The ecology of dogs and canine rabies: a selective review *

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Summary: Although dogs are the most widespread and abundant of all carnivores, the role of the dog in human cultures and its impact on the environment have rarely been studied. These subjects are reviewed in the context of canine rabies.

To understand the epizootiology of canine rabies, the ecology and population biology of the dog must be considered. Information on dog populations (in relation to different habitats, cultures, social strata of human populations and epizootiological situations) was collected in Nepal, Sri Lanka, Switzerland and Tunisia.

In Switzerland (and Western Europe in general), rabies is maintained and spread by red foxes. The low prevalence of rabies in dogs may be explained by restrictive practices of dog-keeping and high rates of vaccination. In the other areas examined, dogs are poorly supervised and their population densities are high enough to support rabies, although it is questionable whether canine rabies exists independently of a wildlife reservoir. Dog-keeping practices, high rates of exposure and various cultural factors may lead to a high human rabies mortality rate. Nevertheless, dogs in these areas remain sufficiently accessible for vaccination and well-executed control programmes could prove successful.


INTRODUCTION

Tremendous progress has been made in recent decades in the understanding of the biology of the rabies virus and the pathogenesis, prevention and epidemiology of the disease (9). Dreams of controlling rabies in wildlife through vaccination have become a reality. Molecular biology has led us to the threshold of a new era in disease prevention. But the number of human rabies deaths in the world has not diminished accordingly. The majority of these fatalities occur in developing countries as a result of virus transmission by dog bites.

* This paper is dedicated to the memory of the late Dr A. Kuruneru, former Chief of Veterinary Public Health in Colombo, Sri Lanka.

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ECOLOGY OF THE MOST COMMON CARNIVORE SPECIES

Estimates of the world-wide dog population can rise as high as 500 million or more. No other carnivore species occurs so widely and with such a high average population density, and few other carnivore species reach peak densities similar to those observed for dogs. Domestic dogs are present on every continent and practically every island settled by humans. Only in a small minority of cultures are dogs completely rejected. The dog:human ratio most commonly lies between 1:10 and 1:6, but considerable variation exists (88, 102, 113, 120, 126). Recent investigations have often found this ratio to be considerably higher than assumed by local authorities (72, 111). Dogs may even outnumber humans in some areas, as in the Athapaskan villages described by Savishinsky (129). In 1967, the 75 inhabitants of one settlement kept 224 dogs, primarily for pulling sledges.

In urban areas of eastern North America, Beck (16, 17, 19) and Daniels (55) estimated a street dog population density of approximately 150 individuals per km$^2$. Much higher densities of poorly supervised dogs were observed in suburban and rural settlements in south-western Sri Lanka, where estimates of up to 3,000 dogs per km$^2$ were made.

The abundance of the dog population is dependent on the habitat, especially the availability of resources such as food, water and shelter. Access to these resources depends on settlement patterns, rubbish and waste disposal, rules for keeping animals and other cultural practices. For an understanding of the population biology of the species, it is important to keep in mind that individual dogs may have different ownership status, different degrees of restriction on their movement, social interaction and reproduction, and different levels of dependence on human care (19, 76, 77, 81, 148, 156, 158). A dog owner may feel responsible for certain aspects of the behaviour and well-being of the animal, while other dogs are ownerless. The laws of most nations oblige people to keep owned dogs under control and to care for them. The responsible dog owner both provides and limits access to resources. In addition, the owner theoretically restricts movement, social interaction and reproduction. However, the reality is often different. The meaning of ownership varies in different cultural and social settings (150). In many parts of the world, a large proportion of animals receive little or no supervision. Movement is not restricted, or restricted only for part of the day. Along with food received from their owners, dogs may have access to waste, refuse and other food sources. Reproduction is not under control, but litters are born and raised under the protection of a household. Dogs which do not have individual owners or a referral household may still be accepted by the neighbourhood as belonging to the community. These animals are “community-owned” (155) or, to use a better term, “neighbourhood” dogs (158). Members of the neighbourhood assume occasional responsibility for these dogs, when it comes to protecting them from dog catchers or bringing them to anti-rabies vaccination clinics. Human care for family and neighbourhood dogs practically eliminates interspecific competition for resources and greatly reduces intraspecific competition.

