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Wildlife Rabies and Urban Expansion:
Environments of Risk in Ottawa-Carleton

by

Carolyn Anne Fielding
B.Sc.(Hons.), McMaster University

A thesis submitted to the
Faculty of Graduate Studies and Research in partial
fulfilment of the requirements for the degree of
Master of Arts

Department of Geography

Carleton University
Ottawa, Ontario

September 1986

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Abstract

The spatial distribution of red foxes and striped skunks submitted to Agriculture Canada for rabies diagnosis is correlated with the land use characteristics of the urban and near-urban region. The environments of vector/human interaction, and therefore possible human exposure to rabies, are identified. Urban areas of risk are generally restricted to the periphery while the rural region is, by far, the environment of highest risk, especially those areas dominated by mixed non-intensive agricultural use. The land use and population changes associated with urban growth are shown to promote the risk of human exposure to rabies through the provision of vector habitat and the increase of human population in the risk environments. The cyclic nature of rabies incidence suggests the RMOC is due for a fox rabies outbreak and thus the compulsory immunization of cats and dogs is recommended.

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CHAPTER ONE

Rabies Exposure and Urban Growth: The Hypotheses

1.1 Introduction and Purpose

Few studies have considered the impact of the growth of large urban centres on wildlife populations. Those that have concentrate on the negative aspects of consumption of the habitats of endangered species and the increased proximity of humans to the habitats of timid animals (Real Estate Research Corporation, 1974; Warren and Rump, 1981). Many species, however, can tolerate the presence of man and thrive in the environments his activities create, including those which support rabies epidemics (Kappus et al., 1970; Bigler et al., 1973; Toma and Andral, 1977; Hassel, 1982; Meredith, 1982; Nicholls and Davies, 1982; Beck, 1984; Rosatte, 1985 c; d). Is it possible, then, that the land use changes induced by urban growth have provided habitats for vector species close to, or within large human population centres thereby increasing the risk of human exposure to rabies?

The purpose of this study is to identify the land uses supportive of Ontario's two main rabies vectors, the red fox (Vulpes vulpes) and the striped skunk (Mephitis mephitis), and to determine if urban growth has increased the risk of human exposure by encouraging an increase in these uses.

1.2 Hypothesis One

The preferred habitat of the red fox and striped skunk is of mixed agriculture interspersed with woodlands - typical of rural Ontario (Tinline and Pond, 1976; University of Guelph, 1980; Johnston and Voigt, 1982). The fringe-habitat this heterogeneous landscape creates provides shelter, hunting grounds and suitable denning sites. Audy (1959) states that such "patchwork" vegetation must be considered an ecosystem in itself and "a single square mile of mosaic vegetation may contain miles of fringe-habitats." It can, therefore, be appreciated that it is the configuration or pattern of the preferred land uses, rather than the areal extent, that determines the relative suitability of an area as vector habitat and that a measure of this suitability may be given by the amount or linear length of those "edge-terrains" created by these land uses. Presumably, the more fringe, the greater the carrying capacity of the area.

Of diseases in general, Audy (1958), also, states that:

... the parasite-pattern alone gives a great deal of information about the habitat and habits of the host which have largely decided that particular pattern

and, although the reported incidence of rabies is thought to represent only a small percentage of the actual cases (Verts and Storm, 1966; Prior, 1969; Lewis, 1972; Toma and Andral, 1977; Bacon and Macdonald, 1980), Meredith (1982) states:

...data on rabies if collected over a sufficiently long period to minimize or eliminate error, will indicate both population density, and by extrapolation, suitability of habitat.

Furthermore, Hayles and Dryden (1970) believe that the distribution of wildlife rabies over time may point out related topographical features. Thus the first hypothesis of the study states that within the "rural" (natural) environment, the length of the preferred type of "edge-terrain(s)" (as characterized by land use) will be positively correlated with the incidence of rabies (submissions) as both variables should reflect habitat suitability. The testing of this hypothesis should identify the rural land uses supportive of the vectors and may prove length of edge-terrain to be a useful measure of relative vector population density and, thus, susceptibility of an area to a rabies outbreak.

1.3 Hypothesis Two

Within the urban environment certain land uses (such as parklands and institutional grounds) may serve as reservoirs of wildlife. Rosatte (1985 a; b) for example, notes the prominence of skunks within Metropolitan Toronto and identifies greenspaces, as well as many man-made features as serving as foraging and denning sites. Furthermore, access from the outlying rural region into the city may be channelled by linear service routes such as transportation and utility corridors which typically "double" as greenspace.

Thus, the second hypothesis states that within the urban environment itself, due to the nature of the land use(s); and because it is in close proximity to concentrations of human population, areas of "high-risk" of exposure to rabies exist and

are, again, identifiable through submission records. Just how urban growth may be a factor in human exposure is subsequently postulated under both hypotheses.

1.4 Urban Growth

The intensity of influence of an urban centre on its region is a function of many factors but is generally accepted as decreasing with distance from the city boundary and extending at least to the limit of the 1-hour commuting distance (Troughton, 1976; Gertler and Crowley, 1977; Russwurm, 1977 a; b; Yeates and Garner, 1980; McCuaig and Manning, 1982). This region will be referred to as the "zone or sphere of urban influence." Representing a transition zone between the built-up city and the truly rural environment beyond (Russwurm, 1977b) it is characterized by a large exurbanite population and scattered non-farm development and urban-oriented activities.

The growth of large North American cities is characterized by sprawl defined as "the haphazard conversion of rural land use to more urban uses" (Coleman, 1978). As a consequence of such land use change, pressures are exerted on the surrounding environment, and it is generally acknowledged that, within the zone of urban influence, fragmentation and abandonment of farmland occurs and active agriculture is reduced and replaced by an increase in idle land and the passive use of farmland (Troughton, 1976; Gertler and Crowley, 1977; Russwurm, 1977a; Coleman, 1978; Bryant and Russwurm, 1979; McRae, 1981). Thus, surrounding the city, superimposed on the original

agricultural land use patchwork is further fragmentation, effectively increasing the amount of "fringe" or "edge-terrain" - a direct response to urban growth. If hypothesis one is supported then the corollary is that as urban sprawl promotes an increase in the length of edge-terrain, man may have created an increase in the potential risk of his own exposure to rabies.

Furthermore, within the city itself, urban growth stimulates a demand for greenspace (both parkland and natural environment areas), institutional facilities, new residential areas and service corridors (such as transportation and hydro routes) (Troughton, 1976; Bryant and Russwurm, 1979). If, as hypothesis two suggests, it is found that any of these land use types support vector species or provide them with access to the urban centre from the rural surrounds, then one can, again, conclude that through urban growth man may have increased his risk of rabies exposure.

The two hypotheses will be tested in the Regional Municipality of Ottawa-Carleton (RMOC), located in Eastern Ontario (Figure 1).

1.5 The Regional Municipality of Ottawa-Carleton

The RMOC supports the land use change characteristics outlined in the previous scenario of urban growth. An agricultural area surrounding a growing urban complex, urban-oriented uses are consuming rural land at an increasing rate. Between 1961 and 1971, 27.8 hectares of land were consumed for urban uses for each population increase of 1000

FIGURE 1 THE LOCATION OF THE REGIONAL MUNICIPALITY OF OTTAWA-CARLETON

people. Between 1971 and 1981 this rate increased to 64.8 hectares (RMOC Planning Dept., 1982). The Region, consequently, continues to suffer the effects of sprawl (Coleman, 1969; 1978; Mayo, 1976; German, 1979). Indeed one reason for the establishment of the N.C.C. greenbelt (1958-1965) was to counter sprawl and preserve agriculture (Coleman, 1969). Mayo (1976), however, states that this was unsuccessful and Coleman (1978) believes it ultimately failed to preserve the rural surrounds and actually encouraged sprawl characteristics over a more extensive area.

Characterizing the Region, Coleman (1978) concluded that much of the rural area suffers from a "chronic excess" of idle and derelict land, "unnecessary land disuse", farm abandonment and fragmentation and a decline in productive farmland as a result of the pressures of urban growth and non-farm development. The urban environment, likewise, suffers from an excess of idle land but also supports a heavy complement of institutional lands and greenspace as a consequence of its status as the nation's political capital (Coleman, 1969; Mayo, 1976). Furthermore, the growth of satellite communities (especially within the past 15 years) has spurred an increased need for service corridors and allowed the extension of sprawl characteristics further afield (Coleman, 1978; Wright, 1978; German, 1979; RMOC Planning Dept., 1984b; 1985).

The Regional Municipality of Ottawa-Carleton, therefore, provides a suitable environment for the testing of both hypotheses.

1.6 Selection Criteria

1.6.1. The Study Area

The Regional Municipality of Ottawa-Carleton was chosen as the study area for several reasons;

- a) as shown, it supports and promotes the land use characteristics hypothesized to be conducive to the red fox and striped skunk
- b) the Official Plan of the Region ensures the maintenance and possibly the extension of these characteristics as it calls for an increase in rural non-farm development and promotes urban expansion outside the greenbelt
- c) it is large enough that, although entirely within the 1-hour commuting limit (loosely defined as 70-80 km from the urban centre (Troughton, 1976; Gertler and Crowley, 1977; Ruaswura, 1977a)), it supports a range of rural environments under varying degrees of influence from urban sprawl
- d) it does not practise effective rabies control as its policy of "prevention" consists solely of "education" and post-exposure treatment (RMOG Health Unit-Fifteenth Annual Report, 1983).
- e) it is the location of Agriculture Canada's Animal Disease Research Institute (ADRI) and, thus, the submission of suspect rabid animals should not be discouraged by the increased costs associated with delivering specimens from greater distances and
- f) it represents an area of rabies persistence and exhibits the classic 3-4 year cycle of incidence (Voigt and Tinline,

1982) indicative of a supply of excellent vector species habitat (as discussed in Chapter Two);

1.6.2 The Spatial Scale

The study was conducted at the regional/county level as;

- a) the Region/County is the level of government responsible for Public Health
- b) the investigation of a larger area would increase the amount of data unmanageably while reducing the scale of consideration of the landscape characteristics thereby creating a reduction in accuracy and reducing the potential quality of the results
- c) suspect animals submitted to ADRI are identified by county, thus simplifying data acquisition and
- d) the Region or County represents a relatively homogeneous area with respect to distance to the diagnostic laboratory, and perception or education of the population towards the disease as Marx (1966, as cited in Smart and Giles, 1973) and Walker (1969) suggest that the local media have an important influence on the population's awareness of the problem of rabies.

1.6.3 The Temporal Scale

The time period considered is July 1, 1970 to June 31, 1985.

This was chosen because:

- a) the Regional Municipality of Ottawa-Carleton was formed in 1969, thus providing a uniform information source for the study area and period.

- b) prior to 1970 submissions of suspect rabid animals to ADRI were not listed with reference to county, making locations less accurate and their reconstruction too time-consuming and
- c) the annual rabies cycle does not follow the calendar year, but (allowing for the delay in disease expression due to the incubation period) is more accurately represented by the period of July 1 to June 30.

1.7 Assumptions

The development of the hypotheses requires that certain assumptions be made. They are:

- a) that relative vector population densities are determined by the relative quality of the habitat
- b) that the better the quality of habitat, the greater the vector population density and thus the greater the potential for human/wildlife contact
- c) that the pattern of disease submission cases (for the given time period) adequately reflects the relative suitability of an area as a vector species habitat
- d) that the entire Region is represented in the rabies submission data and
- e) that each submitted case is equally weighted in value whether representative of a period of animal migration or settlement, or a peak or low incidence year.

1.8 Study Limitations

There are three main limitations to this study. Initially, as rabies submission data are a function of human intervention, only environments with known cases are included in the data set. Thus, it is possible that certain high vector species-density landscapes may be over-looked or underrated due to the lack of human presence in those areas. Furthermore, the seasonality of human outdoor activity may also promote this problem. It can be argued, however, that it is the environments of human (and domestic animal) contact that are of prime concern with respect to the health threat of rabies and, thus, it is precisely these environments which must be identified. The value of these data for use in control schemes, however, is reduced as effective rabies control must be practised in high vector population density habitats rather than those representative of high human/wildlife contact. It is hoped, however, that the collection of data over several years will help reduce the risk of environment misrepresentation.

Secondly, due to the very slow nature of land use change, the relatively short period of the study and the fact that rabies is a fairly recent phenomenon in Ontario, the penetration of wildlife, and thus wildlife diseases, into "man's environment" cannot be shown but must initially be assumed and, indeed, this is the main point of the study. If land use and rabies data existed for a period prior to the onset of rapid urban growth, a comparison of the distribution of the rabies cases may have shown a measurable increase in the number of

human contacts having occurred within the region where man had altered the landscape. As this is impossible, one must be satisfied with a statement that the environments created by urban growth are capable of supporting rabies-carrying species and thus, being created in close association with large numbers of people, they may promote a higher risk of human exposure.

Finally, the study assumes that wildlife habitat can be described based solely on the land use characteristics of a region. It does not acknowledge the possible influence of factors such as slope, soil or vegetation type, inter-species competition for resources or the presence of enemies, all of which may have significant influence on the quality or suitability of habitat.

The study, therefore, has some major shortcomings mainly due to the limited nature of the data available. It is hoped, however, that it may prove useful to rabies control schemes through the identification of high vector density environments. Furthermore, the study may serve as a preliminary investigation for future more comprehensive research into the impact of man's activities on wildlife populations.

1.9 Study Organization

This chapter has introduced basic concepts and has attempted to synthesize the seemingly unrelated ideas of urban growth, wildlife habitat and human exposure to rabies.

Chapter Three elaborates on the methodologies used - the acquisition and organization of both submission and land use

data, the testing and analysis procedures and the problems encountered and concessions made. Chapter four discusses the results, while chapter five presents the implications for control and recommendations for further study. First, however, it is necessary to understand rabies itself and its status in Ontario. Hence Chapter Two consists of a more detailed discussion of rabies - the virology and ecology of the disease, the vectors involved in Ontario and how habitat plays an important role in the support and maintenance of the disease.

CHAPTER TWO

Rabies: Occurrence, Characteristics and Epidemiology

2.1 Occurrence in Canada

Rabies, one of the oldest recorded diseases, was recognized in dogs by both Democritus and Aristotle (Sikes, 1970) and is even believed referenced in Babylonian writings of the 23rd century B.C. (Tierkel, 1959). Wildlife rabies, however, possibly masked by the more obvious threat of domestic animals, was not reported until the thirteenth century in wolves of Asia (Sikes, 1970). Today only the continents of Australia and Antarctica are free of endemic rabies (Walker, 1969; Wandeler, 1980).

