

BEHAVIOR, MOVEMENTS, AND DEMOGRAPHICS OF RABID RACCOONS IN ONTARIO, CANADA: MANAGEMENT IMPLICATIONS

Authors: Rosatte, Rick, Sobey, Kirk, Donovan, Dennis, Bruce, Laura, Allan, Mike, et al.

Source: Journal of Wildlife Diseases, 42(3) : 589-605

Published By: Wildlife Disease Association

URL: <https://doi.org/10.7589/0090-3558-42.3.589>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

BEHAVIOR, MOVEMENTS, AND DEMOGRAPHICS OF RABID RACCOONS IN ONTARIO, CANADA: MANAGEMENT IMPLICATIONS

Rick Rosatte,^{1,4} Kirk Sobey,¹ Dennis Donovan,¹ Laura Bruce,¹ Mike Allan,¹ Andrew Silver,¹ Kim Bennett,¹ Mark Gibson,¹ Holly Simpson,¹ Chris Davies,² Alex Wandeler,³ and Frances Muldoon³

¹ Ontario Ministry of Natural Resources, Rabies Research and Development Unit, Trent University, Science Complex, PO Box 4840, Peterborough, Ontario K9J 8N8, Canada

² Ontario Ministry of Natural Resources, Wildlife Research and Development Section, 300 Water St., Peterborough, Ontario K9J 8N8, Canada

³ Canadian Food Inspection Agency, Ottawa Laboratory Fallowfield, PO Box 11300, Station H, Nepean, Ontario K2H 8P9, Canada

⁴ Corresponding author (email: rick.rosatte@mnr.gov.on.ca)

ABSTRACT: During 1999–2003, 127 cases of raccoon variant rabies were reported in raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) in Ontario, Canada. Raccoons accounted for 98% (125/127) of the reported cases with behaviors/conditions including aggression, fighting with dogs, ataxia, vocalizations, appearance of being sick, and the presence of porcupine (*Erethizon dorsatum*) quills. Seventy-eight percent of the rabid raccoons were adults. Juveniles were underrepresented (22%) compared with the adult/juvenile ratios found in nonrabid Ontario raccoon populations. Of the known aged raccoons, 83% were ≤ 3 yr of age, and 22% of the rabid adult female raccoons had evidence of having had a litter during the year in which they were found to be rabid. The majority of rabid raccoons were reported during the fall, winter, and spring, suggesting a relationship between raccoon behavioral activities such as denning and breeding and the timing of rabies outbreaks. Multiple cases of raccoon rabies occurred at several barns, suggesting that those structures serve as focal points of rabies transmission as a result of denning activities. Movements of five rabid raccoons (range 1,564–4,143 m) were not different from movements of nonrabid raccoons in Ontario. Sixty-six percent of the rabid animals were submitted by government staff, stressing the importance of those agencies in rabies control and surveillance operations. Increased knowledge of the behaviors of rabid raccoons should assist in the development of management strategies for rabies.

Key words: *Procyon lotor*, rabid raccoon, rabid raccoon behavior, rabies, raccoon, raccoon rabies.

INTRODUCTION

More than 57,400 animals were reported with rabies in Ontario, Canada, during 1954–2003 (Canadian Food Inspection Agency, unpubl. data). The majority (62%) of those cases were red foxes (*Vulpes vulpes*, 43%) and striped skunks (*Mephitis mephitis*, 19%), and most of those were infected with an Arctic fox variant of rabies virus (Johnston and Beauregard, 1969; MacInnes, 1987; Rosatte, 1988; Nadin-Davis et al., 1994; Canadian Food Inspection Agency, unpubl. data). Fortunately, the Arctic fox strain of rabies has nearly been eliminated from Ontario with an oral rabies vaccination campaign targeting red foxes (MacInnes, 1987; Johnston et al., 1988; Rosatte

et al., 1992a, b, 1993; MacInnes et al., 2001). In July 1999, the first confirmed case of the raccoon variant of rabies virus was reported in Ontario, Canada (Wandeler and Salsberg, 1999; Rosatte et al., 2001). Since that time, 127 cases (125 raccoons [*Procyon lotor*], two skunks) were confirmed positive with the raccoon variant of rabies (to 31 December 2003; Figs. 1, 2).

The Ontario Ministry of Natural Resources (OMNR) has implemented a raccoon rabies control program utilizing point infection control (PIC), trap-vaccinate-release (TVR), and oral rabies vaccination (ORV) tactics to attempt to contain and eliminate the disease (Rosatte et al., 2001). Behavior and location data for raccoons confirmed positive with the raccoon var-

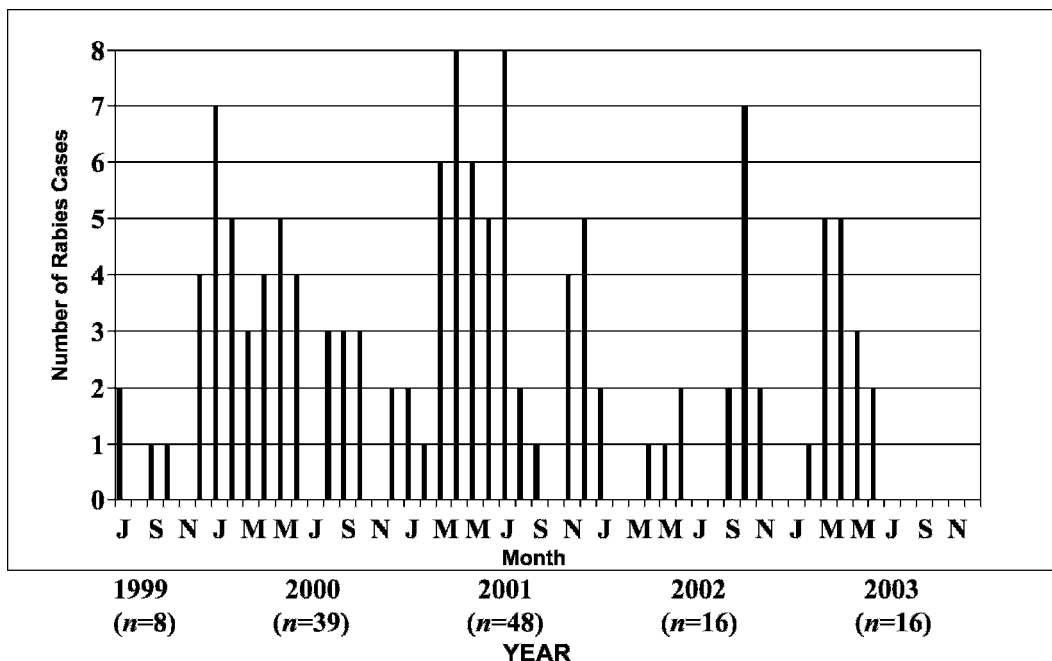


FIGURE 1. Cumulative monthly number of raccoon rabies cases in Ontario, Canada, 1999–2003. Figure includes 127 total cases—125 cases were in raccoons; 2 of the 48 cases during 2001 were in skunks. Case occurrence is based on date the specimen was acquired from the field. n =number of rabies cases per year.

iant of rabies virus, as well as the circumstances relating to the acquisition of those animals were collected while these rabies control programs were conducted. In this paper, we analyze those data and provide recommendations for the management of raccoon rabies in Ontario.

MATERIALS AND METHODS

This study focused on the analysis of data from 127 raccoons and skunks collected from eastern Ontario, Canada (44°45'N, 75°50'W), during 1999–2003 that were confirmed positive with the raccoon variant of rabies. Specimens were tested for rabies with the fluorescent antibody technique at the Canadian Food Inspection Agency (CFIA), Ottawa Laboratory, Nepean, Ontario (Webster and Casey, 1988). The variant of rabies virus was determined with a panel of monoclonal antibodies. Characteristics of rabid raccoon behaviors and circumstances relating to the collection of survey and suspect rabid animals were gathered from a variety of sources, including residents of eastern Ontario, as well as federal, provincial, and municipal govern-

ment employees. Complete information sets were not available for all rabid animals in the sample.