Dogs without owners, a referral household or social bonds to humans are described as “feral”. As Daniels and Bekoff (60) explain, feralisation is not a reversal of domestication, but a process by which individual animals become desocialised from humans or, because born in the wild, never become socialised. Such animals may still depend heavily on resources provided by man. Neighbourhood and feral dogs often
scavenge for food in dumps, markets, slaughter areas, roadside areas and temples. Abandoned structures, parked cars and natural shelters provide refuge (16, 17, 18, 19, 55, 56, 58, 59, 62).

DOGS AND ANTHROPOLOGISTS

Wolves were among the first animals to be domesticated by man, some 12,000 or more years ago (50, 63, 144). Mutual benefits and tolerance must have been so important (66, 76, 101, 124, 127) that the descendant of the wolf, the dog species, rapidly spread to all areas colonised by humans. The useful attributes of dogs include the ability to hunt cooperatively, to guard and defend people, livestock and other property, to pull vehicles and carry goods, to remove refuse and human faeces from the environment, to serve as objects of barter and a meat source, and to act as social partners and companions. Clutton-Brock (50) hypothesised that the change of weaponry observed during the mesolithic period reflected new hunting methods, which also favoured dogs as hunting partners. Indeed, the anthropological literature contains numerous indications that dogs may contribute to the success of a hunter (84, 116, 161; for older references see 78, 100). However, few investigators present evidence that the accomplishments of a hunter using dogs are greater than those of one without dogs (151). A closer look often reveals that dogs may not be particularly efficient for hunting (85, 112, 162), or that they can be used only for certain types of game (36, 43, 161). The widespread use of dogs among northern circumpolar peoples as draught animals to pull sledges and travois (83) has attracted some attention (11, 85, 116, 117, 121, 129, 142). This is an example of the cultural and economic value of dogs changing with different circumstances. The practice developed relatively late in the American Arctic: dogs became important in transportation only after native peoples became heavily involved in fur trading (98, 129). The popularity of dogs for traction is now declining with the greater use of snow-mobiles (98, 116).

Dogs would not have such widespread distribution if their only value was as hunting aids or to pull vehicles. Dog functions are mentioned in numerous studies of cultural anthropology. The vast majority of references relate to the consideration of dogs as mythical or supernatural beings. A comprehensive review of the literature on dogs in African cultures was published by Frank (78), and Latocha (100) produced a similar review on dogs in native South America. Both publications make it clear that attitudes and cultural values regarding dogs vary enormously. In a specific cultural setting, there may be multiple reasons for keeping dogs. Harner (87), for instance, mentions that the Jivaro Indians keep at least one or two dogs in every household, to serve as watchdogs against surprise attacks, to protect garden crops from rodents, for hunting and also as companions which receive care and protection. Among the Jivaro, dogs are also given hallucinogenic drugs to help them obtain supernatural power. There exist only a few other, more detailed accounts of dog/human relationships (e.g. 104, 112, 129).

However, the reasons for the association of people with dogs are often not so obvious. More than the literature suggests, dogs may be kept or tolerated as social companions and pets; as something to care for, something to make one feel safe; as a social partner of inferior rank or simply as a focus of attention. The psychological importance of owning a pet is well documented for a wide variety of social settings in industrialised nations (53, 73, 91, 94). To own an animal companion might also be more important in non-Western societies than recognised to date (104, 112, 129; see also 78, 100). Savishinsky (129) points
out that the dogs kept by an Athapaskan band play an important part in social and psychological processes, especially among children. But this seems to be a troublesome concept for most investigators. One gets the impression that anthropologists have certain difficulties in dealing with the omnipresence of dogs and their possible role as pets. An interesting example is the analysis by Crocker of the keeping of animals by the Bororo in central Brazil (54). Crocker attributes pet qualities to the macaws and parrots tamed by the Indians, but not to dogs. He suggests that a distinction should be made between commensal association _per se_ and the fostering of creatures as pets. Crocker admits that dogs have certain attributes of pets in that they are given names and are never eaten. Only the owner knows which of the dozens of dogs lying about the village are actually his, while taking a minimal interest in them. The animals are so unimportant as not to be included in the disposal of property following the death of the owner. The situation described by Crocker obtains in many rural areas of Latin America, Africa and Asia.