In North America, rabies was initially recorded in Virginia in 1753 (Tierkel, 1959). It is believed to have existed well before European colonization, however, as symptoms are recounted in Canadian Inuit folklore, possibly having arrived via the Bering land bridge 30-75,000 years ago (Winkler, 1975). Vampire bats, also, were recognized to be transmitting a "rabies-like" disease to cattle and man in 16th century Central America (Tabel et al., 1974). The lack of interaction between bats and carnivora observed today, however, tends to refute the theory of diffusion of rabies to North America by migrating bats (Beuregard and Steward, 1964; Winkler, 1975). By the early 1800s the disease was well established in the eastern and central United States and was believed endemic in the Canadian arctic (Tabel et al., 1974; Winkler, 1975; Nicholls and Davies, 1982).

The first confirmed cases of the disease in Canada were two recorded incidences of human rabies - the Governor-in-chief of Canada in 1819, and a man from Quebec City in 1839 (Tabel et al., 1974; Mutton, 1982). Both were believed exposed to rabid dogs. Rabies did not officially reappear until 1905 when a series of sporadic outbreaks began across the country, the majority of which were directly attributable to contact with dogs imported from the United States (Tabel et al., 1974).

Until 1945 the dog was the main vector of rabies in Canada (Tabel et al., 1974). In the late 1940's, however, a major epidemic originated amongst arctic foxes (Alopex lagopus) and grey wolves (Canis lupus) in the Northwest Territories and spread southwards, eventually involving all provinces from British Columbia to New Brunswick. The disease migrated along the coastlines of Hudson Bay and James Bay and by 1956 was introduced into Southern Ontario via Quebec by the red fox (Johnston and Beaugregard, 1969; Johnston, 1970; Tabel et al., 1974; Webster et al., 1974; Nicholls and Davies, 1982) (Figure 2). In 1958 Ontario experienced a rabies "explosion" with over 2000 diagnosed cases, the highest ever for one province. The red fox represented approximately 50% of these cases (Tabel et al., 1974). The epidemic eventually died out except in Southern Ontario and adjacent parts of Quebec where the disease remains endemic (Johnston and Beaugregard, 1969). Rabies is again, however, being reported in New Brunswick and the north eastern United States (Johnston, 1970).

FIGURE 2 THE EPIDEMIC SPREAD OF RABIES IN CANADA, 1945-1972

Strict regulations regarding strays and vaccination schemes have been successful in reducing the prevalence of rabies in the domestic dog (McLean, 1970). Sylvatic rabies, however, persists and maintains the disease. In northern Canada rabies remains endemic in the arctic fox while in Ontario persistence in the red fox and striped skunk has continued since 1958. In the Prairies, skunk rabies is believed to be a recent extension of the north-central United States endemic skunk-rabies area (Tabel et al., 1974; Gunson et al., 1978). Since 1957 several species of bats have been found rabid in several provinces, but cases have been few and are generally believed unrelated to "terrestrial" rabies (Tabel et al., 1974). Figure 3 shows the distribution of fox and skunk rabies in Canada for an average year.

2.1.1 Southern Ontario

Southern Ontario supports the highest incidence of rabies in North America with over 1400 cases diagnosed each year (Table 1). The red fox accounts for nearly 50% of these cases while the striped skunk adds 15 to 20% (Johnston and Beauregard, 1969; Lawson et al., 1982; Tinline et al., 1982; Rosatte, 1985c; Voigt et al., 1985). Wildlife species account for 60-70% of all reported cases; pets 10% and livestock 30% (Tinline et al., 1982; Ontario Ministry of Health, 1985). Over 80% of human exposures to rabies, however, result from contact with domestic animals (Walker, 1969; Toma and Andral, 1977; Honig, 1985) and

FIGURE 3 THE DISTRIBUTION OF FOX AND SKUNK RABIES IN CANADA 1978

(Agriculture Canada)

Table 1

Confirmed Ontario Rabies Cases, 1970-1984

Year	Wildlife	Livestock	Household Animals	Total
1970	840	519	166	1525
1971	811	450	150	1411
1972	1269	712	208	2189
1973	718	519	135	1372
1974	785	634	157	1576
1975	1129	730	157	2016
1976	819	440	144	1403
1977	786	511	140	1437
1978	1007	392	120	1519
1979	1037	332	131	1500
1980	1036	359	117	1562
1981	1160	436	129	1736
1982	1645	456	180	2281
1983	1466	377	145	1988
1984	1069	278	103	1450

(Ontario Ministry of Health, 1985)

every year over 1000 people in Ontario receive post-exposure treatment (University of Guelph, 1980). From 1980 to September of 1985, however, over 10,000 individuals were treated for possible rabies exposure (Honig, 1985; Ministry of Natural Resources, 1985c) (Table 2).

In addition to the health hazard, Ontario's sylvatic rabies also represents an economic burden. The cost for vaccinations (human and pet), testing and reporting services, compensation for livestock loss and research is estimated to be \$15-20 million annually (University of Guelph, 1980; Tinline et al., 1982; Johnston and Voigt, 1982; Voigt, 1983; Rosette, 1985d; Voigt et al., 1985).

In Southern Ontario, all counties are susceptible to periodic increases in the incidence of rabies although intensities and frequencies of increase vary (Johnston, 1982; Watt and Johnston, 1984). The eastern counties and those bordering Lake Huron and southern Georgian Bay exhibit a persisting problem (Nicholls and Davies, 1982). As observed also in Europe (Toms and Andral, 1977; Bacon and Macdonald, 1980; Wandeler, 1980; Anderson et al., 1981; David et al., 1982) incidence within a region seems to follow cycles, peaking every three years in areas of favourable fox habitat and every four to five years in less suitable regions (Johnston and Beauregard, 1969; Tinline et al., 1982; Voigt, 1983).

The persistence and cyclical nature of rabies can be related directly to the characteristics of the disease in the species

Table 2

Vaccine Distributed by the Government Pharmacy
for Post - Exposure Treatments

1970	1164
1971	960
1972	1252
1973	1020
1974	974
1975	1050
1976	935
1977	957
1978	816
1979	1002
1980	1096
1981	1833
1982	2402
1983	2481
1984	2027

(Ontario Ministry of Health, 1985)

affected and the ecology of those same species (Winkler, 1975; Wandeler, 1980).

2.2 The Characteristics of the Disease

2.2.1 The Virus

Rabies is caused by a virus belonging to the family Rhabdoviridae. Although no immunologically differing strains have been recognized (Tierkel, 1959; Sikes, 1970) different "strains" have been identified based on host associations and experimental responses (Baer et al., 1977, as cited in Wandeler, 1980; Carey and McLean, 1983). The virus is sensitive to air exposure, temperatures greater than 56°C, ultraviolet radiation and pH lower than 3.0 (Tierkel, 1959; Sikes, 1970; Wandeler, 1980). The virus attacks the central nervous system (CNS) after travelling from the site of infection, via the peripheral nerves, to the brain. Replication is slow in tissue, but proceeds rapidly once reaching the nervous system (Macdonald and Bacon, 1980; Wandeler, 1980). Centrifugal migration from the CNS and replication in various non-neural tissues, including the kidneys, urinary system, esophagus and lungs, may occur but the virus demonstrates a particular affinity for the salivary glands (Sikes, 1962; Parker and Wilsnack, 1966; Debbie and Trimarchi, 1970; Winkler, 1975; Wandeler, 1980). Hence bite transmission is the main and most efficient means of conveying the virus in nature (Kaplan, 1969; Preston, 1973; Tome and Andral, 1977; Wandeler, 1980; Carey and McLean, 1983).

2.2.2 Transmission

Successful bite transmission is dependent on the presence of sufficient quantities of virus in the saliva of the infected individual (Tierkel, 1959). This occurs in 54-90% of the cases, being more prevalent in the fox and skunk cases than dog (Tierkel, 1959; Sikes, 1962; Parker and Wilsnack, 1966; Wandeler et al., 1966 as cited in David et al., 1976). Although rodent species can contract the disease and emit virus-laden saliva (Winkler et al., 1972; Winkler et al., 1976), these species are likely to be so quickly overcome by the virus itself or a predatory attack that they are of no consequence to the spread of rabies (Winkler et al., 1972; Tabel et al., 1974; Wandeler, 1980).

Non-bite transmission routes do exist although their epidemiological importance is uncertain (Ramsden and Johnston, 1975; Charlton and Casey, 1979). Experimental infection of wild carnivores (including the red fox and striped skunk) via ingestion of infected rodent species, using both "fixed" (laboratory refined) and "street" virus isolates, has been well documented (Bell and Moore, 1971; Ramsden and Johnston, 1975; Charlton and Casey, 1979). The ability of the virus to remain viable in animal tissue for short durations at room temperature (Debbie and Trimerchi, 1970) and for lengthy periods when kept frozen or at very low temperatures (Tierkel, 1959; Bell and Moore, 1971; Wandeler, 1980) enhances the possibility of oral infection of scavengers (Ramsden and Johnston, 1975; Carey and McLean, 1978).

The presence of virus in non-neural tissue and organs, such

Table 3

The Occurrence of Rabies Antigen in Tissues of
the Red Fox

Specimen Tissue	1	2	3	4	5	6	7	8	9	10	11	12	Total
Brain	+	+	+	+	+	+	+	+	+	+	+	+	12/12
Spinal Cord	+	+	+	+	+	+	+	+	+	+	+	+	12/12
Salivary Gland	+	-	+	+	+	+	+	+	+	+	+	+	11/12
Esophagus	+	+	+	+	+	+	+	+	+	+	+	+	12/12
Stomach	-	-	-	-	+	-	+	+	+	+	-	+	6/12
Small Intestine	+	-	-	-	-	-	-	+	+	-	-	-	3/12
Large Intestine	-	-	-	-	-	-	-	+	-	-	-	-	1/12
Thyroid	+	-	ND	+	-	+	+	+	-	-	-	-	5/11
Lung	+	-	-	-	+	+	-	+	+	+	-	+	7/12
Heart	+	-	+	+	+	+	+	+	-	-	-	+	8/12
Adrenal	+	-	+	+	+	+	+	+	+	+	+	+	11/12
Kidney	+	+	+	+	+	+	+	-	+	+	-	+	10/12
Kidney capsule	+	-	+	+	+	-	+	-	+	+	-	+	8/12
Ureter	+	-	+	+	-	-	-	-	+	-	-	-	4/12
Bladder	+	+	+	-	+	+	+	+	+	+	-	+	10/12
Prostate	+	-	+	-	+	+	-	-	+	+	+	-	7/9
Urethra	+	-	+	-	+	-	-	-	-	+	+	-	5/9
Uterus	-	-	-	-	-	-	-	-	-	-	-	-	0/3
Ovary	-	-	-	-	-	-	-	-	-	-	-	-	0/3
Testicle	-	-	-	-	-	+	-	-	-	+	-	-	2/9
Fetus	-	-	-	-	-	-	-	-	-	-	-	-	0/1

(Debbie & Trimarchi, 1970)

as the esophagus, salivary glands and urinary tract, may provide additional routes of infection (Debbie and Trimarchi, 1970; Carey and McLean, 1978) (Table 3). The possibility of aerosol infection has generally been accepted since originally demonstrated by Constantine in 1962 and may be an important transmission route in species, such as the skunk and raccoon, which practise communal winter denning. Ramsden and Johnston (1975) and Charlton and Casey (1979) believe such nasal infection may occur more readily than oral, as passage of the virus is more directly to the brain.

Organs and tissues of excretion and secretion such as the intestine, urinary tract and salivary glands, if infected, may also allow rabies transmission in species where behaviours such as licking, sniffing and scent-marking are practised (Debbie and Trimarchi, 1970; Carey and McLean, 1978; Howell 1982).

Transmission via milk and transplacental routes is believed possible although test results have been inconclusive (Tierkel, 1959; Gough and Niemeyer, 1975; Wandeler, 1980). Bite transmission, however, remains the most important route of rabies infection in nature.

2.2.3 Susceptibility

All mammals are susceptible to rabies but not equally so. Certain species may be more resistant than others while certain "strains" of virus may have differing pathogenicities for different species (Tierkel, 1959; Constantine, 1966; Parker and Wilanack, 1966; Constantine et al., 1968; Bell and Moore, 1971;

Ramsden and Johnston, 1975).

The fox is particularly susceptible to rabies (Parker and Wilsnack, 1966; Winkler, 1975; Black and Lawson, 1980; Wandeler, 1980). Sikes (1962; 1970) using a fox virus isolate, has shown that doses successfully infecting foxes had to be increased 100-fold before skunks contracted the disease. Furthermore, skunks emitted greater quantities of virus per volume of saliva than the fox, with the amount being sufficiently high to allow skunk infection but representing an overwhelming dose for the fox. Parker and Wilsnack (1966) found similar results.

Winkler et al. (1972) found grey squirrels and kangaroo rats to be more susceptible to bat isolates than other rodent species. Bell and Moore (1971) found cats more resistant than skunks to various orally administered "street" viruses (striped skunk and several bat isolates) although, they state, Kaplan (1969) found the opposite! They, nonetheless, offer this as an explanation for why cats do not seem to acquire rabies from the ingestion of bats. Furthermore, Conatantine (1966a; b) found variable results from carnivores exposed to a variety of bat rabies isolates and Ramsden and Johnston (1975) concluded that differences in infectivity of various "strains" may account for the unpredictability of rabies contraction.

Whatever the mechanism, susceptibility differences between species do seem to exist. These differences have often been offered as explanations for the sometimes observed species-discreteness of rabies areas and cycles (Sikes, 1962; 1970; Parker and Wilsnack, 1966; Verts and Storm, 1966; Kaplan, 1969;

McClean, 1970; Winkler, 1975). In North America, for example, fox and skunk rabies overlap in Ontario and the east-central United States. In the prairie regions, however, skunk rabies persists in the absence of fox rabies while raccoons, previously only considered as incidental hosts, have experienced rabies epidemics in the southeastern states since the 1950's - the only known region of raccoon rabies. General avoidance and slightly differing habitat preferences may also be factors to consider (Verta and Storm, 1966; Winkler, 1975).

2.2.4 Latency, Abortive and Non-fatal Infections and Recovery

Rabies is not a uniformly fatal disease. Latent and abortive cases are believed to occur in nature but, in general, once the signs appear, death is imminent (Wandeler, 1980).

