Density, movements, and survival of raccoons in Ontario, Canada: implications for disease spread and management

Rick Rosatte,* Mark Ryckman, Karen Ing, Sarah Proceviat, Mike Allan, Laura Bruce, Dennis Donovan, and J. Chris Davies

Ontario Ministry of Natural Resources, Wildlife Research and Development Section, Trent University, DNA Building, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada (RR, MA, LB, DD, JCD)
Manitoba Conservation, 200 Saulteaux Crescent, Winnipeg, Manitoba R3J 3W3, Canada (MR)
University of Toronto, Centre for Environment, 33 Wilcocks Street, Toronto, Ontario M5S 3E8, Canada (KI)
Summit Environmental Consultants Ltd., 1212 1st Street SE, Calgary, Alberta T2G 2H8, Canada (SP)

* Correspondent: rick.rosatte@ontario.ca

During 1994–2007 a total of 156,416 raccoons was live-captured in Ontario, Canada, as part of mark–recapture studies to estimate raccoon density during rabies-control operations. Mean density in southern Ontario ranged between 3.4 and 13.6 raccoons/km^2 when density in northern Ontario was $<$1.5 raccoons/km^2. Raccoon density also was significantly higher in mixed cropland and deciduous habitats than in large tracts of deciduous forest in southern Ontario. Raccoons generally travelled $<$5 km between years during 1994–1997 mark–recapture movement studies in Niagara; however, movements as great as 45 km and among-year differences in movements were observed. Raccoons in rural habitats also moved more extensively than those in urban areas in 1994. Mean home range (minimum convex polygon) for raccoons in eastern Ontario during 2003–2007 was 3.9 km^2 for very-high-frequency–collared raccoons and 3.4 km^2 for global positioning system–collared raccoons. Mean movement from the release site by collared raccoons over the study period was 1.5 km with the longest movement being 10.3 km. No single habitat was used more or less by collared raccoons than expected. Survival of radiocollared raccoons over the course of the study was 0.62 with survival of raccoons initially captured and released as juveniles and adults being an average of 964 and 786 days. Knowledge of the ecology of raccoons should be used during planning for disease management, and was critical to evaluating the success of rabies-control programs in Ontario, Canada. DOI: 10.1644/08-MAMM-A-201R2.1.

Key words: density, home range, movement, Ontario, *Procyon lotor*, rabies control, raccoon

Raccoons (*Procyon lotor*) have adapted well to both urban and rural environments in North America, using human dwellings and associated buildings for denning and shelter and finding adequate sustenance from resources in habitats ranging from croplands to residential lawns and ornamental gardens. It is this close association with humans that has made raccoons a prominent species with respect to conflicts with humans (Rosatte and MacInnes 1989). In addition, raccoons harbor a number of diseases and parasites that are transmittable to humans, in particular, rabies and *Baylisascaris procyonis* (Kazacos 2001; Rosatte 2000; Rosatte et al. 2007b). Raccoons also may be infected with distemper, which is of concern for wildlife as well as domestic animals (Rosatte et al. 2007b; Schubert et al. 1998). Raccoon population models also have been used in planning for disease control (Broadfoot et al. 2001). Knowledge of the ecology of raccoons, especially density, movements, and survival, will assist in determining the ecological and public health impact of these diseases and parasites, and the validation of models.

Historically, a variety of tactics have been used to manage raccoon populations, including public education, exclusion, population reduction, relocation, and sterilization (Debbie 1991; Rosatte 2000; Rosatte and MacInnes 1989). However, because of their adaptability, resiliency, and high reproductive rates, raccoon populations that are reduced in size soon return to their precontrol density levels (Rosatte 2000; Rosatte et al. 2007d). Knowledge of pre- and posttreatment densities and movements of raccoons will be critical in assessing the success of the various control programs.
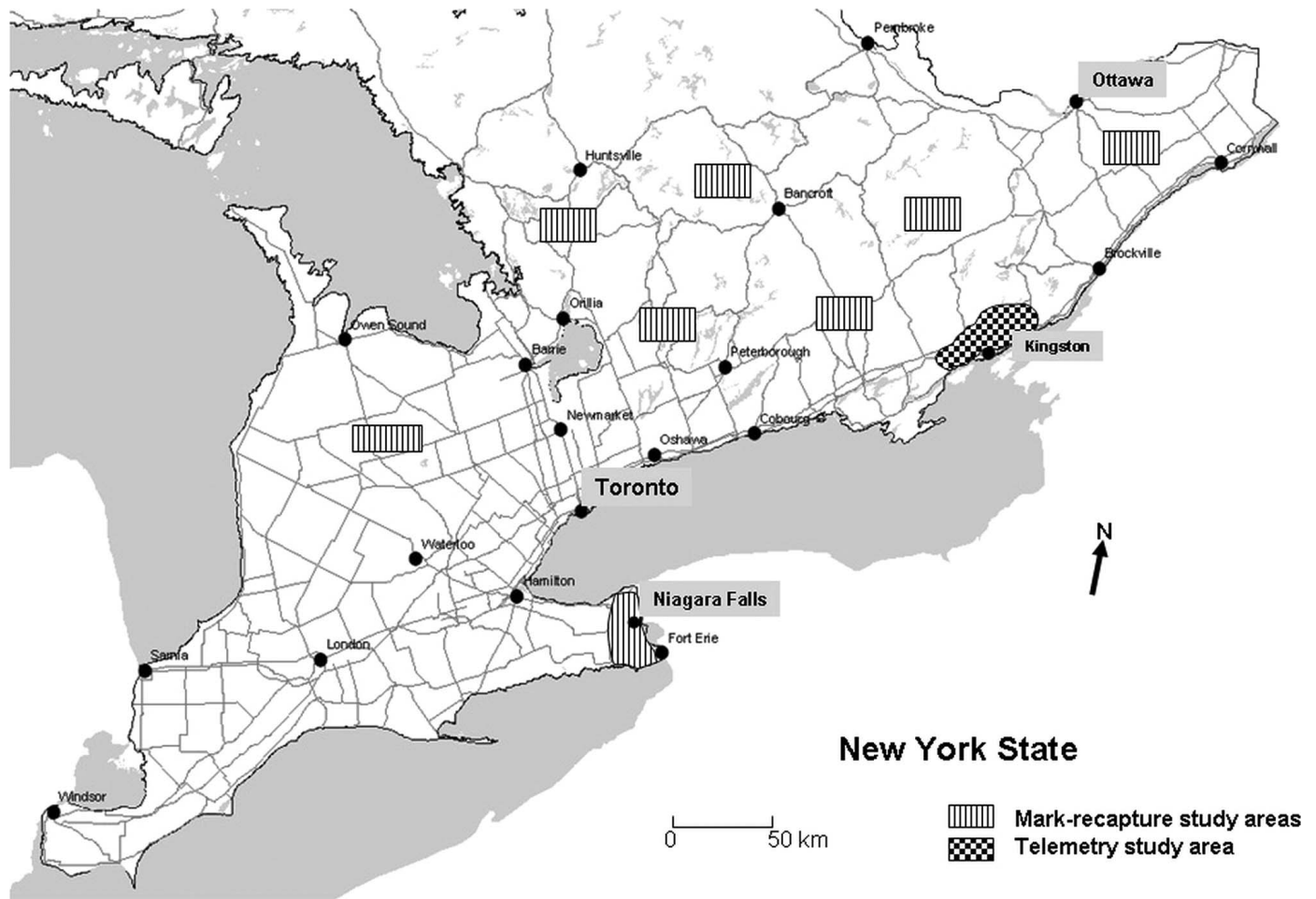
Fig. 1.—Location of the raccoon density and movement study areas in southern Ontario, Canada. The St. Lawrence density study area is the same area as that denoted by the Telemetry study area. The northern Ontario raccoon density study area is not shown on this map but the location is noted in the ''Materials and Methods'' section.

