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Population density, survival, and rabies in raccoons in an urban national park

Seth P.D. Riley, John Hadidian, and David A. Manski

Abstract: Density and survival of a raccoon (*Procyon lotor*) population in Rock Creek Park, an urban national park in Washington, D.C., were estimated using mark–recapture and radio-tracking over an 8-year period following the appearance of the mid-Atlantic States (Mid-Atlantic) rabies epizootic. Raccoon density ranged from 333.3 to 66.7/km^2, with an overall park estimate of 125/km^2. This density places the Rock Creek population within the range of other urban and suburban populations and is many times greater than raccoon densities reported from other habitats. Density was particularly high in one thin spur of parkland with the smallest ratio of area to urban edge. Raccoon survival rates were high except among juveniles during the rabies epizootic. Data on rabies prevalence from Washington, D.C., indicate a cycle with peaks in 1983 during the initial epizootic and again in 1987 and 1991, a pattern similar to that seen in other carnivores and in rabies models. We found evidence of decreased raccoon density during and after the 1987 rabies resurgence relative to the years following the original epizootic, when rabies prevalence was low. While hunting and trapping represent a major mortality factor for many rural raccoon populations, urban and suburban populations and protected populations may frequently be subject to epizootics of diseases such as canine distemper and rabies, even years after initial contact with a disease.

Résumé : La densité et la survie d'une population de ratons-laveurs (*Procyon lotor*) ont été estimées par capture–recapture et par radiotélémétrie dans le parc Rock Creek, un parc national urbain de Washington, D.C., au cours d'une période de 8 ans consécutive à l'éclatement de l'épidémie de rage dans les états du milieu de la côte atlantique. La densité des ratons-laveurs s'échelonnait de 333,3 à 66,7/km² pour une densité globale de 125/km² dans tout le parc. Cette densité place la population de Rock Creek au même rang que les autres populations urbaines et suburbaines et est beaucoup plus élevée que la densité des ratons-laveurs d'autres habitats. La densité s'est avérée particulièrement élevée dans une projection étroite du parc où le rapport surface/périmètre de la zone urbaine était faible. Sauf chez les jeunes, les taux de survie des ratons-laveurs sont demeurés élevés au cours de l'épidémie. Les données sur l'évolution de la rage au sein de la population de ratons-laveurs de Washington, D.C., indiquent que la fréquence de la maladie a atteint un sommet en 1983 au début de l'épidémie, un autre en 1987 et un autre en 1991, suivant les mêmes tendances que chez les autres carnivores et conforme aux modèles théoriques. La population de ratons-laveurs a subi un déclin durant la résurgence de la maladie en 1987 et par la suite, comparativement aux densités enregistrées après l'épidémie originale alors que la fréquence des cas était faible. La chasse et le « trappage » constituent des facteurs de mortalité importants pour les populations rurales de ratons-laveurs, mais les populations urbaines et suburbaines ou les populations protégées sont souvent sujettes aux épidémies de maladies comme la maladie de Carré ou la rage, souvent même plusieurs années après le premier contact avec la maladie.
[Traduit par la Rédaction]

Introduction

The study of urban wildlife ecology is a growing but still neglected field despite the rate of urbanization throughout North America and other parts of the world. An understanding of wildlife ecology in urban and suburban areas and in adjacent nature preserves is crucial to the continued persistence of wild populations in the face of human impacts (Murphy 1988). The raccoon (*Procyon lotor*) is a common urban species that thrives in many habitats throughout North America (Kaufmann 1982), including in and around Washington, D.C. The 1983 arrival of the mid-Atlantic States (Mid-Atlantic) rabies epizootic in raccoons in Washington, D.C., raised interest in raccoon ecology and disease ecology in urban areas, particularly because of the high densities of both humans and raccoons and the increased possibility of transmission of disease from raccoons to humans or domestic animals (Jenkins et al. 1988). Researchers in urban and suburban areas have found dense populations of raccoons (Schinner and Cauley 1974; Hoffman and Gottschang 1977; Slate 1980; Jacobsen 1982; Rosatte et al. 1990), and dense populations are more likely to be subject to epizootics of contact diseases such as rabies and canine distemper and may be more likely to continue to harbor a disease after the initial epizootic. In this study we wanted to increase our understanding of the population dynamics of this important urban species and of urban

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wildlife in general by measuring the density and survival of raccoons in Rock Creek Park, an urban National Park in Washington, D.C., by tracking rabies and measuring the impact of the disease on raccoon density and survival.

Because urban habitats are drastically altered, fewer species survive in them, but those that do may benefit from more exclusive use of available resources. Mammals other than raccoons also exist at high densities in urban areas, including small mammals (Babinska-Werka et al. 1981) and other carnivores such as red foxes (Harris 1981). High urban densities have also been reported for certain bird populations (Nuorteva 1971; Emlen 1974; Vale and Vale 1976; DeGraaf and Wentworth 1981; Beissinger and Osborne 1982). Dense populations of urban wildlife may result from an increased availability of resources such as food, refuges, or den sites. The distribution of resources in the landscape may also influence wildlife densities in developed areas. Concentration of foraging or denning habitat in restricted natural areas can lead to a higher expressed density of animals in urban habitats (Vale and Vale 1976; Matthiae and Stearns 1981; Dickman 1987; Dickman and Doncaster 1987).

Dense wildlife populations are more likely to be impacted by diseases transmitted by contact and may be more likely to maintain the disease. The Mid-Atlantic rabies epizootic in raccoons began in the late 1970s in Virginia and reached Washington, D.C., in late 1982 with 5 cases, peaking in 1983 with 158 cases (Jenkins and Winkler 1987). The disease may have particularly impacted high density urban populations, such as those in Baltimore and Washington, D.C. (Winkler and Jenkins 1991). Anthony et al. (1990), using vehicle fatalities as a population index, note a decline in raccoons in Baltimore following the rabies epizootic.