The question of why dogs are kept or tolerated becomes even more relevant when one considers the costs involved; for the benefits of dog-keeping may turn into disadvantages. The impact of owned dogs on wildlife was probably of minor concern to colonists, for instance, who introduced dogs into new geographical locations; however, the ecological consequences of the introduction are becoming increasingly evident (65; see also 12, 118, 122, 135). Dogs probably played a significant role in the extinction of native wildlife when they were introduced onto islands previously free of vertebrate predators (13, 89, 95, 103). Other costs related to the presence of dogs were most prominently formulated by Feldmann (70; see also 18, 44, 71). Dogs prey not only on wildlife (12), but also on livestock (52); they bite and occasionally kill humans, especially children (8, 20, 41, 57, 110, 128, 130, 141, 159). Originally, they may have helped to offset some of the dangers of living in fixed settlements by removing human faeces and recycling refuse (67); however, in a modern urban environment dogs are often a nuisance and a source of pollution. Cohen (51) suggests that the domestication of animals must have had various health consequences for human communities. High densities of human populations and accompanying dogs must provide ample opportunity for transmissible parasites to evolve into these epidemiological niches. Indeed, dogs are associated with more than fifty zoonotic disease agents (1, 18, 90, 132, 152, 153, 154) of which echinococcosis/hydatidosis, toxocarosis and rabies are the most prominent. Human attitudes towards dogs, dog-keeping practices and other aspects of human behaviour influence disease transmission (98, 114, 132). A well-documented example is echinococcosis in Kenya, where the highest known incidence of human hydatid disease is found among the Turkana (79, 80, 105, 106, 107, 108, 115). The Turkana keep more dogs and have more intimate contact with them than other tribes in the same area (108). Two main factors may account for a high prevalence of _Echinococcus granulosus_ worms in dogs. Although the prevalence of _Echinococcus_ cysts in ruminants is low, transmission of the worms may be increased by the fact that dogs have unlimited access to offal and forage on the numerous livestock carcasses which become available during periodic droughts. Dogs also scavenge on human corpses, which are neither buried nor cremated. The fact that humans are active intermediate hosts (105) must influence the evolution of parasite adaptation.

**DOG POPULATIONS: TWO CASE STUDIES**

As Beck (16) points out, dogs lend themselves perfectly to field studies and testing methods recommended for game biology (154, 158).
Dogs in Tunisia: a long-term investigation

The human-dog relationship has a long tradition in North Africa (7, 78, 101). It is interesting to note that Islam obviously does not discourage people from keeping dogs in these countries (5, 6, 24, 25, 33, 130), contrary to other parts of the Islamic world (29, 120, 133).

In 1982, a National Programme for Rabies Control was adopted in Tunisia. Annual mass vaccination campaigns were organised: first in a limited area in the north-east and later covering the whole country. These activities resulted in a marked regression of the incidence of rabies. However, the goal of total eradication of the disease was not achieved (26, 27, 28, 86). In order to collect the data needed for population management and disease control, dog populations in rural and urban environments were studied between 1986 and 1990 (111, 156, 157). Five rural and eight urban or suburban study sites were selected in northern and central Tunisia. In general, urban and suburban study sites were highly populated, predominantly residential areas which were economically depressed. The methods applied included capture-mark-recapture techniques, questionnaire surveys, individual marking, focal animal and ad libitum observations (3) and radio-telemetry.

A surprising uniformity was observed in the structure and dynamics of the populations under study; however, dog densities differed markedly between rural and urban/suburban zones. Between 7 and 30 dogs per km² were counted in rural zones, where more than 80% of all households kept one or more dogs (3.0-5.5 inhabitants per dog). In urban and suburban zones, dog population density varied between 700 and 1,000 dogs per km². The percentage of households keeping dogs was less than 20% and sometimes even less than 10% (16 to 46 inhabitants per dog). The percentage of ownerless dogs was determined in four study sites. In three areas – one rural, one suburban and one urban – the percentage ranged from 7.0% to 8.3%. In another suburban zone, ownerless dogs accounted for 14.3% of the total dog population, due to the proximity of this area to a large dump site on the outskirts of a provincial capital. However, most dogs in Tunisia are owned. The proportion of ownerless dogs exceeds 10% only in zones where an accumulation of resources is available which attracts unsupervised and ownerless dogs from less favourable areas. These findings are consistent with results from other countries (40, 88, 109, 113).