In Ontario, Canada, a program to eliminate terrestrial rabies from the province has been in place for more than 4 decades. Raccoons, red foxes (*Vulpes vulpes*), and striped skunks (*Mephitis mephitis*) are primary terrestrial vectors of the disease in Ontario (Rosatte et al. 2007a). The effective management of diseases such as rabies requires knowledge of the ecology of the vector species in question. This knowledge will provide insights to understanding how ecological variables such as vector density and movement affect epizootics (Rosatte et al. 2007c). Studies on the density, movements, and survival of raccoons were initiated to design and evaluate the most effective strategies to control rabies in that species and assess the effectiveness of control programs. We tested the following hypotheses: the annual movement of raccoons will be at a level such that a 50-km radial control zone will be adequate to contain an epizootic of raccoon rabies; raccoon survival will be at a rate that will necessitate annual control programs until the disease is eradicated; and use of raccoon ecological data will improve the validity of a disease model for raccoon rabies in Ontario. This paper reports on the results achieved by those studies during 1994–2007.

MATERIALS AND METHODS

During 1994–2007 raccoon density and movement studies were conducted in various regions of Ontario, Canada. The density studies using mark–recapture methodologies during those years occurred in 5 areas of the province. Movement studies using mark–recapture took place during 1994–1997 in southern Ontario. In addition, movement studies using radiotelemetry occurred during 2003–2006 in eastern Ontario.

Study areas.—Raccoon density studies occurred in 5 different areas of Ontario (Fig. 1), including the Niagara Falls area (approximately 700 km^2; 43°03′N, 79°07′W); the St. Lawrence area (approximately 125–892 km^2; 44°45′N, 75°50′W); southwestern Ontario (the Wingham and Owen Sound areas, 108 km^2; 44°02′N, 80°55′W); south-central and eastern Ontario (160 km^2; 44°31′N, 79°00′W to 45°09′N, 75°02′W); and northern Ontario (600 km^2; 46°24′N, 79°23′W to 49°48′N, 92°51′W). The raccoon movement studies using mark–recapture methodologies occurred in the Niagara Falls area and in eastern Ontario (Fig. 1). The raccoon movement study using radiotelemetry was conducted in southeastern

Ontario (Fig. 1), between the cities of Napanee (44°13′N, 76°58′W) and Brockville (44°49′N, 75°31′W), a study area of approximately 6,800 km^2. All research studies were approved by the Ontario Ministry of Natural Resources, Animal Care Committee, and the research meets the guidelines of the American Society of Mammalogists for animal use in research (Gannon et al. 2007).

Raccoon density.—Raccoon populations were sampled across the province of Ontario between 1994 and 2007 during programs with different objectives. To obtain data on raccoon density to predict whether raccoon rabies could spread and become enzootic provincially, raccoons were sampled in the Wingham and Owen Sound areas of southwestern Ontario during 1994, south-central and eastern Ontario during 1995, and in northern Ontario during 1996. Raccoon populations also were sampled in southern Ontario to determine the effectiveness of proactive and reactive rabies-control programs (Rosatte et al. 2001) in the Niagara area during 1994–2007, and along the St. Lawrence River during 1995–2007.

The methodology for capturing and processing raccoons was essentially the same in all areas but the time of year in which studies were carried out varied. Study areas were divided into a series of trapping cells so that trappers would know where to set traps. Cells were about 12 km^2 in rural habitat and 3 km^2 in urban habitat in Niagara—about 91% of the cells were rural and 9% urban in 1994. In Niagara, baited (sardines) live traps (Tomahawk #106 and #108; Tomahawk Live Trap Co., Tomahawk, Wisconsin) were distributed in the study area during June or July to October or November, 1994–2007, as part of a provincial rabies-control program. All captured raccoons were ear-tagged for identification (numbered size 3; National Band and Tag Co., Newport, Kentucky), vaccinated against rabies with an intramuscular injection of inactivated rabies vaccine, and released at the point of capture.

Trap effort for the study areas was variable depending on raccoon density and study objectives: generally 75–100 traps were placed in each of the trapping cells during the initial trapping period, which was either 8 nights over a 2-week period or 12 nights over a 3-week period. Cells that were trapped only for 8 nights were retrapped for 4 or 8 nights with 25 traps between 1 and 6 weeks after the initial trapping period. The majority of cells were retrapped 1 week after the initial trapping period. However, on a few occasions, because of rabies outbreaks and a resultant focus of effort elsewhere in the study areas, the retrapping period was 6 weeks posttrapping. Both trapping and retrapping period data were used to estimate raccoon density for that particular trapping cell. Some cells with low raccoon density were trapped for only 4 nights and retrapped for 4 nights. Normally, cells that were thought to support high densities of raccoons were trapped for a longer period than cells with few raccoons.

In the St. Lawrence study area (1995–2007), trapping cell size averaged 12.3 km^2, with about 95% of the cells being rural. Trapping was initiated in June or July and continued into late October or early November. Cell size for the southwestern Ontario, eastern Ontario, and northern Ontario studies during 1994, 1995, and 1996 was about 9 km^2. Trapping occurred in 12 cells (108-km^2 area) in southwestern Ontario, in 16 cells (160-km^2 area) in eastern–south-central Ontario, and in 64 cells (600-km^2 area) in northern Ontario. Each cell was trapped during July or August for 4 nights (100 traps) and then retrapped the following week for 4 nights. In the northern Ontario study, 25 traps/cell were used to capture raccoons because abundance is low in northern boreal forest habitat.

Niagara raccoon movement.—The data used for this project were collected during the trap–vaccinate–release rabies-control program carried out in the Niagara region between 1994 and 1997. Movement data were necessary to determine whether the control zones were wide enough to prevent the spread of rabies. Raccoon mark–recapture data, recorded as Universal Transverse Mercator coordinates (Schwarz and Wade 1990) using a global positioning system (GPS) unit, were used to estimate raccoon movements in the Niagara area. Methods for capturing and processing raccoons were the same as noted above for the Niagara study.

St. Lawrence raccoon movement.—Raccoon movement data using telemetry were required to determine the size of control zones required in eastern Ontario to contain an outbreak of raccoon rabies. These data and data from the above programs would be used to validate a raccoon rabies model. During the telemetry study we captured raccoons in numbered 106 (65 × 23 × 23-cm) and 108 (81 × 25 × 30-cm) Tomahawk live traps baited with sardines between September 2003 and April 2006. Captured raccoons were immobilized with an injection of ketamine (hydrochloride) and xylazine at a dosage rate of ketamine at 15 mg/kg and xylazine at 3 mg/kg. Anesthetized raccoons were sexed and aged using a combination of body size, tooth wear, and reproductive status. Raccoons were considered adult if they were >1.5 years old at time of capture. All raccoons were marked with individually numbered ear tags and fitted with either a very-high-frequency (VHF) or GPS radiocollar (Lotek Engineering Inc., Newmarket, Ontario, Canada, and Advanced Telemetry Systems, Isanti, Minnesota).

Diurnal rest sites of radiocollared raccoons were estimated once weekly using standard ground telemetry techniques. Telemetry equipment consisted of a portable telemetry receiver, handheld GPS unit, compass, and 3-element yagi antenna. A minimum of 3 bearings were recorded for each animal. Location estimates were calculated in LOCATE II (Pacer Inc., Truro, Nova Scotia, Canada). To minimize the effects of telemetry error, location estimates whose 95% error ellipses were >1 km^2 were discarded. However, error ellipses were generally much smaller (0.59 km^2 ± 0.34 *SD*). GPS collars were programmed to record location estimates at 0600, 1200, and 1800 h, and at each hour between 1800 and 0600 h, to capture nocturnal movement patterns during the spring, fall, and summer months (May–October). From November to April, GPS collars were programmed to obtain a location every 4 h.

To assess accuracy of ground telemetry techniques and equipment, we calculated straight-line distances between locations estimated manually (using the VHF component of

GPS collars) and GPS-estimated locations. Because GPS-collared raccoons were found in different portions of the study area, we assumed this produced a random sample. To increase accuracy of the location estimate, we eliminated any locations that were estimated with fewer than 3 satellites. To test the accuracy of both VHF and GPS locations, 100 daytime locations were randomly selected for which both VHF and GPS data (fixes acquired at approximately the same day and time) were available. Raccoons were assumed to be resting during daylight, thus reducing the likelihood that an animal was moving at the time of location. Mean distance between VHF and GPS location estimates was 43 m $\pm$ 31 SD.

