latter **is** laying paralysed in the vicinity of the common boundary), or whether an aggressive rabid fox (madness) is more likely to attack a healthy fox. The observation by George et al. (1980) that only 11% of captive foxes exhibit furious symptoms would favour the first hypothesis. Our observations of recently acquired wounds on three of the foxes found dead suggest that transmission is effected by aggressive contacts between rabid and healthy foxes, rather than by a more passive transmission (e.g. grooming).

Post-mortem examinations of 1,259 foxes from eastern France between 1976 and 1980 allowed comparison of the age-structure of fox populations from rabies-enzootic areas and rabies-free areas (Artois and Aubert, 1982). These results suggested that rabies reaches yearling foxes (i.e. five to 13 months old and considered non-settled) less frequently than adults (considered to have a home-range). Indeed the former age class is significantly less numerous in the sample of rabid foxes (48.5% of 309 foxes) than in the sample of non rabid foxes (69% of 116) within the enzootic area (see also Wandeler et al., 1974). This characteristic should induce a higher survival rate of young foxes in rabies invaded areas where the yearling age class is present in higher proportions (69% of 116 non rabid foxes) than in rabies free areas (54% of 274 foxes).

These results and the above mentioned data on rabies transmission corroborate the hypothesis that rabies is transmitted largely between foxes living in close proximity to each other, either owners of neighbouring home-ranges or individuals sharing part of the home range.

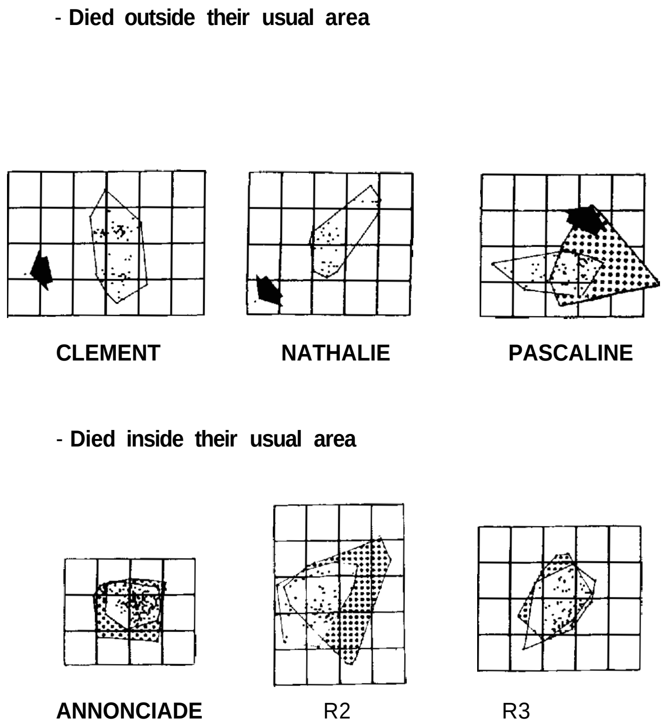
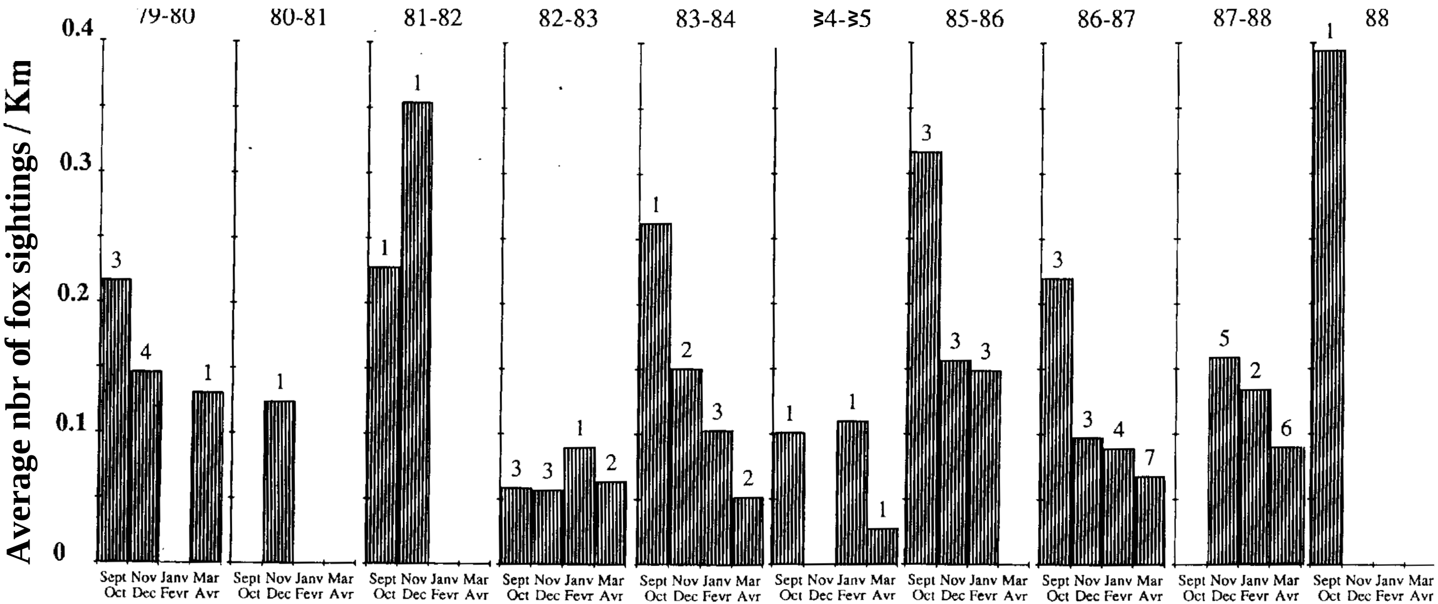


