Demography and Habitat Relationships of Raccoons in Western Tennessee

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Abstract: Winter densities, age structure, and sex ratios of 9 populations of raccoons (*Procyon lotor*) in western Tennessee were compared to 16 habitat variables and between aquatic-associated and upland habitats for 3 pairs of sites. Densities ranged from 0.8 to 18.3 raccoons/km^2. Highest densities and proportions of juveniles and females occurred in bottomland deciduous forests; lowest estimates were in upland, pine-deciduous forests. The proportions of females and juveniles and the density estimates were correlated with habitat variables that reflected a bottomland-upland gradient, such as the distance to deciduous shoreline and the basal areas of conifers and large deciduous trees. In addition to supporting larger raccoon densities, aquatic-associated habitats may also have relatively more on-site reproduction than upland habitats.

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Studies evaluating the importance of habitat type to a wildlife species often assess the absolute or relative abundance of the species in different habitats, assuming that density is correlated with habitat quality. Van Horne (1983) stressed that in some situations this assumption may be false. For instance, when dispersal rates are high, density estimates in a given habitat may be influenced greatly by conditions in surrounding habitats. Assessment of habitat-specific differences in age-specific mortality, fecundity, emigration, and immigration rates would eliminate this problem, but data are often difficult to obtain. Consideration of other demographic variables, such as age and sex ratios, in addition to abundance, might better reveal the importance of a habitat to a species.

Lotze and Anderson (1979), Kaufmann (1982), and Minser and Pelton (1982) have reviewed previous investigations concerning the abundance of the raccoon. Because of differences in methods and trapping periods, direct comparisons among

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previous studies are difficult. Yet, prior studies have identified habitats with high or low densities and suggested a relationship between raccoon abundance and habitat. In general, aquatic-associated or bottomland deciduous habitats are reported to sustain the greatest abundance of raccoons in the southeastern United States (Minser and Pelton 1982), and mixed pine-deciduous and pine forest support lowest densities. Johnson (1970) suggested that habitat-related factors may limit raccoon populations in many areas of Alabama. Only 2 attempts have been made to quantify such relationships. McKeever (1959) and Sonenshine and Winslow (1972) reported that capture rates of raccoons were higher in aquatic-associated habitats than in upland forests. However, assessing abundance from capture rates has been criticized (Smith and Brisbin 1984). No studies have estimated density of raccoons on more than 2 sites or demonstrated the relationship between habitat type and density. Additionally, little attention has been given to the relationship between either raccoon density or other demographic variables, such as sex and age ratios, and specific habitat variables.

Moore and Kennedy (1985*a*) reported factors affecting trap response of raccoons in western Tennessee. Seasonal differences in trap success were significant, with greatest success during winter (late-Dec through Mar). The relationship between a species' abundance and a critical resource should be greatest when the resource is limited. Stuewer (1943), Johnson (1970), and Moore and Kennedy (1985*b*) reported that the weights of raccoons were lowest in winter, suggesting that this may be a period of stress or low food availability. Thus, winter appears to be a favorable period for evaluating the relationship between habitat factors and raccoon population characteristics in Tennessee.

Our objectives were to estimate the winter density of raccoons in different habitat types and to determine if there were any associations between the sex or age structure of raccoon populations and habitat type. We thank the personnel of the Ames Plantation, Hatchie National Wildlife Refuge, Land Between The Lakes, C. Middlecoft Farm, Shiloh National Military Park, and Tennessee Department of Conservation for permission to work on their lands. We are grateful to F. R. Tabatabai and D. W. Moore for use of data collected in their studies. Thanks are also extended to J. P. Leberg, R. M. Lee, III, P. O. Lewis, C. Lydeard, M. E. Ritke, R. R. Snellgrove, and F. W. Weckerly for assistance in data collection. Earlier drafts of this manuscript were criticized by I. L. Brisbin, G. A. Heidt, G. R. Hepp, A. S. Johnson, J. M. Novak, H. R. Pulliam, K. T. Scribner, and M. H. Smith. Research and manuscript preparation were partially supported by Federal Aid to Wildlife Restoration, Tennessee Wildlife Resources Agency, W-46R Pittman-Robertson, and by Contract DE-AC09-76SROO-819 between the U.S. Department of Energy and the University of Georgia's Savannah River Ecology Laboratory.