The mean age in owned dog populations varied between 1.8 and 3.3 years: 12% to 23% were less than one year of age. High turnover rates were observed, with 23%, 30% and 40% of the owned dog population changing within six months in rural, suburban and urban areas respectively. One- and two-year-old bitches had the highest reproductive rate of all age classes.

However, only 20% of live-born pups survived the first three months of life in a rural area. In spite of the high mortality rate (many owners killed undesired pups) the population was self-sustaining and showed a high reproductive potential. The mean age of well supervised dogs in the United States of America and in the canton of Bern, Switzerland, is approximately 4.5 years (16, 110, 113, 131). In Tunisia, the situation is closer to that of Mexico City (126), where only 12% of dogs are older than five years. Interestingly, dogs in south-western Sri Lanka also reach a relatively high age. The slower population turnover in these areas is probably linked to frequent reproductive failures (partly caused by Brucella canis). This may be taken as an indication that life expectancy increases when production of viable offspring decreases.
The percentage of owned dogs allowed to roam freely is twice as high in rural areas as in urban and suburban areas of Tunisia. However, as a consequence of high population densities, numbers of free-roaming owned dogs in urban and suburban zones were 10- to 100-fold higher than in rural areas. Non-restricted dogs occasionally or regularly moved away from their owners to satisfy fundamental needs such as food, shelter and mates. It is on these occasions that owned dogs frequently come into contact with ownerless dogs. Observations on almost 250 owned dogs in one rural study site revealed that male dogs left their referral household significantly more often and covered greater distances than bitches. However, maximal distances of eight kilometres between localisation site and household were observed for dogs of both sexes, although in most cases (57.7%) dogs were observed at less than 500 metres from their household.

In 1986 and 1987, over a period of 22 months, 34 ownerless dogs (17 males and 17 females) were studied in a rural area in north-western Tunisia. At the time of first observation, thirty of the dogs were adult and four juvenile. Eleven had been born to ownerless bitches, while another seven had been chased away or abandoned by their original owners. The origin of sixteen dogs was unknown. Fourteen litters (59 pups) from the observed ownerless bitches were localised. Mortality was relatively high early in life: eleven pups were known to have been killed by residents, five died from natural causes and twenty-one disappeared. Twenty pups were adopted by residents; however, these also suffered extremely high mortality. Lastly, only two pups born in the wild survived and joined a pack of dogs. The overall rearing success of ownerless bitches was insufficient to compensate for the losses of this population segment.

The social organisation of urban and rural dog populations has been described and discussed on several occasions (21, 32, 52, 55, 56, 61, 74, 76, 77, 134). Beck (16, 17) and Daniels and Bekoff (61) found a stronger tendency for dogs to avoid each other than to form groups. There were more single dogs, fewer pairs and slightly more large groups than expected when comparing the observed frequency distribution of groups to a 0-truncated Poisson distribution. Font (74) criticised this statistical approach as an inappropriate means of analysing the social tendencies of free-roaming dogs. In fact, pack formation has been described both in urban (52, 74, 77) and, more frequently, in rural environments (13, 41, 95, 102, 118, 122, 135). The traditional definition of a group is based on temporal, spatial and behavioural components (125), and therefore tends to be impractical in field work (55). In the Tunisian study, grouping was described by spatial distribution only. This allowed measurement of social tendencies by calculating for each dog the overall relative frequency with which it was observed together with other dogs, and the individual relative frequency of observation together with any specific dog within the study area.

