

## Oral Vaccination against Rabies and the Behavioural Ecology of the Red Fox (*Vulpes vulpes*)

A. Vos

Address of author: Impfstoffwerk Dessau, Tornau GmbH, IDT GmbH, PSF 214, 06855 Rosslau, Germany.  
E-mail: ad.vos@idt-direct.de

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### Summary

As a result of oral vaccination of foxes (*Vulpes vulpes*) against rabies, this virus disease has almost been completely eradicated from West- and Central Europe. In most countries, vaccine baits were distributed twice a year: during spring (March to May) and autumn (September to October). This strategy has shown to be able to control and eventually eradicate rabies. However, it remains to be clarified if this is the most cost-effective strategy. Astonishingly, the behavioural ecology of the target species, the red fox, did receive only limited attention selecting the periods when baits should be distributed. Considering the behavioural ecology and rabies epidemiology of foxes, territory owners seem to play a key role in the spread and maintenance of rabies. Thus, oral vaccination campaigns should be targeted primarily at these animals. It is suggested that the optimal timing for bait distribution in Europe is late autumn (November) or early winter (December), depending on the prevailing climatic conditions. Additional campaigns, when financially feasible, can be implemented in order to maintain a high vaccination coverage during the remaining year. Furthermore, different baiting strategies can be selected in case of re-infection or persistent residual foci.

### Introduction

Oral vaccination of foxes against rabies has been developed into the most effective method to control and ultimately eradicate fox rabies (Stöhr and Meslin, 1996; Müller and Schlüter, 1998; MacInnes et al., 2001). The purpose of distributing vaccine baits is to lower the population density of susceptible foxes below a certain threshold. Thus, the probability that a rabid fox encounters and infects a susceptible non-vaccinated fox becomes too low to maintain the chain of infection. A vaccination coverage of approximately 60–70% was considered sufficient to break the transmission cycle (Voigt et al., 1985; Schlüter and Müller, 1995), although values greater than 80% for complete eradication of fox rabies have been mentioned as well (Tischendorf et al., 1998). During the first field studies with oral vaccination in Switzerland at the end of the 1970s the feasibility of this novel approach was clearly demonstrated (Steck et al., 1982). Only few scientifically validated recommendations were available on how and when to distribute baits and most decisions had to be made on the basis of assumption. For example, the initial bait density (15 baits/km<sup>2</sup>) was based on the assumption that the number of baits had to be 10–15 times greater than the number of animals targeted (Linhart, 1993). Baits were distributed twice a

year; in spring when the fox density was at their lowest levels, and in autumn when the juveniles started to disperse (Steck et al., 1982). However, these periods were also selected as a result of vaccine bait performance during winter and summer. During the winter months, the liquid vaccine could freeze and rendering it useless, and high temperatures in the summer would damage and inactivate the vaccine virus within a short period of time after distribution (Steck et al., 1982). Nevertheless, the initial successes of the campaigns supported the concept of a spring and autumn campaign and was copied by many other countries (e.g. Schneider et al., 1983; Brochier et al., 1988; Schmid, 1988). Unfortunately, in the following years set backs were observed in several countries and the complete eradication of vulpine rabies in the European countries practising oral vaccination was protracted (Stöhr and Meslin, 1996; Müller and Schlüter, 1998). The increased fox population density was often blamed for the difficulties encountered during the final eradication phase. It was assumed that to control rabies with oral vaccination in areas with an increased fox density the overall vaccination coverage had to increase as well. Several studies had found a positive relationship between the number of baits distributed and bait-uptake (Cliquet et al., 2000). Consequently, in order to increase the vaccination coverage the number of baits was often increased in areas where rabies persisted (Frost et al., 1985). Nowadays, it is widely accepted that an increased bait density does not necessarily result in a higher bait uptake by the target species (Farry et al., 1998; Thomson and Algar, 2000). As a result of the setbacks encountered, the existing baiting strategies were adapted or even completely new concepts were introduced; e.g. additional vaccination campaigns, double baiting and distribution of baits at fox dens (Breitenmoser and Zanoni, 1995; Müller, 1995; Schlüter and Müller, 1995; Vuillaume et al., 1998). All these adaptations and new concepts aimed at maximizing the overall vaccination coverage, but a decrease in the rabies incidence does not only depend on the proportion of foxes consuming a vaccine bait. For example, in order to increase the vaccination coverage of the juvenile fox population an additional summer campaign was implemented in several areas (Müller, 1995; Masson et al., 1999). Although, these summer campaigns allowed for a significant increase in bait uptake, especially of the target sub-population of juveniles, they proved to be less efficient in decreasing the rabies incidence than spring campaigns with a lower overall bait uptake rate (Masson et al., 1999). It seems that not every member of the fox population is exposed to the same risk of becoming infected with rabies. A possible sex and age biased