Epizootic rabies has the potential to affect survival rates in raccoons. A few researchers have measured raccoon survival, although generally with an interest in the effects of human harvesting, which can significantly reduce survival rates (Fritzell and Greenwood 1984; Clark et al. 1989; Hasbrouck et al. 1992). Brown et al. (1990) reported raccoon survival before and after harvest season during the onset of the rabies epizootic in Pennsylvania, but they found no rabies mortality. A raccoon population in rural Virginia experienced increased mortality during the epizootic (Seidensticker et al. 1988). Raccoon survivorship and mortality factors may be different in urban settings, where recreational hunting and commercial trapping are generally prohibited but the probability of being struck by a vehicle, trapped as a nuisance animal, or infected by an epizootic disease such as rabies or canine distemper may be greater. Epizootics of these diseases have been studied in urban raccoon populations (e.g., Bigler et al. 1973; Roscoe 1993), although raccoon survival was not directly measured in these studies.

Raccoon rabies cycled upwards again in Virginia in 1986, perhaps because of an increase in susceptible animals after the epizootic (Torrence et al. 1992; Winkler and Jenkins 1991). Torrence et al. (1992, p. 374) note that “The fact that the positive percent of rabid raccoons was still decreasing in 1989 may mean that rabies will continue to decline to an endemic level and then disappear, or assume a cyclic pattern over a longer period of time than was analyzed in this study,” and Roscoe (1993) found 4-year cycles of canine distemper in raccoons. Mathematical models of rabies in red foxes produce cycles every 3–5 years, and density and rabies prevalence in red foxes in Europe and Canada cycle with the same period (Anderson et al. 1981). Seasonal mating, reproduction, and dispersal, which are thought to lead to rabies cycles in foxes (Anderson et al. 1981), are also characteristic of raccoons. However, raccoons exhibit a different immune response to rabies than red foxes, both in their response to different types of vaccines (Rupprecht et al. 1986) and in the ability of some raccoons to develop some immunity to the disease (Carey and McClean 1983). A model of raccoon rabies that includes a class of animals which survives and develops natural immunity to rabies produced cycles at 4- to 5-year intervals but with smaller amplitudes in subsequent peaks and shorter dampening times than the red fox models (Coyne et al. 1989). Coyne et al. (1989) speculate that no cycling in disease prevalence or raccoon density should be detectable in the field.

We hypothesized that raccoons in Rock Creek park would exist at high densities relative to populations in rural areas, both because of plentiful food and denning resources and because the park represents a concentrated source of resources adjacent to less hospitable urban habitats, thus perhaps elevating raccoon density in the park. We hypothesized that survivorship would be lower in Rock Creek raccoons during the epizootic because of increased mortality from rabies. We also measured rabies prevalence in Washington, D.C., raccoons for 12 years, starting with the epizootic in 1983, to look for long-term trends and for evidence of cycling. Finally, we hypothesized that raccoon density would be affected by any post-epizootic increases in rabies prevalence.

Materials and methods

Study area

The study was conducted at four sites in Rock Creek Park (Fig. 1), a 710-ha National Park located within metropolitan Washington, D.C. (38°57′N, 77°02′W). The park was established in 1890 by an Act of Congress that expressly prohibited any “injury or spoilation” of animals and other natural resources. Approximately 85% of the park consists of natural areas of mixed mesophytic forest with a deciduous overstory dominated by tulip poplar (*Liriodendron tulipifera*), oak (*Quercus* spp.), and beech (*Fagus grandiflora*).

For each of the four study sites, Piney Branch, Hazen, Colorado Avenue, and H-2 (Fig. 1), we estimated the density of the human population and housing units in the area surrounding each site from census tract data (Anonymous 1988*a*, 1988*b*). We also calculated the total area of each site and the length of its urban edge with a planimeter, and we then calculated the interior to edge ratio. The Hazen study area is the smallest (30 ha) and thinnest area, with an interior to edge ratio of 12.7 m^2/m. Hazen also has the highest adjacent human population density, 45.9 individuals/ha, and housing unit density, 35.5 units/ha. The other spur of parkland, Piney Branch, is larger at 61 ha, with an interior to edge ratio of 16.6 m^2/m and adjacent human and housing unit densities of 25.2 and 11.2/ha, respectively. The Colorado Avenue and H-2 areas, both part of the main body of the park, cover 80 and 56 ha and have much larger interior to edge ratios, 57.3 and 61.5 m^2/m, respectively, than the two spurs. The Colorado Avenue and H-2 sites have similar demographic features to Piney Branch, with adjacent human densities of 25.2 and 28.2/ha and adjacent housing unit densities of 11.2 and 11.8/ha, respectively.

We measured raccoon density at the Piney Branch, Hazen, and Colorado Avenue sites. We chose the Piney Branch and Hazen areas because they are thin strips of parkland surrounded by urban area and the Colorado Avenue area because it forms part of the main body of