Methods

Raccoon densities and habitat variables were examined at 9 sites in western Tennessee between 1979 and 1984. Detailed information for each site is given in

Leberg (1985). Sites 1 and 2 were located in the Stewart County portion of Land Between The Lakes. Site 1 was an upland, deciduous forest with rolling topography. Water was confined to several temporary streams and 2 small ponds. Site 2 was similar to Site 1 in vegetation and topography. The eastern boundary of Site 2 was formed by the shoreline of Lake Barkley, which provided a source of permanent water. Hunting on these sites was restricted to 3 nights a week between 1 December and 31 January.

Sites 3 and 4 were located on the Ames Plantation in Fayette County. Site 3 was a mixed pine-deciduous, upland forest. Topography consisted of gently rolling hills, and water was confined to several temporary streams. Site 4 was a bottomland forest on flat terrain adjacent to Site 3. Several large streams transversed the area. Both areas were hunted during the regular state season (Oct-Feb).

Sites 5 and 6 were located on Shiloh National Military Park in Hardin County. Site 5, an upland, deciduous forest, was located on a bluff above the Tennessee River. Topography of Site 5 consisted of alternating ridge tops and hollows with steep slopes. Site 6, a mature bottomland forest, was transversed by several streams, and was adjacent to Site 5. Topography of the site was generally flat. Several large agricultural fields and mowed areas comprised 10%-15% of both sites. No hunting was permitted on either site.

Sites 7 and 8 were located on portions of the Merman Biological Field Station and the Shelby Forest Wildlife Management Area in Shelby County. Both sites were on a bluff between the Mississippi River flood plain and surrounding uplands and contained both upland and bottomland deciduous forest. Several streams and small agricultural fields were located on or near both areas. Slopes varied from quite steep on the bluff to almost flat in bottomlands. These sites were open to raccoon hunting during the regular state season.

Site 9 was located on Hatchie National Wildlife Refuge in Hatchie County. It was an upland area dominated by pine, with remnant deciduous stands. Several agricultural and old fields also were present. Topography was moderately flat, and small streams and ponds were common. The area was open to raccoon hunting during the regular state season.

Density values used in comparisons with habitat variables at Sites 1 and 2 were taken from Kennedy et al. (1985) and Kennedy et al. (1986), respectively. Values for Sites 3–9 were taken from Leberg and Kennedy (1987). A complete capture history of each animal used in this study is given in Leberg (1985). Trapping and animal handling procedures followed those of Kennedy et al. (1986). Individuals were sexed and were classified as juveniles (<14 months old) or adults based on tooth wear (Grau et al. 1970). Density estimates for all sites were based on trapping data for the period between December and March to control for seasonal variation in raccoon catchability (Moore and Kennedy 1985*a*). With the exception of Sites 2 and 9, population sizes for all sites were estimated using the Jackknife estimate of the program CAPTURE (White et al. 1978, Otis et al. 1978). Due to the small number of raccoons captured at Site 9, only a minimum density could be obtained. The density estimate for Site 2 was derived using a census-assessment line technique modified from O'Farrell et al. (1977). The density estimates for the remaining sites were based on the maximum distances raccoons moved between recaptures (Wilson and Anderson 1985). Two commonly used measures of relative abundance, individuals per trap night and individuals per unit area trapped (unadjusted for area of effect), also were determined. The second measure could not be calculated for Site 2 because a grid was not used. Standard errors for the percentages of females and juveniles were based on the hypergeometric distribution for finite populations (Steel and Torrie 1960). Leberg (1985) and Leberg and Kennedy (1987) present detailed information on trapping and density estimation procedures.

Since estimates of the demographic characters for Site 9 were based on a small sample size, and since the density estimate for Site 2 was based on different methodology from that used on other sites, statistical analyses were conducted both including and excluding these sites. Results were not changed by the exclusion of either site; therefore, results based on all 9 sites are presented.

Sixteen habitat variables (Table 1) were measured at each study site during June-September 1984. To summarize habitat variation among sites, the first 3 prin-

Table 1. Sixteen variables measured to characterize raccoon habitat on 9 study sites in western Tennessee.