Abortive infections have occurred in laboratory tests from Pasteur's time to present (Bell, 1975). They may represent cases of insufficient dosage or virulence, local acidity or oxygen deficiency due to swelling, high temperatures (fever), or the presence of an inhibiting substance preventing virus replication and/or spread to the CNS, or antibodies from previous rabies or rabies-related virus exposure (Bell, 1975; Wandeler, 1980; Howell, 1982; Carey and McClean, 1983). The presence of neutralizing antibodies (NA) in individuals not displaying symptoms is considered, by some, evidence of abortive cases. Bell (1975), however, states that only high NA titre represents abortive cases and Wandeler (1980) and Carey and

McLean (1983) caution against considering these individuals as immune. Naturally occurring abortive and immune cases, being very few, are not considered critical to rabies epidemiology (Sikes, 1962; Bell, 1975).

Latent rabies is often cited as an explanation for rabies recurrence but its actual existence in nature is questioned (Bell, 1975; Wandeler, 1980). Latency may result from the failure of the virus to move from the site of exposure (shown experimentally (Bell, 1975)) and may possibly be activated by stress or temperature increases such as follow hibernation (Parker and Wilanack, 1966; Hayles and Dryden, 1970; Mutch and Aleksuk, 1977; Wandeler, 1980; Howell, 1982). Wandeler (1980) and Bell (1975), however, state that latency may be mistaken for lengthy incubation periods, a quality characteristic of rabies in some species.

The presence of virus in the saliva, brain or other tissues, yet the absence of symptoms has often been stated as proof for non-fatal or carrier cases of rabies. Bell (1975), again however, cautions that virus may be present in the CNS and salivary glands before the onset of symptoms and individuals must, therefore, be held for observation to determine accurately their status - i.e. pre-symptomatic or actually non-fatal. Furthermore, no set criteria of visible rabidity exist as manifestations of the disease vary greatly. Thus the observation of "lack of symptoms" is subject to definition (Bell, 1975).

Actual recovery from clinical rabies is generally believed

impossible. Isolated cases, however, of recovery from paralysis have been documented - including one boy from Ohio. These are believed isolated instances and genuine cases of "luck" (Bacon and Macdonald, 1980). Johnson (1965 as cited in Bell, 1975), however, believes that the paralysis experienced in some rabies cases may not result from neurological cell damage inflicted by the virus, but rather from an "allergic edema" causing swelling of the brain and thus may account for the few documented cases of "recovery".

2.2.5 Incubation and Expression

The incubation period of rabies is extremely variable: rarely less than 10 days or more than 6 months for carnivorous species. Sikes (1970) states 2-12 weeks as the average duration under experimental conditions. Approximately 1 month for the red fox (Sikes, 1962; Parker and Wilanack, 1966; David et al., 1982), the average incubating period is much longer in the striped skunk, often extending up to 6 months (Parker, 1975; Parker and Wilanack, 1966). Captive skunks, however, have shown an average incubation period of approximately 40 days (Gough and Nieneyer, 1975; Gunson et al., 1978).

Duration of the expression of clinical rabies is, again, variable and often longer in the skunk than the fox. An average duration of 2-4 days in the fox and 4-9 days in the skunk is generally accepted (Sikes, 1962; 1970; Parker and Wilanack, 1966). The presence of virus in the saliva is greatest during the period of clinical symptoms (Sikes, 1970). It can, however,

be present several days prior to the onset of symptoms (Sikes, 1970; Parker, 1975; Winkler, 1975) often for 8 days or more (Parker and Wilsnack, 1966). This, together with the survival of the individual over several days of clinical symptoms, allows rabies transmission over a lengthy period.

The symptoms of rabies are, also, extremely variable and often there is a complete lack of signs (Sikes, 1962; Gough and Niemeyer, 1975). Generally, however, the disease is manifest in two forms - the furious, characterized by aggression, irritableness, restlessness, convulsions and progressive paralysis, and paralytic or dumb rabies, characterized by listlessness, incoordination, prostration and paralysis. Disease transmission is promoted through both these forms in the fox and skunk as aggression leads to bite transmission while dumb rabies still allows close contact enabling transmission via the non-bite routes such as aerosol infection during communal denning (Houseknecht, 1969; Preston, 1973; Parker, 1975; Bacon and Macdonald, 1981; Voigt and Tinline, 1982).

Daytime appearances, loss of fear of man and anorexia can generally be considered good indicators of rabies in foxes and skunks (Toms and Andral, 1977; Parker, 1977; Canadian Wildlife Service, 1978; Wandeler, 1980) and Sikes (1970) concludes that "the atypical is typical".

The variability in the expression of the disease, the length of incubation and clinical illness, and the individual's susceptibility to rabies may depend on many factors including dose, virulence, source and route of infection and the age and

physical condition of the individual (Sikes, 1962; Winkler, 1975; Wandeler, 1980; Carey and McLean, 1983). Thus the outcome of contact with an infected individual is uncertain. Furthermore, these variable characteristics of the disease make rabies unpredictable and difficult to control and, in association with the life cycles of the red fox and striped skunk, very well adapted to persistence.

2.3 The Ecology of the Ontario Vectors

Characterization of the rabies cycle necessitates not only an understanding of the disease, but also the life cycle and behaviour of the vector species. The flexible and adaptable red fox and striped skunk occupy a wide variety of habitats and thus population structure and resulting behaviour vary greatly between populations. This section will, therefore, describe the general characteristics shared by all populations and, where known, the details of the Southern Ontario populations will be given. It will become evident that certain aspects of the red fox and striped skunk lifestyles encourage the persistence of rabies.

2.3.1 The Red Fox

Habitat and Diet

The preferred habitat of the red fox is one of rolling, open fields interspersed with forests, streams and marshes (Toma and Andral, 1977; Canadian Wildlife Service, 1978; Voigt, 1981; Carey, 1982; 1984; Mutton, 1982). Active between dusk and dawn,

the fox beds down in thickets and heavy bush during the day. During the breeding season it occupies a den, usually an excavated squirrel or groundhog burrow, shallow cave or hollow tree, that is preferably situated on a slope with a clear view of the region (Tone and Andral, 1977; Canadian Wildlife Service, 1978).

Red foxes occupy overlapping home ranges, consisting of high use areas connected by a series of pathways, the size and shape of which varies depending on seasonal needs (Stora, 1965; Voigt and Macdonald, 1984). Overall size of the home range is a function of habitat suitability (Stora, 1965; Preston, 1973; Macdonald, 1980; 1982; Macdonald and Bacon, 1982; Voigt and Macdonald, 1984) and in Ontario varies between 6-9 km² (Voigt, 1983).

The diet of the largely carnivorous red fox consists mainly of rodents and other small mammals, but is supplemented by frogs, insects, birds, fruits and berries, and carrion depending on season and availability (Tone and Andral, 1977; Canadian Wildlife Service, 1978; Carey, 1982; Voigt and Macdonald, 1984).

Life Cycle

Ontario red foxes pair for life (Canadian Wildlife Service, 1978; Voigt and Macdonald, 1984) and mating occurs in January and February. Females are capable of reproduction within their first year, and in Ontario, Voigt and Macdonald (1984) state that very few vixens fail to breed (11% of yearlings, 1% of older vixens) - the lowest rate known (Voigt, 1983). A den is

established and young are born in late March/early April. Average litter size in Ontario is 7-8 vs. the world average of 5 and sex ratios of 1:1 are maintained into adult populations (Tone and Andral, 1977; David et al., 1980; University of Guelph, 1980; Voigt, 1983; Voigt and Macdonald, 1984). Both the male and female take part in rearing, and pups become increasingly independent. In September and October juveniles (and a few adults) disperse with the intent of establishing their own home range. Those that fail to do so die (David et al., 1982). Adult pairs may separate over winter if resources are scarce, but will reunite during the mating season (Canadian Wildlife Service, 1978).

Enemies of the red fox include the larger carnivores such as the wolf, coyote and dog, but also man (Canadian Wildlife Service, 1978). Trapping in Ontario takes a significant toll (Voigt and Macdonald, 1984), but it is rabies that is the main enemy of the fox. Foxes over 4 years of age are rare in Southern Ontario (Johnston, 1970; University of Guelph, 1980; Voigt, 1983).

Activity

Red fox activity is high during the mating season, but decreases during pup rearing. Adults are active near the den site, but increase their range as pups become increasingly independent. Activity is again high during the fall dispersal of juveniles. Initially, more males than females disperse, travelling not only farther, but faster and earlier; but by their second year, most females, too, have dispersed. The

highly mobile fox can travel great distances and straight-line movements up to 400 km have been recorded. Juvenile male dispersal in Ontario, however, generally ranges from 3-150 km, while female dispersal ranges up to 50 km (Voigt, 1983). Dispersal is not clearly understood as many foxes pass through excellent habitats without settling (Preston, 1973). Juveniles at this time, however, represent over 70% of the active population and thus contact is great as foxes inevitably trespass over established territories.

Behaviour

Red foxes are extremely tolerant of each other (Carey, 1982) and, although scent-marking is practised (Tone and Andral, 1977; Howell, 1982; Voigt and Macdonald, 1984), the overlapping of home range is accepted. Home range defense is not stringent but rather involves the continued harassment and chasing of the intruder by the male (Preston, 1975). The fox will fight only as a last resort (Canadian Wildlife Service, 1978).

Very little is known of the behaviour of rabid foxes or the reaction to them by healthy individuals. Macdonald and Bacon (1982) believe rabid foxes increase their hours of activity, and Anderson et al. (1981) believe they have higher contact rates. Wandering tendencies are debated, but Johnston (1970) states that their behaviour "probably leads them to situations in which they are killed otherwise there would be isolated cases of domestic rabies but no wildlife cases reported". Furthermore, he states an attraction for animal manure as an explanation for

the reporting of so many rabid individuals on farms. It is also generally believed that rabies is manifest equally in its two forms in foxes - i.e., 50% experience furious rabies; 50% paralytic (Johnston and Beuregard, 1969; Preston, 1973; Toma and Andral, 1977). This, however, is difficult to conclude as the nature of dumb expression may reduce the chance of human contact. The loss of fear of man, however, is the one behavioural change agreed upon.

2.3.2 The Striped Skunk

Habitat and Diet

The striped skunk, like the red fox, thrives in agricultural regions, preferring open areas of mixed forest and grasslands (Stora, 1972; Canadian Wildlife Service, 1978). Home ranges overlap and are about 3 km² for Ontario skunks (Voigt, 1983). The skunk, however, has become very adept at filling its needs within the urban environment (Rosette, 1985a; b; Voigt et al., 1985). Foraging mainly at night, daytime retreats are usually found near buildings, fencerows and waterways where disturbance by farm work is unlikely (Stora, 1972). Overwintering and maternity dens are generally underground in the abandoned dens of other mammals or under buildings and porches, but may also be found in stumps, culverts and rock or woodpiles (Stora, 1972; Canadian Wildlife Service, 1973; Gunson and Bjorge, 1979; Rosette, 1984; 1985c). Omnivorous, the diet of the skunk consists of small mammals (especially rodents), insects, larvae and plant matter (Canadian Wildlife Service, 1973).

Life Cycle

Communal denning is characteristic of the striped skunk with dens consisting of several females, often related, and one dominant adult male. Juvenile males usually must den alone. Females enter the den when temperatures reach 0°C while males remain active until -9°C (Canadian Wildlife Service, 1973). Skunks overwinter in a state of "semi-hibernation" with body temperatures decreasing, and feeding does not occur. Body weight may drop as much as 60% as the skunks remain underground often for over 120 days (Houseknecht, 1969; Mutch and Aleksiuk, 1977; Gunson and Bjorge, 1979; Schowalter and Gunson, 1982; Rosatte, 1985a). The number of skunks per den varies, often up to 20, but is believed to increase with latitude as an adaptation to colder climates (Gunson and Bjorge, 1979).

Breeding occurs in late February/early March just before or after emergence from the winter den. Males frequently mate with several females. Young are born in late April/early May and litter size averages 4-6 (Canadian Wildlife Service, 1973). Sex ratios of the litter are 1:1 but in adults favours the female (Bjorge et al., 1981). Adult males remain solitary over the summer while the female alone rears the young which become independent at 3 months of age. At this time (July, August and September), adult and juvenile dispersal occurs, with many juvenile females remaining with the adult female.

Activity

Overwinter activity is low as most skunks remain underground. Males, however, occasionally wander from the den, especially as the breeding season approaches. Activity of both sexes increases during the breeding season, and decreases again during spring and summer rearing when females remain near the den while males wander alone. Activity increases steadily into the autumn when dispersal occurs.

Adult females may remain within the same region for extended periods, but this does not mean they do not travel extensively (Bjorge et al., 1981). Adult males disperse farther than females while juvenile males must travel even further as they attempt to find a female den unoccupied by a male. Male dispersal to distances over 100 km have been reported. Average distances, however, appear to range 10-20 km (Gunson and Bjorge, 1979; Bjorge et al., 1981; Sargeant et al., 1982; Schowalter and Gunson, 1982). Activity again decreases in the period prior to overwinter denning.

Behaviour

Male skunks are generally intolerant of other males. Competition for dens and females often leads to conflict in autumn and spring. Furthermore, females are very intolerant of males during rearing, as males are often responsible for kit mortality (Sargeant et al., 1982). During the breeding season there is considerable antagonistic behaviour between males and females, and Varta (1967, as cited in Rosette, 1984) states that

biting often occurs as part of the ritual mate.

Verts (1967, as cited in Parker, 1975) states that rabid behaviour in skunks is most often manifest in the furious form. Parker (1975), however, disagrees, stating the signs are extremely variable. Gough and Niemeyer (1975) found very little antagonistic behaviour occurring in captive female skunks and their offspring into which a "rabies epidemic" was introduced. Storm and Verts (1966), radio-tracking a rabid female juvenile, found that although its movements were "somewhat aberrant during the last week of her life", its wanderings were of no greater distance than similar non-rabid skunks. Thus, rabid behaviour in skunks is even less understood than that of red foxes.

2.4 Rabies Cycles

Rabies transmission generally occurs within species rather than between. Contact with susceptible individuals is necessary for the maintenance of infectious diseases within a population. Contact rates depend on the social characteristics of the species but are also a function of population density and activity. The incidence and/or spread of rabies in fox and skunk populations reflects changes in both these factors (Houseknecht, 1969; Johnston and Beauregard, 1969; Prior, 1969; Lewis, 1972; Davis, 1974; Bogel and Abdussalam, 1975; Parker, 1975; Tome and Andral, 1977; Capay et al., 1978; Macdonald et al., 1981; David et al., 1982; Macdonald and Bacon, 1982; Sargeant et al., 1982; Showalter and Gunson, 1982; Tinline et al., 1982).