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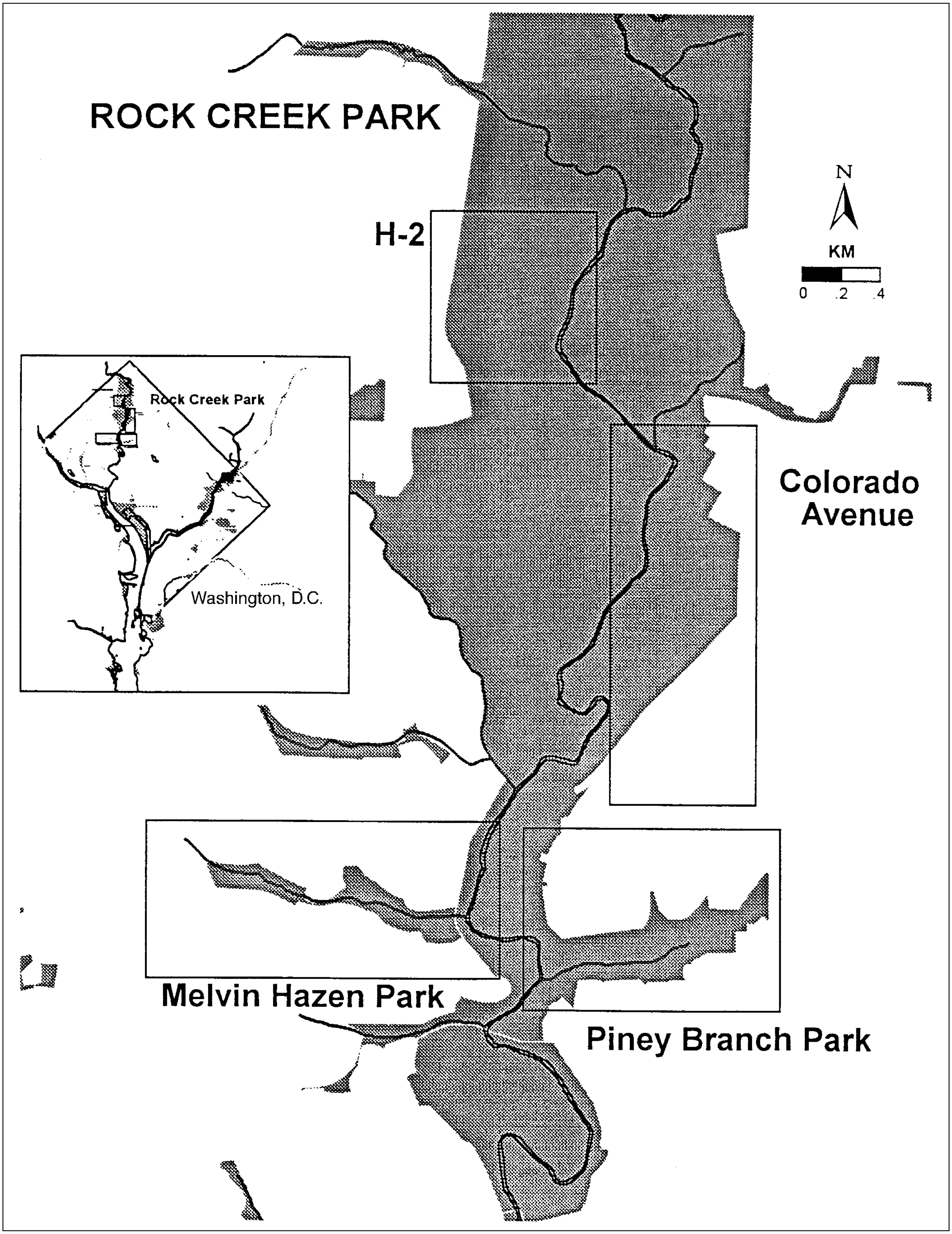
Fig. 1. Study areas in Rock Creek Park.



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the park and served as a comparison for the other two areas. We treated these three sites as separate units for population analyses because, although they shared some borders, they are separated by roads and a large stream (see Fig. 1) and because only 10 of 129 raccoons recaptured during the study were recaptured in a neighboring site.

We measured raccoon survival at the Piney Branch and H-2 sites. The Piney Branch site was chosen for intensive radio-tracking work at the beginning of the study, and a later study of raccoon family relationships at the H-2 site provided survivorship data from long after the original epizootic.

Trapping protocol

We livetrapped raccoons to obtain data for mark–recapture estimates and to radio-collar animals for survival estimates. We set live traps (Tomahawk No. 207, Tomahawk Live Trap Company, Tomahawk, WI 54487, U.S.A.) for 5 consecutive nights during each trapping period. We used 10 sites in Hazen (0.32/ha), 12 sites in Piney Branch (0.20/ha), and 15 sites in Colorado Avenue (0.19/ha). Two traps were set at each site to allow for multiple captures. We baited traps in late afternoon or early evening and examined them at first light. We took all captured raccoons to a quarantine facility for examination unless they had been previously captured and examined during the trapping period. We immobilized raccoons with ketamine hydrochloride (Ketaset, Bristol Laboratories, Bristol-Myers Co., Syracuse, NY 13221, U.S.A.) at dosages of 10–12 mg/kg (Bigler and Hoff 1974) or a mixture of ketamine and xylazine hydrochloride (Rompun, Mobay Corp., Shawnee, KS 66201, U.S.A.) at 5:1 and 7:1 ratios at the same dose rate. All subjects were ear-tagged in both ears with Monel No. 4 metal ear tags (National Band and Tag Co., Newport, KY 41072, U.S.A.) and tattooed on the chest with a unique number. We determined the age and sex of each animal. We classified males with a fully extrudable baculum measuring 95 mm or larger as adults (Sanderson 1961) and females with teats of 5 mm or larger as adults (Steuwer 1943). We fitted animals chosen for radio-tracking studies with a radio collar (Telonics, Inc., Mesa, Ariz., U.S.A., or Advanced Telemetry Systems, Isanti, Minn., U.S.A.). Following recovery we released animals at their respective capture sites in the afternoon or evening of the same day.

Data analysis

Population density

We estimated population size at each study site using mark–recapture techniques (Otis et al. 1978; Seber 1982; Nichols 1992). We trapped for 11 periods in the Piney Branch area, 7 in the Hazen area, and 4 in the Colorado Avenue area. We defined four seasonal periods: winter (January–March), spring (April–June), summer (July–September), and fall (October–December). Sampling intensity varied between study sites because we were particularly interested in long-term data for the Piney Branch area and because trapping was conducted for purposes other than population estimation alone, particularly early in the study.

We estimated population size using the program RECAPTURE, which employs a modified version of the Jolly–Seber model (Seber 1982) for open populations. The model modifications account for animals known to have died during the study (tag returns), eliminate negative birth and immigration values and survival rates greater than 1, and allow for periods during which no influx or outflow occurs (Buckland 1980, 1982). Of available population estimation techniques, the Jolly–Seber model is considered the most appropriate for raccoon populations (Hallet et al. 1991). We were able to estimate population size for 16 of the 22 trapping periods, since open-population models such as the Jolly–Seber model do not generate estimates for the first or last period of any single analysis. In order to take both capture probability and survivorship into account in looking for sexual differences, for each trapping period we constructed a 2 × 2 contingency table of the numbers of males and females captured in that period which were later recaptured or were never seen again (J.D. Nichols, personal communication).