Data analysis.—Mark–recapture data were used to estimate raccoon density via a Petersen model (using animals marked at time 1 and captures and recaptures at time 2) and Ecological Methodology software (Krebs 1989). Annual densities were calculated using mark–recapture data for the entire study area (i.e., cumulative trapping cell data). However, for density estimation at the trapping-cell level and for comparisons of densities in urban and rural habitats, densities were calculated using mark–recapture data from individual trapping cells. Differences in raccoon density in urban and rural cells were compared using a Student's *t*-test and Statistica 6.0 (Statsoft, Inc. 1999). Because we could detect no differences, urban and rural capture data were pooled for density estimation. A subset of the Niagara data (1994–1997) was analyzed at the trapping-cell level to provide density data for a raccoon rabies contingency plan for urban and rural habitats that was finalized during the late 1990s.

A subset (1994–1997) of the Niagara trap–vaccinate–release mark–recapture data also was used to determine raccoon movements in urban and rural habitats for use in the raccoon rabies contingency plan. The Niagara movement study data were significantly right-skewed. Consequently, a Mann–Whitney test (Statsoft, Inc. 1999) was chosen to test the majority of 2 group hypotheses (e.g., male versus female) that were being explored in relation to raccoon movement in Niagara, and the Kruskal–Wallis test (Statsoft, Inc. 1999) was used to test the significance of >2 groups (e.g., seasons).

For analysis of raccoon movement, the year was partitioned into 4 distinct seasons: denning (December–February; communal or solitary); breeding (March–May; male polygamous then leaves); rearing (June–August; by adult females—males play no role); and dispersal (September–November). Because the grouping comparison by seasons involves a time component, we used the data set in which multiple recaptures of the same raccoon were treated as individual cases. From 1995 through 1997 trap–vaccinate–release took place between June and November and encompassed only the rearing and dispersal seasons. However, in 1994 trap–vaccinate–release started in May and included the breeding, rearing, and dispersal seasons. The Mann–Whitney test (Statsoft, Inc. 1999) was used for the 2-season comparison (1995–1997 data), and the Kruskal–Wallis test (Statsoft, Inc. 1999) was used on the 3-season comparison (1994 data).

We calculated seasonal and annual home-range sizes of raccoons (radiotelemetry data) using minimum convex polygon (MCP) and 95% and 50% fixed kernel home-range estimators with Hawth's Tools (Beyer 2004) in ArcGIS 9.1 (ESRI, Redlands, California). Least-squares cross-validation was used to choose the smoothing parameter for kernel home ranges. Exploratory data analysis suggested that annual raccoon home-range size reaches a plateau at approximately 25–30 locations. We therefore calculated annual home ranges for animals having a minimum of 30 locations and >8 months of tracking. We calculated seasonal home ranges for animals with $\geq$15 locations. If an animal had insufficient locations to estimate either of the seasonal home ranges or an accurate kernel home range, data were ignored for that animal in analyses of home-range size. For animals fitted with GPS collars, we randomly chose 15 locations (for seasonal home-range analysis) and generated MCPs from these locations. This process was repeated 20 times per animal to obtain an average MCP home-range size for GPS-collared animals. Seasons for VHF-collared animals were defined as breeding (1 January–30 June) and rearing (1 July–31 December). Because of the higher number of locations obtained for animals fitted with GPS collars, we defined seasons as follows: winter–breeding (1 December–31 March), rearing (1 April–31 July), and predenning–dispersal (1 August–30 November). We compared seasonal home-range sizes using repeated-measures analysis of variance. We also calculated mean and maximum linear distances from release sites to each telemetry location as well as movement rates for each animal (distance moved/h). A multivariate analysis of variance (MANOVA) was used to test for the influence of sex and age on all home-range and movement variables. If no differences were found, sex and age classes were pooled for further analysis. All statistical tests were performed in SPSS (version 10; SPSS Inc., Chicago, Illinois) with $\alpha = 0.05$.

Habitats used by radiocollared raccoons were delineated using geographic information system data obtained from the Ontario Ministry of Natural Resources (http://www.mnr.gov.on.ca). We used the Southern Ontario Interim Landcover data layer, which represents the landscape in the study area from 2000 to 2002. Similar habitat types were combined to reduce the number of habitat variables. Agriculture included annual crops (monoculture), rotated annual–forage (mixed agriculture), and any other rural land use. Wooded Areas included forests with $\geq$60% canopy cover and trees $\geq$2 m in height. Hedgerow had the same restrictions as wooded area with linear features between 10 and 30 m wide. Water included wetlands, water bodies, and waterlines. Development included human settlements. Transportation included the Ontario Road Network. Waterlines included streams, rivers, and creeks. Pits & Quarries included licensed land from which aggregate is currently, or was formerly, excavated. Unclassified included features that did not fit into other categories. Buildings included houses, barns, and garages.

We employed the Euclidean distance method (Conner and Plowman 2001) to test for the presence of nonrandom habitat

Table 1.—Raccoon density in the Niagara and St. Lawrence regions of southern Ontario, Canada, during 1994–2007.[a]

| Year | Niagara | | St. Lawrence | |
	Study area (km^2)	Raccoon density (individuals/km^2) $\bar{X}$ (95% CI)	Study area (km^2)	Raccoon density (individuals/km^2) $\bar{X}$ (95% CI)
1994	680	9.9 (8.6–11.3)	NA	NA
1995	680	8.6 (8.3–8.9)	470	4.8 (4.4–5.2)
1996	700	7.4 (7.2–7.8)	801	4.7 (4.2–5.5)
1997	700	8.4 (7.9–8.8)	720	6.4 (6.0–6.8)
1998	700	8.8 (8.4–9.2)	720	5.4 (5.0–5.9)
1999	700	10.1 (9.5–11.0)	650	6.8 (6.1–7.7)
2000	700	11.8 (11–12.8)	764	8.5 (8.2–8.8)
2001	700	10.4 (9.9–11.0)	892	6.8 (6.6–7.1)
2002	700	12.9 (12.3–13.5)	690	8.3 (8.0–8.5)
2003	680	13.6 (12.9–14.5)	595	7.2 (6.9–7.5)
2004	640	12.8 (12.1–13.8)	224	9.8 (9.6–10.2)
2005	679	12.3 (11.8–12.9)	416	7.1 (6.9–7.3)
2006	577	12.2 (11.7–12.7)	416	7.4 (7.2–7.6)
2007	596	9.3 (9.0–9.7)	125	8.3 (7.8–9.0)

[a] Trapping occurred during late June–early July annually except in Niagara during 1994, when trapping commenced in early May. Sample size was 154,678 raccoons during 1994–2007. NA = not applicable.

use by raccoons using ArcGIS 9.1 (ESRI Inc., Redlands, California). This method did not exhibit inflated type I error rates when compared to other methods (Bingham and Brennan 2004). VHF and GPS telemetry data were divided into seasons as listed above. GPS collar data were further divided into diurnal locations (0600–2200 h) and nocturnal locations (2200–0500 h), from which we generated MCPs. For animals fitted with VHF collars, we generated 200 randomly distributed points within the MCP home range of each animal using Hawth's Tools (Beyer 2004). For GPS-collared animals, we generated 500 random locations. Because variance measures are not included in analysis of Euclidean distance, generating too many points is not a concern (Conner and Plowman 2001). We then calculated straight-line distance from each telemetry location and each random point to the nearest representative of each habitat type, obtaining mean distances for each animal and expected mean distance to each habitat type. We calculated ratios of actual distance to expected distance to each habitat type and used MANOVA (Wilks' lambda statistic—Statsoft, Inc. 1999) to determine if nonrandom habitat use was occurring. If nonrandom use was occurring, we conducted *t*-tests to determine which habitats were being used disproportionately. We also performed paired *t*-tests (Statsoft, Inc. 1999) on all possible habitat combinations to determine which habitats were used more or less than others. Statistical significance was set at $\alpha = 0.05$ for all tests, and unless otherwise noted, standard deviation (*SD*) was used in the analyses.