infection rate could be generated by certain ecological and physiological traits. Preferably, baiting strategies should be selected that would optimize bait uptake by the segment of the fox population with the highest risk of becoming infected. To complicate matters even more, it can be assumed that not every fox has an equal chance of detecting and consuming a bait. For example, temporal and spatial restrictions of the activity pattern can reduce bait availability to the individual animal. Hence, efficient and cost-effective oral vaccination programmes require detailed knowledge of the behavioural ecology of the red fox. Astonishingly, the latter has received little or no attention in the development and evaluation of baiting strategies. In this paper, the behavioural ecology of the red fox will be analysed in the context of rabies epizootiology to evaluate baiting strategies for oral vaccination of foxes against rabies. This may seem overdue because in West- and Central Europe, terrestrial wildlife rabies has been completely eradicated, with the exception of some residual foci. However, oral vaccination is becoming an important tool in rabies control in an increasing number of East European countries. Because of limited financial resources available here for rabies control, the selection of the most cost-effective baiting strategy is of utmost importance.

### Rabies Transmission

The fox rabies incidence in Europe shows a clear seasonal pattern. A peak is observed in March, followed by a rapid decrease to an annual low in June, after which the number of rabies cases starts to increase slowly till January, followed by a more rapid increase till the annual peak in March (Moegle et al., 1974; Macdonald, 1980a; Wachendörfer and Frost, 1980). Rabies can be transmitted by different routes, although the most important one is assumed to be through biting. Johnston and Beauregard (1969) found that 40% of rabid foxes showed evidence of 'ferocious contacts'. However, it remains to be clarified if these aggressive contacts were initiated by the infected animal, or if it was attacked. Unfortunately, little or nothing is known about the behaviour of rabid foxes under natural conditions. Artois and Aubert (1985) described the movements of three rabies-infected foxes fitted with a radio transmitter. All three animals remained in their territory during the entire incubation period. Only during the last phase, the animals strayed for several hundred meters beyond their normal range, but all three died at the border of their own territory. Direct observations of contacts between rabid and healthy foxes are only available from animals kept in captivity. Winkler (1975) observed how a healthy fox turned away from a rabid animal. Another observation by the same author showed completely different behaviour, the normal fox approached and sniffed the entire body of the infected animal. In both cases, the rabid fox did not attack the healthy animal. When the rabid fox showed abnormal behaviour, like seizures, the healthy animal clearly tried to avoid contact. Most rabid foxes exhibit the apathetic form of the disease, also called 'dumb rabies'. Extremely aggressive behaviour is not very common, Winkler (1975) never observed such behaviour in over 100 captive rabid foxes. Rabies transmission probably involves contact between a rabid passive fox and a healthy animal (Blancou et al., 1991). For the spread of fox rabies under natural conditions contacts between aggressive territory owners and impassive rabid intruders are the most likely

scenario (Kappeler, 1985). Although physical aggressive interactions do not belong to the regular behavioural pattern of the territory owners, if necessary, intruders will be expelled by aggressive confrontations (Storm and Montgomery, 1975; Macdonald, 1980a; Henry, 1986). Between foxes sharing a territory the virus could also be transmitted through non-aggressive encounters. Rabies virus can be excreted in saliva before the onset of symptoms, so an apparently healthy fox that behaves completely normal can already transmit the virus (West, 1972; Aubert et al., 1991). Thus, an infected fox can easily transmit the virus to territory members during non-aggressive social contacts. Although, Rupprecht et al. (2002) mentioned that non-bite exposures across mucous membrane are less efficient and rarely result in disease. However, territoriality seems to play a key role in the spatial propagation of rabies. Therefore, a more detailed look at fox territoriality and which animals are involved in territory defence is required for a better understanding of rabies transmission among foxes.