We converted population size to density by dividing each population-size estimate by the size of the area of parkland in which we trapped. We had attempted, through the number and placement of trap sites, to effectively sample each study site. Since we knew from radio-tracking data that many raccoons had home ranges which included both parkland and adjacent neighborhoods, this estimate may overestimate the density of raccoons using a larger area that includes urban habitats. Ultimately, however, we are interested in the density of raccoons that use the park, so this density estimate seemed most applicable.

Survival

We measured raccoon survivorship using radio-tracking data collected in 1983–1984 in the Piney Branch area and in 1989–1990 in the H-2 area. We estimated survival on the basis of radio-days of survival (1 radio-day is 1 day on which one raccoon was being radio-tracked) with the program MICROMORT (Trent and Rongstad 1974; Heisey and Fuller 1985). Survival is defined as the probability of a radio-collared animal surviving from the beginning through the end of a specified time period. We used the "bias-corrected" estimates of survival computed by MICROMORT because the maximum-likelihood estimator for survival over periods longer than 1 day has a small bias directly related to increasing interval length, decreasing sample size, and decreasing daily survival rate (Heisey and Fuller 1985). We also estimated cause-specific mortality rates, or the probability of dying from a specific cause over a certain time interval, for rabies and non-rabies mortality.

Locations were obtained on each radio-collared animal at least three times per week. All radio collars included a motion sensor or "mortality mode," so that if the radio did not move for 12 h, the pulse rate of the signal doubled. Therefore, when an animal died, we were able to recover the body within 2 days. Although Heisey and Fuller (1985) suggest computing a minimum estimate of survival based on the assumption that each animal which disappears has died, we computed maximum estimates of survival based on the assumption that animals whose signals were lost were still alive. Using maximum survival estimates provides a more conservative test for disease effects. Maximum estimates also seem more reliable because a number of animals whose signals were lost were later known to be alive and because radio-collared raccoons exhibited long-range dispersal movements. All animals that died and were recovered were necropsied at the National Zoological Park's Department of Pathology. Brain tissue was removed from all subjects and tested for rabies by the District of Columbia Department of Human Resources with the use of fluorescent rabies antibody tests (Abelseth and Trimarchi 1983).

We computed survival rates for the entire 1983–1984 telemetry study, for each season, for the period when rabies prevalence was high (August 1983 to March 1984), and for the remaining 9 months when rabies prevalence was lower (April 1984 to December 1984). For the 1989–1990 study we computed survival for the whole study period (April 1989 through April 1990) for the adults, and for July 1989 to April 1990 for adults and juveniles because no juveniles were radio-collared before July, and for each season.

Between May 1983 and October 1984 all captured raccoons, and therefore all radio-collared raccoons, were experimentally immunized (Jenkins et al. 1988) using a killed rabies vaccine (IMRAB, Mieureux Laboratories, Paris, France). This procedure probably affected survival during the initial rabies epizootic, although we cannot quantify these effects. Animals followed in the 1989–1990 study of raccoon family relationships in H-2 were not immunized.

Rabies

Data on the number of positive raccoon rabies cases and the total number of raccoons tested for rabies each month from 1983 through 1994 were obtained from District of Columbia's Animal Control

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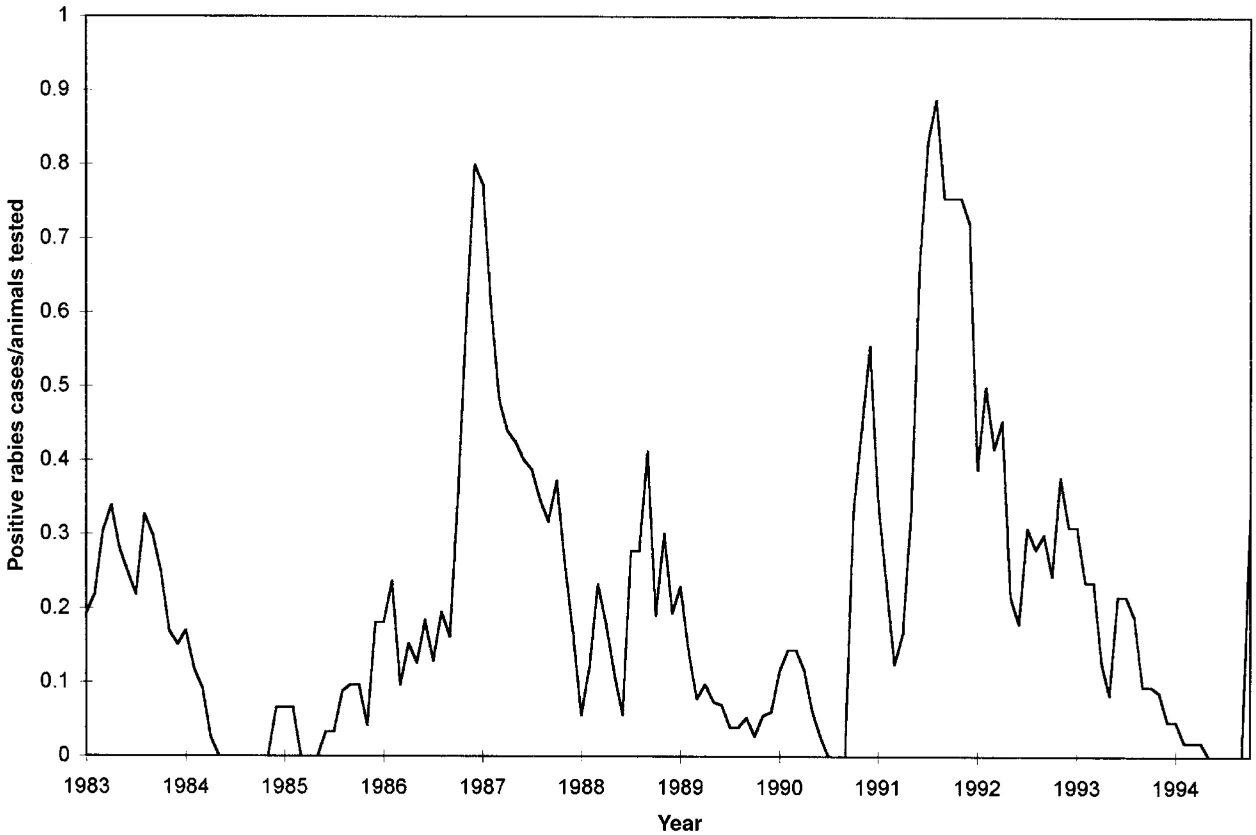
Fig. 2. Three-month running average of ratio of number of rabies cases to number of animals tested, for raccoons in Washington, D.C. (February in all years).