We estimated raccoon survival (using the telemetry data) via the Kaplan–Meier method modified for staggered entry (Pollock et al. 1989). The study period extended from September 2003 to June 2007. Each year was divided into 2 periods, 1 January–30 June and 1 July–31 December. We tested for equality of survival functions between age and sex
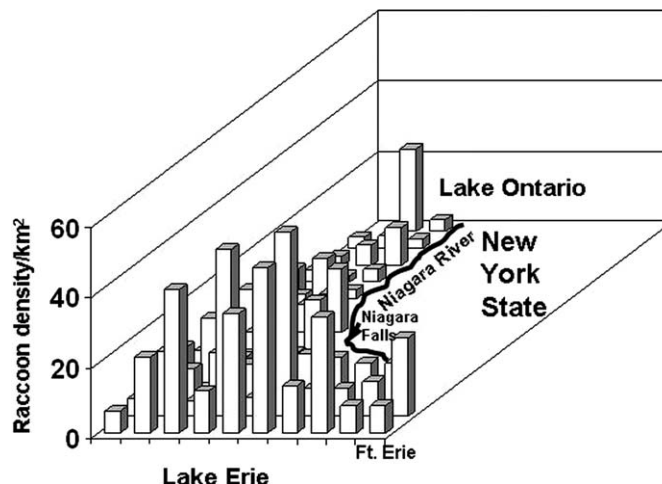

Fig. 2.—Raccoon density per trapping cell in the Niagara Falls, Ontario, Canada, area during 1994. Location of cells is approximate. Each cell represents an approximately 12-km^2 area. Urban cells in the Niagara Falls and Ft. Erie areas were combined to make 12-km^2 cells. Total area of cells is about 700 km^2.

classes using the Tarone–Ware statistic (Zar 1999), which weighs all time points by the square root of the number of cases at risk at each time point. Statistics are reported as mean ± standard error (*SE*).

RESULTS

Raccoon density.—A total of 97,312 raccoons (64,778 individuals) was live-captured and released in the Niagara Falls area (about 700 km^2) during 1994–2007 (Rosatte et al. 2009). Mean raccoon density varied annually (Table 1). In addition, dispersion of raccoons throughout the Niagara landscape varied considerably (Fig. 2). We observed much variation in raccoon density on a trapping-cell basis. For example, during 1994–1997, 89% of the cells in the Niagara study area had 1–20 raccoons/km^2, and 11% of the cells had densities of 21–52 raccoons/km^2 (Fig. 3). We could find no differences in raccoon density among trapping cells in urban and rural habitats during those years (rural cells, $\bar{X} = 10.3 \pm 8.1$ raccoons/km^2, range = 1–52 raccoons/km^2; urban cells, $\bar{X} = 12.1 \pm 10.9$ raccoons/km^2, range = 1–47 raccoons/km^2; $t_{306} = 1.61$, $P = 0.11$).

In the St. Lawrence study area 57,366 raccoons (34,321 individuals) were captured during 1995 and 2007. Mean raccoon density ranged between 4.7 and 9.8 individuals/km^2 during those years (Table 1). Again, much variation in density occurred in trapping cells. For example, during 2005 and 2006, raccoon density per cell ranged between 1.5 and 23.0 individuals/km^2.

In the southwestern Ontario study 884 raccoons (645 individuals) were captured during July and August 1994. Raccoon density was significantly higher ($\bar{X} = 11.7 \pm 4.0$ individuals/km^2; $t_{10} = 3.41$, $P < 0.01$) in habitats that were 50% cropland and 50% deciduous forest compared to raccoon density in habitats that were >75% cropland ($\bar{X} = 9.0 \pm 3.4$
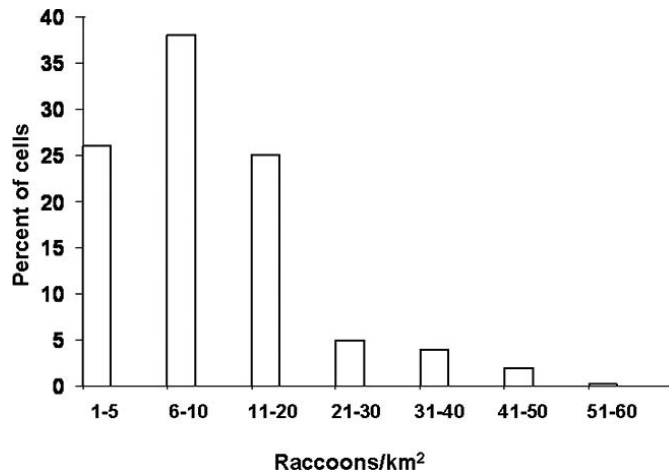
FIG. 3.—Percent of trapping cells in the Niagara Falls, Ontario, Canada, area that had a specific range of raccoon densities during 1994–1997. Sample size was 26,637 raccoons captured in 77 trapping cells in the 700-km^2 study area during 1994–1997.

individuals/km^2) or >75% deciduous forest ($\bar{X} = 6.9 \pm 2.1$ individuals/km^2).

A total of 804 raccoons (645 individuals) was captured during July and August, 1995 in the south-central and eastern Ontario study areas. Raccoon density was significantly higher in habitats consisting of >75% croplands ($\bar{X} = 10.4$ individuals/km^2; 95% confidence interval [95% CI] = 6.8–24.7, $t_2 = 11.82$, $P < 0.01$) than in habitats with 50% cropland and 50% deciduous forest ($\bar{X} = 6.5$ individuals/km^2; 95% CI = 5.5–8.2), or >75% deciduous forest ($\bar{X} = 3.4$ individuals/km^2; 95% CI = 2.4–6.8; $t_8 = 3.43$, $P < 0.01$).

A total of 50 raccoons (47 individuals) was captured in the northern Ontario plots during 1996. Only 13 of 64 plots produced raccoon captures, primarily in the North Bay/Sudbury area. In those 13 plots, raccoon density was extremely low, ranging from 0.3 to 1.5 individuals/km^2.

Niagara raccoon movement.—Raccoons were recaptured from 1 to 10 different times and from 1 to 120 days subsequent to the initial trap event during 1994–1997. The number of recaptures of the same raccoon showed a fairly consistent pattern between 1995 and 1997 with approximately 60–70% of the raccoons recaptured only once and 80–90% of the raccoons recaptured 2 or fewer times. However, the recapture pattern differed greatly in 1994, when more than 85% were

recaptured just once and more than 98% were recaptured 2 or fewer times.

With the exception of 1994, monthly movement patterns of raccoons were very similar between 1995 and 1997 (Table 2). Median values across these 3 years were within the range of 0.2–0.5 km with an upper and lower quartile range of no more than 1.2 km. However, in 1994 the movement distribution spanned greater distances than other years ($t_9 = 2.6$, $P < 0.03$), with September having the greatest median quartile values.

Only during 1994 and 1996 did we find any significant difference between sexes in distance traveled (Table 3). Although female raccoons traveled farther than males in 1994, the opposite trend was found in 1996 (Table 3). We found no difference in distance traveled between adult and juvenile raccoons across years; however, rural raccoons traveled greater distances in 1994 and 1996 than did their urban counterparts (Table 3). In 1994 we saw a progressively increasing median value with the progression of raccoon biological seasons, but in 1996 we saw an opposite trend where distance traveled during the rearing season was greater than during the dispersal season (Table 3).

Only 1994 and 1996 showed significant differences in distance traveled among 3 of the 4 groupings tested: sex, habitat, and biological season. We detected no consistent trends associated with the groups because patterns observed in 1994 were often opposite to those found in 1996. The only consistent pattern found in the 3 significant groupings was within habitat; rural raccoons always were found to travel greater distances than urban raccoons (Table 3). In all years movement by raccoons varied little with age. In the more detailed seasonal analysis of 1994 and 1996, movement by the 4 sex–age groups of raccoons was significantly different only in the rearing season of 1996 (Table 3). However, in the age–sex comparisons across seasons, we found that movement by all 4 of the sex–age groups of raccoons was significantly different (see Table 3 for group differences) among the seasons in 1994 and that movement only by adult male raccoons was significantly different from other groups in 1996.

Across all 3 years, the majority of raccoons (1996 and 1997 = 95%; 1995 and 1996 = 91%; 1994 and 1995 = 63%) traveled less than 5 km from the original site of capture the previous year (Table 4). However, there were cases ($n = 11$) of raccoons moving up to 45 km from the site of 1st capture.