Fig. 3 – Radio-tracking of six rabid foxes. Clement, Nathalie and Pascaline were naturally infected, Annonciate, R2 and R3 were inoculated. Clement and Nathalie were not followed during the last days of their life. The four other foxes, covered a new area (dotted) outside the previous one in the last four to six days before death.



Janv = January   Fevr = February   Avr = April

Fig. 1 – Night-time spotlight counts of foxes in the study area over ten years. Only the counts for the September to April period are reported. The numbers of counts are reported above each bar. This small population recovers fast after the outbreak of rabies.

The population kinetics of foxes (as revealed by night-time counts) can be depicted as successive annual waves. From the very beginning of autumn (September-October) until the vegetation begins to grow again in spring (March-April) the fox population seems to decrease slowly but steadily (Fig. **4).** This pattern is similar with that recorded by Storm et al. (1976), concerning a central North American population of foxes.

The population level in spring represents an index of the breeding population. The level is roughly the same each spring (Fig. **4);** a decrease from one year to the next, if it occurs, is usually less marked than intra-annual decreases. On the other hand, levels reached in autumn can vary considerably between years as was the case in 1984-85 and in the year following the intense rabies outbreak of **1981-82.** In this last case the population had fully recovered the space of one year. From this result we suggest that enzootic rabies does not decrease a local **fox** population (or sub-population) either markedly or over a long period of time.

This observation agrees with the results of large scale population survey in French enzootic areas. Indeed, the annual number of bounties per 1000 km2 delivered in France (considered as a fox population index) does not significantly change from year to year (Fig. 5).

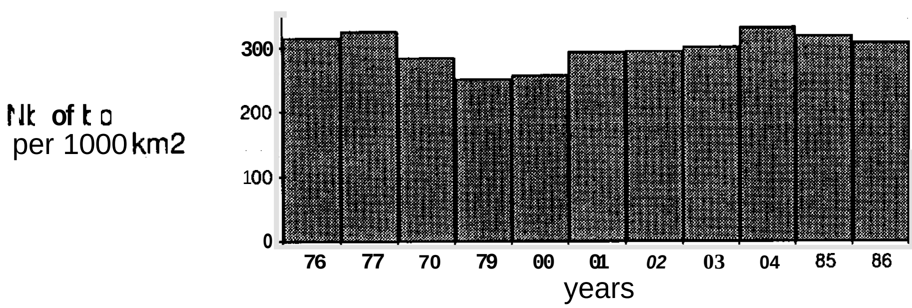


Fig. 5 – Record of **bounties given** for **dead foxes in rabid endemic area** of **France. The ratio of the number of bounties given to the surface of the endemic area is considered as an index** of **mean fox density, This index is rather even despite fluctuations in rabies outbreaks.**

