Wildlife Session

Relationships Between Landscape Characteristics and Space Use of Raccoons in Two Managed Pine Forests

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Abstract: Raccoons *(Procyon lotor)* are ecological generalists that use a variety of landscape and habitat types. Although space and habitat use are well understood for raccoons throughout the southeastern United States, relationships between space use and landscape characteristics are not. We examined relationships between space use and landscape characteristics for 95 radio-marked raccoons monitored during 1996–1997 on two adjacent forested landscapes that differed in forest management strategies. We noted relationships between space use and patch richness, proportion and size of riparian habitats on the landscape, and size of patches providing soft mast resources. Raccoons within an intensively-managed forest maintained spaces with reduced patch richness and less of the landscape in riparian habitats, likely attributable to forest management strategies that optimize wood fiber production. However, raccoons within this system consistently maintained spaces with larger patch sizes of riparian habitats and habitats containing soft mast (early successional plant communities). Our findings suggest that raccoons living on landscapes with intensive forest management select larger patch sizes of quality habitats relative to raccoons living on forested landscapes with less intensive management regimes. Because raccoons in intensively-managed forests may maintain smaller spaces than raccoons in other forested systems and appear to be influenced by landscape patterns, managers should recognize influences of forest management practices on raccoon behavior.

Key words: forest management, landscape, *Procyon lotor*, raccoon, space use

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Landscape characteristics and patterns may influence biotic (e.g., space and movement patterns) and abiotic (e.g., nutrient flows) processes in ecological systems (Li and Reynolds 1994, Turner et al. 2001). Although mesocarnivores have been extensively researched, we know little of how these species respond to changes in landscape pattern (Crooks 2002). Many landscape-scale studies of mesocarnivores have focused on edge-effects and relationships between landscape pattern and nest predation (Dijak and Thompson 2002, Kuehl and Clark 2002, Stephens et al. 2003). Relationships between space use and landscape characteristics have not been well-studied, although space use is commonly used to make inferences about ecology and behavior. Specifically, space use can be an important indicator of food density and efficiency of movement (Schoener 1971), but influences of the spatial arrangement of resources and habitat patches on space use are poorly understood (Ims 1995, Kie et al. 2002).

Raccoons have been extensively studied and space use throughout the southeastern United States is well understood (Johnson 1970, Hoffman and Gottschang 1977, Chamberlain et al. 2000, Chamberlain et al. 2003). Raccoons are habitat generalists and have adapted to a wide range of landscape condition. The literature is replete with information detailing habitat use of raccoons in a variety of landscapes, ranging from prairies (Fritzell 1978) to mixed deciduous forests (Leberg and Kennedy 1988) and intensively-managed pine forests (Chamberlain et al. 2002). However, these studies have not examined relationships between raccoon behavior and landscape patterns.

The forest products industry is an important economic factor in the southeastern United States. The demand for wood fiber continues to increase and forests continue to be converted to managed plantations; this conversion is expected to exceed 18.6 million ha by 2030 (Allen et al. 1996). Likewise, forest management strategies on public lands continue to evolve and are dynamic. Increasing acreages of publicly-owned forests are being managed for the federally-endangered red-cockaded woodpecker *(Picoides borealis),* which results in increases in prescribed burning and structural changes to plant communities (Bowman et al. 1999). Chamberlain et al. (2000) reported that raccoons in intensively-managed pine forests exhibited reductions in space use and movements relative to raccoons in a mixed forest with differing management strategies. Following Chamberlain et al. (2000), our objective was to examine relationships between space use of raccoons and landscape characteristics. We examined these relationships for raccoons on two forested landscapes with differing forest management scenarios to better assess effects of forest management on raccoon behavior.