### Territoriality

Most foxes in Europe are territorial and live in pairs or in small family groups with three to six adults (>12-months old). Other foxes are non-territorial and are more or less itinerant and roam over a larger area and often use (temporarily) the border zones between established territories (Macdonald, 1987; Niewold and Jonkers, 1999; Mulder, 2000). It can be expected that in areas with high mortality (diseases, hunting) family-groups and non-territorial animals are not very common, while most foxes are able to locate and establish a territory on their own. Brief meetings between foxes sharing a territory are quite common, but contacts between foxes of adjacent territories are generally avoided (Harris, 1986; Macdonald, 1987; White and Harris, 1994). Territoriality is primarily claimed by olfactory (markings) and perhaps vocal signals (Preston, 1975; Niewold and Jonkers, 1999). However, critical areas, like rich food patches, are sharply defended and intruders are not tolerated and will be expelled by visual and tactile signals (Preston, 1975; Macdonald, 1987). These territorial fights are also important in setting-up, and subsequently stabilizing, the borders between adjacent territories (Niewold, 1980). Border zones of neighbouring territories do not seem to overlap (Macdonald and Voigt, 1985; Meia and Weber, 1996). However, territories are not static, they shift, are combined or are split up, become smaller or larger, etc. (Macdonald, 1987; Mulder, 2000). Although territory drifting can occur at any given time during the year, the highest rates are observed during the winter months, November to April. It is predominantly a consequence of social instability caused by among others the high annual mortality rate (Macdonald, 1987; Doncaster and Macdonald, 1991). Mulder (2000) calculated that every year 29% of the territory holders died in an undisturbed fox population (no hunting and infectious diseases). However, in areas with increased mortality risks (hunting, disease), a high number of territories will become vacant and are (partially) taken over by neighbouring foxes or itinerants, increasing the number of territorial fights considerably. For example, at the height of a rabies or sarcoptic mange outbreak more than 50% of the foxes can succumb to these diseases (Wandeler et al., 1974; Baker et al., 2000).

## Fox Population

### Cubs

Although rabid cubs ( $\leq 3$ -months old) are sometimes reported, the numbers are insignificant, and these animals are most likely infected by adult territory members. Most cubs are born in early Spring (March to April) and during this time up to 60% of the fox population are cubs (Lloyd, 1980). In the first month after parturition a high cub mortality rate is observed, mainly through the loss of entire litters. The vixen remains in or near the den for 6–10 days after parturition, after which she starts to make longer excursions throughout her home-range. However, she will continue to spend most of her time near the cubs. The cubs emerge from the den when they are about 4-weeks old, and start to eat solid food. At this time, the vixen returns to her old activity pattern (Macdonald, 1987). The cubs start to investigate and search for food in the immediate surroundings of the den at 8–10 weeks of age, from the end of May to late June (Lloyd, 1980). The parents will continue to bring food to their cubs until they are about 14-weeks old (Henry, 1986). The limited spatial activity of the cubs reduces the probabilities of encountering a rabid (or healthy) intruder considerably. Their intraspecific contacts are limited to group members. Thus, cubs are not involved in the maintenance of the chain of rabies infection, and can be considered as dead-end hosts.