Variable	Description
Stand height[a]	Height of tallest tree used in basal area determinations at each plot.
Slope[a]	The greatest vertical decrease (in meters) from plot center to a downhill point 30 m away.
Deciduous BA[a] (10–20 cm dbh) (20–50 cm dbh) (>50 cm dbh) Conifer BA[a] (10–20 cm dbh) (20–50 cm dbh) Snag BA[a] (10–20 cm dbh) (20–50 cm dbh) (>50 cm dbh)	Basal areas (BA) per hectare were determined using a 10 factor wedge prism for 3 size classes of deciduous trees, conifers, and snags (standing dead trees over 3.0 m in height). These variables reflected both stand density and volume. See Husch et al. (1972) for a detailed discussion of the methodology. Size classes were based on tree diameter at breast height (dbh) which was taken at 1.3 m above the ground. Very few conifers over 50 cm dbh were located on any of the study areas so this variable was not included in analyses.
Distance to shrub[a]	Average distance (m) to the nearest shrub (woody vegetation 0.5 – 3.0 m high) in each of 4 quadrats. Quadrats were determined by the transect line used to locate the plot center and by a bisecting perpendicular line.
Distance to[b]	
Shoreline	Distance to the nearest permanent water.
Deciduous shoreline	Distance to the nearest permanent water aligned with deciduous trees.
Road	Distance to nearest hard surface or gravel road open to public use.
Cropland	Distance to nearest field containing an agricultural row crop.
Dwelling	Distance to nearest area of high human utilization. These areas included homes, campgrounds, and visitor centers.

[a] Measurements were taken at 30 points on 3 randomly selected transects. Points were located 50 m apart.

[b] Measurements were taken, to the nearest 10 m, from 10 randomly selected points using aerial photographs and topographic maps.

cipal components were extracted from a matrix of correlations (standardizing variables with different measurement scales) between habitat variables. Nonparametric Spearman's rank-order correlations (*rho*) were used to assess associations between demographic and habitat variables. Analyses were conducted with the Statistical Package for the Social Sciences (SPSS) of Nie et al. (1975).

Since inter-site variation in hunting regulations, annual population dynamics, and the seasonality of trap response might bias the results of the correlation analysis, comparisons of demographic variables also were made between the upland and aquatic-associated habitat pairs of Sites 1 and 2, Sites 3 and 4, and Sites 5 and 6. Aquatic-associated sites included both bottomland deciduous forest (Sites 4 and 6) and upland deciduous forest adjacent to permanent water (Site 2). There was a clear dichotomy of upland and aquatic-associated habitat for each pair of sites allowing for direct tests of habitat-specific demographic differences while controlling for between-pair differences in population dynamics and hunting regulations. Sites within each pair were trapped during the same time period and were separated by less than 1 km. The estimates of each demographic variable for each pair of sites were compared with a Z test. The probability of significant differences between upland and aquatic-associated habitats across all 3 pairs of sites was obtained by the method of combining probabilities (Sokal and Rohlf 1969).

Results

Density estimates (Table 2) were highly correlated with both individuals per trapnight ($rho = 0.708, P < 0.05$) and individuals per km^2 trapped ($rho = 0.893$, $P < 0.01$). Because correlations of both measures of capture rate and the density estimates with the habitat variables were similar, only the latter are presented (Table 3). In general, all demographic variables were positively correlated with basal area

Table 2. Results of raccoon capture-recapture studies for 9 sites in western Tennessee (± 1 SE).

		Density[b] (raccoons/km^2)		% juveniles		% females	
Site	*n*[a]	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
1	12	2.9	0.6	9	4	27	7
2	18	5.8[c]		12		54	
3	6	1.4	0.3	0	2	17	6
4	23	16.1	3.8	39	7	39	7
5	21	8.9	1.9	14	5	67	7
6	17	18.3	3.8	29	9	63	9
7	16	18.2	4.5	35	8	39	8
8	32	7.6	1.5	14	2	29	2
9	2	0.8[c]		0		0	

[a] Total number of raccoons captured on each grid.
[b] From Leberg and Kennedy (1987).
[c] Methodology did not permit calculation of standard errors.

Table 3. Spearman rank-order correlation (*rho*) between habitat and raccoon demographic variables for 9 sites in western Tennessee.