Study Area

We conducted research on an approximately 5,000-ha portion of the 14,410-ha Tallahala Wildlife Management Area (TWMA) and a 2,000-ha area owned by the Timber Company (TC) in sections of Jasper, Newton, Scott, and Smith counties, Mississippi. The TWMA contained 30% mature (>30-year-old) bottomland hardwood forests, 37% mature pine (loblolly, *Pinus taeda;* shortleaf, *P. echinata*) forests, 17% mixed pine-hardwood forests, and 11% in one-15-year-old loblolly pine plantation. The eastern portion of TWMA was substantially altered prior to our study by a tornado, creating approximately 1,000 ha of early successional habitat. Forest management activities (thinning, prescribed fire) did not occur in this portion of TWMA; therefore, we did not include it in our study. Throughout the remainder of TWMA, prescribed burning occurred in mature pine stands. TWMA contained active RCW colonies, and extensive burning and hardwood midstory removal occurred within stands available to these colonies. The TC area, located adjacent to TWMA, was managed primarily for wood fiber production with 90% of the area composed of 1–35-year-old loblolly pine plantations, and the remaining 10% in Streamside Management Zones (SMZs) along creek drainages. No prescribed burning occurred two years prior to or during our study. Topography was gently to moderately rolling, with 0–20% slope. Climate was mild, with a mean annual temperature of 20 C and mean annual precipitation of 152 cm (Chamberlain et al. 2000).

Methods

We captured raccoons for radio-marking using wire cage traps from January 1996 to June 1997. We checked traps daily and baited them with various mixtures of fish, jelly, and molasses. We trapped raccoons on a 50-trap grid system on TC during March and June–August, with each grid block measuring approximately 40.5 ha. On TWMA, we trapped on two similar grid systems given the size of the study area. One cage trap was set/block in areas selected for maximum trap success. We sampled each grid 16–17 consecutive nights during each of the two trapping periods each year. Additionally, we recaptured raccoons systematically during January–March, focusing on areas devoid of radio-marked raccoons. Using these trapping systems, we attempted to capture as many raccoons as possible across the landscape and to radio-monitor individuals uniformly across all habitat types.

We anesthetized captured raccoons using ketamine hydrochloride (Ketaset, Veterinary Products, Fort Dodge Laboratories, Fort Dodge, Iowa) at a rate of 10 mg/kg of estimated body mass (Bigler and Hoff 1974). We fitted adult (≥ 1-year-old) raccoons with a 100-g mortality-sensitive radio transmitter and released them at the capture site the following morning. We conducted research under Mississippi State University IACUC Protocol No. 93-032 and its associated amendments.

We determined raccoon locations by triangulation (White and Garrott 1990) using a hand-held 3-element Yagi antenna (Wildlife Materials, Carbondale, Illinois) from fixed telemetry stations (N = 480) ≥2 times/week. We conducted all radiotelemetry throughout the diel period to ensure equitable and representative samples of raccoon movements. Azimuths for a single radio location were recorded within a 15-min interval to reduce error due to raccoon movement; however, most (94%) consecutive azimuths were recorded within 7 min (4.8 ± 0.03, mean ± SE). We maintained triangulation angles between 45 and 135° to reduce error. Telemetry accuracy tests indicated that standard deviation from true bearing was 5.9° (Chamberlain et al. 2000).

We developed a Geographic Information System (GIS, ARC/INFO, Environmental Systems Research Institute, Redlands, California) with color infrared aerial photographs and 1:24,000 U.S. Geological Survey 7.5-min quadrangles. We used stand data and U.S. Forest Service records to classify stands into habitat types based on forest type (i.e., hardwood, pine) and stand age. We used year-specific stand maps and data to create annual habitat coverages ($N = 2$) for TWMA and TC. We delineated habitats as mature hardwood (≥30 yr), mixed-pine hardwood (≥30 yr), pine (TWMA: 0–8 yr, 9–15 yr, 16–29 yr, and ≥30 yr; TC: 0–8 yr, 9–15 yr, and ≥16 yr), and other habitats (agricultural and Conservation Reserve Program lands ≤2 yr; Chamberlain et al. 2002, Chamberlain et al. 2003).

We converted raccoon locations to a coordinate system using program TELEBASE (Wynn et al. 1990). We estimated annual home ranges (95%) using a kernel estimator in the Animal Movement extension of ArcView (Environmental Research Systems Institute, Redlands, California) for raccoons with at least 30 radio-locations. We delineated a buffer of 870 ha around the center of each home range (estimated with Real Centroid Generator extension of ArcView). We selected the spatial scale, two times the largest patch size on the landscape, to minimize calculation bias of landscape metrics (O'Neill et al. 1996, Turner et al. 2001). We intersected each circular buffer with landcovers of TWMA and TC to calculate landscape metrics thought to be important to raccoons (e.g. Oehler and Litvaitis 1996, Kuehl and Clark 2002, Gehring and Swihart 2003, Henner et al. 2004).

