Characteristics of the spread of a wildlife rabies epidemic in Europe

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The control of rabies in wildlife by reducing the fox population has led in Europe to inconsistent results, since little was known of the dynamics of the fox population and the interaction between rabies epidemics, host populations, and control measures. As part of the WHO/FAO Coordinated Research Programme on Wildlife Rabies in Europe, data on epidemics and persisting reservoirs of the disease were processed by computer. The results led to a better understanding of the mechanism of spread of the epidemic and to proposals for the improvement of rabies control in animals and the protection of man.

Within the WHO/FAO Coordinated Research Programme on Wildlife Rabies in Europe, intensive epidemiological and ecological studies have been carried out on the interaction between fox populations, rabies, and control measures under different topographical conditions. Moreover, the role of other wild carnivores and the effect of rabies and fox control on these species, as well as on small game and rodents, have been investigated (5, 6, 7, 8). In some European countries, these research projects were supplemented by ecological studies on the composition and annual turnover of stable fox populations and on the recovery rate of fox populations after reduction by rabies and control measures (1, 3, 9).

Not all projects provided a basis for a numerical analysis of different phases of the wavelike spread of the disease. Country- or state-wide rabies records that could be evaluated for this purpose were not accurate enough and special surveys with the most intensive investigations were in areas too small for this analysis.

The location of statistically reasonable numbers of rabies cases was therefore determined with ade-

quate precision for an area in the south of the Federal Republic of Germany. Preliminary results obtained by electronic data processing (EDP) have already been published (4) concerning the seasonal relationship between the spread of the epidemic, the frequency of rabies cases, and the density of fox populations. These results are summarized in this report and supplemented by further analyses of the front-wave of rabies and its aftermath.

DATA AND METHODS

Area and period of investigation

All available data on animal rabies cases recorded in the former administrative area of Südwürttemberg-Hohenzollern and two adjacent districts (Stockach and Überlingen) of the Land Baden-Württemberg, Federal Republic of Germany (Fig. 1) were stored for computer analysis. The size of the study area is 11 273 km². The period under investigation was from January 1963, when rabies first spread into the area, to 31 March 1971 when the wave of rabies had spread from north to south over the whole area. As the frontwave of the epidemic moved, large-scale gassing of fox dens was carried out in each district until the disease disappeared.

For special studies, the area was divided into the following three zones according to the different landscapes, fox population densities, and the status of the rabies epidemic observed:

A. Black Forest, comprising mostly unbroken coniferous woodland, with a relatively low fox density.

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Fig. 1. Study area and sub-divisions. Zone A="Black Forest", zone B="Swabian Jura", zone C="pre-alpine area".

B. Swabian Jura, including agricultural and mixed forested areas, part of which is characterized by steeply sloping valleys transecting the spine of the Jura and where wildlife rabies is difficult to control and tends to persist.

C. Pre-alpine regions, comprising a moraine landscape which, towards the south, merges with alpine areas. Woodland, agricultural, and pastoral areas are evenly represented. These areas produced the highest number of foxes shot per km² and per year (HIPD, see below) before rabies and control operations reduced the fox populations.

Collection of data

For each of the 2822 recorded and laboratory confirmed cases of rabies in animals (for species see Table 1), the following information was stored on magnetic tape: date; species; locality (longitude and latitude of community); code number of community; and name of district. Moreover, the number of foxes shot per km² and per year (Hunting Indicator of Population Density=HIPD, see ref. 5) was recorded for each district.