Overall relative frequencies varied between 0% and 86% (mean: 62%; standard deviation: 15%). One male dog, which had been abandoned by its owner near a dump, was never observed in contact with other dogs. For five months (until death), this dog did not move from the site of abandonment and limited its activity range to a minimal area of 0.06 km$^2$ as estimated by the convex polygon method. In the same study area, the home range sizes of twenty-one ownerless dogs, calculated on the basis of more than 4,300 localisations, averaged 1.9 km$^2$, ranging from 0.2-8.5 km$^2$. Similar behaviour of recently abandoned dogs was observed by Daniels and Bekoff in New Mexico (61, 62). A very low contact rate was also determined for a pregnant female. Before and after parturition, this bitch avoided any contact with other dogs except her own pups. The existence of four stable non-oestrous groups was demonstrated by tabulating the individual relative frequency of grouping for all dogs in the study area. Group size
varied mainly due to the death of group members and, in one case, due to integration of two wild-born pups (group A: 5-8 members; B: 4-6 members; C: 2-4 members; D: 2 members). At least two factors seemed to contribute to group formation in the study area: genetic relatedness and familiarity between non-related individuals (111). Of the observed non-oestrous groups, 80% were formed exclusively by ownerless dogs. However, the situation is quite different in oestrous groups. Up to 55% of observed oestrous groups consisted of both owned and ownerless dogs. Ownerless males attempted to mate with owned bitches in heat and owned males joined oestrous groups with ownerless oestrous females. This regular contact between ownerless dogs and occasionally or permanently free-roaming owned dogs may be of special importance in the transmission of rabies and other pathogens affecting dogs and man (33, 90).

**Lalitpur: an example of operational research**

Human rabies is not uncommon in Nepal, especially in the Kathmandu Valley and in the Terai areas (92). Dogs are the main source of disease. Access to proper post-exposure treatment is far from optimal. In the 1980s, there were fewer than 500 medical doctors employed in government services in Nepal; only a small fraction were serving in rural areas, whereas 95% of Nepalis live in such areas (137). Local authorities are greatly in need of a programme of mass vaccination for dogs, in order to reduce the number of human exposures to rabid dog bites. In 1989, the French non-profit organisation *Vétérinaires sans frontières* sponsored a dog vaccination campaign in the city of Lalitpur (Patan) in Nepal. The World Health Organisation (WHO) supported the collecting of information on the dog population size in the project area and the vaccination coverage achieved.

Lalitpur is a traditional city, highly structured, both socially and architecturally, which is situated on the southern banks of the Bagmati River, in the immediate vicinity of Kathmandu. Plans called for vaccination of a minimum of 75% of the dog population of the city against rabies within one month. To achieve this goal, a strategy of temporary “neighbourhood clinics” was adopted, as opposed to door-to-door vaccination. Five teams each operated a vaccination clinic every morning for three hours. The location was changed daily. Each dog presented at a clinic was vaccinated, registered, and marked with a plastic collar, colour-specific for a given clinic. Within 19 working days, vaccination clinics had operated at a total of 110 locations, covering almost the entire area. After this regular campaign, two mobile teams vaccinated unmarked dogs in those areas of town where the percentage was below the desired target (D.D. Joshi, unpublished findings). The number of dogs collared during vaccinations and the proportion of collared dogs registered during re-observation surveys were used to estimate the total population size and the percentage of vaccinated dogs. At the end of the regular vaccination campaign, a total of 6,886 dogs had been vaccinated. Each of the five teams had treated between 8 and 195 dogs per morning (average: 72). The daily total for all five clinics varied between 141 and 614 (average: 362). Another 1,090 dogs were vaccinated by the two mobile teams during the follow-up campaign. An additional 520 were treated in the Lalitpur Veterinary Hospital over the whole period of the initial and follow-up campaigns. Taking into account that some dogs had lost their collars between the regular campaign and the follow-up, an estimated total of 8,200 dogs were vaccinated.

After the regular campaign, 1,135 dogs were observed in the course of eighteen re-observation surveys: 753 were wearing collars. With a total of 6,886 dogs vaccinated and marked, the total dog population of Lalitpur was estimated to be 10,375, using Bailey's
direct sampling method (45). Collar loss rates were estimated to be about 0.75% per day on the basis of information collected by "photographic recapture" (154) in a limited number of areas. If these losses are taken into account, an additional 14 of the 1,135 dogs can be assumed to have been vaccinated, reducing the population estimate to 10,186. The method of direct observation tends to underestimate numbers of puppies. With a correction factor of 5%, a conservative estimate for the total dog population is 10,700. Frith (unpublished findings) found a ratio of people to dogs of 9.42:1, based on questionnaire survey data. Estimating the human population as 117,875 (which is probably too high), Frith calculated the dog population to be 12,513 animals. With a corrected estimate of the human population, this figure is reduced to 11,054 dogs, a figure which is relatively close to the estimate based on mark-recapture data. From direct observation, the overall vaccination coverage after the initial campaign was estimated to be 66.3%. If a correction is made for collar losses, a coverage of 67.6% is calculated. Vaccination coverage achieved within specific control areas varied considerably (between 46% and 89%). The best coverage was found in the "Old Town", where the density of operating points for vaccination centres was highest. Finally, the follow-up campaign increased vaccination coverage to approximately 75%. This relatively easy accessibility of Kathmandu dogs for vaccination was predicted by Bögel and Joshi (39). The same seems to be true in many parts of the world (23, 28, 29, 30, 31, 48, 49, 99). Similar vaccination coverages were observed in south-western Sri Lanka and Tunisia but, in both areas, high percentages were reached only in close vicinity to temporary vaccination clinics (see also 42).