Fox and skunk population densities vary temporally and spatially. Spatially, densities vary with habitat suitability and thus "good" habitats support more individuals over smaller areas (Audy, 1958; Jennings et al., 1960; Hayles and Dryden, 1970; Storm, 1972; Bogel, 1976; Macdonald, 1980; Wandeler, 1980; Anderson et al., 1981; Carey, 1982; Hassel, 1982). Temporally, large litter sizes allow the population density to swell annually with susceptible juveniles (as they become active in late summer and early autumn), and "densities" effectively increase during communal denning of the skunk in winter. Longer term density changes occur in response to hunting pressures, prey cycles, climatic conditions and, of course, disease. Johnston and Beaugerard (1969) noted that Ontario rabies outbreaks were preceded by high populations. Indeed, threshold densities (at which epidemics are likely to occur), have been recognized in rabies epidemiology. These threshold levels, however, vary between populations; densities quoted as necessary to curtail fox rabies in Europe are values at which fox rabies persists in Ontario (Tinline et al., 1982).

Heightened activity such as experienced during dispersal and the mating season also promotes contact. Furthermore, the mobility of the fox and skunk and their innate tendency to disperse enhances the chance of possible infection over great distances.

Behaviour, too, may promote the spread of rabies. With the red fox, the tolerant nature results in the possibility of

multiple contacts that would otherwise not occur if aggressive "fights-to-the death" occurred (Carey, 1982). Furthermore, tolerance of trespassing removes the desire for avoidance, and thus contact is not actively averted. For the striped skunk, its aggressive nature does not promote a peaceful outcome when contact occurs.

Finally, susceptibility to disease may be a factor in the rabies cycle. Stressful periods occur annually with autumnal dispersal, winter hardships and spring-time parturition (Johnston and Beauregard, 1969; Preston, 1973; Carey, 1974; 1982; Webster et al., 1974; Macdonald, 1982). Stress may also be a factor over lengthier time periods, as overcrowding, harsh climatic conditions and resource shortages may increase a population's susceptibility to disease (Toma and Andral, 1977; Bjorge et al., 1981; Pool and Hacker, 1982). In Texas, for example, Pool and Hacker (1982) found that peaks in rabies incidence coincide with periods of water shortages. Although they noted the stress factor, they also argued that increased contact may have occurred due to increased competition for resources.

2.4.1 The Annual Cycle

2.4.1.1 The Red Fox

The incidence of fox rabies in Ontario is low in summer. At this time stress is at a minimum as resources are plentiful and activity is centred around the den, reducing the likelihood of contact with neighbours. In the fall, however, incidence

increases, coincident with juvenile dispersal, and is maintained throughout the winter (Johnston and Beauregard, 1969; Nicholls and Davies, 1982; Tinline et al., 1982). The delay in female dispersal may sustain the high percentage of susceptibles in the active population and thereby support the increased incidence over time. Indeed, Johnston and Beauregard (1969) reported a higher incidence of juvenile male rabies cases in the early fall, followed by an equal male/female ratio in January and February. The harshness of winter conditions may also contribute to the high incidence.

The activity associated with the January/February mating period may be responsible for the peak in incidence which occurs in March. Furthermore, the stress of parturition may be a factor, and Johnston and Beauregard (1969) believe hormonal changes in females may enhance susceptibility. Again, they found a higher incidence of rabid yearling females in March through June. From March, incidence steadily decreases to the summertime low as, again, activity is reduced due to the rearing of young.

2.4.1.2 The Striped Skunk

Similar to the red fox, the incidence of rabies in the striped skunk in Ontario is low in the summer when female activity is centered about the den, and males wander solitarily, generally avoiding each other. Incidence increases in the fall and peaks in December, possibly due to increased activity occurring with dispersal and denning preparation. Webster et

al. (1974) found this December peak to be composed equally of males and females, but over 60% were juveniles.

Incidence declines in January and February, as would be expected, due to denning. This, however, may be a period of rabies transmission via the non-bite routes, as contact in the communal dens is very close (Houseknecht, 1969; Parker, 1975). Incidence does not increase drastically in March, even though activity is high due to emergence from the den and mating, but does increase, however, in April, possibly representing the expression of over wintering transmission. Incidence then slowly decreases into the summertime low, with these late springtime cases possibly the expression of rabies transmission during the mate.

2.4.2 Long Term Fluctuations

As stated earlier, all Southern Ontario counties experience periodic increases in the incidence of rabies, although intensities and frequencies vary. Peaks in fox rabies incidence tend to occur every 3-5 years, and similar cycles have been observed in Europe (Bogel et al., 1976; Toma and Andral, 1977; Wandeler, 1980; Anderson et al., 1981; Bacon and Macdonald, 1981; David et al., 1982). These cycles, as with the annual cycle, can be understood through the examination of fox ecology.

Fox rabies outbreaks do not occur simultaneously throughout all areas of the province, but rather occur "out-of-phase". This phenomenon reflects varying population densities and helps ensure a constant supply of rabid individuals for re-infection

(Johnston, 1970). Areas in which the fox population density exceeds the threshold experience outbreaks. The result is a population crash so that in the following years, density in that area remains below the threshold level. The high reproductive capability and mobility of the red fox ensures rapid repopulation through the successful rearing of young and immigration (Toma and Andral, 1977; Wandeler, 1980; Anderson et al., 1981; Carey, 1982; David et al., 1982). Thus densities again exceed the critical threshold and reinfection occurs via outside juvenile dispersal. Voigt et al. (1985) modelled the Ontario situation and found ingressing foxes were necessary to maintain the cycle, and they state that, indeed, peninsular areas of Ontario have a lower "re-introduction potential", and do show lower incidences of fox rabies. Disease re-introduction has also been speculated as arising via a second vector species or as a result of reactivation of latent cases. Due to the lack of interaction between species and the believed rarity of latent cases, however, these routes are questionable.

The frequency of these cycles has been tied to habitat suitability in that areas of excellent habitat are more quickly and densely repopulated and thus support shorter cycles. Poorer regions exhibit longer (5-7 years) cycles. Similar conclusions have been reached in European studies (Bogel et al., 1976; Toma and Andral, 1977; Anderson et al., 1981; David et al., 1982).

It is generally believed that Ontario skunk rabies developed from a "spillover" of the late 1950's fox epidemic. The incidence of skunk rabies, however, does not display the same

obvious cyclical trends. Peaks and troughs do occur, but not with such strict regularity (Webster et al., 1974). In general, skunk rabies is less clearly understood than fox rabies, but Verts (1967 as cited in Webster et al., 1974) believes that factors other than density alone may affect incidence.

Lengthier incubation periods, shorter dispersal distances and aggressive behaviour may be important factors, and climate may have a greater impact than originally considered. For example, Voigt (1983) notes that the serious 1979-80 Ontario skunk rabies outbreak (where for the first time skunk cases outnumbered rabid fox cases) occurred over a mild winter when skunk activity might have been considerably greater over the winter.

Thus, the nature of the incidence of rabies in the red fox and striped skunk reflects characteristics of their respective ecologies, and given the characteristics of the disease, it is easy to see why the fox and skunk have become "successful" and persisting hosts.

2.5 Landscape Epidemiology

The landscape characteristics of a region play a major role in the rabies phenomenon in two ways. First of all, the nature of the region determines the density of vector species it is able to support and, therefore, the relative incidence of rabies and secondly, it influences the direction and route of possible epidemic spread.

Consider the density factor. As stated previously, population density of a species is largely a function of habitat

suitability. Areas of preferred vector habitat, therefore, would be expected to support higher incidences of rabies (Johnston, 1970; Carey, 1974; Bacon and Macdonald, 1980; Anderson et al., 1981; Meredith, 1982). Pool and Hacker (1982), for example, were able to associate specific biotic regions in Texas with fox and skunk rabies areas. These regions, obviously providing favourable habitat, were able to support adequate densities of the respective vectors and thus supported persistent rabies within the specific region.

Davis (1974) claimed the increased abandonment of farmland in Georgia between 1945 and 1950 promoted an increase in the incidence of fox rabies in that state as abandoned farmland provided excellent fox habitat. Similarly, Tinline and Pond (1976), in Ontario's Grey County, were able to find, at the township level, a significant relationship between the amount of unimproved land and the total cases of rabies reported.

Thus, these examples show how the characteristics of a region influence the relative incidence of rabies. Furthermore, as discussed earlier, the periodicity of the cycles of fox rabies reported in Ontario and Europe reflect, in the same way, the influence of the region's physical characteristics on rabies incidence.

The physiography of an area may also guide the spread of rabies by providing physical barriers or conduits that block or channel vector movement such as large rivers, lakes or mountain ranges (Jennings et al., 1960; Carey, 1974; Toma and Andral, 1977; Wandeler, 1980) or by providing directional regions of

continuous preferred habitat whereby high densities promote the directional spread of the disease. Such areas may include waterways, railway lines or valley systems (Carey, 1974; Tinline and Pond, 1976; Toma and Andral, 1977; Carey et al., 1978; Bacon and Macdonald, 1980; Cummings, 1982).

For example, Carey et al. (1978) found the epidemic spread of rabies in their Virginia study area followed a linear northeast-southwest pattern mirroring the orientation of the region's valley systems. Tinline and Pond (1976) concluded that the spread of rabies into Grey County in the late 1950's was guided by the linear configuration of woodlands, dividing farms, which ran in an east-west orientation paralleling the road network. These two examples demonstrate the influence that a region's physical characteristics can have on the direction of spread of rabies.

Thus, knowledge of a region's physical characteristics is important to the understanding of the rabies phenomenon, as influence is exerted over both the relative incidence and possible direction of spread of rabies.

2.6 Control

Past rabies control strategies have recognized the concept of threshold density and the role of the landscape and, thus, schemes have been directed at reducing the reservoir and vector species densities below the critical value in regions of persistent rabies or in advance of an epidemic front. Den gassing, trapping, hunting and poisoning have met with little

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success for two reasons: high productivity and mobility of the target species allows the rapid re-establishment of population levels, and intervention disrupts the species social structure so that its characteristics change. In their European study, Toms and Andral (1977) state that for effective rabies control via population reduction, it would be necessary to remove 75% of the red fox population. Such "control" methods also need to be practised every year, making them inefficient and expensive. Furthermore, low density areas may actually encourage the spread of rabies elsewhere by allowing outside rabid foxes to travel quickly and extensively through these "controlled" regions due to reduced encounters (Toms and Andral, 1977; Bacon and Macdonald, 1980). Also, Tinline et al. (1982) found that heavy fox trapping, although it may alter the severity and timing of rabies outbreaks, may induce fox movement and thereby increase the contact rate within the population.

Two solutions have been offered. The obvious is reducing the carrying capacity of an area for the vector species as suggested by Davis (1974). Winkler (1975) states this to be impractical. This idea, however, might be considered in the planning of parks and recreational areas and practised in the maintenance of idle land found close to areas of dense human population. It is oral vaccination of wildlife, however, that is considered the most practical, efficient and cost-effective method of rabies control as the social characteristics of the vector species are not upset while the success of disease transmission is reduced.

The Ontario Ministry of Natural Resources has been working for several years on an effective delivery system in anticipation of the development of a successful vaccine. Taking into account the characteristics of the red fox and striped skunk populations of Ontario, their system consists of the airborne delivery of liver-coated sponges, containing a vaccine, to areas of optimal fox and skunk habitat over a region. The spongy nature of the bait ensures the individual will chew, rather than bolt the bait, and thus the vaccine is absorbed into the system from the mouth, rather than the stomach where the chance of successful immunization is reduced. Through this method, over 500 km² can be baited in less than 8 hours and acceptance rates determined by biomarkers approach 70% for foxes (University of Guelph, 1980; Johnston and Voigt, 1982). The acceptance rate in the skunk, however, is lower and Voigt (1983) believes a more intensive distribution pattern may be needed to reach them.

Rosatte (1985a; b; c), however, points out that skunk rabies is most prominent in the urban areas of Ontario, and that airborne delivery of baits is impossible in such environments. Furthermore, the oral vaccine-bait method has not proved very successful with skunks (Ministry of Natural Resources, 1985a; Rosatte, 1985b). Thus, research is continuing for an effective vaccine while the Ministry is presently testing the effectiveness of a "trap-vaccinate-release" campaign in Metropolitan Toronto whereby the vaccination of skunks is conducted by hand by Ministry personnel.

Until recently, live vaccines were considered too dangerous

to use in oral vaccination schemes as ingestion by non-target species might trigger new epidemics, for example, in rodent species (Winkler et al., 1972; 1976; Black and Lawson, 1980; Lawson et al., 1982). Killed vaccines, however, were of reduced effectiveness, and absorption into the system was not guaranteed in a good percentage of the cases (Tinline et al., 1982; Voigt, 1983). Connaught Laboratories in Toronto, however, have recently developed a safe live vaccine that has proven effective in 80% of the laboratory foxes tested (Ministry of Natural Resources, 1985c). The Ministry must now determine what percentage of the population needs to be vaccinated to control rabies.

As the vaccine is effective only for one year, annual baiting of the entire endemic region of the province would be costly (\$4 million/annum) (Voigt et al., 1985). Tinline et al. (1982) propose the classification of rabies "regions", based on physiography, carrying capacity and intensity of hunting and trapping pressures, whereby control programs could be managed at this level, with particularly troublesome areas identified and treated annually. The effectiveness of any wildlife rabies control scheme, however, whether through vaccination, culling or a combination of both, depends upon knowledge of vector habitat characteristics and preferably, the identification of quality landscapes (Tierkel, 1959; Davis, 1974; Bacon and Macdonald, 1980; Macdonald et al., 1981; Tinline et al., 1982; Rosatte, 1985a; d). Thus the purpose of this study is to investigate the environments of vector species in an attempt to identify characteristics of quality habitat.

CHAPTER THREE

Methodology

The characterization, by land use, of the environments of wildlife/human contact, involves the use and comparison of two types of information - land use maps and rabies submission data. This chapter discusses the sources, preparation, problems and limitations of these data and of the study methodology.

3.1 Data Sources

Rural land use data were obtained from the 1977 RMOC Agricultural Land Use Systems map series (1:50,000) produced by Agriculture Canada, and the 1981 Canada Land Inventory (CLI) land use series for the Urban-Centred Region of Ottawa-Hull (1:50,000), published by the Lands Directorate of Environment Canada. The CLI maps identified the land uses within the greenbelt and the adjacent area known as "Mer Bleue"; the RMOC series covered the remainder of the rural region. Although not as temporally compatible with the RMOC maps, the improved classification system of the 1981 CLI series dictated its use over the earlier 1976 series.

Land use descriptions from within the urban region were obtained using the RMOC 1981 Urban Land Use map (1:25,000) contained in the 1982 RMOC Planning Department report entitled Land Use in Ottawa-Carleton.