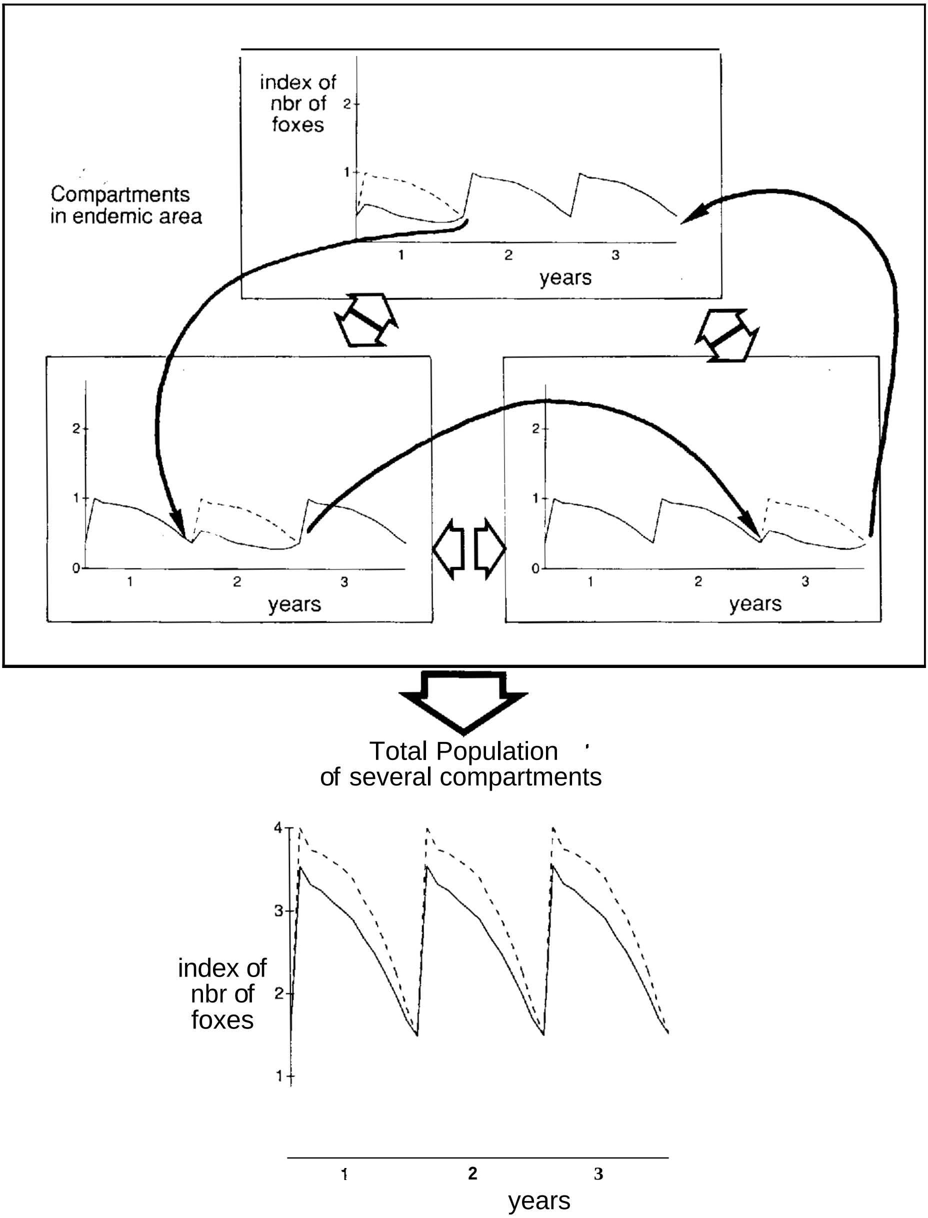


Fig. 6 – Interpretation of the evolution of fox population levels according to the scale of the prospected area. The large scale population is made up of local populations (three **are** pictured here) more or less separated by geographical or sociological barriers. Rabies (curved arrows) travels from one compartment to another. **As** a result of a "vacuum effect", foxes move from neighbouring compartments (double arrows). The dashed lines are theoretical levels of fox populations without rabies.