### Juveniles

During the summer months, the juveniles (4–12-months old) will limit their movements to the territory of their parents and do not participate in territory defence. This latter behaviour is reflected in the small proportion of juveniles found rabid during the summer months (Macdonald and Voigt, 1985). At the end of the summer the gradual transition to independence of the juveniles is now completed, and they start making exploratory trips preceding the actual dispersal period (Mulder, 2000). Also, juveniles that eventually do not disperse make these exploratory trips occasionally (Woollard and Harris, 1990). These excursions are probably used to familiarize the animal with the surrounding areas and to locate suitable areas to establish their own territory. Most of these trips are made in random directions, and little time is spent either resting or foraging (Woollard and Harris, 1990). In the beginning, these trips will last only several hours and the animal returns every time to its natal grounds. These trips become longer with time and the animal does not return every night anymore. Eventually, a proportion of the juveniles will leave the territory of their parents permanently. Generally, the dispersal season varies from August to March, with a clear peak in October (Voigt and Macdonald, 1984; Zimen, 1984; Macdonald, 1987; Trehella and Harris, 1988; Labhardt, 1990; Mulder, 1991). Although dispersal is mostly done by juveniles, females living in family groups can also disperse in their second year (Mulder, 1988). When the juvenile does not become successful in establishing its own territory, its activity area becomes smaller and it becomes a local itinerant, sometimes also called a 'floater' (Mulder, 2000). These itinerants often occupy the border zones of neighbouring territories (Mulder, 1988; Zabel and Taggart, 1989; Niewold and Jonkers, 1999). The reason why the juveniles disperse is still not completely understood. Aggressive behaviour of the parents towards their offspring

has often been suggested (Zimen, 1984; Harris, 1986; Henry, 1986), but other authors dismiss the expulsion through aggressiveness (Storm et al., 1976; Hough, 1980). Woollard and Harris (1990) claim that juveniles may disperse because they are in some way excluded from the best feeding sites within their natal area. This is most likely not a matter of rapid or violent expulsion from these areas but a rather gradual exclusion through continual harassment by the dominant animals.

The overall increase in rabies incidence in autumn has often been linked to the onset of the dispersal season of the juveniles (Wachendörfer and Frost, 1980; Kaplan, 1985). However, the role of the juveniles is still not completely understood. As mentioned previously, the number of rabies cases already starts to increase during summer, thus considering a mean incubation period of 2–4 weeks an increasing number of foxes becomes infected in late spring to early summer, when the movements of the cubs are still limited to the direct surroundings of the den. The role of the dispersing juveniles in the epizootiology of rabies may simply be overestimated (White et al., 1995). Infected dispersing juveniles can of course transport the virus over larger distances than during normal transmission from territory to neighbouring territory. However, in Europe most juveniles do not disperse over large distances. Furthermore, these cases far ahead of the rabies front do not accelerate or alter the movement of the epizootic (Moegle et al., 1974), indicating the minor importance of these cases in the spread of the disease. Woollard and Harris (1990) found no evidence for an increase in contact rate between foxes during the dispersal period and post-mortem studies showed no increase in bite wounds of juveniles during this period. Thus, the behavioural ecology of the (dispersing) juveniles and the rabies epizootiology do not support the often assumed dominant role of these animals in rabies transmission during this season. The final attempts to obtain a territory by the dispersers occur late winter or early spring (Mulder, 2000).

### Adults

The mating period (January to February) is characterized by intense activity and males are often found far outside their own territory, probably sexually attracted by a female in oestrus (Mulder, 1985). During the mating season, the virus is initially transmitted among males during aggressive encounters. The infected males can transmit the virus to the females during the actual mating period, when the animals stay closely together. Consequently, first male foxes dominate in the annual winter peak of the rabies incidence followed by an increasing number of rabid females. The higher number of rabies cases among females has also been linked with pregnancy and lactation. The energetic costs of pregnancy and maternal care, plus the immunosuppressive effects of some hormones produced during parturition and lactation, may increase the susceptibility of females to infectious diseases (Festa-Bianchet, 1989; Dobson and Meagher, 1996). After the mating season and when the vixens have selected a suitable den, territorial stability returns and territorial behaviour is less pronounced than during the rest of the year. This behaviour is reflected in the annual low in rabies number during late spring and the early summer months (Moegle et al., 1974; Macdonald, 1980a; Wachendörfer and Frost, 1980). Adult foxes make regular excursions outside their territories in this period. These trips are often directed towards