Habitat vriable	Density (raccoons/km^2)	% juveniles	% females
Stand height	0.109	−0.025	−0.277
Slope	−0.059	−0.122	0.311
Deciduous BA			
(10–20 cm dbh)	0.527	0.312	0.226
(20–50 cm dbh)	0.317	0.403	0.167
(>50 cm dbh)	0.762[b]	0.781[b]	0.444
Conifer BA			
(10–20 cm dbh)	−0.694[a]	−0.727[a]	−0.310
(20–50 cm dbh)	−0.451	−0.592[a]	−0.162
Snag BA			
(10–20 cm dbh)	−0.191	−0.360	−0.313
(20–50 cm dbh)	0.373	0.376	0.254
(>50 cm dbh)	0.445	0.427	0.333
Distance (in m) to			
Shrub	0.268	0.384	0.360
Shoreline	−0.300	−0.395	−0.233
Deciduous shoreline	−0.733[a]	−0.790[b]	−0.717[a]
Road	−0.267	−0.261	−0.250
Cropland	−0.100	0.168	0.017
Dwelling	0.083	−0.008	0.167

[a] $P \leq 0.05$.
[b] $P \leq 0.01$.

of deciduous trees (>50 cm dbh) and negatively correlated with basal area of conifers (10–20 cm dbh) and distance to deciduous shoreline.

Significant interlocality variation existed for all habitat variables ($P < 0.05$; ANOVA). Three principal components accounted for 73.3% of the variation among sites. Thus, there was little distortion of the relationships between sites created by reducing the matrix of 16 habitat variables to 3 principal components. Loadings, indicating the correlation of characters with principal components, are given in Table 4 for the first 3 components. Component I had high loadings for factors associated with overstory and distance to shoreline. Basal area of snags (20–50 cm dbh), distance to roads, and distance to houses loaded highly on Component II. Component III had high loadings for slope and basal area of snags (>50 cm dbh).

Principal Component I was correlated with density ($rho = -0.95$, $P < 0.01$), the percentage of juveniles in the population ($rho = -0.94$, $P < 0.01$), and the percentage of females in the population ($rho = -0.67$, $P < 0.05$). Characters that were highly correlated with raccoon age ratios, sex ratios, or density, such as distance to deciduous shoreline, deciduous basal area >50 cm dbh, and conifer basal area 10–20 and 20–50 cm dbh, loaded highly on Component I (Table 4). Components II and III were not correlated with any of the demographic variables ($P \geq 0.18$).

Table 4. Variable loadings on the first 3 principal components of interlocation variation in the habitats of the raccoon.

Habitat variable	Principal components I	II	III
Stand height	−0.058	0.133	0.543
Slope	0.154	−0.222	0.858
Basal area			
Deciduous (10–20 cm dbh)	−0.496	0.327	0.439
Deciduous (20–50 cm dbh)	−0.795	0.483	0.203
Deciduous (>50 cm dbh)	−0.816	−0.338	0.083
Conifer (10–20 cm dbh)	0.772	−0.493	−0.372
Conifer (20–50 cm dbh)	0.912	−0.280	−0.245
Snag (10–20 cm dbh)	0.325	0.153	0.216
Snag (20–50 cm dbh)	−0.552	0.583	−0.573
Snag (>50 cm dbh)	−0.482	0.262	−0.670
Distance to shrub	−0.667	−0.554	−0.156
Shoreline	0.686	0.593	0.237
Deciduous shoreline	0.864	0.396	−0.042
Cropland	−0.050	0.360	0.568
Road	0.226	0.940	−0.228
Dwelling	0.045	0.716	−0.096
Percentage of variance explained	33.5	22.6	17.2

A comparison of density estimates in Table 2 for the upland and aquatic-associated habitat pairs of Sites 1 and 2, Sites 3 and 4, and Sites 5 and 6 indicated that densities were highest in the aquatic-associated habitats in each case ($P < 0.01$). The percentage of juveniles was higher on Site 4 than on Site 3 ($P < 0.01$) and on Site 6 than on Site 5 ($P < 0.07$). The percentage of females was higher on Site 2 than on Site 1 ($P < 0.01$) and on Site 4 than on Site 3 ($P < 0.01$). The test of overall differences (combining probabilities from the pairwise tests) across all three pairs of sites indicated that density and the percentages of both females and juveniles were all greater in the aquatic-associated habitats than in the upland habitats ($P < 0.01$).

The correlation between the percentage of juveniles and density was significant ($rho = 0.92, P < 0.01$). Similarly, the association between the percentage of females and density was significant ($rho = 0.67, P < 0.05$).