Division of the Department of Public Health (T. Harper, personal communication). This agency has routinely tested all suspect raccoons submitted to it since the rabies epizootic reached Washington, D.C., in the fall of 1982.

Disease incidence, or the number of positive cases of a disease, is an uncertain measure of disease prevalence because of the often large variation in the numbers of animals tested (MacInnes 1987; Torrence et al. 1992). We used the ratio of positive rabies cases to the number of animals tested as a measure of rabies prevalence that reduces the impact of this variation in sample size (Winkler and Jenkins 1991). We used a 3-month running average of this ratio to reduce the impact of any single month that might also constitute a small sample (Fig. 2). We used spectral analysis to test for cycles in raccoon rabies prevalence (Shumway 1988).

Statistical tests

We compared estimates of population size and survivorship between different time periods, such as periods of high versus low rabies incidence, different age and sex groups, and different study areas, using z tests for simple comparisons (Rosner 1982) and the χ^2 test of Sauer and Williams (1989) for more complex comparisons using the program CONTRAST (Hines and Sauer 1989). Fisher's exact tests and χ^2 tests were used to look for sexual differences in recapture probability and Yates' correction was used with χ^2 with 1 degree of freedom (Rosner 1982). We decided that three estimates of population size with coefficients of variation of 1.00 or more (Table 1) were too imprecise and they were not used in comparisons.

Results

During the study we captured 386 different raccoons 525 times. Of these, 57 (14%) were recaptured at least once and 30 (8%) were recaptured two or more times. We captured significantly more males (223 animals caught 295 times) than females (163 animals caught 230 times) ($\chi^2 = 9.02$, $p < 0.005$, df = 1). The overall sex ratio (M:F) of animals trapped was 1.37:1. Only 1 trapping period of the 19 that we could test was associated with a significant difference in recapture probability between males and females ($\chi^2 = 5.25$, $p < 0.05$, df = 1; 16 Fisher's exact tests, 3 χ^2 tests), so we used population estimates that combined the sexes.

Population density

We estimated population density for 16 trapping periods over the three different study sites (Table 1). Density estimates ranged from a high of 333.3 raccoons/km^2 during August and November 1985 in the Hazen area to a low of 67/km^2 in March 1988 for the Piney Branch population.

We found a significantly higher density of raccoons in the Hazen study area than in the Piney Branch ($\chi^2 = 11.07$, two-sided $p < 0.001$, df = 1) or Colorado Avenue ($\chi^2 = 10.03$, two-sided $p < 0.001$, df = 1) area. Densities did not differ significantly between the Piney Branch and Colorado Avenue study sites ($\chi^2 = 0.31$, two-sided $p = 0.58$, df = 1). These comparisons are affected by the fact that we did not always sample the three study areas during the same periods, in particular we sampled different sites during different periods of rabies prevalence (see "Rabies and population density" below). We sampled the Piney Branch area during the 1984–1985 decrease in rabies after the initial epizootic, as well as during and after the first post-epizootic rabies peak in 1986–1987.

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Table 1. Population size estimates, 95% confidence intervals, coefficients of variation, and density estimates from mark–recapture data for raccoons in the Piney Branch, Melvin Hazen Park, and Colorado Avenue study areas in Rock Creek Park, Washington, D.C.

	Mean	95% CI	CV	Raccoon density (no./km^2)
Piney Branch				
Jan. 1984	90	49–154	0.32	147
Aug. 1985	105	67–162	0.25	172
Nov. 1985	103	44–146	0.27	169
Apr. 1986	65	28–131	0.45	106
Dec. 1986	60	19–265	1.20	98
Dec. 1987	45	26–76	0.27	76
Mar. 1988	40	20–62	0.28	65
Dec.–Jan. 1988	66	24–103	0.29	109
Jan. 1990	53	10–330	1.92	87
Melvin Hazen Park				
Jan. 1984	95	28–193	0.54	313
Aug. 1985	100	60–151	0.26	333
Nov. 1985	100	45–138	0.26	333
Apr. 1986	77	27–131	0.35	256
Sept. 1987	60	11–191	1.00	200
Colorado Avenue				
Oct. 1986	82	28–164	0.43	102
July 1987	66	18–115	0.42	83

We sampled the Hazen area predominantly during the 1984–1985 period (the September 1987 estimate has a high coefficient of variation and is not useful for comparisons), while the Colorado Avenue area was sampled only during 1986–1987. A comparison of Piney Branch and Hazen using only common sampling periods (January 1984, August and November 1985, and April 1986) still reveals a significantly higher raccoon density in the Hazen area ($\chi^2 = 6.68$, $p = 0.01$, df = 1). A similar comparison is not possible for Hazen and Colorado Avenue or for Piney Branch and Colorado Avenue (the December 1986 Piney Branch estimate has a high coefficient of variation), although the latter comparison showed no difference even with all estimates included and would not be expected to change.