To determine the age of rabid and nonrabid raccoons, canine teeth were extracted from specimens and processed and aged according to Johnston et al. (1987). Age structure of nonrabid raccoons in eastern Ontario was derived by averaging 5 yr of postaerial baiting surveillance data (1998–2002) across year classes to derive a representative age class distribution ($n=1,242$). Distribution of age classes of rabid and nonrabid raccoons was compared with a Kolmogorov-Smirnov two-sample test. This test was also used to test for differences in age class structure between male and female raccoons that were rabies positive. Statistical analyses were completed with the use of Statistica 6.0 (StatSoft Inc., 2004).

When a raccoon was recaptured in a given year, several values were possible for time and distance moved between captures. The maximum distance traveled was used in the analyses (to avoid pseudoreplication). Lack of replication for rabid raccoon movement distances precluded an inferential statistical analysis. Instead, movement distances and time intervals for different nonrabid raccoon

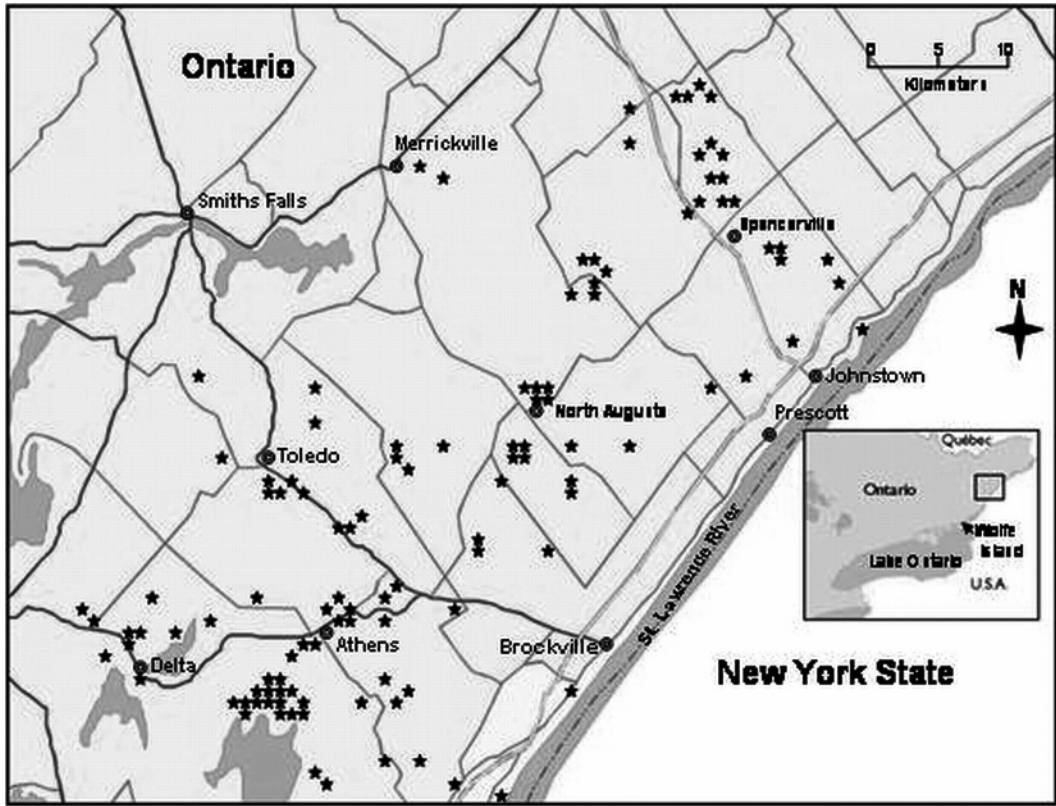


FIGURE 2. Spatial distribution of raccoon variant rabies cases in Ontario, 1999–2003. Six cases of raccoon strain rabies occurred during 1999–2000 on Wolfe Island, shown in the inset. Wolfe Island ($44^{\circ}10'N$, $76^{\circ}25'W$) is approximately 35 km SE of Brockville, Ontario. Case locations are approximate to protect the privacy of landowners. Some stars represent multiple cases at that location.

demographics were determined with descriptive statistics, to which we compared the movement of rabid raccoons.

A multiway frequency table was created for rabies-positive raccoons that included data on age, sex, and month of collection. Log-linear analysis was performed to test relationships among variables in this contingency table. The objective of using a contingency table was to reflect various main and interaction effects that add together in a linear fashion resulting in the observed table of frequencies and to find the simplest model that adequately explains the data (Fienberg, 1970; Bishop et al., 1975; Knoke and Burke, 1983; Christensen, 1990). Increasingly complex models were fitted to the observed data until there was no significant improvement in the goodness-of-fit statistic. The goodness of fit of a particular model was evaluated via the maximum likelihood ratio chi-square statistic. This test evaluated whether the expected cell frequencies in the model being considered were

significantly different from the observed cell frequencies. When this was true, the model being considered for the frequency table was rejected.

Associations between symptomatic manifestations of raccoon rabies or circumstances and raccoon demographics (age and sex) were uncovered by correspondence analysis (CA). Correspondence analysis was designed to analyze multiway frequency tables containing some measure of association between rows (demographics) and columns (symptoms or circumstances) of categorical variables (Greenacre, 1984). The primary purpose of this technique was to produce a simplified representation of the information in complex frequency tables; CA is a method of decomposing the overall calculated chi-square statistic by identifying a small number of dimensions in which the deviations from the expected values can be represented (StatSoft Inc., 2004). In decomposing the chi-square statistic, the inertia value was calculated as the

chi-square value divided by the total number of cases. Symptom and occurrence data were assembled opportunistically from reports surrounding positive cases. Unfortunately, no established protocol had been developed a priori by which to collect this information, and the initial multiway table contained too many zero values to permit analysis. Standardized categories of symptoms or circumstances were developed post hoc, to which all rabies-positive raccoons could be assigned. Standardization of symptoms was based on the premise of the disease manifesting itself as either Dumb, Furious, or Normal. Classification was as follows: Dumb included friendly, approachable, sick, unhealthy, ataxia, impaired mobility, loss of muscle coordination, circling, and staggering; Furious included fighting with domestic animals, fighting with livestock, impaled with porcupine quills (fighting with other wildlife), attacking inanimate objects, and acting aggressively toward humans; Normal meant the animal did not display any signs or symptoms of the disease. Although the majority of rabies-positive cases fell into one of these three categories, some reports also included comments on vocalization including abnormal chirping, peeping, hissing, squealing, chattering, and growling. Therefore, categories of Dumb-Vocalization, Furious-Vocalization, and Normal-Vocalization were also created. Less commonly, a combination of symptoms (i.e., ataxia, porcupine quills, hissing) were reported. The final two categories created were Furious-Dumb and Furious-Dumb-Vocalization. This standardized manifestation of symptoms data set was used in the CA analysis.

RESULTS

Submission of specimens

Of the 127 cases of raccoon variant rabies reported during July 1999 and 31 December 2003, 125 (98.4%) were in raccoons and two (1.6%) were in skunks (Figs. 1, 2). Sixty-six percent (82/125) of the rabid raccoons were collected and submitted by government (OMNR, Municipal Health Units, CFIA) staff during rabies control operations (OMNR staff submitted 51% [64/125] of the rabid animals). Eighteen of those were collected and submitted by government staff after notification of the location of a potentially rabid animal by a member of the public.

The public submitted 34% (43/125) of the specimens (Table 1).

Eighteen percent (22/125) of the rabies-positive raccoons were live trapped by OMNR staff during rabies control operations during 1999–2003 (Table 1). In addition, 36% (45/125) of the rabies-positive raccoons were shot (primarily by residents), 30% (37/125) were found dead, and 9% (11/125) were collected as road kill (collision with automobiles) (Table 1). About 24% (30/125) of the rabid raccoons were found in residential yards, and 21% (26/125) were found in close association with barns (Table 1).