specific food sources, for example to find sufficient food for their offspring (Niewold, 1980; Meek and Saunders, 2000; Mulder, 2000). The inevitable confrontations between territory owners and intruders during these excursions could be responsible for initiating the increase after the annual low in rabies incidence. Thus, this increase after the annual low in rabies incidence is caused by adults, and not by the young fox population. During autumn, not only the juveniles show increased activity (exploratory trips and dispersal), but also the locomotive activity of territorial adult foxes increases during this season (Labhardt, 1990; Capt and Stalder, 1991). Most authors link this behaviour of the territory owners with territory defence against the increasing number of intruders (Labhardt, 1990). Capt and Stalder (1991) however explain the increased activity of the foxes to a higher food intake during this period. During autumn fat reserves are built up to overcome the food shortages encountered during the winter months (Lindström, 1983; Suchentrunk, 1991). The increased food intake during autumn could explain that bait uptake by foxes is generally higher during autumn than during spring (Frost et al., 1985; Brochier et al., 1988; Masson et al., 1999). Territoriality and overall activity continues to increase till it reaches its peak during the mating season.

### Oral Vaccination

Although disentangling cause and coincidence is not without problems, from the above presented data it seems that, with exception of the mating season, territory owners are responsible for the persistence and transmission of the disease. This subpopulation will attack intruders, irrespective of the behaviour of the latter, and are therefore extremely susceptible of becoming infected. Thus, oral vaccination of foxes should be targeted mainly at the territory owners, as 'core' transmitters of this infectious disease. This could greatly improve the effectiveness of the vaccination campaigns. Maximizing bait availability to a certain subpopulation, meanwhile minimizing bait depredation by the remaining fox population, clearly sets limits to the timing of oral vaccination campaigns.

The traditional early spring campaign seems very attractive, because (i) the overall fox density and number of adult non-territorial foxes have reached its lowest levels, (ii) the territories are relatively stable and excursions outside their own territories are rare and (iii) the adults have sufficient time to develop an immune reaction before the period of enhanced risk of transmission in late spring to early summer. Also, the climatic conditions would generally not hinder bait distribution anymore, this in contrast with the first months of the year (sub-zero temperatures). In countries with a relatively mild climate bait distribution in the first months of the year would also be feasible. However, bait delivery during this period would not protect the animals against infection during the mating season, when most aggressive encounters between foxes are observed. It should not be forgotten that after bait consumption it will take several weeks before an adequate immune response has been developed. Although, antibodies were already detected in fox sera 2 weeks after bait consumption, the highest titer was observed 1 month post-vaccination (Schneider and Cox, 1983). Therefore, it is suggested to distribute baits during November or December, depending on the prevailing climatic conditions, to vaccinate the animals prior to the onset of the mating period. In case that an

additional spring vaccination campaign aimed at the adult foxes is carried out, it should take place before the cubs start to eat solid food. It was suggested that the period of limited spatial activity of the reproductive-active vixens in the first week(s) post-parturition would limit bait availability to these animals during early spring vaccination campaigns (Linhart, 1993; Marks and Bloomfield, 1999; Vos et al., 2001). However, this does not have to be the case. For example, Macdonald (1980b, 1987) observed that during this period of confinement food was deposited at the entrance of the den or cached in the immediate vicinity by the male partner or other group members. Later on, when the cubs start to eat solid food items, evidence is accumulating that cubs compete for baits through the transportation of baits by the parents to the den (Vuillaume et al., 1998; Saunders et al., 1999). Ironically, many of the cubs can not be vaccinated successfully. Partially because they are not yet immuno-competent or maternally transferred immunity interferes with active immunization (Vuillaume et al., 1998; Blasco et al., 2001; Müller et al., 2001, 2002). Distribution of baits during late spring and summer will predominantly reach the young fox population. These animals are inclined to locate and consume baits more rapidly than adults, while they are less successful at foraging and concentrate on finding more easily obtained food sources (Harris, 1986; Marks and Bloomfield, 1999). As stated previously, the young fox population is not responsible for rabies transmission, thus summer campaigns targeted at the young fox population have little or no effect on the persistence and spread of rabies as shown by Masson et al. (1999). Furthermore, trying to reach a very high vaccination coverage of the young fox population at this stage can also be cost-ineffective. In spring, around 60% of the fox population are cubs, but at the time the animals become independent this has been reduced to 40%. Evidence from ear-tagging studies suggest that between 40–55% of all cubs have perished before the animals become completely independent (Englund, 1980; Harris, 1986; Mulder, 2000). In autumn, overall activity increases, including territoriality. Therefore, campaigns carried out early in this season could protect territory owners against a rabies infection when confronted with a rabid intruder. However, the fox population in early autumn consists out of a large segment of non-territorial animals competing for baits, among others the dispersing juveniles. It is not likely that dispersers have less chance of locating a bait than non-dispersers. Woollard and Harris (1990) could not observe a marked difference between the activity patterns of dispersers and non-dispersers. In addition, Linhart et al. (1997) found no difference in bait-uptake between territorial and non-territorial coyotes (*Canis latrans*). Distributing baits after the dispersal peak in October would therefore reduce depredation of baits by non-territory holders and coincide with the suggested period to vaccinate the animals prior to the mating season. Of course there is no simple relationship between the timing of vaccination campaigns and the eradication of rabies. Too many other factors, unrelated to fox ecology, determine the outcome as well. For example, bait uptake is also influenced by bait distribution system, bait palatability, quantity and quality of other available food sources and the presence of other non-target species (Linhart, 1993).