TABLE 2.—Monthly movement (km) of raccoons in the Niagara, Ontario, Canada, region, 1994–1997.[a]

Month	1994	1995	1996	1997
May	3.17 (54) (2.75/3.91)	NA	NA	NA
June	3.02 (40) (1.82/5.60)	0.51 (173) (0.20/1.40)	0.32 (84) (0.22/0.58)	0.36 (106) (0.12/0.77)
July	7.98 (40) (2.36/14.98)	0.41 (520) (0.14/1.20)	0.50 (238) (0.22/1.10)	0.18 (749) (0/0.45)
August	8.94 (26) (4.11/12.66)	0.36 (235) (0.10/0.85)	0.58 (238) (0.28/1.30)	0.16 (523) (0/0.45)
September	20.16 (51) (5.41/33.97)	0.40 (217) (0.14/0.93)	0.50 (143) (0.22/1.17)	0.29 (316) (0/0.75)
October	4.05 (37) (2.35/16.60)	0.40 (113) (0.14/0.81)	0.40 (187) (0.22/0.71)	0.26 (298) (0/0.58)

[a] Median values are given for each month, followed by the corresponding sample size (*n*) in parentheses, then the lower/upper quartiles in parentheses. NA = not available because no samples were collected that month.

TABLE 3.—Raccoon movement (km) by group in Niagara Falls, Ontario, Canada, 1994–1997 based on mark–recapture data.

Group	n	Median	Minimum	Maximum	25% quartile	75% quartile	P-value
1994							
Male	326	11.70	0	84.2	4.03	24.45	0.0051
Female	253	16.83	0	75.94	5.52	26.35	
Adults	437	13.27	0.85	75.94	4.84	26.78	0.9007
Juvenile	264	13.27	0	53.27	6.02	26.35	
Urban	22	2.34	0.85	44.05	1.72	5.38	<0.0001
Rural	675	16.31	0	84.20	7.09	26.79	
Breeding	55	3.33	0.95	12.15	2.75	3.91	<0.0001
Rearing	286	9.73	0	43.50	3.21	19.76	
Dispersal	787	16.83	0	41.90	6.98	26.35	
1995							
Male	409	1.04	0	20.66	0.41	2.01	0.8001
Female	387	0.850	0	13.26	0.36	1.84	
Adults	495	1.05	0	16.54	0.40	2.11	0.6527
Juvenile	318	0.89	0	20.66	0.40	1.70	
Urban	119	0.81	0	4.47	0.36	1.40	0.3636
Rural	603	0.81	0	8.36	0.32	1.63	
Rearing	1,108	0.45	0	16.31	0.14	1.25	0.2765
Dispersal	431	0.41	0	20.66	0.14	1.07	
1996							
Male	416	0.75	0.02	26.94	0.36	1.64	0.0065
Female	301	0.61	0.10	25.22	0.30	1.20	
Adults	431	0.70	0.02	26.94	0.32	1.46	0.6510
Juvenile	295	0.65	0.04	25.22	0.32	1.36	
Urban	110	0.60	0.10	12.15	0.28	1.00	0.0058
Rural	650	0.71	0.02	26.94	0.33	1.58	
Rearing	720	0.50	0	26.94	0.22	1.11	0.0476
Dispersal	418	0.44	0	8.08	0.22	0.85	
1997							
Male	778	0.44	0	45.95	0.10	1.12	0.1388
Female	745	0.34	0	24.01	0.07	0.86	
Adults	907	0.41	0	44.15	0.12	1.03	0.9781
Juvenile	629	0.35	0	45.95	0.02	0.97	
Urban	235	0.37	0	20.05	0.08	0.85	0.1620
Rural	1,304	0.38	0	27.08	0.07	1.00	
Rearing	967	0.34	0	45.95	0.06	1.00	0.1115
Dispersal	498	0.41	0	24.23	0.10	0.96	

TABLE 4.—Number of raccoons (and percent of total in parentheses) in the Niagara, Ontario, Canada, region that traveled x distance between 2 consecutive years from 1994 to 1997.[a]

Distance traveled (km)	Year		
	1994–1995	1995–1996	1996–1997
0	38 (5.9)	7 (1.0)	0
0 < x ≤ 5	408 (63.3)	656 (91.4)	757 (94.4)
5 < x ≤ 10	59 (9.2)	20 (2.8)	29 (3.6)
10 < x ≤ 15	26 (4.0)	10 (1.4)	7 (0.9)
15 < x ≤ 20	20 (3.1)	10 (1.4)	7 (0.9)
20 < x ≤ 25	21 (3.3)	7 (1.0)	1 (0.1)
25 < x ≤ 30	20 (3.1)	3 (0.4)	1 (0.1)
30 < x ≤ 35	35 (5.4)	3 (0.4)	NA
35 < x ≤ 40	8 (1.2)	1 (0.1)	NA
40 < x ≤ 45	10 (1.6)	1 (0.1)	NA

[a] Total sample size in 1994–1995 = 645, 1995–1996 = 718, 1996–1997 = 802. NA = not applicable.

Interannual travel decreased in a more recent year (1996–1997) as evidenced by the decreasing numbers in the higher distance categories (Table 4). Median travel was smallest in 1996 and 1997 and greatest in 1994 and 1995. In each of the 3 years, males traveled significantly greater distances than did females (Table 5).

St. Lawrence raccoon movement.—A total of 98 raccoons was captured and fitted with radiocollars (86 VHF and 12 GPS) between 10 September 2003 and 30 September 2006 and tracking continued until 15 May 2007. We captured 33 adult females, 43 adult males, 10 juvenile females, and 12 juvenile males. These are maximum samples sizes and the actual samples sizes used vary depending on the criteria set to screen the data (see ''Materials and Methods'').

Home-range estimates were based on a mean of 43 ± 10.6 locations. Annual home-range estimates (*n* = 30) of VHF-

TABLE 5.—Summary statistics of distance traveled (km) between 2 consecutive years for various subgroups of raccoons captured in the Niagara, Ontario, Canada, region trap–vaccinate–release rabies-control program. Mann–Whitney U-tests are for comparisons of males and females.

Group	n	$\bar{X}$	SD	Median	Quartile range (upper 75% − lower 25%)	Mann–Whitney U-value	P-value
1996–1997							
All	802	1.24	2.64	0.54	0.84		
Males	296	1.87	3.25	0.71	1.53	55,262	<0.0001
Females	491	1.01	2.06	0.46	0.63		
1995–1996							
All	718	2.20	4.57	0.90	1.48		
Males	295	2.98	5.49	1.12	1.94	47,807	<0.0001
Females	408	1.67	3.77	0.79	1.12		
1994–1995							
All	645	7.20	10.70	1.92	7.80		
Males	258	7.37	10.03	2.49	8.43	41,234	0.0060
Females	367	7.06	11.16	1.65	5.50		

collared raccoons (Table 6) did not differ by sex ($F_{5,23} = 0.615$, $P = 0.689$) or age ($F_{5,23} = 0.514$, $P = 0.763$). Mean annual MCP home-range size for pooled age and sex classes was 3.91 ± 6.15 km^2. Mean 95% kernel home range was 0.83 ± 0.87 km^2, and 50% kernel home range was 0.17 ± 0.22 km^2. Breeding-period home ranges were 1.00 ± 1.14 km^2, and rearing-period home ranges were 1.67 ± 1.53 km^2. Raccoon home ranges were significantly larger during the rearing period than during the breeding period ($F_{1,34} = 7.963$, $P = 0.008$; Table 6).

Annual MCP home-range sizes of GPS-collared animals ($n = 12$) were similar between sexes (Table 7). Mean annual MCP home-range size for pooled sex classes was 3.29 ± 2.41 km^2 ($n = 12$). Seasonal MCPs did not differ by sex ($F_{1,7} = 1.326$, $P = 0.675$). Seasonal home-range sizes were as follows: breeding, 1.63 ± 1.74 km^2; rearing, 1.88 ± 1.85 km^2; predenning and dispersal, 2.1 ± 1.53 km^2. Comparisons of seasonal home ranges revealed no significant differences between seasons ($F_{2,14} = 0.554$, $P = 0.587$). Kernel home-range estimates were similar between sexes (95%, $F_{1,10} = 2.625$, $P = 0.136$; 50%, $F_{1,10} = 3.770$, $P = 0.081$; Table 7).