Dimensions extracted from CA of the raccoon rabies surveillance methods and demographic data explained 93.5% of the inertia, with approximately 10% more of the inertia captured on dimension 1. This dimension distinguished between adults and juveniles with respect to surveillance methods for detecting rabies-positive raccoons. Cosine² values of 0.80 and 0.82 revealed that live trapping or the killing of suspicious raccoons, respectively, as methods to detect rabid raccoons were strongly correlated with dimension 1. This was interpreted to indicate that rabid adult raccoons, particularly adult females (AFs), were more likely to be detected by killing and testing suspect animals than by live trapping. The distribution of points related to finding raccoons dead or live trapping on the right of the vertical axis suggests these were more important methods for detecting rabid juveniles, with some difference between males and females suggested by positioning of points above and below the horizontal axis. Cosine² values of 0.89 and 0.58 for AFs and adult males (AMs), respectively, revealed stronger correlation with dimension 2. The positioning of these points above and below the horizontal axis indicated a difference in surveillance methods to detect rabies-positive cases in these two demographics. Road kill and finding dead raccoons were also more strongly correlated with dimension 2 with Cosine²

TABLE 1. Circumstances that led to the submission of rabid raccoons for diagnostic rabies testing; Percent positive (number of positives/number tested).

Age/sex ^a	% Positive for rabies								Government submitted specimen ^c
	Live trapped	Shot	Road kill	Found in/near barn	Found in residential yard ^b	Found alive	Found dead	Public submitted specimen	
AM	19 (7/37)	41 (15/37)	14 (5/37)	22 (8/37)	19 (7/37)	73 (27/37)	27 (10/37)	27 (10/37)	73 (27/37)
AF	17 (8/46)	37 (17/46)	7 (3/46)	17 (8/46)	28 (13/46)	74 (34/46)	26 (12/46)	33 (15/46)	67 (31/46)
A?	0 (0/14)	29 (4/14)	7 (1/14)	36 (5/14)	21 (3/14)	36 (5/14)	64 (9/14)	50 (7/14)	50 (7/14)
JM	33 (4/12)	25 (3/12)	8 (1/12)	17 (2/12)	25 (3/12)	83 (10/12)	17 (2/12)	33 (4/12)	67 (8/12)
JF	25 (3/12)	25 (3/12)	8 (1/12)	25 (3/12)	17 (2/12)	67 (8/12)	25 (4/12)	42 (5/12)	58 (7/12)
J?	0 (0/3)	67 (2/3)	0 (0/3)	0 (0/3)	33 (1/3)	100 (3/3)	0 (0/3)	33 (1/3)	67 (2/3)
?M	0 (0/1)	100 (1/1)	0 (0/1)	0 (0/1)	100 (1/1)	100 (1/1)	0 (0/1)	100 (1/1)	0 (0/1)
ALL	17.6 (22/125)	36.0 (45/125)	8.8 (11/125)	20.8 (26/125)	24.0 (30/125)	70.4 (88/125)	29.6 (37/125)	34.4 (43/125)	65.6 (82/125)

^a AM = adult male; AF = adult female; A? = adult unknown; JM = juvenile male; JF = juvenile female; J? = juvenile unknown; ?M = unknown male.

^b Residential yards primarily included houses associated with farms.

^c Government represents Ontario Ministry of Natural Resources, Municipal Health Unit, or Canadian Food Inspection Agency staff who collected or submitted the specimen or were involved in the acquisition or collection of the specimen (i.e., it was not acquired or collected solely by a member of the public).

values of 0.77 and 0.58, respectively. With respect to these two surveillance methods, this observation was interpreted to indicate that AMs were more likely to be detected through collection of road kill, whereas rabid AFs were more likely to be found dead.

Correspondence analysis on source of rabies-positive sample submission captured 94.5% of inertia along dimension 1. The small amount of inertia (5.6%) meant very little difference in the distribution of demographic or submission points along the vertical axis. Cosine² values revealed little correlation of points with dimension 2, but strong correlation of all points with dimension 1. Results were interpreted to indicate that joint submission of positive cases differed from OMNR or public with respect to AMs along dimension 1. The demographic AM was the most prominent among joint submissions by the public, OMNR, and Ministry of Health. Submission of other demographic cohorts by OMNR or the public were relatively similar, led by AFs, then AMs, and finally juveniles.

Age and sex distribution of rabies raccoons

Teeth were available for age estimation from 89 of the 125 rabid raccoons. Of those, 21% (19/89) were juveniles and 79% (70/89) were greater than 1 yr old (Fig. 3). Eighty-three percent (74/89) were 3 yr of age or younger (Fig. 3). Of the raccoons for which a tooth was available for age estimation, and the sex of the raccoon was known ($n=76$), no difference was found between the number of males ($n=37$) and the number of females ($n=39$) that were reported as rabid ($P>0.05$) (Fig. 4).

Adult raccoons accounted for 78% (97/125) of the reported rabies cases (raccoon variant in raccoons) during 1999–2003 ($P<0.05$); 22% (27/125) were juveniles (young of the year), and the age was unknown for one male raccoon (Table 2). Of the adult raccoons reported rabid, the sex was known for 83 individuals. Fifty-

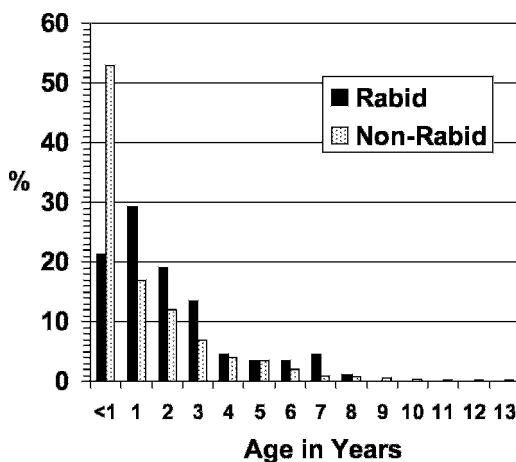


FIGURE 3. Age distribution of a sample of rabid and nonrabid raccoons in Ontario. The number of nonrabid and rabid raccoons in the sample was 1,242 and 89, respectively. Nonrabid samples were collected during 1998–2002; rabid specimens were collected from 1999 to 2003.

five percent (46/83) of those were AF raccoons and 22% (10/46) of the AFs were lactating or had other evidence of having recently produced a litter of young (e.g., enlarged hairless nipples; Table 2). Forty-five percent (37/83) of the rabid adult raccoons were males (for which the sex was known). No significant difference in rabies-positive age class structure between male and female raccoons was detected ($P>0.10$). Of the juvenile raccoons that

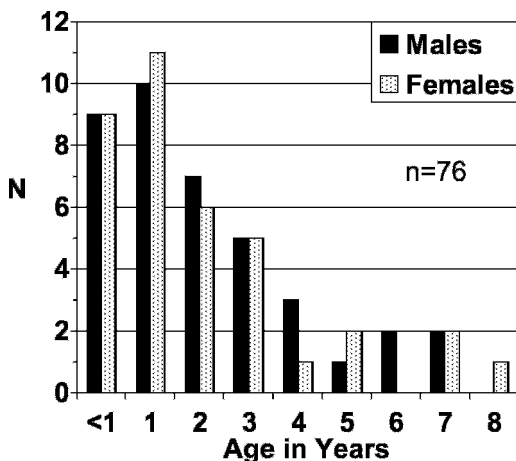


FIGURE 4. Sex and age distribution of a sample of rabid raccoons in Ontario, 1999–2003.