DISCUSSION

RESPONSES BY FOXES TO RABIES PRESSURE

Although the number of observations carried out is inadequate to substantiate generalizations it is worth conjecturing that foxes may react to the presence of rabies in several ways:

- At the individual level we argue that a high proportion of foxes that are not definitively settled is able to move or emigrate towards an improved or simply different life space at is becomes empty (e.g. after the death by rabies of a neighbour). The predominantly solitary behaviour of foxes is likely not only to limit contact with rabid foxes, it should also induce emigration as an avoidance of close proximity. This could appear as an effective response against rabies. These hypotheses are in accordance with the findings of Doncaster (1985) on foxes living in Oxford city, in which human induced mortality (comparable to rabies induced mortality) favours the existence of continually drifting territories. They also accord with the study by Mulder (1985), showing how yearlings occupy the little used parts of a family territory before settling in an empty space.
- At a population level, a relatively high proportion of yearlings might make such movements more frequent. Studies in Europe (Jensen, 1973; Lloyd, 1980; Zimen, 1984) and in North America (Storm et al., 1976; Pils and Martin, 1978; Tullar and Berchielli, 1980) have shown that juveniles and yearlings are more frequently involved in long range dispersal than are adults. However emigration distances seem to be related to average home-range size (Macdonald and Bacon, 1982). A fox population thus might react to rabies induced mortality more by drawing in "new" members from a neighbouring non-rabid reservoir, (as conjectured by Zimen, 1980), than by increasing the rate of reproduction (which is already very high and perhaps at the upper limit for the species, Artois et al., 1982). This speculative explanation of behavioural adaptation to rabies appears efficient enough to allow a fast recovery of the initial popuiation level after an outbreak of rabies.

Our last hypothesis to explain the high speed of recovery is that fox "metapopulations" could behave like a network of "micropopulation" compartments, while one compartment is suffering from rabies another is recovering, sending emigrants into the depopulated neighbouring patch. This patch progressively becomes more populated and more susceptible to invasion by rabies (Fig. 6).

Because of the absence of a long term effect on the fox population index, we conclude that rabies depresses but does not control fox population dynamics. Consequently, efficient rabies control must take into account the natural balance with rabies achieved by the fox population. Culling of foxes in France, for example, cannot reduce the fox population for a long period and is probably not successful enough to stop the spread of the disease (Artois, 1983; Aubert et al., 1988; Aubert, 1988). Oral vaccination, however, is likely to reduce the mobility of foxes by decreasing the mortality due to rabies and then decreasing the probability of transmission between foxes in close proximity by an increase in the number of immune individuals.

We are currently involved in a long term study in order to test this hypothesis, especially the availability of food versus rabies **as** control on population dynamics and the question of the foxes' fidelity to their home-range when rabies is eliminated by vaccination.

REFERENCES

ABLES, E.D. **1969.** Home-range studies of red foxes (*Vulpes* wipes). J. Mammal. 50: **108-120.**

ARTOIS, M. **1981.** Méthodes de dénombrement des populations de renards **roux.** Bull. Mens. O.N.C. **47: 23-32.**

ARTOIS, M. **1983.** Evolution de la rage dans les Alpcs françaises. Actes du VIIè Colloque National de Mammologie, Grenoble, **37-45.**

ARTOIS, M. & SALMON, D. **1981.** Délermination expérimentale du sexe et de l'âge chez le renard roux (*Vulpes vulpes*): validité et reproductibilité des techniques choisies. Mammalia **4 5 373-378.**

ARTOIS, M. & AUBERT, M.F.A. **1982.** Structure des populations (âge et sexe) de renards en zone indemne ou atteinte de rage. Comp. Immun. Microbiol. Infecl. Dis. **5: 237-245.**