The location of a case was defined by the coordinates officially given to a central point of the com-

Table 1. The role of different animal species in the spread of rabies: study area in the southern part of the Federal Republic of Germany, 1963-1971

Species	Observed cases			
	ahead of frontline ^a		behind frontline ^a	
	No.	%	No.	%
Foxes	414	97.2	1912	79.8
Roe deer	6	1.4	175	7.3
Badgers	2	0.5	55	2.3
Martens	—	—	50	2.1
Other wildlife	—	—	4	0.2
Wildlife total	422	99.1	2196	91.7
Cats	3	0.7	54	2.3
Dogs	1	0.2	50	2.1
Other domestic animals	—	—	96	4.0
Grand total	426		2396	

^a Frontline determined for each preceding month.

munity (Gauss-Krüger's system of coordinates) in which the animal was shot or found. As the communities in the study area are rather small, the average territory being 11 km² in area, this definition appeared to be sufficiently exact for further computation. Considering that approximately 3000 cases were recorded, it was impossible to define the localities more precisely.

Definition of the frontline

Initially maps were produced by plotting cases monthly, both with and without the cases from the preceding months. These maps afforded an analysis of the movement of the frontwaves through the study area (Fig. 2). All attempts to draw frontlines and to determine the distances of new cases from the frontline by graphical and semi-graphical procedures were found unsatisfactory. The "frontline" was therefore defined for the computer programme as follows:

In view of the general trend of the epidemic to spread from north to south (Fig. 2), the study area or its zones A, B, and C were subdivided into north-south strips each about 2.3 km wide (exact width on west-east axis as defined by printing conditions). The frontline is composed of straight lines (latitude) that are drawn

Fig. 2. Spread of rabies through the study area.

through the sites of the most southerly cases. The centres of each of these straight lines are called frontline points, and these points have been used for the calculations. In strips without cases, the frontline goes through the most northerly geographical point (community) in this particular strip.

Distance of new cases from the frontline

The frontline of the epidemic was determined at the end of each month. All cases observed south of the frontline until the end of the subsequent month were considered as "new cases south of the frontline". The distance of a case from the frontline was taken to be the distance from the central point in

the 2.3-km-wide strip, at the latitude of the new case, to the nearest frontline point in the same strip and the five strips west and east (Fig. 3).

Initially we examined the extent to which the results may be influenced by fixing the frontline at 2-month intervals and by using different numbers of strips for the determination of the distance of new cases. Modification of these components of the computer programmes had very little influence on the results reported in this paper. The assumptions made were, therefore, technical aids for computation rather than scientific determinants.

The maximum and mean distances of new cases from the frontline are very important characteristics

Fig. 3. Scheme for computing the distance of a new rabies case from the frontline.

of an epidemic since they are measures of what can be expected to happen around a new case during the 30 days following its detection. Since these values refer only to new cases found south of the frontline and do not consider any stagnation of the spread of the epidemic, they should not be confused with the velocity of spread of the whole frontwave (see below).

Movement of frontwave

For the total of zones A, B, and C all observed cases were projected monthly on the y-axis (north-south direction). This frequency distribution based on latitude over time for the whole area and for the different zones is shown in Fig. 4-7. A tabulation of the cases was also made for further calculations and graphical analysis.

In view of the results, a computer programme was developed to further characterize the movement of the centre of the frontwave and the seasonal appearance of index cases in the rabies-free areas towards the south. It proved most useful to project the cases on the y-axis for all months but including not only the cases of the current month but also of the five

preceding months. Thus, 6-month periods were plotted and tabulated at monthly intervals. For graphical evaluation, every third projection has been chosen (Fig. 8). Each quarterly projection on the y-axis in Fig. 8 therefore gives the smoothed distribution over the latitude of all cases recorded during the preceding 6-month period.

Definition of the frontwave and its separation from a persisting reservoir

Fig. 2 shows clearly the southward movement of a frontwave. However, from the 50th month onwards cases continued to appear a certain distance north of the frontwave. Practically all of these cases, which also appear in Fig. 6 and 7 for zones B and C, belong to a persisting rabies reservoir in the area of the Swabian Jura. For further computation it became necessary to separate these cases from the frontwave. A fairly accurate determination of the rear edge of the frontwave was made by drawing a line in Fig. 4 to reflect this continuing flow, although the longitudinal distribution of cases is missing in this computer printout.