Fox and skunk rabies submission data were obtained from the records of Agriculture Canada's Animal Diseases Research

Institute (ADRI) in Nepean. This federal laboratory is the diagnostic centre for all suspect rabies cases reported in Ontario. Specimens, submitted by federal and private veterinarians, local law authorities (police and by-law officers) and the general public, are dated upon receipt and assigned a consecutive file number. Annual catalogues (January 1 - December 31) identify submission county, the type of animal involved and the test results (positive, negative or unfit for testing). Case particulars are recorded on a standard form and stored in the archives. This form lists the specific location of the find (requested as Lot and Concession), name and address (if different from the location of find) of the person(s) involved; a space for a brief comment regarding the circumstances surrounding the contact is also provided. Over the study period, 606 red fox and 498 striped skunk submissions were identified from the catalogue as being from the Region of Ottawa-Carleton, and the date, diagnosis and file number of each was recorded. Locational information for 503 of these foxes and 418 skunks was obtained from the archival files (see Problems).

3.2 Data Preparation and Organization

3.2.1 Land Use

The "rural" region considered in hypothesis 1 is defined as the dominantly agricultural area outside the inner limit of the greenbelt. This region entirely encompasses the three developing "urban" satellites of Kanata, Barrhaven and Orleans and the two "intra-greenbelt" communities of Bell's Corners and

Blackburn Hamlet (see Figure 4). Given the proximity of the rural environment it is difficult to consider the wildlife cases found within their limits as a truly urban phenomenon. Indeed, no point within Barrhaven, Bella Corners or Blackburn Hamlet is more than 1 km away from the defined edge of the rural environment. The urban centres of Kanata and Orleans, although physically larger, are dominated by scattered low-density residential development and vast expanses of land left idle in anticipation of future growth. Thus, the specimens submitted from within their limits, as defined by the RMOC Planning Department Urban Land Use Map (1981), (10 foxes and 37 skunks) are considered as part of the rural environment. Consequently, the "urban" environment considered in hypothesis 2 is confined to the region bounded by the inner limit of the greenbelt (see Figure 4).

Within the defined rural environment, simplification of the land use categories used in the RMOC and CLI maps to five (5) basic groups was necessary to create a manageable data set and ensure compatibility between the two different source map series. The five categories chosen were, Active Agriculture (A) - loosely defined as intensive crop production with frequent field disturbance; Passive Agriculture (P) - where the intensity and frequency of field disturbance is reduced in comparison to the Active category; Grazing or Idle lands (G) - where agricultural land is left relatively unattended and uncultivated; Woodlands (W); and Urban areas (U) referring to areas of human concentration and lands associated with urban and

FIGURE 4 URBAN AND RURAL RMOC

urban-oriented activities. Tables 4 and 5 show the original classifications found in the RMOC and CLI source maps, respectively, and their reclassification into the 5 basic uses outlined above. An overlay map of land use types in rural RMOC was produced using the simplified classification scheme from which ten (10) different boundary or edge types were produced (see Table 6).

No preparation of the urban land use data was necessary, as descriptions required for hypothesis 2 were simply taken directly from the RMOC Urban Land Use map.

3.2.2 Rabies Submission Data

As stated in Chapter 1, the pattern of a zoonose (disease of animals) can reflect the pattern of relative habitat suitability for the host species as - ceteris paribus - a greater and persisting number of disease cases would be reported from areas of higher population densities. The pattern of all submissions, regardless of diagnosis, likewise, should be indicative of population densities and thus habitat suitability. Thus, as access to this information was available, the locations of all suspect cases submitted from the RMOC, for the period commencing July 1, 1970 through to June 30, 1985, were identified. The location of encounter of rural specimens was noted by Lot and Concession while urban cases were identified by street address.

Table 4

Reclassification of RMOC Land Use Source Map

Original System Classification	Definition	Study Reclassification Category
Monoculture		
Corn	<ul style="list-style-type: none"> - Continuous cultivation of corn or cereal grain without crop rotation. High fertilizer application rates used - Corn, cereal, grain, hay and pasture in rotation with corn comprising between 30 and 90% of the total acreage, fertilizer application rates are moderate but use is universal - Orchards, market gardens, sod farms 	Active Agriculture (A)
Specialty Agriculture		
Mixed	<ul style="list-style-type: none"> - Corn, cereal grain, hay and pasture in rotation with corn comprising less than 30% of total acreage, land quality, capital investment and animal density are appreciably lower - Hay, grain and pasture in rotation with hay dominant in area. Fertilizer application rates and crop yields are average 	Passive Agriculture (P)
Pasture	<ul style="list-style-type: none"> - Hay and pasture in approximately equal proportions but without crop rotation, low labor and capital investment input, yields below average 	
Grazing	<ul style="list-style-type: none"> - Livestock grazing on permanent or native grass pasture, with minimal cultivation and mechanical harvesting 	Grazing/Idle Land (G)
Abandoned Farmlands	<ul style="list-style-type: none"> - Weeds, grasses, willows and small trees - Unproductive - bedrock, sand, etc. 	
Scrubland		
Woodland	<ul style="list-style-type: none"> - Continuous cover over 6 metres in height, includes reforestation 	Woodlands (W)
Swamp or Marsh		
Built Up, Recreation Extraction	<ul style="list-style-type: none"> - Urban related uses, industrial, etc. - Parks, golf courses, etc. - Sand, gravel, topsoil 	Urban (U)

Table 3

Reclassification of CLI Land Use Source Map

Original System Classification	Definition	Study Reclassification Category
A111	Grain Growing - Annual Tillage Crop	Active Agriculture (A)
A112	Vegetable Growing - Annual Tillage Crop	
A117	Corn Growing - Annual Tillage Crop	
A131	Tree Fruit Production - Orchards	
A140	Ornamental Shrubs and Trees	
V110	Row Crops - Annually Cultivated	
V120	Close Grown Crops - Annually Cultivated	
A121	Growing Forage Crops	Passive Agriculture (P)
V120	Improved Grass and/or Legume Crop	
N000(W120, Z000)	See Text	
A122	Grazing	Grazing/Idle Land (G)
B100	Unused, Idle Land - Former Agricultural Activities	
L100	Land in Transition	
V220	Unimproved Grasslands, Reeds, Sedges, Etc.	
W223	Shrubs and Bushes (less than 0.5 metres in height)	
W120	Irregular Spaced (Natural) Woody Vegetation-Mature Woodlands (W)	
D111	Dwelling - Permanent Homes	Urban (U)
H111	Transportation by Expressway	
H163	Transportation of Electricity-Related Activities	
H230	Broadcasting	
J200	Providing Protective and Custodial Services	
J310	Providing Primary and Secondary Education	
J900	Undifferentiated Institutional Services	
M631	Treatment and Disposal of Domestic Solid Wastes	
M900	Undifferentiated Manufacturing and Storage Activities	
R000	Recreational Activities	
Y100	Constructed Covers - Structures	
C000	Commercial Activities	

Table 6

Land Use Edge-Terrain Types

1. Active Agriculture/Passive Agriculture (A/P)
2. Active Agriculture/Grazing (A/G)
3. Active Agriculture/Woodland (A/W)
4. Active Agriculture/Urban (A/U)
5. Passive Agriculture/Grazing (P/G)
6. Passive Agriculture/Woodland (P/W)
7. Passive Agriculture/Urban (P/U)
8. Grazing/Woodland (G/W)
9. Grazing/Urban (G/U)
10. Woodland/Urban (W/U)

3.3 Problems

3.3.1 Land Use Data

Reclassification of the CLI land use categories, periodically, proved difficult due to the use of more than one land use label on a given parcel of land. In several cases, the multiple labels (usually one major category with minor subscripts) under the new classification system did not match. Nowhere was this problem more evident than in the case of Mer Bleue.

The original CLI classification for this area was listed as N000 (W120,2000). According to the series legend N000 is defined as "no perceived activity with no evidence of former activities". The subscripts W120 and 2000, however, are respectively defined as "dominantly irregular spaced (natural) woody vegetation" and "water". Visual inspection of the area in question revealed a low-lying region of mixed vegetation including reeds and swamp, but also extensive fields of grass and hay, some mature trees and scrublands. According to the 1976 CLI classification scheme, the area was defined as "intermittently wet hay-land". Thus, rather than label it as "idle" or "woodland", as indicated by the 1981 CLI classification, based on the author's visual inspection, the area was reclassified as Passive Agriculture. Thus the CLI system, at times, proved difficult, clumsy and contradictory.

The second major rural land use data problem arose from the use of two different source maps and their apparent differing mapping resolutions. Although neither series specified the

resolution to which land units were mapped, the smallest areal unit found on the RMOC maps was 2.5 hectares vs. 1 hectare on the CLI maps. In order to "equalize" the two, no land use unit smaller than 2.5 hectares was included on the overlay map. There were fewer than 3 dozen such omissions.

3.3.2 Rabies Submission Data

As rabies submission cases were listed by file number in the ADRI general catalogue, those submitted from the RMOC were identified by the county (Regional Municipality) name. A secondary location is also listed identifying the general area within the county where the specimen was found. Periodically, counties were mislabelled for the given secondary location. This was a chronic problem in the case of submissions from within the Township of Cumberland - part of the RMOC. Several dozen cases were labelled as "Russell County" when the secondary location clearly indicated a Cumberland locale. All Russell listings, therefore, also had to be examined. Those found to be "Carleton" cases were included in the data set.

A second problem lay in the identification of the specific location of find (Lot and Concession or street address). This information was obtained from the individual case file, but was not available for 17% (103) of the fox cases and 16.1% (80) of the skunks for any one of the following reasons:

- a) files were missing or misfiled,
- b) data were illegible or illegitimate (such as a non-existent lot or concession),

c) absence of, or vagueness of the data. This was especially the case when local law authorities were involved. Forms often simply read "Road kill, Nepean" or "Greenbelt Farm" and thus locations could not be pinpointed. Attempts to acquire this information through the records of the authorities involved met with limited success. Requests for access to the records were denied, the data had been destroyed or were never recorded, the information available from the ADRI file was insufficient for record identification, or the records contained no more locational information than was found on the ADRI files.

d) information was contradictory. In such cases an address (presumably that of the person(s) involved) was listed under the "location of find" while the brief details of the event implied the find was elsewhere. For example: John Smith of 100 Smith Street in Ottawa comments that the family dog fought with the animal in question "at the cottage". In several of these such cases it was unclear as to whether the specimen was even encountered within the Region.

e) no location given (or simply a RR or P.O. Box number given) with a name supplied. 1984 or 1985 assessment roles were used to identify the lot (or part lot) and concession, or street address, owned by the individual named but only in those cases where the commentary supported that the animal was found in the home environment (i.e., "fox found in backyard with dog"). If more than one property was owned or the individual was not listed in the assessment, the case was not included.

f) some animals (especially skunks) were listed as pets or

in a "human-altered" state (for example, fox found skinned). Such cases were not used.

Thus of the 606 foxes and 498 skunks listed in the general catalogue as contacted within the Regional Municipality of Ottawa-Carleton, locational information was available for 503 and 418 of the cases, respectively.

3.4 Methodology

Initially, to determine the nature of rabies incidence within the RMOC, annual (July 1-June 30) totals of all fox and skunk cases diagnosed positive, regardless of location, were plotted over the period of 1970 to 1985.

Second, to test the first hypothesis, the newly developed 5-category rural land use map was divided into quadrats using an 8x8 km grid. This provided a sufficient number of quadrats, of relatively uniform land use characteristics, for statistical analysis. Within each quadrat the total length of each of the ten edge-types, created by the juxtaposition of two of the 5 land uses, was determined using a computer digitizer. The MICS program "LINEDIST", developed at the Carleton University Computer Cartographic Centre, calculated the straight-line distance between any two points (or series of points). The distance of any curvilinear edge was, therefore, calculated using the sum of the distances of a series of shorter straight-line segments, and the total length of a given edge-type determined by summing the lengths of all similar types. Similarly, due to the irregular physical shape of the

RMOC beneath the fixed grid network, land areas "contained" in the quadrats were determined by the program "POLYAREA" and ranged from 0.8 to 64 km².

The location of each rural fox and skunk submission (481 foxes, 328 skunks) was plotted in the centre of the Lot and Concession reference and the number of cases found within each quadrat was noted. Thus for 59 quadrats, the length (km) of each of the 10 types of edge-terrain, the total length of edge (the sum of the ten), quadrat area (km²), and the number of fox and skunk submissions found within each were recorded (see Appendix A). To determine the relationship, if any, between submission counts and length of edge, a series of regression analyses were conducted for each species sample, using the statistical software package MINITAB, developed at Pennsylvania State University.

Each of the following independent variables was individually regressed against the number of submissions (the dependent variable):

- the length of each of the 10 edge-terrain types
- the total length of edge (the sum of the above 10)
- the sum of those edge-types sharing a common land use category (for example, the total length of wooded-edge)
- quadrat area

Furthermore, multiple regressions of:

- combinations of the lengths of edge-types sharing a common land use category (for example, again, the four types of wooded-edge lengths)

- all 10 edge-type lengths
- all 10 lengths plus quadrat area
- the total length plus quadrat area.

Table 7 clarifies this. Regression significance was determined by the testing of the coefficient of correlation (R) (adjusted for the degrees of freedom) using the F statistic at the .01 level of significance. The results of these regressions are discussed in Chapter Four.

Characterization of the urban environments of vector species/human (and/or domestic animal) contact (hypothesis 2) was undertaken in a less structured manner. Simply, fox and skunk cases for which locational data was available, were plotted on the Urban Land Use source map by street address. The general type of area was noted (i.e., residential, institutional, etc.) and land use features found within a 1/2 km radius were identified (i.e., cemeteries, parklands, greenbelt) (see Appendix B). Descriptions were compared and similarities noted. Furthermore, the spatial distributions of these urban cases were plotted in relation to linear "corridor" land uses. The "testing" of hypothesis 2, therefore, is based on descriptive, rather than statistical, analyses. Again, the results are discussed in Chapter Four.