Discussion

Previous work suggested raccoon densities tended to be higher in aquatic-associated than in upland habitats (Lotze and Anderson 1979, Kaufmann 1982). However, no study examined densities across habitat types to quantify this relationship. Our results indicate that raccoon density is highest in bottomland deciduous forests, intermediate in upland deciduous forests adjacent to permanent water or bottomland, and lowest in upland pine-deciduous forests. For adjacent pairs of sites, raccoon densities were 2 to 11 times higher in the site closer to permanent water. Density estimates in the bottomland sites (4 and 6) were 13 to 23 times higher than those in the upland pine-deciduous sites (3 and 9). Two variables, deciduous-lined shoreline and basal area of large deciduous trees, appeared to be important components of raccoon habitat. Many studies have noted the importance of water as a source of food and refuge for raccoons (e.g., Johnson 1970, Minser and Pelton 1982). Similarly, deciduous trees provide den sites and foods, such as mast (Johnson 1970, Hudson 1978). If either of these components were rare or absent at a site (e.g., such as water from Site 1 or large deciduous trees from Site 9), raccoon densities were low.

The strong associations of the proportion of females and juveniles with the bottomland-upland habitat gradient were unexpected. Direct comparisons of demographic variables between upland and aquatic-associated habitats at 3 locations support the analysis of correlations between habitat variables of density and the age and sex structure of raccoon populations.

It is possible that the associations of the sex and age structure of the study populations with habitat type were the result of demographic phenomena. Both sex and age ratios were correlated with density. Sanderson (1951) found that the proportions of females and juveniles in state-wide raccoon harvests increased as the total harvest increased. He suggested that higher proportions of females and juveniles indicated the population was growing; however, there are other explanations for changes in these ratios. In the present study, there was little reason to believe that densities in all upland habitats were stable or decreasing relative to densities in the aquatic-associated habitats surveyed. Furthermore, scent-station surveys did not suggest any large changes in the abundance of raccoons on any of the study sites over the length of the investigation (Leberg and Kennedy 1987).

The differences in sex and age structure of raccoons may be the result of habitat-specific reproductive differences (Van Horne 1983). Specifically, most annual reproduction may occur in bottomland or other forest riparian sites, with the majority of the individuals in upland habitats representing immigrant individuals. Radio-telemetry studies have suggested that young raccoons remain on their mother's home range until after their first winter (Schneider et al. 1971, Fritzell 1978), that yearling males, but not yearling females, disperse from the maternal home range (Fritzell 1978), and that adult males, but not adult females, are territorial (Johnson 1970, Schneider et al. 1971, Fritzell 1978). The disproportionally high numbers of juveniles found in aquatic-associated habitats suggests that reproduction was relatively higher on these sites. Dispersal and territorial tendencies of males may have resulted in adult males occupying less favorable upland sites. Schantz (1981) presented an analogous scenario to explain red fox (*Vulpes vulpes*) population dynamics in high and low quality habitats.

The differences in sex and age ratios observed between habitats may also be explained by different movement patterns of the sex and age classes. In this explanation, both sexes and age classes most heavily use bottomland hardwoods and other forested riparian habitats during the winter. Because adult males tend to have larger home ranges and move greater distances than females or juveniles (Fritzell 1978), they may be over-represented in samples from upland sites. This explanation is more parsimonious than one based on habitat-specific reproductive rates because it makes no assumptions about where reproduction occurs. However, both explanations suggest that wetlands may be more important to regional raccoon populations than density values alone suggest. It is not possible to distinguish between these alternate explanations with our data.

Care in the interpretation of these results is needed because estimates of demographic variables were based on small numbers of individuals, especially from upland sites. The measurement errors of the density estimates and the age and sex ratios may be large. Furthermore, because only 9 sites were sampled, it was not possible to determine whether relationships between variables were linear. It is encouraging that results of correlations of demographic variables with habitat were supported by direct comparisons of adjacent upland and aquatic-associated sites, but these analyses were not independent. Further studies, measuring both raccoon movement between upland and wetland sites and habitat-specific fecundity and mortality rates are needed to more completely understand the importance of these habitats to raccoons.

Because our conclusions are still tentative, caution should be used in altering raccoon management programs based on our results. The 2 explanations (habitat-specific reproductive differences and age- and sex-specific movement patterns) proposed to explain the associations of the sex and age ratios with habitat type have similar implications for resource managers. A local wetland may not only support a large number of raccoons on the site, but may also serve as the source of raccoons (mostly adult males) in surrounding upland habitats during the winter. Destruction of the wetland area could affect raccoon abundance in the surrounding areas. Additionally, heavy harvest of raccoons from upland areas during the winter would affect regional population dynamics differently than harvest of raccoons from bottomland habitats. In the first case, more males would be removed, while in the second case the number of juveniles and adult females in the area would be reduced.