RABIES IN WESTERN EUROPE AND SRI LANKA:
A COMPARISON

Fox rabies in Western Europe has been described and analysed by numerous authors (e.g. 35, 139). For rabies virus to survive, it is essential that the virus be transmitted by an infected fox, during the short period of virus excretion, to enough other susceptible individuals. The rate of infective contacts is dependent on population density; rabies transmission ceases when population density drops below a certain level. In summer and autumn, only a small proportion of juvenile foxes are found to be rabid; juveniles attain the same level of infection as adults only during winter. This difference must be due to the higher probability of adults exposing themselves to infectious bites when they attack disoriented rabid foxes intruding into their territory, whereas juveniles avoid outsiders. The slow spread of a fox rabies epizootic suggests that the disease is usually transmitted by an infected animal to the occupants of a neighbouring territory and only rarely over larger distances. This is also suggested by the observation of radio-tagged infected foxes dying from rabies within their original home range or not very far from it (4). Only occasionally is rabies introduced into a new area during dispersal movements of an infected subadult animal. The progress of epidemic waves is halted by zones of low fox density (139) and areas where more than 60% of the fox population has been immunised (through oral vaccination with baits containing attenuated rabies virus) (140). Where the fox population has been reduced below a certain level (by rabies itself and/or fox control), rabies disappears not only in foxes, but also in all other terrestrial mammal species (but not in bats). Even though the disease can be eliminated under these circumstances, a number of questions still
remain with regard to fox rabies (149). In Western Europe, only 0.1-5% of the rabies cases reported annually are in dogs (139). Three factors may account for the low prevalence of rabies in dogs:

- most dogs are restricted in their movements
- dogs are kept indoors or in enclosures and are kept on leashes when outside
- vaccination of dogs is strongly recommended or even compulsory.

It may also be that virus strains adapted to wild species are not very well suited for propagation within dog populations. There is no recent evidence that fox rabies gives rise to epizootics in urban stray dog populations.

The situation is different in large parts of Asia, Africa and Latin America, where rabies virus circulates in the dog population, accounting for 95% or more of all diagnosed rabies cases (10, 34, 46, 47, 143, 145, 154). Despite the easy access to dog populations, little is known about the epizootiology of rabies. Most accounts give the impression that dog rabies is highly enzootic with only moderate fluctuations in prevalence (22, 69, 82, 97, 136, 138, 147).

Sri Lanka can serve as an example for pointing out some of these problems. In Sri Lanka, rabies is endemic in all provinces and dog population densities are extremely high. The human settlement pattern allows the existence of a continuous dog population along the coast and into the areas of cultivated paddies. Most dogs are owned, and between 65% and 85% are accessible for parenteral rabies immunisation. Many dogs living with families are adopted or are tolerated strays. When interviewed, a respondent may decide arbitrarily to declare such an animal as owned or unowned. Less than one-third of all dogs are permanently confined to gardens or houses. Approximately one-third of the owned dogs are always free. Most owned dogs may move freely in or out of the houses of their owners.

The majority of animal rabies cases are observed in dogs. But, as in so many other countries with “endemic” dog rabies, there are also a few confirmed wild animal cases. These may be dog rabies offshoots, but could also be the tip of an iceberg of wild carnivore rabies. Sri Lanka has a rich wild carnivore fauna. Jackals (*Canis aureus*), civet cats (*Viverricula indica*) and mongooses (*Herpestes edwardsi* and *H. fuscus*) occur at densities potentially high enough to support independent cycles of epizootic rabies. The question is not unimportant; dog rabies eradication is an easier goal if the occurrence of the disease in dogs is independent of wildlife rabies.