Between the frontwave thus determined and the reservoir defined by borderlines drawn on maps by hand, there were still 60 intermediate cases. However, by further analysis these could be related to either the reservoir (29 cases) or the frontwave (31 cases); of the intermediate cases attributed to the frontwave, 27 were visually very closely linked with the frontwave as plotted in the right lower corner of Fig. 4. They were recorded in the districts of Wangen and Ravensburg, south of y-coordinate 5309, between May 1970 and March 1971 (see also Fig. 7 for zone C).

Protrusions from the persisting reservoir to the south and east were observed for limited periods of time and accounted for 18 cases. An additional 11 cases were located very close to the borderlines of the reservoir. Thus, 29 of the 60 questionable cases could be attributed to the reservoir.

Subdivision of frontwave and persisting reservoir

In order to study the frequency of cases in different animal species during the flow of the epidemic, all cases were categorized according to the scheme shown in Fig. 9. The frontwave was defined and its flow considered as described in the preceding sections. Also, the definition by EDP of new cases recorded monthly south of the frontline was described.

The rear edge of the frontwave was defined by the most northerly case recorded per month in

Fig. 4. North-south distribution of rabies cases at monthly intervals over total study area (2822 cases).

Fig. 5. Progression of frontwave in zone A (479 cases).

Number of cases			
• = 1	•• = 4	✕ = 7	■ = 10
••• = 2	•••• = 5	✕✕ = 8	■• = > 10
••••• = 3	✕• = 6	✕✕• = 9	

zones A, B, and C (compare Fig. 5-7). We added to these 157 cases 31 cases of the aftermath of the epidemic which could not be related to the graphically determined reservoir (see preceding section).

The animal cases attributed to the reservoir were mapped and thus determined. Moreover, these animals accounted for the difference between all 2822 cases and the cases of the frontwave. Where information on the species was not available from EDP

direct, a separate printout of all case data and monthly maps permitted identification.

RESULTS

Distance of new cases from the frontline

Of the new cases recorded ahead of the frontline within a month, 93.4% were less than 10 km from the frontline. The maximum distance observed was

Fig. 6. Progression of frontwave in zone B (929 cases).

WHO 75918

Number of cases

- = 1	= = 4	* = 7	⊗ = 10
- = 2	† = 5	⋈ = 8	⊞ = > 10
+ = 3	* = 6	⋈ = 9	

Fig. 7. Progression of frontwave in zone C (1075 cases).

20.5 km (Table 2 and Fig. 10). There were no significant differences among zones A, B, and C regarding the mean distance of new cases south of the frontline. These values were close to the 4.8 km per month determined for the entire study area. This mean distance appeared to be independent of the frequency of rabies cases and of the number of foxes shot per km² and per year as an indicator of the population density (Table 3).

This observation is further supported by analysis

of a new epidemic in 1971–1972 in part of the area, starting from the district of Sigmaringen. The disease spread from the focus in different directions, and the distance of 83 cases from the nearest cases that had occurred in preceding months was determined on maps. Although the mean distance of 4.85 km calculated for the 83 cases was the same as that determined by EDP for the 1963–1971 epidemic, the frequency of rabies cases was extremely high in this new epidemic. In one reinfected district,

Fig. 8. Movement of the epidemic wave of rabies through zone B of the study area. Cases for 6-month periods are shown at successive intervals of 3 months. The band width is determined by the printout conditions of the computer. The reference latitude is 5383.480 km according to Gauss-Krüger's coordinates.

0.33 cases per km² were recorded during the year with the highest frequency, representing a value 60% higher than the maximum frequency (about 0.2 cases per km² and per year) observed in districts during the 1963–1971 endemic.

In Fig. 11, the mean distance of new cases and the frequency of cases are compared for each month of the year; data were compiled for all Januaries,

Februaries, etc., of the 1963–1971 epidemic. In this seasonal analysis, mean distances and rabies frequency seem to parallel each other, except in February, August, and September.

Movement of the frontwave

Maximum and mean distance of new cases from the frontline, as described in the preceding section,

Fig. 9. Categories of rabies cases in an epidemic moving from north to south.