Literature Cited

Fritzell, E. K. 1978. Aspects of raccoon (*Procyon lotor*) social organization. Can. J. Zool. 56:260–271.

Grau, G. A., G. C. Sanderson, and J. P. Rogers. 1970. Age determination of raccoons. J. Wildl. Manage. 34:364–372.

Hudson, E. M. 1978. The raccoon (*Procyon lotor*) on St. Catherines Island, Georgia. 2. Relative abundance in different forest types as a function of population density. Am. Mus. Novitates 2648:1–15.

Husch, B., C. I. Miller, and T. W. Beers. 1972. Forest mensuration. Ronald Press Co., New York. 410pp.

Johnson, A. S. 1970. Biology of the raccoon (*Procyon lotor various* Nelson and Goldman) in Alabama. Agric. Exp. Sta., Auburn Univ. Bul. No. 402, Auburn, Ala. 148pp.

Kaufmann, J. H. 1982. Raccoon and allies. Pages 567–585 *in* J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America: Biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, Md.

Kennedy, M. L., G. D. Baumgardner, F. R. Tabatabai, O. S. Fuller, and M. E. Cope. 1985. Density estimation of a raccoon population in western Tennessee. J. Tenn. Acad. Sci. 60:86–87.

———, ———, M. E. Cope, F. R. Tabatabai, and O. S. Fuller. 1986. Raccoon (*Procyon lotor*) density as estimated by the census-assessment line technique. J. Mammal. 67:166–168.

Leberg, P. L. 1985. Density and habitat relationships of the raccoon, *Procyon lotor,* in western Tennessee. M.S. Thesis, Memphis State Univ., Memphis, Tenn. 78pp.

——— and M. L. Kennedy. 1987. Use of scent-station methodology to assess raccoon abundance. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies. 42:394–403.

Lotze, J. H. and S. Anderson. 1979. Procyon lotor. Mammal. Species 119:1–8.

McKeever, S. 1959. Relative abundance of twelve southeastern mammals in six vegetative types. Am. Midl. Nat. 62:222–226.

Minser, W. G. and M. R. Pelton. 1982. Impact of hunting on raccoon populations and management implications. Univ. Tenn. Agric. Exp. Sta. Bul. No. 612, Knoxville. 32pp.

Moore, D. W. and M. L. Kennedy. 1985*a*. Factors affecting response of raccoons to traps and population size estimation. Am. Midl. Nat. 144:192–197.

——— and ———. 1985*b*. Weight changes and population structure of raccoons in western Tennessee. J. Wildl. Manage. 49:906–909.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Brent. 1975. Statistical package for the social sciences, 2nd ed. McGraw-Hill Book Co., New York. 675pp.

O'Farrell, M. J., D. W. Kaufman, and W. D. Lundahl. 1977. Use of live-trapping with the assessment line method for density estimation. J. Mammal. 58:575–582.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62:1–135.

Sanderson, G. C. 1951. Breeding habits and a history of the Missouri raccoon population from 1941 to 1948. Trans. North Am. Wildl. Nat. Resour. Conf. 16:445–461.

Schantz, T. V. 1981. Female cooperation, male competition, and dispersal in the red fox *Vulpes vulpes*. Oikos 37:63–67.

Schneider, D. G., L. D. Mech, and J. R. Tester. 1971. Movements of female raccoons and their young as determined by radio-tracking. Anim. Behav. Monogr. 4:1–43.

Smith, L. M. and I. L. Brisbin, Jr. 1984. An evaluation of total captures as estimates of furbearer abundance. J. Wildl. Manage. 8:1452–1455.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco, Calif. 776pp.

Sonenshine, D. E. and E. L. Winslow. 1972. Contrasts in distribution of raccoons in two Virginia localities. J. Wildl. Manage. 36:838–847.

Steel, R. G. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., New York. 481pp.

Stuewer, F. W. 1943. Raccoons: their habits and management in Michigan. Ecol. Monogr. 13:203–257.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893–901.

White, G. C., K. P. Burnham, D. L. Otis, and D. R. Anderson. 1978. CAPTURE, a FORTRAN IV program for general computer use. Share Program Library Agency, Research Triangle Park, N.C.

Wilson, K. R. and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. J. Mammal. 66:13–21.