The conclusions presented here concerning the timing of oral vaccination campaigns partially contradict the recommendations of the European Commission (2002). Here, it was

suggested to conduct oral vaccination campaigns on a bi-annual basis in spring (May to June) and autumn (September to October), with a den vaccination campaign complement to the regular Spring campaign. This, to increase the availability of the cubs to vaccine baits. Such a strategy may have proven its effectiveness in the past, but it does not implicate that other more (cost-) efficient approaches exist. Other strategies have shown to be also highly effective. For example, in Texas (USA) and Ontario (Canada) single annual vaccination campaigns have been extremely effective (Fearneyhough, 1999; MacInnes et al., 2001). Here, baits were distributed in autumn or early winter, as suggested in this paper. Although, the motives for selecting these periods in North-America were not based on the ecology of the target species alone, also issues like availability of the airplanes for bait distribution and prevention of depredation of baits by certain non-target species played a role. Countries considering oral vaccination campaigns, but that do not have the financial resources to distribute baits on a bi-annual basis, could implement a single annual vaccination campaign preferably in late autumn or early winter. In case of re-emergence of rabies or persistent residual foci additional campaigns can be considered. The financial burden should not be underestimated, several eastern European countries have discontinued their vaccination programme as a result of financial problems.

## Conclusion

From the presented data we can distinguish two key periods that seem to determine the annual rabies cycle in Europe; the mating period from January till February and the more inconspicuous period during late spring and early summer. The annual rabies peak in March is mainly a result of the mating season of the red fox. This period is characterized by the highest number of (aggressive) encounters between, predominantly, male foxes searching outside their own territories for females. This period of increased activity greatly enhances the spread of the virus. Later on, the males will infect the female foxes. When the cubs are born, in the beginning of spring, the fox population is relatively stable and the dispersal season is also over. The number of rabies cases decreases rapidly to its annual low in early summer. Outside the mating period, rabies is most likely transmitted to territory owners by rabid intruders. When confronted with the territory owner, the infected animals does not flee and the virus is transmitted to the susceptible territory owner in the attempt to expel the intruder. Although young foxes will not leave the territory of their parents during the summer months and are also not actively defending this area, they can become infected through contacts with adult territory members. From August on, the juveniles will start to wander off, first on exploratory trips and later most juveniles will disperse from their natal area. However, there is no evidence that the dispersing young foxes are responsible for the increase in rabies incidence observed during this season. Therefore, the oral vaccination campaigns to reach especially the young fox population are not very effective to halt the temporal and spatial spread of rabies. The main target population of oral vaccination must be the animals that are actively involved in territory defence. During the mating season, practically the whole population is at risk of becoming infected. Thus, the optimal timing of oral vaccination campaigns is late autumn and/or early winter, depending

on the local climatic conditions. Supplementary vaccination campaigns can be implemented when financial resources are available or under specific epidemiological conditions.

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