Seasonal averages varied significantly between years for Piney Branch (fall, $\chi^2 = 26.4$, $p < 0.001$, df = 2; winter, $\chi^2 = 21.92$, $p < 0.001$, df = 3). We examined our most consistently sampled study area, Piney Branch, for seasonal variation in raccoon density and found that although mean density from July to December (131.6/km^2) was higher than mean density from January to June (88.5/km^2), the difference was not statistically significant at the 0.05 level ($\chi^2 = 2.04$, one-sided $p = 0.08$, df = 1). The average density of Rock Creek raccoons from mark–recapture estimates was 125/km^2.

Rabies and population density

The Mid-Atlantic rabies epizootic moved into the Washington, D.C., area in the fall of 1982 (Jenkins and Winkler 1987), with an initial epizootic peak occurring in the spring and summer of 1983. The ratio of rabies cases to animals tested shows that the initial epizootic was followed by a drop in rabies prevalence through late 1984 and 1985, followed by peaks in late 1986 and 1987 and again in late 1991 and early 1992 (Fig. 2). Spectral analysis of these data confirms the cycle and shows statistically significant cycling ($\chi^2 = 34.25$, 7 point smoothing, $p < 0.005$, df = 8) with a period of 41 months (0.0245 cycles per point, 1/0.0245 = 40.8 months), or about 3½ years.

We used the data from the Piney Branch area to test for changes in population size relative to rabies prevalence. Population size from January 1984 to April 1986 ($n = 4$ estimates) was significantly higher than from December 1987 through March 1988 ($n = 2$ estimates; $\chi^2 = 8.86$, $p < 0.005$, df = 1). The higher population estimates between January 1984 and April 1986 coincided with a period of low rabies prevalence after the epizootic, and the lower population estimates between late 1987 and early 1988 occurred after the rabies resurgence in 1986–1987 (Fig. 2).

Survival

We radio-tracked 49 animals (33 adults and 16 juveniles) between August 1983 and February 1985 at the Piney Branch study site and 19 animals (10 adults and 9 juveniles) between April 1989 and April 1990 at the H-2 study site. Seven adult radio-collared raccoons died in the Piney Branch area during 1983–1984. One animal tested positive for rabies, two were killed by cars, three were trapped and euthanized as nuisance animals, and one drowned. The much higher mortality (11 of 16 animals) occurring among juveniles during the same period was partly attributable to deaths from rabies (4 animals), but also included 1 animal that was hit by a car, 3 that were trapped and euthanized as nuisances, 2 that died of gastroenteritis, and 1 that died of unknown causes. In the 1989–1990 study, two adults died, a male of pneumonia and a female of unknown causes, and one juvenile male died of rabies. In the 1983–1984 study, radio signals were lost for 8 of 49 animals (2 juvenile females, 2 adult females, and 4 adult males). In the 1989–1990 study, signals from 7 of 19 radio-collared animals were lost, but 4 animals were later recaptured or resighted and so were known to have been alive at least through the end of the study in April 1990.

For the 1983–1984 study, we combined juvenile males and females into one group for computing survivorship because of small sample sizes for each sex. Survival of adult males was generally higher than that of adult females, but the difference was only significant for one of six seasons (spring 1984, $z = 2.06$, two-sided $p < 0.05$) and over the period from April to December 1984 ($z = 2.15$, two-sided $p < 0.05$). Moreover, z values were inflated because only two adult males died during the study, both in winter 1984, resulting in a survival variance of 0 for all other periods. Survival was therefore computed for a single adult class. The sexes were also combined for the 1989–1990 study because sample sizes were small (2) for the adult male and juvenile female groups, and for purposes of comparison with the 1983–1984 data.

For adults, survival during the height of the initial rabies epizootic (the 9-month period between August 1983 and

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Table 2. Estimates of raccoon density from mark–recapture studies.

Raccoon density (no./km^2)	Urban/rural	Mortality sources[a]	Source
250.0	Rural	Protected	Twichell and Dill 1949
125.0	Urban	Rabies and distemper	This study
111.1	Urban	Distemper	Schinner and Cauley 1974
66.7	Suburban	Unknown	Hoffman and Gottschang 1977
55.6	Suburban	Distemper	Slate 1980
55.6	Urban	Rabies and distemper	Rosatte et al. 1990
55.6[b]	Rural	Protected and distemper	Lehman 1977
43.5[c]	Rural	Protected and distemper	Hable et al. 1992
35.7	Urban	Unknown	Jacobsen 1982
27.0	Rural	Unknown	Jacobsen 1982
17.5	Rural	Harvested	Urban 1970
17.5	Rural	Harvested	Hasbrouck 1991
17.2	Rural	Harvested	Sonenshine and Winslow 1972
13.9	Rural	Harvested	Moore and Kennedy 1985*a*
12.8	Rural	Harvested	Slate 1980
12.7	Rural	Harvested	Kennedy et al. 1991
11.8	Rural	Harvested	Johnson 1970
11.8	Rural	Harvested	Lehman 1984
11.8[c]	Rural	Harvested	Perry et al. 1989
10.5[d]	Rural	5 harvested, 2 protected	Leberg and Kennedy 1988
8.0	Rural	Harvested	VanDruff 1971
6.5[c]	Rural	1 harvested, 1 protected	Nixon et al. 1993
5.9	Rural	Protected and distemper	Rabinowitz 1981
5.7	Rural	Protected and distemper	Keeler 1978
5.6	Rural	Harvested	Lehman 1980
3.6	Rural	Harvested	Nottingham et al. 1982
1.4	Rural	Protected and distemper	Mech et al. 1968
0.9	Rural	Harvested	Orloff 1980

[a]Mortality sources indicates whether the population is harvested or protected and other major sources of mortality mentioned in the reference.

[b]Averaged from counts in several years.

[c]Averaged from two different sites.

[d]Based on an average of density estimates from seven sites in western Tennessee. The estimate for a protected National Park area was 5.5 ha per raccoon.