TABLE 2. Monthly cases of rabid raccoons by age and sex category in Ontario during 1999–2003.^a

Month	No. of rabid raccoons							All (n)
	Adult males (n)	Adult females ^b (n)	Juvenile males (n)	Juvenile females (n)	Adult unknown (n)	Juvenile unknown (n)	Unknown male	
January	4	7	0	1	1	0	0	13
February	2	0	2	1	0	0	0	5
March	5	5	2	2	2	0	0	16
April	5	6	1	0	5	0	0	17
May	2	7	0	0	3	0	0	12
June	6	7	0	0	1	0	0	14
July	0	4	2	0	2	1	0	9
August	3	1	0	1	0	0	0	5
September	2	3	2	0	0	0	0	7
October	2	3	2	2	0	1	1	11
November	1	1	1	2	0	0	0	5
December	5	2	0	3	0	1	0	11
Total	37	46	12	12	14	3	1	125

^a On the basis of collection date of the animal.^b Ten of 46 adult female raccoons were lactating or had evidence of producing a litter of young that year.

were reported rabid and the sex was known, 50% (12/24) were males and 50% (12/24) were females (Table 2).

Rabies-positive age class data was pooled with respect to sex and compared to nonrabid age class data (Fig. 3). Age structure of rabies-positive raccoons was significantly different from the age structure of nonrabid raccoons collected in eastern Ontario as part of postaerial baiting surveillance ($P < 0.001$). A large sample size ($n = 1,242$) of nonrabid raccoons from 5 consecutive yr (1998–2002) of sampling, revealed very few raccoons in Ontario older than 8.5 yr of age. Rabies-positive raccoons have not been reported in these older age classes. The majority (83%) of rabies-positive raccoons detected in Ontario were less than 3.5 yr of age. Animals less than 3.5 yr of age also formed the bulk of the nonrabid raccoon population in Ontario. The dominant age class of nonrabid raccoons was less than 1-yr-old (juvenile), which made up over 50% of the population (Fig. 3). This was different ($P < 0.001$) from the age distribution among rabid raccoons, in which juveniles accounted for only 21.3% of the sample (Fig. 3). The dominant age class for rabid raccoons (29%) was young adults (≥ 1 and

< 2 yr), whereas this age class comprised less than 20% of the nonrabid raccoon population (Fig. 3).

Monthly prevalence of rabid raccoons in relation to raccoon age and seasonal raccoon behavior

Sixty-three percent (79/125) of the cases of raccoon strain rabies (in raccoons) occurred during the denning and breeding/parturition periods (November–May, winter/spring; Table 2 and Fig. 1). Only 22% (28/125) of the cases occurred from June to August and 14% (18/125) in September and October (Table 2 and Fig. 1). Log-linear analysis revealed that the best model to fit the age, sex, month, contingency table for rabies-positive raccoons in Ontario consisted of the interaction between age and month (Table 2). Numbers of rabies-positive juvenile raccoons were lowest from April to June. During this time, reported incidence of rabies in adults was at its highest. From July to November, the number of rabies-positive juveniles increased, while cases in adults decreased significantly relative to other months. During November, cases of rabies in adults fell below that reported in juvenile raccoons. December and January marked

TABLE 3. Percentage of rabid raccoons that exhibited a specific behavior or condition at the time of collection in eastern Ontario.^a Percent positive (number of positives/number tested).

Age/sex ^b	% Positive for rabies						
	Aggressive ^c	Appeared sick or unhealthy	Fought with a dog	Abnormal vocalization ^d	Ataxia/mobility impaired ^e	Impaled with porcupine quills	Normal behavior
AM	22 (8/37)	24 (9/37)	8 (3/37)	11 (4/37)	19 (7/37)	11 (4/37)	14 (5/37)
AF	33 (15/46)	11 (5/46)	20 ^f (9/46)	15 (7/46)	13 (6/46)	13 (6/46)	9 (4/46)
A?	7 (1/14)	14 (2/14)	0 (0/14)	7 (1/14)	14 (2/14)	29 (4/14)	0 (0/14)
JM	8 (1/12)	25 (3/12)	8 (1/12)	17 (2/12)	17 (2/12)	17 (2/12)	17 (2/12)
JF	17 (2/12)	33 (4/12)	0 (0/12)	17 (2/12)	17 (2/12)	0 (0/12)	17 (2/12)
J?	33 (1/3)	33 (1/3)	33 (1/3)	0 (0/3)	0 (0/3)	0 (0/3)	0 (0/3)
?M	100 (1/1)	0 (0/1)	0 (0/1)	0 (0/1)	0 (0/1)	0 (0/1)	0 (0/1)
All	23.2 (29/125)	19.2 (24/125)	11.2 (14/125)	12.8 (16/125)	15.2 (19/125)	12.8 (16/125)	10.4 (13/125)

^a Individual raccoons with one to several of the above noted behaviors; 37 of the rabid raccoons were found dead.
^b AM=adult male; AF=adult female; A?=adult unknown; JM=juvenile male; JF=juvenile female; J?=juvenile unknown; ?M=unknown male.
^c Included aggression toward humans, animals, or inanimate objects.
^d Abnormal vocalizations included chirping, peeping, hissing, squealing, chattering, and growling.
^e Ataxia or impaired mobility included loss of muscle coordination, circling, wandering, staggering, and imbalance.

a plateau in rabies cases in juveniles, but an increase in adult raccoons. During February, rabies cases in adults again fell below that of juveniles, which peaked in March. The trend for total number of rabid raccoon cases closely tracks the trend for adults, suggesting that this segment of the population was largely responsible for the observed seasonal pattern of rabies incidence in Ontario. This conclusion is further reinforced by the relative contribution of the juvenile cohort (50%) in the nonrabid raccoon population; juvenile raccoons only represented 22% of the rabid animal sample.

Clinical symptoms of raccoons with the raccoon variant of rabies

The most common symptoms or behaviors/conditions noted among the 125 rabid raccoons were aggression (23%), appearance of being sick or unhealthy (19%), impaired mobility or ataxia (15%), fighting with dogs (11%), abnormal vocalizations (13%), and the presence of embedded quills (13%) (Table 3). Ten percent of the rabid raccoons displayed no abnormal behaviors. Thirty-three percent of the rabid AF raccoons displayed

aggressive behavior (Table 3). The most common manifestations of raccoon rabies in Ontario were, in order of importance, Normal, Furious, and Dumb, with apparent differences across demographics. With the use of CA, the first two dimensions extracted from the symptom manifestation and raccoon demographic frequency table explained 85.2% of the inertia, with dimension 1 accounting for 57.0% of the total. Dimension 1 is characterized by AF on the right of the vertical axis and all other demographics to the left. Juvenile females are in the most extreme left position with male raccoons in a more intermediary position. Similarly, Furious manifestations of rabies symptoms are located to the right of the vertical axis along dimension 1, whereas Dumb manifestations of symptoms occur to the left. Cosine² values can be interpreted as the correlation of the respective point to the dimension being considered (StatSoft Inc., 2004). Adult and juvenile female raccoons had a high degree of correlation (0.94 and 0.77, respectively) with dimension 1. Similarly, Furious, Furious-Dumb-Vocal, Dumb, and Dumb-Vocal were strongly correlated with dimension 1, having values

of 0.83, 0.75, 0.88, and 0.91, respectively. This suggests that much of the total inertia in dimension 1 is due to differences in adult and juvenile female raccoons and that manifestation of Dumb-type symptoms are relatively typical of juvenile female raccoons, whereas Furious forms of the disease are more characteristic of AFs. Cosine² values for AM and juvenile male raccoons of 0.49 and 0.82, respectively, indicated a stronger correlation with dimension 2 than dimension 1. Normal, Normal-Vocal, and Furious-Dumb manifestations of rabies symptoms had Cosine² values of 0.70, 0.72, and 0.69, respectively, for dimension 2. This was interpreted to indicate that whereas rabid male raccoons might typically not exhibit manifestations of the disease (appeared Normal), abnormal vocalization might be characteristic of juvenile males (as for juvenile females), but AMs could also exhibit some mix of Dumb and Furious forms of the disease, as suggested by the relatively lower Cosine² (0.49) along dimension 2.