3.5 Data Limitations

The data and methodology contain several limitations. Initially, while rabies submissions are continuous in time, land use maps characterize an area at a single moment and thus, a

Table 7

Regressions Performed

Dependent Variables	Independent Variable(s)	
	Simple Regression	Multiple Regression
1. Fox Submissions	1. Length of A/W edge	1. Wooded Edge Lengths (A/W, G/W, P/W, U/W)
2. Skunk Submissions	2. Length of A/U edge	2. Urban Edge Lengths (A/U, G/U, P/U, U/W)
	3. Length of A/G edge	3. Grazing Edge Lengths (A/G, G/W, G/U, G/P)
	4. Length of A/P edge	4. Passive Edge Lengths (A/P, G/P, P/W, P/U)
	5. Length of G/W edge	5. Active Edge Lengths (A/W, A/U, A/G, A/P)
	6. Length of G/U edge	6. All Edge Lengths (10 variables)
	7. Length of G/P edge	7. All Edge Lengths plus Area (11 variables)
	8. Length of P/W edge	8. Total Length of Edge plus Area (2 variables)
	9. Length of P/U edge	
	10. Length of U/W edge	
	11. Total Edge Length (sum of 1-10)	
	12. Total Length of Wood Edge (A/W+G/W+P/W+U/W)	
	13. Total Length of Urban Edge (A/U+G/U+P/U+U/W)	
	14. Total Length of Grazing Edge (A/G+G/W+G/U+G/P)	
	15. Total Length of Passive Edge (A/P+G/P+P/W+P/U)	
	16. Total Length of Active Edge (A/W+A/U+A/G+A/P)	
	17. Quadrat Area	

"dynamic" phenomenon is being cast against a "static" feature. Consequently, land uses characterized as supporting the vector species may be misrepresented. Land use change, however, is a continuum by which transformation is generally gradual rather than catastrophic and thus, over a relatively short time period, the degree of modification is minimized. The land use data, therefore, were obtained for a period roughly in the middle of the study period so that the error produced as a consequence of change would be minimized. At the more local scale, again due to the "static" nature of the land use data, agricultural land worked under a rotation system may be similarly misclassified.

The use of two different source maps also results in discrepancies of time and, possibly, definition over the study area. This, however, was unavoidable due to the lack of a comprehensive Regional land use base.

The simplification of the rural land use data into the 5 broad categories creates a loss of information as specific features are concealed. Vegetation type and density of growth, for example, may be critical factors erased by generalization, and this may limit the value of the results.

Finally, the rabies submission data represent a biased population sample. That it is a sample is obvious, as not every member of the population is submitted for rabies analysis, and the bias is the result of dependence upon human contact for recognition. The true distribution of the vectors may not be accurately represented with areas being under or overrated due to the characteristics of the human population. The degree of

bias is unknown in the study due to the omission of human population density as a variable.

Thus, although the data and methodology impose some severe limitations, it is still believed that useful information regarding the rabies phenomenon in or near the urban environment can be extracted from the data. Chapter 4 now discusses the investigation's findings and their possible implications.

CHAPTER FOUR

Analysis and Results

4.1 The Incidence of Fox and Skunk Rabies in the RMOC

During the study period, of the 606 foxes and 498 skunks submitted for rabies testing from within the RMOC, 520 foxes and 189 skunks were diagnosed rabid. This represents 85.8% and 38.0% of the total foxes and skunks submitted. The reported incidence of these cases was cyclical. Fox cycles peaked, noticeably, every 3-4 years with over 80 cases in 1971/72 and again in 1982/83. Lesser peaks of over 30 and 60 cases were recorded in 1974/75 and 1978/79, respectively. The skunk cycle showed less marked regularity and range, with peaks of over 20 cases occurring in 1972/73 and 1979/80 and over 45 in 1982/83. The latter peak coincided with a high fox rabies period while the former two lagged fox peaks by 1 year (see Figure 5).

Of the rabid cases for which location was known 95.8% of the foxes and 84.3% of the skunks were submitted from the rural region.

Discussion

The correlation and lag of fox and skunk rabies incidence peaks is suggestive of inter-species disease transmission with the delay in skunk rabies possibly being due to a lengthier period of disease incubation. If cross-infection were commonplace, however, one would expect an increase in the reported incidence of skunk rabies to have occurred during, or

FIGURE 5 ANNUAL (July 1 - June 30) INCIDENCE OF FOX AND SKUNK RABIES IN THE RMOX 1970-1985

following, the 1974/75 fox peak. Skunk incidence, however, remained low from 1973/74 through to 1978/79. It is more likely that the cycles are independent, given the reported lack of interaction between the two species. The similarity in cycle frequency, therefore, may be indicative of the influence of an overall environmental factor such as climatic conditions, or may represent an effect of reporting due to periodic increased public awareness of the general prevalence of the disease.

Thus, the incidence of fox rabies within the RMOC exhibits a well-defined 3-4 year cycle, while skunk incidence is less easily characterized. This implies the Region supports excellent fox habitat.

Given that the most recent rabies outbreak occurred in 1982/83, it would appear the Region is due for a new eruption. Although within the first 6 months of 1986 Ontario has recorded a substantial increase in the reported incidence of rabies over previous years, this epidemic has been focussed in central Ontario. Especially hard hit have been the counties of Peterborough, Durham, Simcoe, Frontenac and Hastings. The Regional Municipality of Ottawa-Carleton has not been affected, reporting only 12 rabid animals between January and June (Ontario Ministry of Health, 1986). It is possible that the disease has not been re-introduced into the region by the successful ingression of an infected individual from the epidemic area or, due to the severity of the 1982/83 outbreak (in both the fox and skunk) the populations have not recuperated sufficiently to the threshold densities required to support an

epidemic. Whatever the reason, the general incidence pattern suggests the RMOC is due for an increase in fox, and possibly skunk, rabies. As over 85% of the foxes submitted were found rabid compared to only 38% of the skunks, rabies is more likely involved in a fox, than a skunk, encounter, and thus the fox represents a greater threat to human health.

Finally, although the urban area supports over 75% of the Region's population, the majority of rabid foxes and skunks were encountered in the rural environment. This suggests that human exposure to rabies is more likely in the rural environment. As urban growth promotes an increase in the rural population it may also promote an increase in the risk of human exposure to rabies.

4.2 The Rural Environment

Hypothesis One proposed that within the rural environment, fringe-landscapes, generated by the juxtaposition of specific land use types, provided an attractive habitat to the red fox and striped skunk, and, since the spatial pattern of rabies submissions should reflect the variability in habitat suitability, the number of individuals submitted for rabies testing should be correlated with the amount of preferred edge-terrain. From the series of regression analyses performed, several statistically significant relationships were, indeed, found to exist, indicating environments of preferred use. Tables 8 and 9 summarize these relationships. Only those supporting coefficients of determination ($R^2 \times 100$ values) greater than

Table 8

Regression Statistics Summary: Fox

Independent Variable (Simple Regression)	$R^2 \times 100$ (%)	$R = \sqrt{R^2}$	F_{calc} Statistic	F_{crit} Statistic	Reject H_0 ? (0.01)
Length of...					
Active/Wooded Edge	8.6	.293	6.43	7.08	No
Active/Urban Edge	3.8	.195	3.30		No
Active/Grazing Edge	12.6	.355	9.36		Yes
Active/Passive Edge	5.3	.230	4.26		No
Grazing/Wooded Edge	22.6	.475	17.91		Yes
Grazing/Urban Edge	1.5	.123	1.88		No
Grazing/Passive Edge	51.5	.718	62.64		Yes
Passive/Wooded Edge	29.7	.545	25.47		Yes
Passive/Urban Edge	6.0	.245	4.72		No
Urban/Wooded Edge	0.7	.084	1.40		No
Total Edge	39.0	.625	38.12		Yes
Summed Length of Wooded Edges	33.0	.575	29.62		Yes
Summed Length of Urban Edges	4.2	.205	3.52		No
Summed Length of Grazing Edges	42.0	.648	42.92		Yes
Summed Length of Active Edges	10.0	.316	7.46		Yes
Summed Length of Passive Edges	36.4	.603	34.19		Yes
Quadrat Area	45.6	.675	49.66		Yes
<hr/>					
Independent Variables (Multiple Regression)					
Length of...					
Wooded Edges	35.1	.593	8.83	3.74	Yes
Urban Edges	1.4	.118	1.21		No
Grazing Edges	53.2	.729	17.47		Yes
Active Edges	11.4	.338	2.87		No
Passive Edges	50.0	.707	15.49		Yes
All Edge-types Lengths	51.5	.718	7.16	2.72	Yes
All Edge-types plus Area	53.3	.730	7.02	2.65	Yes
Total Edge Length plus Area	44.8	.669	24.57	4.98	Yes

Table 9

Regression Statistics Summary: Skunk

Independent Variable (Simple Regression)	$R^2 \times 100$ (%)	$R = \sqrt{R^2}$	F_{calc} Statistic	F_{crit} Statistic	Reject H_0 ? (0.01)
Length of...					
Active/Wooded Edge	2.8	.167	2.65	7.08	No
Active/Urban Edge	4.7	.217	3.83		No
Active/Grazing Edge	15.4	.392	11.53		Yes
Active/Passive Edge	7.1	.267	5.40		No
Grazing/Wooded Edge	11.4	.338	8.43		Yes
Grazing/Urban Edge	3.8	.195	3.27		No
Grazing/Passive Edge	11.5	.339	8.57		Yes
Passive/Wooded Edge	10.7	.327	7.95		Yes
Passive/Urban Edge	13.8	.372	10.27		Yes
Urban/Wooded Edge	9.9	.315	7.40		Yes
Total Edge	24.8	.498	20.13		Yes
Summed Length of Wooded Edges	19.1	.437	14.69		Yes
Summed Length of Urban Edges	11.9	.345	8.84		Yes
Summed Length of Grazing Edges	21.0	.458	16.44		Yes
Summed Length of Active Edges	10.4	.323	7.74		Yes
Summed Length of Passive Edges	17.0	.412	12.90		Yes
Quadrat Area	24.7	.497	20.01		Yes

Independent Variables
(Multiple Regression)

Length of...					
Wooded Edges	16.7	.409	3.91	3.74	Yes
Urban Edges	14.5	.381	3.45		No
Grazing Edges	20.5	.453	4.75		Yes
Active Edges	10.9	.330	2.78		No
Passive Edges	17.2	.415	4.01		Yes
All Edge-types Lengths	27.2	.522	3.17	2.72	Yes
All Edge-types plus Area	28.8	.537	3.13	2.65	Yes
Total Edge Length plus Area	24.8	.498	10.57	4.98	Yes

40.0% were considered worthwhile for examination. These are presented in Table 10.

4.2.1 The Fox

The numbers of foxes submitted for rabies testing was found to be moderately associated with the linear length of grazing/passive agricultural edge. Of the variability in the number of submissions 51.5% could be explained by the variability in the provision of this fringe environment. The sum of the lengths of all grazing edges was also found to be correlated ($R^2 = 42.0\%$) as, too, were combinations of both grazing and passive fringe types (R^2 values were 53.2% and 50.0% respectively). The multiple regression of all 10 edge-types proved to support no more of a correlation than the simple length of grazing/passive edge while the total length of all edge produced an R^2 value of only 39.0%.

Quadrat area was found to be associated with submission counts producing a moderate R^2 of 45.6%. The inclusion of this variable in the total length of edge regression and the multiple regression of all the edge types did not significantly increase the levels of correlation (R^2 values were 44.8% and 53.3% respectively). Figure 6 shows the distribution of rural fox submissions.

Discussion

These correlations indicate that within the study area edge-terrain is attractive to the red fox and thus should be

Table 10

Significant Regressions: $R^2 \geq 0.40$

Species Regression (Type)		R ²
Fox	Length of Grazing/Passive Edge (Simple)	51.5
Fox	Summed Length of Grazing Edges (Simple)	42.0
Fox	Quadrat Area (Simple)	45.6
Fox	Length of the 4 Grazing Edge-Types (Multiple)	53.2
Fox	Length of the 4 Passive Edge-Types (Multiple)	50.0
Fox	Lengths of all 10 Edge-Types (Multiple)	51.5
Fox	Length of all 10 Edge-Types Plus Area (Multiple)	53.3
Fox	Total Edge Length plus Area (Multiple)	44.8

FIGURE 1. THE DISTRIBUTION OF FOX SUBMISSIONS IN RURAL BRICK 1970-1985

recognized as a factor of habitat suitability. The statement that the preferred habitat of the red fox is "mixed agriculture interspersed with woodlots" should be more accurately restated as "the fringe-environments created by mixed agriculture and the interspersation of woodlots". This more readily identifies the importance of land use configuration. Furthermore, it appears that the red fox prefers the fringe environments of unintensive agriculture over those fringe environments provided by other uses. In the zone of urban influence it is precisely these land uses that are encouraged by urban growth as active farmland is replaced by less intensive agriculture and farm abandonment occurs. Furthermore, farm fragmentation increases the amount of edge-terrain. Thus it is conceivable that urban growth increases the amount or quality of habitat in the zone of urban influence, improving its environmental carrying capacity for red foxes and thereby increasing the possible risk of human exposure to fox rabies.

Despite the strongest fringe/submission correlation being found through the multiple regression of various combinations of edge-terrain types in association with quadrat area, for the extra input involved in the gathering of this information it proved no more valuable a measure of the variability in submission counts than the simple length of grazing/passive edge. This suggests that the length of grazing/passive agricultural edge may be the strongest, simple cartographically-measured land use indicator of fox rabies submissions and, by association, population density or habitat suitability.

Although the weakness of the correlation precludes its use as a single predictor variable, it may be useful in concert with several other variables to categorize fox habitat or predict fox population densities.

Noticeably absent is the lack of strong correlation between any wooded-edge measure and fox submissions. One would expect wooded-edge to be indicative of habitat quality because of its necessity as cover to the fox. It may be, however, that due to the scale of the consideration of land use the subtleties of the landscape are lost, yet these may be critical to fox habitat. For example, the non-delineation of woodland species and/or densities may have obscured the significance of woodlot edge to the fox. Open-deciduous forest may be more attractive than dense-coniferous stands but the agglomeration of all woodlands into one broad category would mask this. Furthermore, it may be that the fox prefers lengthy but narrow woodland cover along which protection and escape-routing is available without effective removal from the hunting grounds. Such "woodlands" may be furnished by the treed field-boundaries, not shown on land use maps, rather than the defined bodies of forest, in which case the value of woodland edge, as determined by a cartographically-obtained measurement, would be under-rated.

Thus, although highly generalized, the comparison of the length of fringe-environments to fox rabies submission counts indicates that the red fox may prefer those environments of unintensive land use and the growth of the urban area through the promotion of such uses may increase the risk of human exposure to rabies.

4.2.2 The Skunk

None of the patterns of edge-terrain lengths proved able to support a worthwhile correlation with skunk submission counts. The strongest association was achieved by the multiple regression of all ten edge-terrain types and quadrat area. For all of this input, only 28.8% of the submission variability could be explained by the land use data.

Discussion

This lack of a worthwhile relationship suggests that the striped skunk is free from a dependence on fringe-environments or specific land use types. Indeed the omnivorous nature of the skunk and its confidence in its defence system may give rise to its exploitation of multiple habitat types. Consequently the threat of human rabies exposure from the skunk may be, spatially, more widespread. Quadrat area, however, also failed to support a significant correlation with submission counts. This suggested the dependence of skunk submissions on additional variables other than land use and area.