Table 2. Distance of new rabies cases from the frontline of the previous month

New cases	Distance from the frontline in km				
	0-5 ^a	5-10	10-15	15-20	>20
Number	238	115	20	5	3
Percentage	66.4	27.0	4.7	1.2	0.7
	93.4				

^a Upper limit included.

disregard the number of rabies cases recorded monthly in previously rabies-free areas. The distribution of cases within the frontwave can, however, be analysed using computer printouts as shown in Fig. 4-7. For all three zones of the study area, certain trends become apparent by the monthly pro-

jection of cases on the north-south axis. In zone A the disease moved southwards, mainly in December/January (in 1965 even in October) and to some extent also in March, whereas the most southerly point appeared to become stationary from April to late autumn. Similarly, in zone B the major advances southwards occurred in November/December, and in 1965 in September/November. Zone C shows southward spread also during October/December, although a second step during March/April was more pronounced in this zone than in zones A and B.

The graphical presentation of the frontwave of zone B illustrates better the periodic movement of the epidemic (Fig. 8). "Amoeboid" protrusions were produced as a first step in autumn and to a lesser extent in March/April, whereas the body of the wave seemed to move much more steadily (at a rather constant rate). According to Fig. 4-7, the centre of the frontwave moved at about 27 km per year.

Fig. 10. Observed mean (solid line) and maximum (broken line) distances of new rabies cases from the frontline of the preceding month.

Fig. 11. Mean distance of rabies cases recorded ahead of the monthly determined frontline (solid line) and rabies cases as a percentage of all 2822 cases recorded from 1963 to 1971 (broken line).

Role of different animal species during the epidemic

As shown in Table 1, the fox has been almost solely responsible for carrying the disease in rabies-free areas. The differentiation of phases of a moving epidemic (Fig. 9), and the attribution of cases to these phases (Table 4), also allow analysis of the roles of different animal species towards the end of an epidemic.

Because of the very high proportion of rabid foxes among the new cases ahead of the monthly determined frontlines, this initial phase of the spread of the epidemic should be excluded from further

Table 3. Frequency and distance of rabies cases in zones of different indicator values for the density of fox populations

	A "Black Forest"	B "Swabian Jura"	C "Pre-alpine area"
HIPD ^a	0.7	1.1	1.5
Frequency of rabies ^b	0.044	0.051	0.065
Distance of new cases ^c	4.98	4.71	4.70

^a HIPD = Hunting Indicator of Population Density: foxes shot per km² per year.

^b Average number of recorded cases of rabies in animals per km² and per year.

^c Mean distance in km of new cases ahead of the monthly determined frontline.

Table 4. Animal species found rabid during different phases of the epidemic

	Foxes	Badgers	Martens	Polecats	Deer	Squirrels	Dogs	Cats	Cattle	Horses	Pigs	Sheep	Total
Reservoir (persisting)	241 75.8 %	6 6.0 %	13 6.0 %	—	35 11.0 %	—	9	3	8	1	1	1	318
Rear edge of frontwave and aftermath	140 74.5 %	8 9.0 %	8 9.0 %	1	15 8.0 %	—	6	4	6	—	—	—	188
Centre of frontwave	1531 81.0 %	41 2.2 %	29 1.5 %	2 0.1 %	125 6.6 %	1 0.05 %	35 1.9 %	47 2.5 %	78 4.1 %	1 0.05 %	—	—	1890
New cases beyond monthly frontline	414 97.2 %	2 0.5 %	—	—	6 1.4 %	—	1 0.2 %	3 0.7 %	—	—	—	—	426
Total	2326	57	50	3	181	1	51	57	92	2	1	1	2822

considerations. For example, the number of recorded rabid mustelids behind the frontline was 0.12 per fox, but in advance of the frontline it was only 0.005 per fox, a difference of 25 times. Other indicators, such as deer and domestic animals, showed a similar pattern of 0.22 per fox behind and 0.024 in advance of the frontline, a difference of 9 times. These differences may be due to differences in the awareness of rabies in wildlife and domestic animals and are therefore most difficult to interpret in detail, except that they show that the fox remains the best indicator of the presence of rabies.