In Ontario during 1999–2003, two of the 125 rabid raccoon cases resulted in human postexposure treatments because of human contact with the rabid raccoons. One exposure occurred when a family handled a dead raccoon brought home by the family dog, whereas the other exposure occurred as a result of a rabid wild raccoon biting a young girl.

Behavior of rabid raccoons found with porcupine quills

From July 1999 to 31 December 2003, a total of 16 of the rabies-positive raccoons (raccoon variant) in Ontario were documented with porcupine quills embedded in the facial area, body, or both (Table 3). Eighty-eight percent of those with quills were adult raccoons (14/16; Table 3). Of the rabid raccoons with quills, 25% (4/16) exhibited aggressive behavior toward humans, animals, or inanimate objects, and two of those fought with dogs. Twenty-five percent (4/16) of the rabid raccoons with

quills appeared sick or unhealthy. Of those four raccoons, two were vocal and two exhibited ataxia.

Evidence of intraspecific transmission of raccoon rabies

In eight instances, two to four rabid raccoons were found either in individual barns or in close association with barns on farms in eastern Ontario during 1999–2003. About 77% (17/22) of those rabid raccoons were found from January to May, when raccoons congregate in barns for denning and breeding activities. The timing (6–53 days between cases) and location of those cases suggest transmission of rabies among raccoons. On one occasion, 10 raccoons were live trapped from one barn. Only one (case 53) of those was diagnosed rabies positive; however, some of those might have been incubating rabies.

Movements of rabid and nonrabid raccoons

Five raccoons that were live trapped, ear tagged, and released during OMNR rabies control and surveillance programs during 1999–2002 were later submitted for rabies testing. All five were positive for the raccoon variant of rabies. Movements from the time of initial release and collection for rabies testing ranged between 1,564 and 4,143 m, with a median value of 1,689 m (Table 4). Movement distance data of nonrabid adult raccoons captured in eastern Ontario during 1999–2002 was nonnormally distributed and was positively skewed. In all four yr, nonrabid adult raccoons were observed to typically move less than 1.5 km, although several individuals were observed to move distances of more than 5.1 km during three of the four recapture yr. Median movement distances for the different age and sex classes of nonrabid raccoons ranged between 700 and 919 m (Table 4). Comparing movement distances between rabid and nonrabid raccoons for a given demographic, it was observed that the movement of rabid raccoons fell within

TABLE 4. Movement distances of rabid and nonrabid raccoons captured during rabies control programs in Ontario during 1999–2002.

Rabid raccoons ^a				
Age/sex ^b	Initial capture date	Date collected for rabies testing	Time from initial capture date to date reported rabid (days)	Distance between initial capture location and where animal was acquired for rabies testing (m)
AM ^c	7 July 1999	30 December 1999	176	1,689
AF ^d	30 September 1999	23 October 2000	389	1,564
AF ^d	28 September 1999	18 April 2001	568	4,143
JM ^c	29 August 2002	12 September 2002	14	1,622
AF ^d	3 November 1999	30 October 2002	1,092	1,762
Nonrabid raccoons				
Age/sex ^c	Year of initial capture	Subsequent capture year	Time between captures (days, median, min/max)	Distance moved (m, median, min/max)
AM (<i>n</i> =51)	1999	1999	3 (0–10)	700 (0–3,160)
AF (<i>n</i> =13)	1999	2000	266 (229–296)	781 (86–14,380)
AF (<i>n</i> =24)	1999	2001	648 (559–686)	908 (53–9,465)
AF (<i>n</i> =13)	1999	2002	1069 (940–1,182)	919 (16–42,112)
JM (<i>n</i> =30)	2002	2002	12 (1–66)	366 (0–1,742)

^a Movement distance of five raccoons from the date they were initially captured and released during raccoon rabies control operations in Ontario until they were collected and subsequently reported as positive for the raccoon variant of rabies.

^b Age refers to age of animal when it was collected for rabies testing: AM=adult male, AF=adult female, JM=juvenile male.

^c Vaccinated intramuscularly with IMRAB® during trap-vaccinate-release operations.

^d Collected during surveillance operations—not vaccinated against rabies.

^e Age refers to age of animal when it was live trapped during the subsequent time period.

the mid to low range of maximum distances moved by nonrabid raccoons (Tables 4). However, the movement distances for every ear-tagged raccoon that became rabies positive exceeded the median movement distance for nonrabid raccoons of the same demographic (Tables 4).

DISCUSSION

Submission of specimens

A well-organized surveillance program is crucial for the early detection of rabies in an area to allow for a rapid control response. A proactive and well-publicized raccoon rabies control program in Ontario ensured that staff were in the field and were vigilant for animals that acted abnormally. Media coverage of the rabies

programs in Ontario was extensive, so residents were aware of the threat and were also vigilant and responsive in the submission of abnormally acting animals for rabies testing (Rosatte et al., 2001). In Ontario, Government staff submitted the majority (66%) of the raccoon variant cases during 1999–2003. The OMNR staff submitted more than half of the rabid specimens. Without OMNR staff in the field, up to 50% of the cases could have gone unreported, with additional infections occurring from those animals. The challenge for the future as terrestrial wildlife rabies is eliminated in Ontario is to maintain surveillance or presence in the field for the early detection of a rabies reinvasion. Also, of critical importance is that 34% of the rabid raccoons were submitted by the public, emphasizing the

importance of publicizing rabies outbreaks.

Eighteen percent of the rabies-positive raccoons were live trapped by OMNR staff during rabies control operations in Ontario during 1999–2003. Thirty-six percent (8/22) of those raccoons exhibited clinical symptoms of rabies. This indicates that raccoons in the later stages of rabies infection can be live trapped during rabies control operations.

In Ontario, 30% of the rabid raccoons were found dead (usually in or near a barn); 9% were collected as road kill. In the southeast and mid-Atlantic US, 3–6% of road-killed raccoons were rabid (Winkler and Jenkins, 1991). In Ontario, searching for rabid animals in barns appears to be more effective than collecting road kill during a rabies outbreak. About 24% (30/125) of the rabid raccoons in Ontario were found in residential yards, and 21% were found in close association with barns. Similarly, in the southeastern US, 24–39% of the rabies cases were found in yards during daylight (Winkler and Jenkins, 1991). Again, this stresses the importance of having ever-vigilant members of the public report abnormal behavior of animals for early detection of rabies in an area and having a resultant rapid control response.

Age and sex distribution of rabid raccoons

Seventy-eight percent of the rabid raccoons in Ontario during 1999–2003 were adults. Only 22% were juveniles. In Virginia, adult raccoons were more often positive than juveniles (Hubbard, 1985), but in the mid-Atlantic region, there was no difference in rabies prevalence between adult raccoons compared with juveniles (Jenkins and Winkler, 1987; Jenkins et al., 1988). The low percentage of rabid juvenile raccoons detected during rabies control operations is in contrast to the percentage of juveniles normally found in Ontario in the absence of raccoon rabies. In Barrie, Ontario, juvenile raccoons represented 38% of a sample of 700

raccoons during 1993–94 (Rosatte, 2000). Similarly, in Niagara Falls, Ontario, juveniles ranged between 33% and 42% of the population during 1994–97 (Rosatte, 2000). Where samples were available for aging, 83% of the rabid raccoons in Ontario during 1999–2003 were 3 yr of age or less. In Barrie, Ontario, 78% of raccoons sampled were 3 yr of age or less. In Barrie, 38% were juveniles and 12% were 1 yr of age, whereas in this study, 22% of the rabid raccoons were juveniles and 29% were 1 yr old. Obviously, juveniles were underrepresented in the rabies-positive sample, whereas 1-yr-old raccoons were overrepresented. The reason for this is unclear. Before raccoon rabies entered eastern Ontario in 1999, juveniles represented 42% and 31% of raccoons ($n=3,985$ different raccoons) caught during TVR operations during 1995 and 1998, respectively. After raccoon rabies was reported in eastern Ontario, juveniles accounted for 30–38% of the raccoons captured (11,526 different raccoons) during TVR operations in 1999–2001. Similarly, juvenile raccoons accounted for 30% and 38% of the different raccoons ($n=1,922$) processed during PIC operations in the raccoon rabies outbreak area during 2001 and 2003 (Rosatte, unpubl. data). Obviously, the few juvenile raccoons reported rabid in Ontario was not because of insufficient numbers of juvenile raccoons being present in the population during 1999–2003 because significantly more juveniles were in the nonrabid samples as in the rabies-positive sample. In fact, on the basis of surveillance samples from the raccoon rabies area of Ontario (Fig. 3), over half of the potential host population was juveniles. Perhaps the maternal rabies antibody passed on to juveniles from immunized AF raccoons is playing some role in protecting juvenile raccoons from rabies; rabies-neutralizing antibody has been detected in unvaccinated wild raccoons in Ontario (Rosatte et al., 1990). Another possibility is that juvenile raccoons are being infected with rabies in

the maternal den and die before they are old enough to exit the den and be noticed by humans.