No sex- or age-specific differences were discovered in the mean or maximum distance movements by 91 raccoons (39 females and 52 males; sex, $F_{2,86} = 1.625$, $P = 0.203$; age, $F_{2,86} = 1.932$, $P = 0.151$). Mean distance from release site was 1.54 ± 1.44 km, and maximum distances averaged 2.79 ± 1.97 km. The longest linear movement was by a juvenile male, which was found 10.3 km from the release site. An adult

male moved the next farthest (9.3 km), followed by juvenile females (6.7 km). The maximum distance moved by an adult female was 4.4 km.

Throughout the study, male and female raccoons moved at a rate of 131.22 ± 67.87 m/h. Movement rates were not statistically different among seasons ($F_{2,28} = 0.123$, $P = 0.885$). Nightly movement rates for raccoons averaged 169.6 ± 78.1 m/h, whereas daily rates averaged 55.9 ± 31.1 m/h. Based on the average movement rate, males left their winter dens between days 25 and 39 of the calendar year (the end of January, beginning of February) for breeding, followed by a lull in activity until about day 56 (end of February).

Habitat analysis.—Raccoon habitat use was not influenced by season ($F_{20,356} = 0.403$, $P = 0.991$), time of day ($F_{10,177} = 0.553$, $P = 0.850$), or collar type ($F_{10,177} = 0.730$, $P = 0.695$). Therefore, all data were pooled together by sex and age class for further analysis. Habitat use by raccoons did not differ by age ($F_{10,49} = 1.669$, $P = 0.115$) but did differ by sex ($F_{10,49} = 2.453$, $P = 0.018$). Specifically, the difference in distance of female (1.18 km) and male (0.94 km) raccoons from water-lines was marginally nonsignificant ($F_{1,58} = 3.748$, $P = 0.058$). Females also were found farther than expected from unclassified habitats (1.13 km), whereas males were found closer than expected (0.94; $F_{1,58} = 7.692$, $P = 0.007$). Results of univariate t-tests suggest that no single habitat was used less or more than expected (Table 8). Likewise, use of a MANOVA and pairwise comparisons of habitat types suggest that no single habitat was used more or less than any other habitat (Table 9).

TABLE 6.—Mean (SD) annual and seasonal home ranges (km^2) of very-high-frequency–collared raccoons in the St. Lawrence study area in eastern Ontario, Canada, during 2003–2007. MCP = minimum convex polygon; n = sample size.

Age and sex	n	Annual MCP	Annual 95% kernel	Annual 50% kernel	Breeding-period MCP	Rearing-period MCP
Adult females	8	2.21 (1.78)	0.46 (0.66)	0.10 (0.16)	0.95 (0.64)	1.87 (1.57)
Adult males	20	4.23 (5.41)	0.67 (0.72)	0.12 (0.02)	1.30 (1.44)	1.74 (1.80)
Juvenile males	2	1.31 (0.76)	0.7 (0.86)	0.12 (0.16)	0.31 (0.12)	1.23 (0.70)

TABLE 7.—Annual and seasonal home range of global positioning system–collared raccoons in eastern Ontario, Canada, during 2003–2007. *F*-statistics are for comparisons of males and females. MCP = minimum convex polygon; K = kernel; *n* = sample size.

	Adult females $\bar{X}$ (*SD*) (km^2)	Adult males $\bar{X}$ (*SD*) (km^2)	*n*	*F*	*P*
Annual MCP	3.33 (2.72)	3.26 (2.39)	12	0.002	0.963
Breeding-period MCP	1.88 (1.72)	3.31 (3.19)	10	0.619	0.462
Rearing-period MCP	1.81 (1.63)	2.95 (1.30)	10	1.201	0.315
Dispersal-period MCP	1.89 (1.80)	1.99 (1.81)	10	0.803	0.466
Annual 95% K	0.37 (0.29)	1.28 (1.22)	12	2.63	0.136
Annual 50% K	0.06 (0.03)	0.17 (0.12)	12	3.769	0.081
Breeding-period 95% K	0.20 (0.14)	1.00 (0.99)	10	2.509	0.164
Breeding-period 50% K	0.04 (0.01)	0.16 (0.16)	10	2.183	0.19
Rearing-period 95% K	0.25 (0.22)	0.78 (0.43)	10	4.757	0.072
Rearing-period 50% K	0.04 (0.02)	0.14 (0.08)	10	5.218	0.062
Dispersal-period 95% K	0.31 (0.27)	0.36 (0.35)	10	4.701	0.101
Dispersal-period 50% K	0.06 (0.01)	0.07 (0.03)	10	5.023	0.093

Survival analysis.—We recorded 18 mortalities and 59 censors (dropped collar or loss of contact) between September 2003 and June 2007. Unknown causes accounted for 50% (*n* = 9) of raccoon mortalities. Predation, vehicular collision, and nuisance animal removal each accounted for the remainder of mortalities (*n* = 3, 17% each). Average survival time was estimated at 816.0 days ± 61.3 *SE* for male raccoons (*n* = 55) and 924.5 ± 108.4 days for females (*n* = 43). This difference was not statistically significant (Tarone–Ware = 0.00, *P* = 0.998). When data were stratified by age, average survival of raccoons released as juveniles was 964.4 ± 139.2 days, but was not significantly different (Tarone–Ware = 2.92, *P* = 0.088) from that of adults (785.5 ± 56.2 days). Cumulative study period survival for pooled sex and age classes was estimated at 0.622 (Fig. 4).

DISCUSSION

Raccoons are one of the most successful carnivore species in North America, occupying a variety of habitats (Rosatte 2000). In the northern part of their range they are subjected to long winters, but their adaptability has enabled them to thrive in locations such as Ontario, Canada. Raccoons also are the

TABLE 8.—Habitat use by raccoons determined by telemetry locations relative to habitat availability in eastern Ontario, Canada, during 2003–2006.[a]

Habitat	$\bar{X}$	*SD*	*t*	*P*
Agriculture	0.949	1.130	−0.656	0.512
Buildings	0.966	0.491	−1.021	0.308
Development	0.989	0.434	−0.371	0.711
Hedgerow	1.008	0.571	0.203	0.840
Waterline	1.048	0.601	1.163	0.246
Pits & Quarries	1.009	0.505	0.257	0.797
Transportation	1.037	0.477	1.149	0.252
Unclassified	1.026	0.512	0.756	0.450
Water Bodies	0.993	0.513	−0.209	0.834
Wooded Areas	1.135	1.069	1.851	0.066

[a] Means represent habitat use relative to habitat availability. The habitat with the lowest value was used most relative to availability, whereas the habitat with the largest value was used least relative to availability.

reservoir for the raccoon variant of rabies in eastern North America, including Ontario (Debbie 1991; Rosatte et al. 2006). Knowledge of raccoon ecology, in particular density and movements, has been an asset in designing tactics that have led to the control of the disease in Canada (Rosatte et al. 2001, 2007a).

We have shown that raccoon density varies throughout the landscape of Ontario and we believe that an accurate portrayal of raccoon density at the landscape level should be a mean estimate over a large area. If only a small portion of the landscape is studied, an inflated estimate of raccoon density may be derived. However, because of the extremely large study areas and sample sizes in our studies, and long sampling periods, we feel confident that our estimates of raccoon density (3.4–13.6 individuals/km^2) for southern Ontario are accurate. Density estimation tends to be less accurate in small study areas because of the effect of the effective trapping area and raccoon movement. That is, if raccoon home ranges average about 4 km^2 in Ontario (Rosatte 2000) and raccoons are capable of moving on average about 1–4 km (Rosatte et al. 2006, 2007a), a study area 1–2 km^2 in size will most likely result in an overestimate of raccoon density because trapping will capture raccoons on the periphery of their range and raccoons that use the 1–2 km^2 as their core area of use. Examples of reported high raccoon densities (64–333 individuals/km^2) derived from extremely small study areas include Hoffmann and Gottschang (1977—2.3-km^2 study area), Smith and Engman (2002—0.72-km^2 study area), and Riley et al. (1998—0.30-km^2 study area).