To study the conditions towards the end of an epidemic it seems more appropriate to compare the rear edge of the frontwave and its aftermath (which equals the final phase of the epidemic) with the centre of the frontwave (equalling the height of the epidemic). In Table 5, all cases observed during these two phases are given, as well as the percentages of these totals recorded during the final phase in foxes, mustelids, domestic animals, and deer. The latter two categories of animal are of no significance as transmitters of the disease and are well recorded by veterinary services. In particular, rabid domestic animals are excellent indicators for the purpose of comparison, since they are almost completely recorded with little variation of public awareness during the height of the epidemic and its final phase.

The proportion of cases found in the final phase of the epidemic varied significantly among the species ($\chi^2=9.084$; $P<0.05$; see Table 5). The main contribution to this value was given by mustelids ($\chi^2=7.418$). The other proportions were very similar.

Mustelid cases also occurred in the persisting reservoir more frequently than expected, but the difference between this and the centre of the frontwave is not statistically significant if the martens and badgers are considered together. However, out of the 42 rabid martens recorded in the centre of the epidemic wave and the persisting reservoir, 13 (30.9%) were observed in the reservoir. The proportion differs significantly from the 12.5% of rabid domestic animals observed in the same persisting reservoir (Table 4).

DISCUSSION

The results will be discussed with respect to (a) the assessment of the risk of human exposure to rabid animals, (b) the improvement of wildlife rabies control in different phases of the epidemic, and (c) the roles of different animal species towards the end of a rabies epidemic.

Table 5. Distribution of species according to phase of the rabies epidemic

Species	Recorded rabies cases		Proportion in final phase	Chi-square values
	centre of frontwave	final phase of frontwave		
Foxes	1531	140	0.084	0.798
Mustelids	72	17	0.191	7.418
Domestic animals	161	16	0.090	0.053
Deer	125	15	0.107	0.815
Total	1889	188	0.091	9.084

Characteristics of the spread of rabies

The definition presented in this paper of a front-line of an epidemic wave and the calculation of distances of new cases from this line should be considered as a first attempt to obtain some information on the distances between rabies cases. Although we did not observe significant differences among the mean distances in zones A, B, and C, it appears to be very important to study distances under other ecological conditions. Where the disease spreads into previously uninfected areas, this can be easily done by mapping the cases, as we have shown for re-infection of the study area in 1971.

The spread of rabies is characterized by several variables. The mean distance between new front-line cases refers to points where new cases occurred within a one-month period and does not describe a movement of the frontline at its whole length. The mean distance between new cases is more informative in conjunction with the total number of cases observed ahead of the frontline per month. Even more instructive is the ratio of new cases ahead of the frontline over the total number of cases observed per month. This ratio defines the progressivity of a rabies epidemic, according to Moegle et al. (4).

The movement of the centre of the frontwave further characterizes the epidemic. Fig. 4-7 suggest that the centre moves at a rather constant rate of about 27 km per year.

All these characteristics of the spread of rabies are not to be confused with frontwave protrusion defined by the geographically most advanced cases in each of the three zones studied (Fig. 5-8). Protrusions coincided with the periods of high rabies frequency in late autumn and in March. The extremely advanced cases recorded in March and April did not seem to give rise to a further spread of the disease since generally about 6 months elapsed

before further progression of the extreme points of infection were observed. Sites of extremely advanced cases were reached during the summer months by the more slowly moving centre of the epidemic wave, from which a further protrusion apparently originated in the autumn (Fig. 8), usually in late November or even in December (Fig. 5-7).

Apart from this production of protrusions, rabies mobility increased in August, as shown by the sharp increase in the mean distance of new cases from the frontline (Fig. 11). This mobility must therefore have occurred behind the most advanced cases in accordance with the movement of the centre of the frontwave (Fig. 8).