No difference could be detected in the number of rabid male raccoons compared with the number of rabid females (adults or juveniles) in Ontario. Similarly, in Florida, no significant difference was noted in the prevalence of rabies in male or female raccoons (Bigler et al., 1973). However, in the mid-Atlantic region, rabies prevalence was higher for female than male raccoons (Jenkins and Winkler, 1987), and in Virginia, more females were rabies positive (Hubbard, 1985). The majority of raccoons in one Illinois study were less than 3 yr of age, with little difference in the sex ratio (Gehrt, 2003). This is consistent with most raccoon populations, in which the sex ratio of males to females is slightly biased toward females or equal (Gehrt, 2003). In support of that, in eastern Ontario during 1998, 50% ($n=2,950$) of the raccoons captured during TVR operations were female.

Twenty-two percent of the rabid AF raccoons in Ontario had litters during the year in which they were reported rabid. The stress of pregnancy might predispose pregnant females to be more susceptible to rabies; however, Hubbard (1985) could find no evidence of this during his study of rabid Virginia raccoons in 1981–82.

Monthly prevalence of rabid raccoons in relation to age of raccoons and seasonal raccoon behavior

Sixty-three percent (79/125) of the cases of raccoon strain rabies (in raccoons) occurred during the denning and breeding/parturition periods of raccoons, and more adult raccoons than juveniles were reported rabid during this period (November–May; Table 2 and Fig. 1). A similar trend was found in the mid-Atlantic US in 1982–83 during peaks of rabid raccoons in October, November, December, and April (Jenkins and Winkler, 1987). This is probably directly related to the amount of intraspecific contact that occurs among raccoons during this period.

In northern latitudes such as Ontario, raccoons compete for denning sites during the fall in preparation for winter denning. Raccoons den during periods of inclement weather in Ontario, which, depending on winter severity, can last from November to April. Also, the potential for transmission of rabies in the den was great because raccoons often den communally (Rosatte, 2000). As a result of predenning and denning activities during October/November to March each year, the potential for intraspecific contact is high with resultant transmission of rabies among raccoons.

Breeding for raccoons in Ontario usually occurs during late February and early March (Rosatte, 2000; Gehrt, 2003). This is a period of high contact as polygamous male raccoons (these may breed up to six females) compete vigorously for females, and male/female behavior during mating can be aggressive (Gehrt, 2003). Raccoons infected during breeding in early February would develop rabies in February–April, depending on the length of incubation period (Tinline et al., 2002). Similarly, Bigler et al. (1973) suggested a relationship between the breeding season for raccoons and a peak of rabies cases in March in Florida. Jenkins et al. (1988) also noted a peak in rabid raccoon numbers during the spring in Virginia and the mid-Atlantic US during the early to mid 1980s.

Female raccoons usually have litters averaging about four in Ontario (Rosatte, 2000), with most young being born in April and May. However, litters have also been reported in late summer/early fall in Ontario (Rosatte, 2000). Twenty-two percent of the AF raccoons that were reported rabid had evidence of producing a litter that year. Therefore, the potential for transmission of rabies is great between the AF raccoon and her young because this social unit often remains in or in close proximity to the parturition den for as long as 2–3 mo. As a result of adult raccoon behavioral activities during breeding and the rearing activities of the mother/young

social unit, the potential for intraspecific contact and transmission of rabies is high from February until July.

An increase in rabid juvenile raccoons was reported during the fall (Fig. 1). This is most likely from juvenile raccoons becoming infected by rabid AFs because AMs generally do not play a role with respect to the family unit during the summer (Gehrt, 2003). In fact, in Ontario during 2004, one live-trapped rabid AF raccoon was found in close proximity (a few meters) to three juvenile raccoons. However, in Ontario, AM raccoons have been found in close proximity to AF raccoons and their young during the late summer/early fall (Rosatte, unpubl. data). Thus, AMs cannot be discounted as playing some role in the transmission of rabies to juvenile raccoons. During the fall, young raccoons become more independent of the AF, travel more, and are in contact with other raccoons as raccoons begin to search for winter dens. In view of this fact, Winkler and Jenkins (1991) suggested that as young susceptible raccoons repopulate rabies endemic areas, secondary epizootic waves could occur.

Clinical symptoms of raccoons with the raccoon variant of rabies

The most common symptoms or behaviors/condition noted among raccoons reported with the raccoon variant of rabies in Ontario during 1999–2003 included aggression, appearance of being sick or unhealthy, ataxia, fighting with dogs, abnormal vocalizations, and the presence of quills. Ten percent of the rabid raccoons displayed normal behavior. Generally, nonrabid raccoons in the wild do not exhibit any of the above symptoms unless they are infected with a disease such as distemper or parvovirus (Rosatte, 2000). Aggressive behavior by raccoons and resultant contact with susceptible individuals provides for an effective route of transmission and spread of the rabies virus, both intra- and interspecifically, especially in view of the relatively high

raccoon population densities that occur in Ontario (Rosatte et al., 1991, 1992a; Rosatte, 2000; Broadfoot et al., 2001; Totton et al., 2002, 2004). In Ontario, 23% of the rabid raccoons exhibited aggression. Similarly, in the SE US, between 33% and 47% of the rabid raccoons were aggressive (Winkler and Jenkins, 1991) and in the mid-Atlantic area, 11–24% of the raccoons exhibited aggressive behavior (Hubbard, 1985; Jenkins and Winkler, 1987). Raccoon contact with dogs was reported in 13–37% of the SE and mid-Atlantic US rabies cases. Fighting with dogs was reported in 11% of the Ontario cases. In the mid-Atlantic and SE US, the percentage of rabid raccoons that acted sick, had uncoordinated movements, or were paralyzed ranged from 7% to 39% (Winkler and Jenkins, 1991). In Ontario, that number was 34% during 1999–2003.

In Ontario during 1999–2003, there was human contact by only two of the 125 rabid raccoons which subsequently resulted in human rabies postexposure treatment. However, the risk of human rabies infection acquired from wild raccoons should not be taken lightly. In the US during 1980/81, 8% of humans who received postexposure treatment had been exposed to wild raccoons (Helmick, 1983). In Florida during 1963–72, 65% of humans exposed to rabid wildlife had contact with raccoons (Bigler et al., 1973). A careful examination of postexposure treatment data for the mid-Atlantic US revealed that most exposures could have been avoided (Winkler and Jenkins, 1991; e.g., do not handle dead animals with bare hands). In Connecticut during 1991–94, 80% of human exposures occurred by indirect contact with infected animals, usually a domestic dog or cat (Wilson et al., 1997). Again, most of these exposures could have been prevented, which indicates a need for increased public education regarding the handling of wild animals. During 2003, the first human to die from the raccoon variant of rabies was

reported in Virginia (Anonymous, 2003). In this case, there was no known exposure to terrestrial animals.