In the late 1970s and 1980s, the Veterinary Public Health Services in Colombo conducted campaigns intended to control rabies (96). The strategy was to remove unsupervised dogs and vaccinate supervised owned animals. Teams of dog catchers worked with great skill, but their effect on the dog population density remained negligible. Less than 5% of the population was removed every year. Such losses are rapidly replaced by offspring. Dogs were immunised by well-trained vaccinators at temporary vaccination clinics. The locations of temporary clinics were posted and announced by loudspeaker just prior to the campaign. Between 40% and 85% of the dogs in the immediate vicinity of a clinic were brought for immunisation. The spacing of vaccination clinics was such that not more than about 30% of all dogs in an area received vaccine during a particular campaign. This relatively low immunisation coverage cannot prevent a relatively high prevalence of dog rabies and, as a result, frequent human exposures.
HUMAN RABIES IN SRI LANKA

Approximately 35,000 persons world-wide die from dog-transmitted rabies each year, and approximately 3.5 million people receive post-exposure treatment annually, mostly after dog bites (37, 38). Almost all human rabies deaths and the vast majority of treated bite exposures occur in developing countries (2). South-East Asia is an area of extraordinarily high density of human rabies occurrence (154) and Sri Lanka provides a typical example.

This island nation has approximately 16 million inhabitants. Every year, between 10,000 and 14,000 persons begin post-exposure treatment in many of the approximately 400 hospitals in the country. The annual death toll is between 100 and 400 registered cases. This may be due, in part, to an unusually high rate of exposure to biting rabid animals. But even if this assumption is correct, it does not fully explain the high number of rabies casualties. In view of the high efficacy of modern post-exposure treatment, nearly all human rabies cases must be considered as failures of the medical system; the correct treatment was not applied, or not applied in time. The appropriate treatment may not be universally available (spatially, temporally, socially or economically), or the appropriate treatment is not in compliance with traditional (religious) beliefs. It is also possible that the necessity of the appropriate treatment is not recognised because other treatments are considered equivalent or superior, or because the disease entity is not recognised (e.g. rabies and tetanus are considered identical). Popular or traditional disease classification affects the selection of medical services (for a West African example and short literature review, see 75).

Information has been collected in several areas of Buddhist Sinhalese Sri Lanka on the following:

- frequency of exposure
- the nature of post-exposure treatment
- the nature of the treatment undergone by people who subsequently died of rabies
- the level of knowledge of the disease among the population.

Those interviewed were asked if they or any member of their household had been bitten by a dog in the previous twelve months and, if so, what kind of treatment had been applied. Depending on the area, between 1% and 12% of the population had experienced dog bites. Some of those bitten were treated for the injury only, while others received prophylactic anti-rabies treatment. In seeking treatment to heal dog bites and provide protection against rabies, a bitten Sinhala patient may choose from among folk medicine, exorcism, Ayurvedic medicine and Western medicine (14, 68, 93, 123, 146, 160, 163). Dog bites are often treated with herbal medications alone. For severe injuries, most Sinhala patients visit several specialists, including a Western physician and the Sinhala rabies healer. The Western physician in Sri Lanka has a choice between European tissue culture vaccine and locally-produced goat brain vaccine. The latter is of questionable potency and safety. Tissue culture vaccine is available only to those patients able to afford it (for a short time, tissue culture vaccine was also provided through the public health system). Since treatment with goat brain vaccine is painful and of uncertain success, many Sinhala patients prefer to use traditional methods of care alone.
The concepts and practices governing health care in Sinhalese Sri Lanka continue past traditions and include the Western medicine introduced by the British (146). When resorting to curers, Sri Lankan patients may apply strategies similar to those of patients in southern India (15). Many Sinhalese resist the idea that diseases are caused by germs. The agent which a rabid animal transmits is considered to be a toxin, and the disease is diagnosed and treated as an intoxication similar to a snake bite (64). Ayurvedic concepts of humoral disorders provide the fundamental principles for traditional Sinhalese treatments (119), although they are not free from shamanistic or magical aspects, which are at least partially in accordance with Buddhist religion (93). In all traditional treatments recorded in this study, offerings to a supernatural power, spells of exorcism and/or protective amulets formed an essential part. These transcendental and spiritual aspects are completely lacking in the post-exposure treatments which a patient receives in a government hospital. Traditional medical systems are more holistic than Western medicine and may therefore be psychologically and culturally more acceptable.