These observations further support the conclusion that the geographically most advanced cases observed in March were of little or no significance for the further spread of the disease. This could be explained by the annual turnover of fox populations and the function of the new fox generations as a basis of the rabies reservoir. The pre-breeding population of adult foxes in spring represents only about one-third of the maximum population present after the birth of the new generation (3). Chains of infection should, therefore, tend to end in the adult fox population in March and April. Behavioural factors related to the period of pregnancy, the establishment of territories, increasing food supplies, etc., may further lower the contact rate and aggressivity between foxes in this season.

The probability that the epidemic spreads from extreme sites such as the protrusions may therefore be very low, whereas the high rabies frequency in the centre of the epidemic wave could provide sufficient chances for a transfer of the virus from the adult population to the new fox generation.

Further studies must be carried out to show whether this break in the chain of infection in ex-

tremely advanced cases, and the shift of the reservoir from adult populations to include the new generation in the centre of the epidemic, do indeed circumscribe the critical paths of the epidemic. In particular, the extent to which this pattern depends on the density of fox populations in spring should be investigated. In the areas described in this report, the gassing of fox dens was in general done only after rabies had reached an administrative district. The process leading to epidemic protrusions could hardly have been influenced by control measures. However, the natural differences between the population densities of the three zones also had no significant influence on the patterns of spread (Table 3, Fig. 5–7).

Suggestions for controlling the spread of the epidemic

It may be essential in the future to include in routine surveillance an annual analysis of the frontwave. This could easily be done by mapping, by the identification of epidemic zones of about the size of zones A, B, and C, and by the projection of cases on an axis representing the major direction of spread, as shown in Fig. 8. Should the hypothesis of the transfer of rabies from the centre of the frontwave to the new fox generation, as presented in this report, be confirmed, it would be most useful to investigate the situation in February, March, and April so that decisions could be made on appropriate control operations. Experience must show whether it is in fact the area between the centre of the frontwave and the most advanced cases where, during the summer months, the transmission takes place and the further movement of the frontwave is prepared. Special efforts should be made to reduce the susceptible fox population rigorously in that area by the gassing of dens, intensified hunting, and any supplementary measures. This concentration of efforts on a selected area during a limited period could actually stop an epidemic wave. Insufficient control operations in areas further ahead of the frontwave could be dispensed with, and areas once infected could then be treated efficiently so that the disease could be eliminated. The results suggest that the speed of the spread of rabies is not influenced by a reduction in the fox population unless the population density falls below a critical level so that the epidemic wave can be completely stopped (5).

Rabies control during the final phase of an epidemic

The method described enabled us to follow the flow of the epidemic and to analyse continuously

its final phase as it moved over the study area. The ratio of rabid foxes to rabid indicator animals remained rather constant from the centre of the frontwave (ratio 5.4 : 1) to its rear edge and afterwards (ratio 4.5 : 1, see Table 4). Apparently, gassing operations and the further reduction of the fox population by rabies did not influence the main pattern of the epidemic in that the fox remained the principal reservoir animal and transmitter.

Wild mustelids, although a minor factor in the rabies epidemic, showed a proportional increase from 3.8% of all cases in the centre of the frontwave to 9% in the final phase of the epidemic. This may either be due to an actual increase in rabies incidence in these species, or it may only reflect a relative increase as the fox population is considerably reduced towards the end of an epidemic wave. Both actual and relative increases, however, would suggest that short chains of infection exist in mustelids and that such chains of infection become more apparent towards the end of an epidemic.

Although martens and badgers do not seem to maintain the epidemic when rabies has disappeared from fox populations, their contribution to the total reservoir of rabies should not be neglected when the reservoir in foxes becomes exhausted. This should be considered particularly where rabies is difficult to control by the reduction of fox populations. An example is the persisting reservoir in the Swabian Jura. Special attention must be paid to martens under these conditions.