Thirteen percent of the rabid raccoons in Ontario during 1999–2003 had contact with a domestic animal such as a dog, cat, or calf. This stresses the importance of having pets or domestic animals immunized against rabies. This is critical to minimize the potential for transmission of rabies from pets and domestic animals to humans.

Behavior of rabid raccoons found with porcupine quills

In Ontario, if a red fox has porcupine quills embedded in its facial area, then that animal is highly suspect for rabies (Arctic fox variant). This assumption was correct for the majority of fox submissions with embedded quills in the past. However, the same cannot be said unequivocally with respect to the raccoon variant of rabies virus in raccoons. Only four of seven raccoons with embedded quills tested positive for rabies. However, it is recommended that raccoons with quills be submitted for rabies testing because they are indicative of an abnormal behavior/condition, possibly because of infection with rabies or distemper virus.

Evidence of intraspecific transmission of raccoon rabies

The close proximity of the locations that rabid raccoons were found on the same farm and the timing between when those animals were found is suggestive of intraspecific transmission of rabies among raccoons. Multiple cases of raccoon rabies occurring in individual barns are also evidence that buildings such as barns serve as focal points for rabies transmission. The denning habits of raccoons (i.e., communal denning during the winter months) results in periods of high contact among individual raccoons in the den and makes for an effective mode of rabies transmission. Breeding by raccoons in Ontario also occurs during the winter

months (February/March) when raccoons congregate in barns. Because male raccoons are polygamous, a single male raccoon infected with rabies could potentially transmit rabies to several AFs during breeding activities in winter dens. As well, female raccoons often bear young in maternal dens in barns. In this situation, an infected female raccoon could transmit rabies to her litter of young.

Movement of rabid raccoons

Movement distance by raccoons from the time they were ear tagged until they were collected for rabies testing and subsequently diagnosed positive for rabies was not dramatically different from non-rabid raccoons (noting that the sample of rabid raccoons was only five). Therefore, it could be cautiously assumed that effective rabies control programs can probably be designed with movement data from non-rabid raccoons. In Ontario, ORV, PIC, and TVR zones encompass a 50-km radial area around isolated raccoon rabies cases. This zone takes into account previous studies in Ontario that determined that 95% of the raccoon movements were less than 50 km (Rosatte, 2000, unpubl. data). Therefore a 50-km rabies control zone (whether it be created with ORV baits, TVR, or PIC) would minimize the potential for rabies progressing beyond the control zone because of the movement of rabies-infected raccoons (Rosatte et al., in press).

Management implications

Surveillance programs should be designed to target the submission of raccoons noted as having a particular behavior/condition described in this study, including aggressiveness toward dogs, vocalizations, presence of porcupine quills, or evidence of ataxia or impaired mobility. In addition, enhanced surveillance programs should be implemented during the fall, winter, and spring when the majority of raccoons were confirmed as rabies positive in Ontario.

This and previous studies (Rosatte et al.,

in press) suggest that maximum movements of rabid raccoons are similar to nonrabid raccoons. Therefore, rabies control tactics such as PIC, TVR, and ORV (Rosatte et al., 2001) should be designed accordingly in Ontario.

Clinical symptoms of rabies in animals generally include evidence of neurological disorders (e.g., ataxia; aggression toward animals, humans, and inanimate objects; activity during daylight hours; lack of human avoidance; and paralysis). Other disease and parasitic conditions that might result in clinical symptoms similar to rabies include canine distemper, ethylene glycol toxicosis (antifreeze poisoning), *Baylisascaris procyonis* infections, and trauma (Cranfield et al., 1984; Kazacos, 2001; Foley and McBurney, 2002). Given the similarity of symptoms, screening should also include distemper, antifreeze poisoning, head trauma, and neural larval migrans (*B. procyonis*).

The majority (66%) of rabid raccoons were submitted by government staff, underscoring the critical input from government sources for rabies surveillance. Strategic use of media outlets should be encouraged to inform the public of their critical role in reporting abnormally acting animals to enhance rabies surveillance.

Because multiple rabies cases occurred within or near barns, tactics to minimize the number of raccoons denning in barns could minimize the potential for intraspecific contact and transmission of rabies. Depopulation of raccoons in barns during the winter could minimize the risk of a rabies outbreak or of the barn serving as a focal point for rabies transmission, especially to cattle (i.e., on at least two occasions, cattle were quarantined as a result of a rabid raccoon found on the farm). Alternatively, vaccination programs (either TVR or ORV) could target barns during the raccoon denning and breeding periods.

Because 48% of the rabid raccoons were either live trapped or found dead in Ontario, an effective rabies surveillance strategy would be to focus efforts in areas

with relatively high raccoon densities (i.e., 10 raccoons/km²) such as farming operations. Given that only 9% of the rabid animals were road kill, it is not recommended that this be the sole method of detection for rabies in Ontario.

About 15% of the rabid raccoons were contacted by domestic animals or humans. To ensure that both humans and domestic animals are not infected with rabies, programs (especially with the use of the media) to promote the vaccination and containment of pets (i.e., on a leash or in a kennel or other type of enclosure) as well as to inform residents of the dangers of handling rabies reservoir species should be implemented. Human contact involving a bite by any animal should be reported immediately to a physician for consideration of rabies postexposure prophylaxis.

ACKNOWLEDGMENTS

The Ontario Raccoon Rabies Control Program was supported by the Rabies Advisory Committee, J. Carlson, Chair, and C. Davies, Manager, OMNR, Wildlife Research and Development Section, Peterborough, Ontario. All members of the OMNR, Rabies Research and Development Unit, Peterborough, contributed immensely to the program. Raccoons were tested for distemper at the Canadian Co-operative Wildlife Health Centre, Guelph (thanks to Ian Barker, Doug Campbell, and staff), and the CFIA, Ottawa Laboratory Fallowfield, Nepean (thanks to Abed Zeib-dawi). Teeth (from rabid as well as nonrabid raccoons) were sectioned by Mark Gibson, and age was estimated by Andrew Silver. Bev Stevenson and Rob Warren contributed to construction of the database. Special acknowledgment goes to all of the dedicated trappers, technicians, and collaborators of the Ontario Ministry of Natural Resources Rabies program and the CFIA staff (especially Doug Hayes), who took the time to record rabid raccoon behavioral data. This is OMNR, Wildlife Research and Development Section, contribution 04-04.

LITERATURE CITED

- ANONYMOUS. 2003. First human death associated with raccoon rabies—Virginia, 2003. *MMWR* 52 (45): 1102–1103.
- BIGLER, W. J., R. G. MCLEAN, AND H. A. TREVINO. 1973. Epizootic aspects of raccoon rabies in