March 1984) was 0.830 and was not significantly different than survival over the next 9 months (0.850) (z = 0.185, one-sided p = 0.425) or for an equivalent period, July through April, in 1989–1990, during which survival was actually lower (0.728) (z = 0.590, one-sided p = 0.288) (Table 3). Juvenile survival (0.254) during the 9-month epizootic period was significantly lower (z =1.73, one-sided p < 0.05) than during the next 9 months (0.640) and during the same period in 1989–1990 (0.825) (z = 3.01, one-sided p < 0.005).

Discussion

Raccoon density in Rock Creek Park was from twice to more than 100 times that reported for the species in non-urban habitats and was consistent with the few estimates published for other urban and suburban raccoon populations (see Table 2). Raccoon populations vary considerably in size, however, and high densities have been reported outside of urban areas (see Table 2; Twichell and Dill 1949; Lehman 1977), although the highest recorded density (Twichell and Dill 1949) was determined by an intensive search of den sites and hand capture of animals, not by mark–recapture estimation. Urban environments likely provide resources, such as food and den sites, and conditions, such as greater protection from exploitation, that directly benefit and support dense raccoon populations.

Higher raccoon densities in urban areas are likely often related to greater survivorship. Where they are hunted or trapped, human harvest is a dominant cause of death for raccoons (Atkeson and Hulse 1953; Sanderson 1961; Johnson 1970), representing up to 78% of mortality (Clark et al. 1989). Starvation and malnutrition in late winter and early spring, perhaps compounded by the effects of parasites and disease, have also been cited as significant mortality factors for rural raccoons (Mech et al. 1968), which can lose from 19 to 50% of their body mass over the winter (Steuwer 1943;

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Table 3. Survival rates and mortality rates from rabies and from other sources for raccoons in the Piney Branch and H-2 study areas of Rock Creek Park, Washington, D.C.

Age-class	No. of days	No. of radio-days	Survival rate	Rabies mortality rate	Other mortality rate
Piney Branch					
August 1983 – December 1984					
Adults (*n* = 33)	519	10612	0.71±0.09	0.04±0.04	0.25±0.09
Juveniles (*n* = 16)	519	3076	0.16±0.10	0.32±0.13	0.49±0.13
August 1983 – March 1984 (during rabies epizootic)					
Adults (*n* = 32)	244	5372	0.83±0.08	0.04±0.04	0.13±0.07
Juveniles (*n* = 16)	244	1716	0.26±0.12	0.32±0.13	0.40±0.14
April 1984 – December 1984 (after rabies epizootic)					
Adults (*n* = 23)	275	5240	0.85±0.08	0.00±0.00	0.15±0.08
Juveniles (*n* = 7)	275	1360	0.64±0.19	0.00±0.00	0.33±0.19
H-2					
April 1989 (adults) and July 1989 (juveniles) – April 1990					
Adults (*n* = 10)	395	2562	0.73±0.16	0.00±0.00	0.26±0.16
Juveniles (*n* = 9)	304	1717	0.83±0.15	0.16±0.15	0.00±0.00

Note: Rates were determined from radio-collared raccoons and are given as the mean ± SD. Number of days is the number of calendar days during the period in question, and number of radio-days is the cumulative number of days that different animals in each age-class were followed during the period: 1 radio-day = one radio-collared raccoon followed (and alive) for 1 day (note that the survival rate does not always equal 1 minus the sum of the mortality rates) because using the bias-corrected survival rate slightly decreases the survival rate estimate; see Methods).

Mech et al. 1968; Johnson 1970; Moore and Kennedy 1985*b*). Raccoon populations in urban areas are free from intense harvest pressure and may also benefit from stable food and denning resources that mitigate the effects of severe winter conditions. Urban and suburban animals lost 16% of their body mass in Ohio (Hoffman 1979) and 10% in Rock Creek (J. Hadidian, unpublished data) over the winter.

Food resources for Rock Creek raccoons are abundant both within and adjacent to the park, although we do not have explicit geographic data on these resources. We know from scat analyses (J. Hadidian, unpublished data) that these animals rely on a variety of food items, such as earthworms and insects, from January until late April. During the rest of the year they focus on abundant fruits, both native and ornamental, including (in seasonal order) mulberries, cherries, wild cherries, raspberries, grapes, peppervine, and persimmons. They also eat acorns in the late fall and by November and December, palpation of the hind pelvic region of Rock Creek raccoons reveals significant fat reserves. Oak trees and fruit trees and bushes exist in the park but also abound in yards and gardens outside the park. Garbage and feeding by humans represent supplemental food sources that may be situationally important, although we think that most Rock Creek animals do not rely on them. The abundant fruit and acorn resources available in and around the park may contribute to the high density of Rock Creek raccoons.

A concentration of resources in small areas of natural habitat may also contribute to high densities of urban raccoons. Spatial models in ecology often assume that density does not change with the size of suitable habitat (e.g., MacArthur and Wilson 1963; Hanski 1991), although some models explicitly vary habitat quality, which can lead to differences in density (e.g., Pulliam 1988; Doak 1995). We speculate that the presence of small or fragmented natural areas surrounded by less suitable denning habitat may lead to larger concentrations of raccoons. This effect may be particularly pronounced if food resources are distributed more widely than dens, as is probably the case in Rock Creek. Matthiae and Stearns (1981, p. 62) note that forest islands in urban areas act as refuges for raccoons and support “numbers greater than carrying capacity.” Our highest raccoon density occurred in the Hazen site, an area distinguished by having both the smallest ratio of interior area to surrounding urban edge and the highest human population density outside. Multi-resident apartment complexes also surround the Hazen area to a greater extent than other study sites, considerably reducing the number of chimneys and yard trees frequently used as den sites in residential areas (Hadidian et al. 1991). The extremely high population density found by Twichell and Dill (1949) may also have been the result of a concentration of resources, since by their description they collected raccoons from a thin strip of ideal riparian habitat.