Visual inspection of the rural pattern of skunk submissions (Figure 7) identifies a clustering of cases around some of the villages. This is especially obvious around Richmond, Stittsville and Fitzroy Harbour and is also evident in the areas of urban development within the satellite communities of Kanata and Orleans and within the greenbelt communities of Bella Corners and Blackburn Hamlet. This suggests that the skunk may be attracted to the less harsh urban environment where buildings

FIGURE 7 THE DISTRIBUTION OF SKUNK SUBMISSIONS IN RURAL RMOC, 1970-1985

provide large, dry denning sites (as found by Schowalter and Gunson (1982) in Alberta skunks) and garbage is in constant supply. If, however, the skunk had a particular preference for the urban landscape over the rural environment, one would expect some significant correlation between the length of urban-edge environment (indicative of the relative amount of urban area available) and the number of submissions. No such correlation was found and, thus, it may be that the clustering is indicative of a dependence of submission data on human population density. Unfortunately, if this is so, then little can be inferred about the characteristics of skunk habitat or distribution over the Region, as submission data will not accurately reflect skunk habitat suitability. It is clear, however, that the skunk can thrive in a range of environments including those under a strong urban influence.

4.3 The Urban Environment

Hypothesis Two proposed that certain urban land uses provide suitable fox and skunk habitat and, being in close proximity to concentrations of the human population, they therefore represent environments of "high risk" of human exposure to rabies. Again, it is believed that they are identifiable through the pattern of rabies submission distribution. Over the study period, ninety skunks were submitted for rabies testing from within the defined urban area, representing 21.5% of the Regional total of (known locational) cases. Only 22 or 4.4% of the foxes, however, were submitted from this area. The details of the land use

characteristics found within 1/2 km of each of the reported locations of contact are included in Appendix B, and although it is impossible to separate the proportion of influence exerted by each of the surrounding land uses or features, the major common characteristics can be identified and general inferences made.

It is notable, however, that due to the proximity of concentrations of the human population, areas supporting urban wildlife were considered to be environments of "high risk" of human-exposure. This must now be qualified as a relative risk, as in Section 4.1 it was shown that the rural environment supports, by far, the highest risk of human-exposure as an overwhelming number of the rabies cases are reported from this area.

4.3.1 The Fox

Of the 22 urban foxes, 19 were submitted from dominantly residential areas, 2 from warehousing/transportation environments and one from Agriculture Canada's Central Experimental Farm. Eighteen of the contact locations, however, were less than 1/2 km from the greenbelt edge and/or were associated with (within 1/2 km) an extensive patchwork system of vacant land that dissects the southern suburban communities and extends into the warehousing/transportation district in the southeast and eastern part of the urban area. Much of this vacant land system is "inter-connected" with the greenbelt or lies adjacent to it. Figure 8 outlines the general extent and pattern of this network.

FIGURE 8 THE EXTENT OF PASSIVE RECREATIONAL AND VACANT LAND USE NETWORKS IN URBAN RMIX

Figure 9 outlines the main railway lines, highways and rivers crossing the urban area and the distribution of submission cases relative to these linear land uses. A strong visual correlation is evident and, indeed 17 of the cases were found less than 1/2 km from such uses, with 13 along the railway lines/highways and 5 along the Ottawa and Rideau Rivers.

Discussion

Several factors suggest the red fox is not overly attracted to the urban environment. Initially only 4.4% of the total cases were submitted from within this region. A comparable area in the rural environment (approximately 16000 hectares) supports 5.9% of the cases. Secondly, 18 of the 22 cases were found in environments that were either within 1/2 km of the greenbelt system or linked to it through the extensive network of vacant land. This suggests the attractiveness of these environments to the fox is a consequence of proximity to the rural region. Finally, a strong association for linear land uses implies these uses, by virtue of their configuration, may serve as corridors of access from the surrounding rural areas, which is a "reservoir" area, channelling fox movement into the urban environment. If they were acting as more than periodic access routes one would expect a greater number and a more extensive distribution of submissions over these networks than is demonstrated in Figure 9.

The presence of urban foxes in the RMOC, therefore, may not be the result of the general provision of habitat by certain

FIGURE 9 THE DISTRIBUTION OF URBAN TOXICS AND TRANSPORTATION NETWORKS IN THE RMOX

land use types but rather, more specifically, the provision of these uses in association with the surrounding rural environment. Indeed "greenbelt proximity" and "linear access" could account for all 22 cases found within the urban environment. Consequently this suggests a strong rural influence and implies that many of the Region's urban foxes may not be true residents but rather transient individuals or part-time dwellers utilizing both those useful urban and rural environments.

However, of the 22 cases, 14 were encountered during March/April/May - the period associated with the concentration of activity about the den, therefore implying these cases as representative of denning sites and thus urban residency. Nonetheless, 9 of the 14 were, again, found under 1000 metres from the greenbelt and thus, could in fact be greenbelt denners. Furthermore, rabies infection may make assumptions regarding behaviour invalid. All but 2 of these 14 cases were diagnosed rabid.

Thus the urban environments that prove attractive to the red fox appear to be the linear transportation corridors (including rivers) and extensive vacant or idle land, when found near the outer limit of the city. These unmanaged lands may represent excellent hunting grounds due to colonization by rodent species and, therefore, may prove to be areas of human rabies exposure. The frequency of contact reported within the nearby residential areas suggests that areas adjacent to such uses may, equally, be considered at risk.

Anticipation of outward urban growth induces the conversion of active land uses (often agriculture) to vacant or idle holdings between the perimeter of the built-up urban limit and the true rural environment beyond. Thus, through land speculation instigated by urban growth, it is possible that a perpetual supply of urban "high risk" landscapes is provided. The establishment of satellite communities may simply act to relocate these risk-areas by inducing speculation further afield or in circles around the new urban nodes. Satellite development provokes an increased need for service corridors through the rural environment into the urban centres, again increasing the amount of risk area provided. Furthermore, the threat of massive agglomeration of built-up urban uses often encourages the secondary use of these service corridors as physical barriers between communities and as urban greenspaces, and thus they are left lined by natural vegetation or open, idle grassland, increasing their attractiveness to the red fox.

Thus, given the urban land uses found to be occupied by the red fox, it is possible that urban growth has maintained and stimulated their supply and, consequently, the risk of human exposure to fox rabies.

4.3.2 The Skunk

Of the 90 striped skunks submitted for rabies testing from within the urban region, 63 were found in dominantly residential areas, 17 in multiple use residential/warehousing/transportation areas, 7 on institutional lands and 3 from within extensive

parke or natural environment areas. Forty-five of the 90 were associated with (within 1/2 km of) the outer network of vacant land or the greenbelt and 37 were associated with areas of passive recreational land uses. Forty-one could be associated with transportation corridors. Figure 10 shows the pattern of distribution of urban skunk submissions.

Discussion

It is extremely difficult to make inferences regarding the urban habitats skunks occupy or prefer due to the apparent dependence of skunk submissions on the human population density pattern. Unlike fox submissions, one cannot assume that the complete range of skunk habitats is accurately represented.

Within the RMOC, however, the pattern of urban skunk submissions is diffuse and widespread with cases found in a multitude of environments and well into the urban region proper. As with the rural data, this implies that the skunk is capable of exploiting a multitude of environments and thus no landscape may be safe from skunk habitation. Furthermore, combined with the sheer number of submissions, this indicates that the skunk is an urban resident rather than a trespasser.

There is, however, a visual correlation between submissions and those residential areas located close to the greenbelt, the outer network of vacant land and/or areas of extensive passive recreational land use (see Figure 8). These environments, therefore, may serve as skunk "reservoirs" and when located near the urban population may represent areas of increased

FIGURE 10 THE DISTRIBUTION OF URBAN SNUNKS AND TRANSPORTATION NETWORKS IN THE RMOX

2 OF 2

MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

likelihood of human/skunk contact and thus rabies exposure. Nonetheless, the risk of human exposure to skunk rabies is not limited to these areas.

The skunk submission pattern exhibits a notable peculiarity. Figure 10 indicates the majority of the diagnosed rabies "positive" cases are found in the outer-margin environments. This supports the theory that rabies re-infection of a population occurs through external contact, rather than latent disease activation, and consequently isolated populations may support a reduced incidence of rabies. Inner-city skunks, therefore, having reduced access to external populations in comparison to the inhabitants of the outer-margin environments may constitute more of a nuisance than a human health hazard.

Finally, it is difficult to conclude that the land use changes induced by urban growth serve to increase the risk of human exposure to skunk rabies within the urban region. The apparent ability of the skunk to make use of a variety of environments no doubt implies that it would be a successful urban colonizer regardless of the land use changes occurring. It may be, however, that the risk of exposure in the inner-city is, in fact, reduced by urban growth due to progressive skunk isolation from the reinfection source.

4.4 Summary

Several inferences have been made regarding the habits and habitats of the red fox and striped skunk populations of the Regional Municipality of Ottawa-Carleton, the implications for human exposure to rabies and the impact of urban growth. Being based solely on land use and rabies submission data, however, these inferences are open to some criticism.

In general, the province's two main vectors of rabies thrive in the environments of the RMOC. Population regeneration after epidemics, in the fox especially, is efficient and thus indicative of quality habitat. Rabies represents mainly a rural problem and thus the risk of human exposure is greatest in the well-populated rural region. In comparison to the skunk, the occurrence of rabies in the fox is more prevalent but the supporting environments more restricted. Specific urban and rural areas can be identified as high use by the fox and thus human exposure-risk areas. These environments represent the idle, unmanaged lands of the urban periphery and the rural fringe-landscapes created in the regions of unintensive agriculture. The skunk is a less likely carrier of the disease but, being more flexible, distributes this "reduced" risk of exposure over a wider range of environments. It may, nonetheless, be particularly troublesome around rural villages. Perhaps the area within the RMOC "safest" from the threat of rabies is the loosely defined "urban centre" where fox penetration is unlikely and skunk reinfection most difficult.

Finally, urban growth can be characterized as a general

perpetrator of human rabies exposure, especially to fox rabies, through the provision of new and/or improved vector habitat and encouragement of human population increases in the "high-risk" rural region.

It is now possible to make some inferences regarding rabies control within the RMOC with respect to the human health risk and to make recommendations for further study.

CHAPTER FIVE

IMPLICATIONS AND RECOMMENDATIONS

The purpose of this study was to identify those land uses - both urban and rural - thought to be supportive of the province's two main rabies vectors, in an attempt to characterize, using an obvious feature (land use), the environments of human risk of exposure to rabies. The study also aimed to determine if man's alteration of the landscape encourages his own risk of exposure, and, if possible, to gain an understanding of the nature of fox and skunk rabies within the Regional Municipality of Ottawa-Carleton. The results (summarized in Chapter 4) have implications for rabies control and yield recommendations for further study.

5.1 Implications for Control

The threat of human exposure to rabies within the RMOC is greatest in the rural environment. Consequently urban control is secondary to rural control. Furthermore, given that the rural environment is the apparent source of urban foxes and skunk reinfection, rural control alone may successfully reduce the risk of human exposure in both environments. The focus of rabies control, therefore, should be the rural landscape.

Within the RMOC fox rabies is more explosive than skunk rabies but the higher degree of habitat specificity shown by the fox may aid the targetting of control schemes and, consequently, give a greater efficiency and likelihood of success. Skunk

rabies - being more diffuse - is more difficult to control. The frequency of reports of skunks near the human environment, however, may argue for the practice of control schemes around "rural" concentrations of human population.

Although land use has been shown to be a factor of vector (mainly fox) habitat, multiple ownership and the pressures of economics, specifically the agricultural cost-price squeeze, clearly show rabies control through rural land use management to be impractical. Possibly the only risk area where such control could reasonably be practised would be the vacant lands of the urban periphery where repeated disturbance, simply through mowing, may reduce their attractiveness to the vectors. Given that the public health risk in these areas, however, is greatly reduced in comparison to the rural environment, such "control" would be insignificant. In any case, as stated in Chapter 2, the only accepted means of effective rabies control is through wildlife vaccination. Unfortunately, in Ontario, the as yet experimental status of wildlife rabies vaccination does not suggest its imminent implementation in the RMOC. The drastic increase (over 100%) in the number of people treated for rabies exposure that has accompanied the recent rabies epidemic in central Ontario, and the overdue status of the RMOC for a rabies outbreak strongly suggests, however, that in the interest of public health, the Region implement some form of control. The present "scheme" of education and post-exposure treatment is not enough. Under the Health Protection and Promotion Act the local medical officer has recently been given the authority to make

compulsory the immunization of all cats and dogs in the jurisdiction. As 80% of all human exposures to rabies occur via domestic animals it is strongly suggested that this regulation be implemented within the RMOC, now, before the epidemic strikes in an effort to reduce the public threat of rabies.

5.2 Recommendations for Further Study

To gain a further understanding of the degree to which man's activities affect wildlife populations and, thus, his possible risk of exposure to rabies, several different avenues of investigation may be pursued.

A comparison of the incidence of rabies within the zone(s) of urban influence with that of the truly rural region may allow speculation as to the actual degree of influence urbanization exerts on vector population densities. Is habitat truly improved, thereby increasing the environmental carrying capacity, or are discrepancies in incidence the result of differences in the reporting population? Furthermore, are increased vector densities responsible for the recent increase in the number of humans receiving treatment for rabies exposure or is this increase a consequence of a change in human recreational habits or lifestyle - that is, are people pursuing a "back-to-nature" trend bringing them into increased contact with wildlife? A comparison of the specific types of environments of exposure (for example, campground vs. farm) may resolve this question.

Finally, an investigation into the specific characteristics of those environments shown to be frequented by the vectors may clarify their attraction to these areas and suggest that it is not the land use that is appealing but rather specific features of the landscape. For example, does the red fox prefer the edges of grazing and passive agriculture because of the types of land usage involved or because of the presence of fencerows or hedges that may be associated with these uses. Similarly, is the skunk attracted to the urban environment because of the garbage supply or the quality denning sites provided by buildings? Answers to these and other questions may lead to an improved efficiency in control schemes, through the identification of vaccination target areas, or suggest new ideas or directions for combatting the threat of rabies.