- Florida. *American Journal of Epidemiology* 98: 326–335.
- BISHOP, Y. M., S. E. FIENBERG, AND P. W. HOLLAND. 1975. Discrete multivariate analysis: Theory and practice. The MIT Press, Cambridge, Massachusetts, 577 pp.
- BROADFOOT, J. D., R. C. ROSATTE, AND D. T. O'LEARY. 2001. Raccoon and skunk population models for urban disease control planning in Ontario, Canada. *Ecological Applications* 11: 295–303.
- CHRISTENSEN, R. 1990. Log-linear models. Springer Texts in Statistics, New York, New York, 408 pp.
- CRANFIELD, M. R., I. K. BARKER, K. G. MEHREN, AND W. A. RAPLEY. 1984. Canine distemper in wild raccoons (*Procyon lotor*) at the Metropolitan Toronto Zoo. *Canadian Veterinary Journal* 25: 63–66.
- FIENBERG, S. E. 1970. The analysis of multidimensional contingency tables. *Ecology* 51 (3): 419–433.
- FOLEY, P., AND S. MCBURNEY. 2002. Ethylene glycol toxicosis in a free-ranging raccoon (*Procyon lotor*) from Prince Edward Island. *Canadian Veterinary Journal* 43: 291–292.
- GEHRT, S. D. 2003. Raccoon. In *Wild mammals of North America biology, management and conservation*, G. Feldhamer, B. Thompson, and J. Chapman (eds.). The Johns Hopkins University Press, Baltimore, Maryland, pp. 611–634.
- GREENACRE, M. J. 1984. Theory and applications of correspondence analysis. Academic Press Inc., London, UK, 364 pp.
- HELMICK, C. G. 1983. The epidemiology of human rabies post-exposure prophylaxis, 1980–1981. *Journal of the American Medical Association* 250: 1990–1996.
- HUBBARD, D. R. 1985. A descriptive epidemiologic study of raccoon rabies in a rural environment. *Journal of Wildlife Diseases* 21: 105–110.
- JENKINS, S. R., AND W. G. WINKLER. 1987. Descriptive epidemiology from an epizootic of raccoon rabies in the mid-Atlantic states, 1982–1983. *American Journal of Epidemiology* 126: 429–437.
- , B. D. PERRY, AND W. G. WINKLER. 1988. Ecology and epidemiology of raccoon rabies. *Reviews of Infectious Diseases* 10: S620–S625.
- JOHNSTON, D. H., AND M. BEAUREGARD. 1969. Rabies epidemiology in Ontario. *Bulletin of the Wildlife Disease Association* 5: 357–370.
- , D. JOACHIM, P. BACHMANN, K. KARDONG, R. STEWART, L. DIX, M. STRICKLAND, AND I. WATT. 1987. Aging furbearers using tooth structure and biomarkers. In *Wild furbearer management and conservation in North America*, M. Novak, J. Baker, M. Obbard, and B. Mallock (eds.). Ontario Trappers Association, North Bay, Ontario, Canada, pp. 228–243.
- , D. R. VOIGT, C. MACINNES, P. BACHMANN, K. F. LAWSON, AND C. E. RUPPRECHT. 1988. An aerial baiting system for the distribution of attenuated or recombinant rabies vaccines for foxes, raccoons and skunks. *Review of Infectious Diseases* 10: S660–S665.
- KAZAKOS, K. R. 2001. *Baylisacaris procyonis* and related species. In *Parasitic diseases of wild mammals*, 2nd Edition, W. M. Samuel, M. J. Pybus, and A. A. Kocan (eds.). Iowa State University Press, Ames, Iowa, pp. 301–341.
- KNOKE, D., AND P. J. BURKE. 1983. Log-linear models. Sage University Paper series on Quantitative Applications in the Social Sciences, series No. 07-020. Beverly Hills, California, 80 pp.
- MACINNES, C. D. 1987. Rabies. In *Wild furbearer management and conservation in North America*, M. Novak, J. Baker, M. Obbard, and B. Mallock (eds.). Ontario Trappers Association, North Bay, Ontario, Canada, pp. 910–929.
- , S. SMITH, R. TINLINE, N. AYERS, P. BACHMANN, D. BALL, L. CALDER, S. CROSGREY, C. FIELDING, P. HAUSCHILDT, J. HONIG, D. JOHNSTON, K. LAWSON, C. NUNAN, M. PEDDE, B. POND, R. STEWART, AND D. VOIGT. 2001. Elimination of rabies from red foxes in eastern Ontario. *Journal of Wildlife Diseases* 37: 119–132.
- NADIN-DAVIS, S. A., G. A. CASEY, AND A. I. WANDELER. 1994. A molecular epidemiological study of rabies virus in central Ontario and western Quebec. *Journal of General Virology* 75: 2575–2583.
- ROSATTE, R. C. 1988. Rabies in Canada—History, epidemiology and control. *Canadian Veterinary Journal* 29: 362–365.
- . 2000. Management of raccoons (*Procyon lotor*) in Ontario, Canada: Do human intervention and disease have significant impact on raccoon populations? *Mammalia* 64: 369–390.
- , D. R. HOWARD, J. B. CAMPBELL, AND C. D. MACINNES. 1990. Intramuscular vaccination of skunks and raccoons against rabies. *Journal of Wildlife Diseases* 26: 225–230.
- , M. J. POWER, AND C. D. MACINNES. 1991. Ecology of urban skunks, raccoons and foxes in metropolitan Toronto. In *Wildlife conservation in metropolitan environments*, L. W. Adams and D. L. Leedy (eds.). National Institute for Urban Wildlife, Columbia, Maryland, pp. 31–38.
- , ———, AND ———. 1992a. Density, dispersion, movements and habitat of skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) in metropolitan Toronto. In *Wildlife 2001: Populations*, D. R. McCullough and R. Barrett (eds.). Elsevier Science Publishers, London, UK, pp. 932–944.
- , ———, ———, AND J. B. CAMPBELL. 1992b. Trap-vaccinate- release and oral vaccination for rabies control in urban skunks, raccoons and foxes. *Journal of Wildlife Diseases* 28: 562–571.
- , C. D. MACINNES, M. J. POWER, D. H. JOHNSTON, P. BACHMANN, C. P. NUNAN, C.

- WANNOP, M. PEDDE, AND L. CALDER. 1993. Tactics for the control of wildlife rabies in Ontario Canada. *Reviews of the Science and Technical Office of International Epizootics* 12: 95–98.
- , D. DONOVAN, M. ALLAN, L. HOWES, A. SILVER, K. BENNETT, C. MACINNES, C. DAVIES, A. WANDELER, AND B. RADFORD. 2001. Emergency response to raccoon rabies introduction into Ontario. *Journal of Wildlife Diseases* 37: 265–279.
- , M. ALLAN, R. WARREN, P. NEAVE, T. BABIN, L. BUCHANAN, D. DONOVAN, K. SOBEY, C. DAVIES, F. MULDOON, AND A. WANDELER. 2005. Movements of two rabid raccoons (*Procyon lotor*) in eastern Ontario, Canada. *Canadian Field-Naturalist* 119: In Press.
- STATSOFT INC. 2004. *Electronic statistics textbook*. StatSoft, Tulsa, Oklahoma, www.statsoft.com/textbook/stathome.html. Accessed August 2005.
- TINLINE, R., R. ROSATTE, AND C. D. MACINNES. 2002. Estimating the incubation period of raccoon rabies: A time-space clustering approach. *Preventative Veterinary Medicine* 56: 89–103.
- TOTTON, S. C., R. R. TINLINE, R. C. ROSATTE, AND L. L. BIGLER. 2002. Contact rates of raccoons (*Procyon lotor*) at a communal feeding site in rural eastern Ontario. *Journal of Wildlife Diseases* 38: 313–319.
- , R. C. ROSATTE, R. R. TINLINE, AND L. L. BIGLER. 2004. Seasonal home ranges of raccoons (*Procyon lotor*), using a common feeding site in rural eastern Ontario: Rabies management implications. *Canadian Field Naturalist* 118: 65–71.
- WANDELER, A., AND E. SALSBERG. 1999. Raccoon rabies in eastern Ontario. *Canadian Veterinary Journal* 40: 731.
- WEBSTER, W. A., AND G. A. CASEY. 1988. Diagnosis of rabies infection. In *Rabies*, J. B. Campbell and K. M. Charlton (eds.). Kluwer Academic Publishers, Boston, Massachusetts, pp. 201–222.
- WILSON, M. L., P. M. BRETSKY, G. H. COOPER, S. H. EGBERTSON, H. J. VAN KRUININGEN, AND M. L. CARTTER. 1997. Emergence of raccoon rabies in Connecticut. 1991–1994: Spatial and temporal characteristics of animal infection and human contact. *American Journal of Tropical Medicine and Hygiene* 57: 457–463.
- WINKLER, W. G., AND S. R. JENKINS. 1991. Raccoon rabies. In *The natural history of rabies*. 2nd Edition, G. M. Baer (ed.). CRC Press, Boca Raton, Florida, pp. 325–340.

Received for publication 1 October 2004.