In our study, raccoon density in southern Ontario averaged 3.4–13.6 individuals/km^2 during 1994 and 2007, depending on location of the study area, and about 11% of sampled cells in Niagara had raccoon densities of 21–52 individuals/km^2. Our estimates generally compare to those from other studies in Ontario (Rosatte and Lawson 2001; Rosatte et al. 1992a, 1992b, 2001; Totton et al. 2004). Our estimates also compare to those from study areas outside of Ontario. Perry et al. (1989) reported median raccoon densities of 11.7 individuals/km^2 (4.4–19.1 individuals/km^2) in a study in Virginia. However, much higher estimates have been reported in other studies. For example, Blackwell et al. (2004) estimated

TABLE 9.—The *t*-statistics (and *P*-values) used to determine if a habitat was used proportionately more than another habitat by radiocollared raccoons in eastern Ontario, Canada, during 2003–2006.

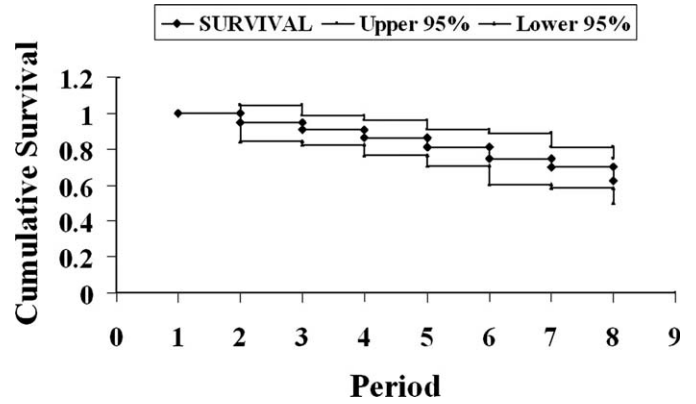|	Agriculture	Buildings	Development	Hedgerow	Waterline	Pits & Quarries	Transportation	Unclassified	Water Bodies	Wooded Areas
Agriculture		0.243 (0.808)	0.435 (0.664)	0.757 (0.450)	1.182 (0.239)	0.595 (0.553)	1.113 (0.267)	0.836 (0.404)	0.437 (0.662)	1.42 (0.157)
Buildings	−0.243 (0.808)		0.561 (0.576)	0.789 (0.431)	1.419 (0.157)	0.917 (0.576)	2.148 (0.033)	1.152 (0.251)	0.478 (0.633)	1.939 (0.05)
Development	−0.435 (0.664)	−0.561 (0.576)		0.388 (0.699)	1.012 (0.313)	0.741 (0.460)	1.067 (0.287)	0.714 (0.476)	0.077 (0.939)	1.684 (0.094)
Hedgerow	−0.757 (0.450)	−0.789 (0.431)	−0.388 (0.699)		0.675 (0.5)	0.019 (0.985)	0.596 (0.552)	0.342 (0.733)	−0.261 (0.794)	1.591 (0.113)
Waterline	−1.182 (0.239)	−1.419 (0.157)	−1.012 (0.313)	−0.675 (0.5)		−0.675 (0.5)	−0.226 (0.822)	−0.512 (0.609)	−1.234 (0.219)	1.092 (0.276)
Pits & Quarries	−0.595 (0.553)	−0.917 (0.576)	−0.741 (0.460)	−0.019 (0.985)	0.675 (0.5)		0.593 (0.554)	0.351 (0.726)	−0.327 (0.744)	1.478 (0.141)
Transportation	−1.113 (0.267)	−2.148 (0.033)	−1.067 (0.287)	−0.596 (0.552)	0.226 (0.822)	−0.593 (0.554)		−0.260 (0.795)	−0.879 (0.381)	1.181 (0.239)
Unclassified	−0.836 (0.404)	−1.152 (0.251)	−0.714 (0.476)	−0.342 (0.733)	0.512 (0.609)	−0.351 (0.726)	0.260 (0.795)		−0.793 (0.429)	1.707 (0.089)
Water Bodies	−0.437 (0.662)	−0.478 (0.633)	−0.077 (0.939)	0.261 (0.794)	1.234 (0.219)	0.327 (0.744)	0.879 (0.381)	0.793 (0.429)		1.872 (0.063)
Wooded Areas	−1.42 (0.157)	−1.939 (0.05)	−1.684 (0.094)	−1.591 (0.113)	−1.092 (0.276)	−1.478 (0.141)	−1.181 (0.239)	−1.707 (0.089)	−1.872 (0.063)	

FIG. 4.—Survival ($\bar{X}$ and 95% confidence limits) of radiocollared raccoons in eastern Ontario, Canada, during September 2003–June 2007. The period of time includes: 1 = September–December 2003; 2 = January–June 2004; 3 = July–December 2004; 4 = July–December 2004; 5 = January–June 2005 6 = January–June 2006; 7 = July–December 2006; 8 = January–June 2007.

raccoon density in an area of Ohio to range from 33.4 individuals/km^2 in August to 13.6 individuals/km^2 in November. In a marsh habitat of western Lake Erie, raccoon density was 181 individuals/km^2 (Urban 1970). Extraordinary densities of 67–333 raccoons/km^2 ($\bar{X}$ = 125 raccoons/km^2) were reported in Rock Creek Park, Washington, D.C., by Riley et al. (1998). However, these are the exception, and we designed and evaluated our rabies-control strategies based on mean raccoon densities found in Ontario.

In our study, we believe than an abundance of food resources and denning sites, and high reproductive potential, are factors that led to considerable densities of raccoons in both urban and rural areas of southern Ontario. In an urban habitat of metropolitan Toronto, where resources were concentrated, Broadfoot et al. (2001) found mean raccoon densities of 23.5 individuals/km^2 across their study area but 53 individuals/km^2 in productive raccoon habitat. In a study in northeastern Illinois, Prange et al. (2003) reported raccoon densities that were higher in urban and suburban habitats than in rural areas. Other studies in Ontario (Rosatte 2000; Rosatte et al. 1992b) also have shown that raccoon densities in metropolitan Toronto are higher than in rural habitats. As a result of differences in raccoon density among habitats, we have had to design and evaluate our rabies-control strategies based on whether rabies cases are in urban or rural areas of Ontario (Rosatte et al. 1997).

Home ranges of raccoons in this study averaged 1–4 km^2 (depending on age and sex) in rural habitats of eastern Ontario using MCP and <1.3 km^2 using a 95% kernel estimator. Obviously, core ranges of raccoons in eastern Ontario are much smaller than their annual ranges. Similarly, Beasley et al. (2007b) found that male raccoons in a study in Indiana had mean home ranges of 92 ha (0.92 km^2) with core-area use of only 20 ha. Home ranges were similar (71.2–182.4 ha) in rural habitats of northeastern Illinois (Prange et al. 2004). Home ranges varied across seasons in a study in Mississippi during 1991 and 1997 (Chamberlain et al. 2003); however, similar-

sized core areas were used during all seasons. Gehrt and Fritzell (1997, 1998) also found that spatial patterns of female raccoons in Texas were determined by resource distribution; however, patterns of males were influenced by distribution of females. Bozek et al. (2007) noted that raccoon home-range size in Illinois was greater in rural than in urban habitats. Mean home ranges for raccoons in Ontario were taken into consideration when we were designing our raccoon rabies-control strategies (Rosatte et al. 2001). We also used home ranges to evaluate and validate our raccoon rabies model (Rees 2007).

Mean and median movements of raccoons in this study averaged 1–17 km, depending on location of the study area, year, and sex and age of raccoons. Other studies in Ontario have yielded similar findings (Rosatte et al. 2007d; Totton et al. 2004). However, in our study, maximum distances of 40–45 km were noted in Niagara. Roscoe et al. (1998) reported maximum movements of 12.9 km for 5 rabid raccoons in New Jersey. By comparison, nonrabid raccoons in that study moved about 2.6 km. Rosatte et al. (2006) also noted that the movements of 5 rabid raccoons (1.6–4.1 km) exceeded the median movement distances of nonrabid raccoons (median = 0.7–0.9 km) in eastern Ontario. Hodges et al. (2000) documented mean ($\pm$ *SD*) male and female raccoon movement rates of 764 $\pm$ 52 m/h and 669 $\pm$ 89 m/h in a study in Mississippi. Rates for Ontario raccoons were much lower, which is probably a function of climate and the resultant impact on raccoon movement. Regardless, the raccoon movement data in Ontario were used for designing and evaluating rabies-control tactics and were valuable for the management of raccoons in the province.