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Appendix A

Summary of Quadrat Characteristics: Length of Edge, Area and Submission Counts

Quadrat	Length of Edge-Type (km)											Area (Km ²)	Submission Counts	
	A/W	A/U	A/O	A/P	G/W	G/U	G/P	P/W	P/U	U/W	Total		Fox	Sauv.
1	15.0	2.1	17.5	30.7	15.7	4.8	22.7	23.9	2.0	0.4	135.2	54.6	15	5
2	7.2	-	6.5	11.0	53.8	1.6	21.6	16.7	-2.6	2.1	107.4	48.7	14	10
3	4.4	0.6	2.1	3.5	27.6	2.3	6.7	10.7	0.5	13.6	72.2	35.1	10	1
4	11.7	1.0	12.9	33.7	22.6	0.6	27.6	21.4	1.0	3.7	135.3	54.0	14	1
5	3.4	-	13.7	15.2	44.6	0.7	27.5	26.7	0.7	-	132.3	64.0	11	11
6	3.9	0.0	6.2	4.9	42.7	3.3	32.8	20.5	1.0	6.1	120.5	60.4	25	1
7	-	-	-	-	6.8	1.0	3.0	0.2	-	6.2	17.2	8.7	1	1
8	1.3	-	5.7	5.7	63.3	0.7	21.4	12.6	-	-	110.5	61.4	11	1
9	3.9	1.0	12.1	37.9	19.2	4.9	9.6	2.7	3.5	4.1	99.1	64.0	14	1
10	0.4	-	3.7	2.5	42.4	3.4	35.6	9.9	0.3	3.0	101.0	64.0	10	10
11	-	-	-	-	22.4	1.9	8.6	2.6	0.9	1.0	37.7	12.3	9	1
12	3.0	-	1.5	1.7	61.1	3.8	17.2	8.7	0.5	1.5	98.9	63.0	6	1
13	9.2	5.5	22.9	8.5	51.5	10.5	25.8	15.3	3.0	13.8	155.9	64.0	14	1
14	4.3	4.8	13.4	11.2	46.1	8.1	29.7	19.8	7.0	9.1	153.6	63.6	15	1
15	-	-	-	-	8.1	2.0	1.0	5.1	1.0	0.7	17.9	7.0	0	1
16	5.0	-	5.7	6.7	78.9	5.3	20.8	14.3	1.2	2.3	140.1	63.9	6	1
17	3.7	0.4	3.6	1.3	73.3	12.2	17.0	20.3	0.7	20.2	152.6	64.0	9	10
18	3.1	3.4	18.4	23.9	31.7	13.6	16.1	9.0	11.1	18.0	146.1	64.0	8	14
19	7.3	1.2	5.4	18.5	16.3	2.7	2.0	7.3	4.7	3.3	68.7	23.6	6	17
20	7.1	0.3	5.5	10.7	49.5	3.9	37.9	40.1	2.3	3.8	160.8	63.8	14	1
21	-	3.2	12.4	10.4	34.7	4.0	21.1	13.4	9.2	3.3	111.5	64.0	15	11
22	12.2	5.6	26.1	47.1	16.3	15.5	19.3	4.6	4.6	7.5	162.7	64.0	4	1
23	3.3	8.4	24.8	35.6	15.2	11.9	28.3	9.3	14.4	2.4	153.5	62.2	8	1
24	0.4	1.1	2.1	1.8	34.2	29.3	15.0	16.1	3.3	10.0	123.6	44.4	4	1
25	20.9	5.6	6.1	33.9	19.0	1.8	12.7	32.4	8.2	23.7	166.0	53.6	7	1
26	13.5	12.5	12.4	14.1	12.4	16.3	39.5	15.6	8.5	13.0	157.7	64.0	18	1
27	7.8	0.6	8.4	15.3	11.3	2.7	40.8	27.1	0.9	2.9	125.5	62.5	8	1
28	4.0	-	0.5	2.7	13.5	2.2	10.6	18.7	5.2	3.7	61.3	22.1	1	1
29	1.3	-	-	-	34.1	-	2.2	2.7	-	-	40.3	13.9	1	1
30	5.0	0.5	7.6	13.6	32.9	0.9	22.9	16.2	0.4	2.4	102.0	64.0	10	11
31	16.6	0.8	10.8	45.6	7.5	3.4	14.3	28.2	12.3	2.3	147.9	64.0	16	11
32	6.0	3.0	11.7	26.0	33.5	14.5	23.0	24.6	7.6	2.3	154.9	64.0	16	1
33	5.9	2.2	5.1	5.8	63.5	35.5	16.0	14.1	13.4	21.8	186.2	64.0	10	1
34	1.6	0.4	25.3	26.4	43.7	5.9	25.4	20.3	1.6	11.0	174.2	64.0	5	1
35	3.2	1.0	4.3	13.2	31.5	17.5	26.5	22.0	3.4	18.0	142.4	64.0	4	1
36	10.4	1.7	15.6	22.8	24.6	4.2	35.2	28.4	6.5	3.8	153.3	64.0	12	1
37	1.9	-	1.6	1.4	5.9	-	11.6	4.1	-	-	25.9	12.6	0	1
38	2.7	-	-	0.5	61.7	-	3.3	9.2	-	-	76.9	64.0	1	0
39	0.7	-	4.8	10.1	53.0	5.5	18.5	18.7	0.7	1.9	119.2	64.0	10	1
40	10.7	3.3	13.4	15.3	28.2	6.0	26.0	15.7	3.8	2.2	124.3	61.5	10	1
41	4.2	1.6	11.8	16.1	32.9	9.9	29.1	26.5	3.5	3.1	138.4	64.0	18	1
42	5.8	1.1	3.2	9.6	53.7	8.6	29.2	22.9	8.7	4.2	146.9	64.0	25	1
43	7.4	0.6	16.1	19.5	33.4	1.4	32.8	19.0	1.0	2.5	134.2	51.6	8	1
44	1.5	3.4	1.7	2.9	5.6	3.9	14.4	7.0	7.3	0.5	49.9	19.9	3	1
45	1.4	0.4	0.7	1.0	15.9	1.8	14.6	16.3	0.5	1.6	59.9	35.0	4	1
46	0.9	-	1.4	1.0	1.2	-	2.9	-	-	-	7.3	7.4	1	1
47	-	-	3.2	5.1	2.0	1.7	3.9	1.1	0.6	0.6	18.0	9.2	1	1
48	-	-	6.5	2.5	3.2	2.1	2.7	-	0.2	0.3	17.4	10.1	1	1
49	1.8	-	6.0	14.7	6.9	-	16.9	15.0	-	-	61.1	34.3	5	1
50	14.0	-	6.1	24.9	12.0	2.3	12.6	26.5	0.9	1.7	101.0	48.0	1	1
51	4.6	1.0	5.2	13.4	2.9	0.5	16.3	8.0	0.2	-	53.0	26.1	1	1
52	-	-	-	-	4.1	0.1	-	0.5	-	2.6	7.3	2.8	1	1
53	-	-	-	-	-	-	-	0.2	-	1.1	1.3	1.0	0	1
54	3.9	1.1	1.2	1.4	2.7	0.7	3.1	2.2	0.3	0.5	16.2	4.6	1	1
55	0.6	1.5	1.3	4.1	16.0	20.6	5.6	8.0	5.1	18.8	81.9	27.0	4	1
56	1.0	0.5	0.9	0.7	5.0	4.5	5.3	2.0	2.3	4.4	26.4	9.9	1	1
57	-	-	-	-	12.8	-	0.2	-	-	-	13.0	8.0	0	1
58	0.2	0.2	-	0.4	12.6	-	1.2	2.4	0.4	-	17.2	9.4	1	1
59	0.6	0.8	-	0.2	-	-	0.2	-	-	-	1.8	0.6	1	1

Appendix B

Land Use Characteristics Surrounding the Site of Urban Fox Submissions

General Land Use	Land Use Features	
	within 1 km	within 1 km
Commercial/Warehousing	Vacant land network, Railway line, creek	Greenbelt, cemetery
Residential/Warehousing	Vacant land network, Railway line	Rideau River
Residential	Greenbelt, Railway line, Hydro field, creek	
Residential	Greenbelt, Railway line, Hydro field, creek	
Residential	Greenbelt, Railway line, Hydro field, creek	
Residential	Greenbelt, Railway line, Hydro field	Creek
Residential	Vacant land network, Hydro field, creek, large cemetery, garden plots	Railway line
Residential	Greenbelt, vacant land network, Hydro field	
Central Experimental Farm	Passive Recreation Area	Rideau Canal
Residential	Vacant land network, creek, school grounds, cemetery	
Residential	Vacant land network, Railway line	
Residential	Greenbelt, maintained open space, vacant land network, school grounds, Highway	Railway line
Residential	Vacant land network, Railway line, Rideau River	
Residential	Rideau River, school grounds	
Residential	Vacant land network, Rideau River, maintained open space	
Residential/Transportation	Railway junction, vacant land network, maintained open space, Highway	
Commercial/Warehousing	Vacant land network, Railway line, creeks	Greenbelt
Residential	Vacant land network, Greenbelt, Highway, creeks	
Residential	Passive Recreation Area, Ottawa River	
Residential	Passive Recreation Area, Ottawa River	
Residential	Passive Recreation Area, vacant network, school grounds, Highway	Greenbelt
Residential	Greenbelt	

Land Use Characteristics Surrounding the Site of Urban Skunk Submissions

General Land Use	Land Use Features	
	within 1 km	within 2 km
Residential	Vacant land network, Railway line, Greenbelt	
Residential	Vacant land network, Railway line, Greenbelt	
Residential	Vacant land network, Railway line, Greenbelt	
Residential	Vacant land network, Railway line, Greenbelt	
Institutional Grounds	Vacant land network, residential area, Hydro field	
Institutional Grounds	Vacant land network, residential area, Hydro field	
Residential	Vacant land network, Railway line, school grounds, cemetery	
Residential	Vacant land network, Railway line, school grounds, cemetery	
Residential	Vacant land network, passive recreation, Railway line, school grounds, Hydro field	
Residential	Vacant land network, passive recreation, Railway line, school grounds, Hydro field	
Residential	Vacant land network, Railway line, school grounds, cemetery	
Residential	Vacant land network, Railway line, school grounds, cemetery	
Residential	Vacant land network, cemetery	
Residential	Vacant land network, Railway line, school grounds, cemetery	
Residential	Greenbelt, Hydro field	
Residential	Greenbelt, Hydro field	
Residential	Greenbelt, Hydro field	
Residential	Park, school grounds	Vacant land network
Residential	Vacant land network, Railway line	
Institutional Grounds	Vacant land network, residential area	
Residential	Vacant land network, Railway line	
Residential	Vacant land network, Greenbelt, Railway line, passive recreation, Hydro field	
Residential	Vacant land network, Greenbelt, Railway line, passive recreation, Hydro field	
Residential	Vacant land	
Residential/Commercial	Cemetery, school grounds	Vacant land
Residential/Commercial	Passive recreation, vacant land, creek, Railway line	Greenbelt
Residential	Passive recreation, vacant land, Railway line, creek	Greenbelt
Residential	Greenbelt, passive recreation, creek	

Skunk cont'd.

General Land Use	Land Use Features	
	within 1 km	within 1 km
Residential	Active recreation, maintained open space, institutional grounds	
Residential	Active recreation, maintained open space, institutional grounds	
Residential	Vacant land network, passive and active recreation, institutional grounds	
Residential	Passive recreation, institutional grounds, extensive cemetery	
Institutional grounds	Passive recreation	Ottawa River
Residential	Institutional grounds, vacant land	
Residential	Passive recreation, extensive cemetery, active recreation, institutional grounds	
Institutional grounds	Ottawa River, passive recreation	
Institutional grounds	Ottawa River, passive recreation	
Residential	Maintained open space, passive recreation, Ottawa and Rideau Rivers	
Residential	Maintained open space, passive recreation, Ottawa River	
Residential	Passive and active recreation, Ottawa and Rideau Rivers	
Residential	Passive recreation, cemetery	Rideau River
Residential	Cemetery	Rideau River
Residential	Passive recreation, cemetery	Ottawa River
Residential	Passive recreation, Ottawa and Rideau Rivers	
Parkland	Passive recreation, Ottawa River	
Residential	Passive recreation, Highway	Ottawa River
Residential/Commercial	Highway	
Residential/Commercial	Passive and active recreation, vacant land, Highway	
Residential/Commercial	Passive and active recreation, creek, Highway, Hydro field	
Residential/Commercial	Passive and active recreation, Highway	
Residential/Commercial	Passive recreation	Experimental Farm
Residential	Highway, maintained open space, passive recreation	
Residential	Passive recreation, creek, Experimental Farm	
Residential	Passive recreation, Experimental Farm, creek	
Residential	Passive and active recreation, reservoir	
Passive Recreation	Residential area, active recreation, Experimental Farm	
Passive Recreation	Residential area, active recreation, Experimental Farm	
Residential/Commercial		Experimental Farm

Skunk cont'd.

General Land Use	Land Use Features	
	within 1 km	within 1 km
Commercial/Warehousing	Vacant land network, Greenbelt, creek, cemetery	
Residential	Vacant land network, Railway line, Rideau River	
Residential/Commercial/Warehousing	Vacant land network, Railway line	Rideau River
Residential	Vacant land network, creek, school and institutional grounds, passive recreation	
Commercial/Warehousing	Vacant land network	Rideau River
Residential	Greenbelt, vacant land network	
Residential	Greenbelt, vacant land network	
Residential	Greenbelt, vacant land network	
Commercial	Residential area, maintained open land, vacant land, creek, Highway	Greenbelt
Residential	Maintained open space, vacant land, creek, Highway	Greenbelt
Residential	Greenbelt, vacant land, Highway	
Residential	Greenbelt, vacant land, passive recreation area, creek, Railway line	
Residential	Greenbelt, vacant land, passive recreation area, creek, Railway line	
Residential/Commercial/Warehousing	Vacant land network, Railway line, creek, Highway, maintained open space	
Residential	Vacant land network, institutional grounds	
Residential	Vacant land network, Highway, maintained open space, creek	
Residential	Vacant land network, institutional grounds	
Residential	Greenbelt, active recreation area, vacant land network, creek	
Residential	Greenbelt, vacant land, creek	
Residential/Commercial	Passive recreation, Railway line, maintained open space, Highway, school grounds	Rideau River
Residential/Commercial	Passive recreation, Railway line, maintained open space, Highway, school grounds	Rideau River
Residential	Active and passive recreation, Rideau River, maintained open space, school grounds	
Institutional grounds	Rideau River, active and passive recreation, maintained open space	
Residential	Vacant land network, Railway line, maintained open space	
Residential	Vacant land network	Rideau River
Residential	Vacant land network, active recreation	Greenbelt

Skunk cont'd.

General Land Use	Land Use Features within 1 km	within 1 km
Warehousing/ Commercial	Maintained open space, vacant land network	
Transportational/ Warehousing	Railway lines, vacant land	
Residential	Active recreation, institutional grounds, vacant land, Rideau River	
Residential	Active recreation, institutional grounds, vacant land	Rideau River
Residential	Passive recreation, maintained open space, Ottawa River	

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