Besides the secondary role of mustelids and the predominant role of the fox as the principal host and transmitter of wildlife rabies in Europe, the results do not indicate the involvement of other animal species in the rabies reservoir. All the characteristics of the wavelike movement of the epidemic and its persistence in certain areas can easily be explained with the fox as the principal host. This supports earlier reports of many European investigators (e.g., 1, 2, 5, 7, 8).

Public health significance of maximum distances between rabies cases

Knowledge of maximum distances between rabies cases could be particularly useful when decisions are being taken on the risk of exposure and the necessity of post-exposure treatment in man. Knowledge of the maximum distances of cases within one-month periods would also be useful for certain control measures, e.g., the vaccination of dogs, cats, and cattle in those communities in the range of one or

two "monthly maximum distances" from recorded rabies cases. Seasonal variations in these distances could be taken into consideration (Fig. 10). Although such control measures will not influence rabies in wildlife, they may considerably reduce the number

of persons receiving post-exposure treatment in areas at risk. Moreover, knowledge of maximum and mean distances could be of great importance where, for legal or economic reasons, control operations should be limited to "infected" fox populations.

RÉSUMÉ

CARACTÉRISTIQUES DE LA PROPAGATION D'UNE ÉPIDÉMIE DE RAGE DES ANIMAUX SAUVAGES EN EUROPE

On a étudié les caractéristiques d'une vague épidémique de rage des animaux sauvages dans une région du sud de la République fédérale d'Allemagne. Le traitement des données sur ordinateur a permis de suivre la progression de cette vague et d'y distinguer à tout moment les cas observés en avant du front mensuel, ceux du centre de la vague et ceux qui venaient en queue ou en arrière-garde. En ce qui concerne les nouveaux cas, leur distance maximale en avant du front déterminé tous les mois a été de 20,5 km; leurs distances moyennes dans des zones différentes quant à la topographie et la densité des populations vulpines étaient très similaires, à savoir à peu près 4,8 km. Sur la totalité des cas, 93,4% se sont produits à moins de 10 km du front.

Quant au centre de la vague épidémique, il se déplaçait à une vitesse à peu près constante de 27 km par an, indépendamment de la topographie des zones. On observait une périodicité pour les cas initiaux les plus avancés, correspondant à des saillants de la vague à la fin de l'automne et, dans une certaine mesure, en mars également. Cette progression, rapportée à une zone entière, coïncide avec les périodes où les cas de rage ont une fréquence élevée. Il y avait cependant une rupture dans ce parallélisme en août, car à ce moment la distance moyenne des nouveaux cas par rapport au front augmentait brusquement. Pour mieux lutter contre la pro-

pagation de la rage des animaux sauvages par la réduction sélective des populations vulpines, il faut vérifier l'hypothèse selon laquelle la rage passerait pendant l'été des adultes aux nouvelles générations de la population vulpine au centre de la vague épidémique. A cette période, cette nouvelle génération représente au moins les deux tiers de la population totale. On estime que les cas qui se produisent très loin en avant du centre de la vague, par exemple ceux qui apparaissent en mars dans la population adulte, sont d'une importance mineure en ce qui concerne la propagation ultérieure de la maladie.

Les renards représentent 97% de la totalité des animaux enrégistrés trouvés en avant du front. Au cours de la phase finale de l'épidémie et dans un réservoir persistant, la proportion de Mustélidés rabiques, en particulier ceux du genre *Martes*, était nettement plus élevée qu'au centre de la vague épidémique. En revanche, les cas se produisant parmi d'autres espèces animales, y compris les animaux domestiques et les chevreuils qui constituent des « indicateurs », ont été distribués très également pendant ces phases de l'épidémie. Bien que le renard soit le principal hôte du virus rabique dans toutes les phases épidémiques, il faut tenir compte du rôle des *Martes* et des blaireaux dans les programmes de lutte vers la fin d'une épidémie. En particulier la chasse aux fouines doit être intensifiée.

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