Raccoons are considered to be ecological generalists and exist in a variety of habitats and landscapes (Chamberlain et al. 2002; Fritzell 1978; Henner et al. 2004).We found that no single habitat type was used more extensively than others. Pedlar et al. (1997) noted that raccoons in one Ontario study used woody vegetation associated with fencerows, denning trees, and deciduous stands. Raccoons also were associated with areas of extensive corn cover. This suggests that although raccoons may be habitat generalists, they are attracted to certain habitats during foraging and denning activities. This also was found in Mississippi during 1997–2001 in a prairie landscape where use of space by raccoons was impacted by dispersion of row-crop fields and resources such as water, riparian habitats, and woodlots (Chamberlain et al. 2007). In Indiana during 2003–2005, selection of agricultural habitats by raccoons was greatest when corn was available and raccoon density and dispersion were dependent on the availability and distribution of forest cover and habitats associated with forests (Beasley et al. 2007a, 2007b). It is advantageous that raccoons are habitat generalists because targeting specific habitats for disease control in raccoons would be a logistical challenge, especially over large landscapes such as Ontario.

Raccoons are not very long-lived. Average survival of raccoons in our telemetry study in eastern Ontario was 816 and 924 days for males and females. Near Barrie, Ontario,

78% of raccoons sampled during 1993–1994 were ≤3 years of age (Rosatte 2000). In our study the majority of known raccoon mortalities were due to predation, collision with vehicles, and nuisance animal removal. Robel and Barnes (1990) also noted that raccoon mortality in a study in Kansas during 1986 was greater in areas of high human disturbance. Rosatte (2000) reported that annual harvest-related mortality in raccoons in Ontario from 1979 to 1996 varied between 1% and 15%. In addition, 5–19% of a raccoon population living within 1–4 km of a major superhighway in Ontario were killed due to collisions with vehicles during 1991–1992 (Rosatte 2000). Mosillo et al. (1999) found no differences in survival of raccoons that were relocated to different habitats in urban and rural areas of Illinois.

Raccoon survival over the course of the telemetry study period was estimated to be 0.62 with juvenile and adult raccoons surviving 964 and 786 days. Generally speaking, the winters during 2003–2007 were not severe in southern Ontario. However, in a study in Manitoba during 2002 and 2005, Pitt (2006) noted that winter severity, as measured by temperature and snow accumulation, was the most significant factor influencing raccoon survival. His estimates of raccoon survival ranged from 0.51 during a harsh winter to 0.84 during a mild winter, and adults had greater survival rates than did yearlings. In a study in Kansas, where winter severity is not a consideration compared to more northern locations, Kamler and Gipson (2004) noted that annual survival of raccoons was 0.71 during 1995 and 2000. Similarly, Gehrt and Fritzell (1999) found high survival (0.84) of raccoons in a study in southern Texas.

Factors other than winter severity also account for significant mortality among raccoons. Adult female and male survival values were 0.58 and 0.37 in a raccoon population in an area of Iowa where hunting and trapping occurred (Hasbrouck et al. 1992). Male and female raccoon survival values were 0.63 and 0.50 in Mississippi, where harvest accounted for 58% of the mortality (Chamberlain et al. 1999). During the 1990s the Ontario raccoon harvest was about 42,000 pelts/year, or approximately 4% of the Ontario raccoon population (Rosatte 2000). Obviously, the harvest in Ontario has little impact on raccoon survival. However, raccoon survival is important when designing and implementing disease-control tactics. For example, if raccoon mortality is high, with resultant rapid population turnover, rabies-control tactics will have to be used annually because the majority of the population will be juveniles.

In Ontario, raccoons harbor a number of infectious diseases and parasites including rabies, canine distemper, and *Baylisascaris* sp. (Rosatte et al. 2007b). Movement of rabid and nonrabid raccoons contributes to the rapid spread of diseases such as rabies (Roscoe et al. 1998). Rosatte et al. (2005, 2007a) concur that raccoon movement plays an important role in disease spread. As such, the width of control zones must take into consideration the movement potential of raccoons. Rosatte et al. (1992b, 1997) used data on movement of rabid and nonrabid raccoons from urban and rural landscapes when

designing a point infection control tactic for rabies in Ontario. In addition, these data were used to design a raccoon rabies contingency plan and determine the size of a high-risk zone around case locations for raccoon rabies (Rosatte et al. 1997, 2001). Recent studies in rabies-control areas of eastern Ontario have found movement of rabid raccoons to be <5 km, whereas nonrabid raccoons moved on average <4 km but some as far as 24 km (Rosatte et al. 2005, 2006, 2007c). In Ontario, the width of raccoon rabies-containment zones is currently 50 km, which takes into consideration the movement potential of raccoons (Rosatte 2007d). As such, our hypothesis that a 50-km-wide containment zone would be sufficient to control an epizootic of raccoon rabies was verified because Ontario has been free of reported cases of raccoon rabies since September 2005 (to September 2009).

Knowledge of raccoon population densities and dispersal patterns and environmental features such as topography can assist with predicting or explaining the irregular wavelike pattern of disease spread (Smith et al. 2002). Russell et al. (2004) assessed the effects of geographical features such as rivers and mountains on disease movement. They noted that knowledge of raccoon habitat use will assist in model prediction of likely areas of disease introduction and assist with the design and evaluation of tactics to manage disease. In view of this, disease-control tactics should consider the topography of the control zone. In the Niagara and St. Lawrence River areas in Ontario during the mid-1990s when raccoon rabies was threatening Ontario from New York State, vaccination barriers were created using the rivers as partial barriers to raccoon movement (Rosatte et al. 2007a). Knowledge of raccoon ecology also was used to develop population models to assist with disease-management planning exercises in Ontario (Broadfoot et al. 2001). In addition, raccoon ecological data were used to validate a raccoon rabies model for Ontario (Rees 2007). The model predicted that raccoon rabies would have spread several hundred kilometers from eastern Ontario to Toronto if control programs were not initiated. The disease was contained using point infection control tactics (Rosatte et al. 2001) and spread only 49 km in 6 years before it was eliminated.

Knowledge of the densities of raccoon populations in Ontario was critical for assessing the effectiveness of control programs such as point infection control. To be successful, population-reduction programs will need to decrease vector density to a point where transmission of rabies does not occur. Rosatte et al. (2001) reduced raccoon density from 5.7–7.1 individuals/km^2 to 0.6–1.1 individuals/km^2, sufficient to contain the 1st case of raccoon rabies in Ontario. Knowledge of raccoon densities allowed the determination of trapping effort required to decrease vector density to a point where rabies transmission ceased (Rosatte et al. 2001; 2007d). Well-designed density studies will assist in the accurate evaluation of disease-control strategies.

Also of importance when designing wildlife disease-control tactics and strategies is the longevity of the target species. We found that raccoon survival in Ontario was generally <3 years, meaning that raccoon population turnover will be rapid. From a disease-management perspective this is not ideal, and control using tactics such as vaccination will have to occur annually because each year the majority of the population will be young-of-the-year animals that have not been vaccinated. In view of this, our hypothesis that raccoon survival will necessitate annual control programs until the disease is eliminated is accepted.

When distributing vaccine baits for rabies control it is important to know whether sufficient baits are on the landscape to provide all raccoons an opportunity to become vaccinated. For example, distributing 20 baits/km^2 in habitat where raccoon density is 40 individuals/km^2 would be considered insufficient. Blackwell et al. (2004) noted that at mean raccoon densities of 24.5 individuals/km^2, an average of 3.3 baits was consumed per raccoon when baits were distributed at 75 baits/km^2. Obviously, this was sufficient bait density to ensure that a significant portion of the raccoon population became immunized against rabies for the given density of raccoons in the target area. Rosatte and Lawson (2001) also determined raccoon density in urban and rural habitats of Ontario when experimenting with densities of baits needed to vaccinate raccoons, with a goal of ensuring that baits were placed in the home range of all raccoons within the target zone. Wise disease-management planning will need to take into consideration the ecology of raccoons when designing disease-management tactics and strategies; otherwise, failure at containment, control, and eradication may be inevitable.

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