CONCLUSIONS AND REMARKS ON DOG RABIES CONTROL

Dogs are kept and/or tolerated in very large numbers in most human societies. This abundance cannot be explained by the economic usefulness of these animals, which is somewhat limited. The tolerance granted to dogs must find an explanation in processes of socialisation and psychology. Cultural practices determine the level of supervision of the social interactions of dogs and access to resources (food, water, shelter and mates). It is assumed that high-density dog populations permit the occurrence of enzootic canine rabies; but this is not very well documented. There are grounds for suspecting that the disease in dogs may not always exist independently of wildlife rabies. However, there is no doubt that rabid dogs are the major source of human infection. The widespread occurrence of human rabies is due not only to the frequency of exposure, but also to the failure to apply proper treatment after bites from rabid animals. In some areas, it might be more cost-effective to bring dog rabies under control than to treat cases of human exposure. Eradication programmes must take into account the biology of the target species. If the target species is the domestic dog, cultural constraints imposed by the human population must also be considered (150).

The WHO (155) and the World-wide Society for the Protection of Animals (158) have issued comprehensive guidelines for dog rabies control and dog population management. Both documents give detailed guidance on the planning and management of control programmes, legislation and techniques for the execution of local programmes. The contents of these documents cannot be reiterated here; however, a few details can be mentioned.

Taking the cost and benefits of a campaign into consideration, it can be suggested that the goal of such a campaign should be disease eradication, rather than a temporary reduction of the incidence rate. The most economical means for achieving this goal is through mass vaccination. There is a need for comprehensive national plans, rather than temporary, local measures. These plans must identify a goal and take account of national structures and resources. Effective intersectoral cooperation is also necessary. In the past, international organisations (WHO, the Food and Agriculture Organisation
of the United Nations [FAO] and the Office International des Epizooties [OIE]) have provided training courses in programme planning and management, and logistics. It can be expected that these programmes will continue in the future, and they could be usefully supplemented by training administrators and organisers in population biology and epidemiology, to increase understanding of the consequences of these campaigns. Pilot projects may help in assessing the following:

- accessibility of dogs
- possible means of cooperating with local residents
- avenues through which information and education may be provided.

Plans for large-scale operations, vaccination strategies and logistic aspects of programmes can then be adjusted to findings in the pilot phase. It is also suggested that some operational research be conducted in future programmes, in order to monitor campaign efficiency.

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Resumen: Aunque los perros son los carnívoros más extendidos y más numerosos, raros son los estudios sobre su papel en la cultura humana y sobre su impacto en el medio ambiente. Los autores abarcan estos temas en el contexto de la rabia canina.

Para comprender la epizootiología de la rabia canina es necesario tener en cuenta la ecología y la biología de las poblaciones caninas. Una serie de datos sobre las poblaciones caninas, reunidos en el Nepal, Sri Lanka, Suiza y Túnez han sido analizados en relación con los distintos hábitats, culturas, estratos sociales de las poblaciones humanas y con las diversas situaciones epizootiológicas existentes.

En Suiza (y Europa occidental en general), la rabia se mantiene y propaga a través de los zorros rojos. La escasa prevalencia de la rabia en los perros se puede explicar por las restricciones impuestas al vagabundeo de los perros y por la alta tasa de vacunación. En las demás regiones estudiadas, los perros son apenas objeto de vigilancia y sus densidades de población son lo suficientemente altas como para permitir que se mantenga la rabia, aunque cabe preguntarse si la rabia canina puede existir independientemente de un reservorio en la fauna salvaje. La ausencia de vigilancia de los perros, las altas tasas de exposición y diversos factores culturales pueden dar lugar a un alto índice de mortalidad por rabia en el hombre. No obstante, la posibilidad de acceso a los perros en esas regiones es suficiente para su vacunación, y programas de control correctamente aplicados podrían dar buenos resultados.