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A prerequisite for dense populations of carnivores is the ability to tolerate more conspecifics in less space, a situation that can lead to behavioral changes. Dense populations of red foxes in urban areas in England exhibit a variable social structure that allows for high densities (MacDonald 1981). Though Fritzell (1978) reported territoriality among male raccoons in a low-density population in North Dakota, our preliminary analysis of telemetry data for Rock Creek raccoons indicates extensive overlap of home ranges for both males and females. Daytime resting sites, particularly den trees, are also shared, both simultaneously and on different days (Hadidian et al. 1991). Barash (1974) found that raccoons caged next to their neighbors from the wild showed fewer signs of aggression than those caged next to totally foreign animals. Perhaps raccoons in high-density populations can adjust their social relationships to allow many adults of both the same and different sexes to coexist without constant conflict.

Epizootic diseases such as rabies and canine distemper may be more easily transmitted in populations where individuals are closely associated. These diseases are the most frequently reported causes of mortality in high-density populations of raccoons and in unharvested populations (Table 2). Of the eight mark–recapture studies with the highest reported densities, all six that mention population regulation cite disease as a major factor. In addition, disease, especially canine distemper, had a significant impact on raccoon populations in every study conducted in protected areas (Mech et al. 1968; Cauley and Schinner 1973; Hable et al. 1992; Hoff et al. 1974; Lehman 1977; Keeler 1978; Slate 1980; Rabinowitz 1981; Rosatte et al. 1990; Roscoe 1993). Although some investigators of harvested populations mention disease (e.g., Johnson 1970), none of them count disease as a major contributor to raccoon mortality. Because urban and suburban raccoon populations are both dense and protected, it is not surprising that all four of the urban and suburban studies that discuss sources of mortality cite disease as a significant one. Rabies epizootics in urban raccoons were first reported more than 20 years ago in Florida, with high concentrations of raccoons being particularly susceptible (Bigler et al. 1973).

Our direct measurement of survival in urban raccoons during and after a disease epizootic revealed that survivorship of adult raccoons in Rock Creek was high and constant both in 1983–1984 and 1989–1990, and specifically during the epizootic in the summer and fall of 1983. The juvenile survival rate during the same epizootic period was significantly lower, more than a third of the deaths being directly caused by rabies. We attribute the high survival rate of adults during the epizootic in part to the efficacy of the immunization program. Young raccoons may be less able to mount an immune response after immunization than older animals, as is the case in dogs (Bunn 1991; S. Jenkins, personal communication). Had we not immunized all radio-collared animals, the adult survival rate may well have also been lower in 1983–1984 than in 1989–1990. However, Brown et al. (1990) followed two groups of adult raccoons, one immunized and one not, along the “leading edge” of the Mid-Atlantic rabies epizootic in Pennsylvania and although harvest mortality was high, they recorded no rabies mortality, even in the group that had not been immunized. Immunization was also not a definitive means of avoiding the disease in our study, as one immunized adult died of rabies. Seidensticker et al. (1988) found a lower survival rate in raccons during the rabies epizootic in Virginia, although they did not test the difference statistically or provide the ages of radio-collared animals. Survival of adult raccoons in Rock Creek appears similar to that in areas with little or no exploitation (Mech et al. 1968; Fritzell and Greenwood 1984) and higher than that found in intensively harvested populations (Glueck 1985; Clark et al. 1989; Brown et al. 1990). The juvenile survival rate in Rock Creek during the epizootic was considerably lower than that found in other studies, regardless of exploitation level.

The tendency of disease to replace human harvest as a significant cause of mortality in urban or protected raccoon populations raises the question of whether harvest mortality is additive or compensatory. Some authors believe that harvest mortality is additive in raccoons (Clark and Fritzell 1992; Nixon et al. 1993). The patterns seen in raccoon mark–recapture studies (Table 2) do not imply that all nonharvested raccoon populations do, or will, undergo epizootics of rabies or distemper. However, protected, urban, and high-density populations should more often endure these epizootics, and epizootic disease may represent another form of additive mortality in raccoons, particularly in young animals.

Raccoon rabies remains endemic in the Washington, D.C., area and in fact the disease appears, through early 1994, to be on a fairly regular cycle (Fig. 2). The 3½-year cycle seen in the Washington, D.C., rabies data is comparable to the 2- to 3-year cycles seen in the percentages of raccoons testing positive in five counties in Virginia (Torrence et al. 1992), the 4-year interval between an initial distemper epizootic and subsequent concurrent rabies and canine distemper epizootics in Florida raccoons and gray foxes (*Urocyon cinereoargenteus*) (Hoff et al. 1974), the 4-year cycles of canine distemper in raccoons in New Jersey (Roscoe 1993), and the 3- to 5-year cycles of red fox density and rabies prevalence in Europe and Canada (Anderson et al. 1981). Using their model of raccoon rabies with a class of immune animals, Coyne et al. (1989) speculate that no cycling in disease prevalence or density should be noticeable in the field for raccoons, and that population density is less likely to fall below the threshold level for disease maintenance, thereby permitting the disease to persist in the population. We were able to see cycles in rabies prevalence in our data, contrary to the model. However, the period of the cycles we found is consistent with models of disease dynamics in foxes and raccoons, and rabies in Washington, D.C., and the southeastern U.S.A. in general does appear to have become endemic, as predicted by the raccoon model.

Unfortunately, we do not have data on population density from before the epizootic in order to measure the initial impact of the disease on raccoon abundance. Nevertheless, a significant drop in the density of the Piney Branch population occurred between the period 1984–1985, when rabies prevalence was low, and the period after late 1986 – early 1987, when disease prevalence increased, indicating that rabies may have seriously impacted the population 4 years after the initial epizootic. Other areas of the Mid-Atlantic and northeastern U.S.A and eastern Canada can expect the rabies virus to maintain itself in raccoon populations and perhaps to impact raccoon density long past an original epizootic.

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