ARTOIS, **M.,** AUBERT, M.F.A, GÉRARD, Y. **1982.** Reproduction du renard roux (*Vulpes vulpes*) en France. Rythme saisonnier et fécondité dcs femelles. Acta Oecol. 3 **205-216.**

ARTOIS, M. & AUBERT, M.F.A. 1985. Behaviour of rabid foxes. Terre *et* Vie, 40: **171-176.**

ARTOIS, M. & AUBERT, **M.F.A.** 1990. Organisation spatiale et déplacements dcs renards roux adultes. Terre et Vic **45:** 29-51.

AUBERT, M.F.A. **1988.** Mesures de contrôle de la rage par réduction des populations de vecteurs. Conséquences sur les populations animales et l'épidémiologie de la rage. Rev. **Sci.** tech. O.I.E. **8: 853-854.**

AUBERT, M.F.A., ROBOLY, O. & MIGOT, P. **1988.** Le tir de nuit du rcnard dans le cadre de **la** prophylaxie de **la** rage. Premier bilan et perspectives. Bull. Mens. O.N.C. **128: *38-46.***

DAGNÉLIE, P. **1975.** L'analyse de la covariance. In: Théorie et méthodes statistiques Les Presses Agronomiques de Gembloux, Gembloux 2: **340-358.**

DONCASTER, C.P. **1985.** The spatial organisation of urban foxes (*Vulpes vulpes*) in Oxford. Ph. D. Thesis, University of Oxford, Waldham College, Oxford, **2** voi.

GEORGE, J.P., GEORGE, J., BLANCOU, J., AUBERT, M.F.A. **1980.** Description clinique de la rage du renard. Etude expérimentale. Rev. Méd. Vét. **131: 153-160.**

JENSEN, B. **1973.** Movements of the red fox (*Vulpes vulpes* L.) in Denmark investigated by marking and recovery. Dan. Rev. Game Biol. 8: **3-20.**

LLOYD, **H.G. 1980.** The red fox. B.T. Batsford Ltd., London, **320** pp.

MACDONALD, D.W. & BACON, **P.J. 1982.** Fox society, contact ratc and rabies epizootiology. Comp. Immun. Microbiol. infect. Dis. **1-3: 247-256.**

MULDER, **J.L.** 1985. Spatial organization, movements and dispersal in a Dutch red **fox** (*Vulpes* wipes) population: some preliminary results. Terre et Vie 40: **133-138.**

PILS, C.M. & MARTIN, M.A. **1978.** Population dynamics, predator-prey relationships and management of the red fox ***in* Wisconsin.** Techn. Bull Dept. Nat. Res., Madison **105, 56** pp.

SALMON, D. & BLANCOU, J. **1980.** Diagnose expérimentalc du sexe du rcnard (*Vulpes vulpcs*). Essais comparés de trois méthodes en w e de l'étude épidémiologique de la ragc. Rec. Méd. Vét. **156: 121-128.**

STORM, G.L., **ANDREWS,** R.D., **PHILLIPS,** R.L., BISHOP, R.A., SINIFF, D.B., TESTER, J.R. **1976.** Morphology, reproduction, dispersal and mortality of midwestcrn red fox populations. Wildl. Monogr. **49, 82** pp.

TULLAR, B.F. & BERCHIELLI, L.T. 1980. Movements of the red fox in central New **York.** N.Y. Ash and Game J. **27: 179-204.**

WANDELER, **A.,** MULLER, J., WACHENDÖRFER, G., SCHALE, W., FÖRSTER, U. & STECK, **F. 1974.** Rabies in wild carnivores in central Europe. III. Ecology and biology of the **fox** in relation to control operations. **Zbl.** Vet. Med. **21B: 765-773.**

ZIMEN, E. 1380. A short history of human attitudes towards the **fox. In** Zimen E. (ed.): The red fox. Symposium on behavior and ecology. Biogcographica 18: **1-5.**

ZIMEN, **E. 1984.** Long-range movements of the red fox, *Vulpes vulpes* L. Acta Zool. Fennica **171: 207-270.**