We used Patch Analyst (Elkie et al. 1999) to measure landscape variables at two levels: landscape-scale metrics, which represent the structure of the entire landscape mosaic ($N = 8$ patch types; McGarigal et al. 2002); and class-scale metrics, which represent amount and spatial distribution of a single patch type (McGarigal et al. 2002, Tischendorf 2001). At the landscape scale, we measured total edge (m; Elkie et al. 1999) and patch richness density (number of patch types/100 ha; McGarigal et al. 2002). We pooled habitat classes into two functional categories for class-scale landscape metrics. Riparian habitat included mature hardwood and pine-hardwood habitats on both areas and likely provided water, high-quality den sites, and hard mast (Chamberlain et al. 2002, 2003). Soft mast habitat included 0–8 yr-old pine and mature pine on TWMA and 0- to 8-yr-old pine and ≥16-yr-old pine on TC, and likely represented high-quality foraging sites based on knowledge of raccoon diet (Johnson 1970) and habitat selection patterns of raccoons on our study sites (Chamberlain et al. 2002, 2003). We calculated two metrics for each habitat class: proportion of habitat (0–1, proportion of each patch type in the buffer; McGarigal et al. 2002) and mean patch size (ha; Elkie et al 1999).

Many landscape metrics are intercorrelated because they use the same basic building blocks in their formulas (Turner et al. 2001, McGarigal et al. 2002). Therefore, we calculated Pearson correlation coefficients for each variable pair and retained the more biologically meaningful member of highly correlated pairs ($r \geq 0.80$). To stabilize variance and correct for nonnormality, we arcsine-transformed proportion of habitat and log transformed mean patch size and patch richness density. We used univariate t-tests to compare each landscape metric between TWMA and TC and did not correct P-values for multiple testing (Moran 2003).

Table 1. Ranges, means with associated standard deviations, and test statistics with probability values for landscape variables associated with space use by raccoons on the Tallahala Wildlife Management Area and properties owned by the Timber Company (TC), Mississippi, 1996–1997.

	Range[a]		Mean ± sd[a]			
Metric	TC	TWMA	TC	TWMA	t	P[b]
N			25	70		
Patch richness density (*N* patch types/100 ha)	0.46–0.92	0.43–0.92	0.70 ± 0.17	0.78 ± 0.08	–3.36	0.022
% of riparian habitat	0.04–0.53	0.02–0.78	0.24 ± 0.15	0.36 ± 0.27	–1.76	0.028
Mean size (ha) of riparian habitat patches	12.9–29.5	8.1–25.3	19.6 ± 5.3	14.7 ± 3.3	5.14	<0.001
Mean size (ha) of soft mast habitat patches	5.9–92.7	8.1–25.3	31.4 ± 25.1	14.0 ± 4.9	4.54	<0.001
Interspersion (%) of riparian habitat	53.3–100.0	58.7–100.0	90.9 ± 12.8	88.0 ± 10.4	–3.75	<0.001
Interspersion (%) of soft mast habitat	40.0–98.7	15.5–100.0	67.2 ± 17.6	83.2 ± 21.0	1.67	0.099

a. Untransformed values.

b. *P*-values not corrected for multiple comparisons. Probability of 5 significant results = 0.025 (Moran 2003).

Results

We noted significant negative correlations ($r = –0.94$) between proportion of the landscape in soft mast habitats and proportion of the landscape in riparian habitats. We excluded the former variable and retained the latter given the known importance of riparian habitats to raccoons in other systems (Leberg and Kennedy 1988). Similarly, we detected a significant negative correlation between mean patch size of soft mast habitats and total edge ($r = –0.80$). We retained the first variable of this pair given the known importance of area of quality foraging habitats to raccoons in other ecosystems (Kaufmann 1982).

We created circular buffers for 70 raccoons on TWMA and 25 on TC monitored from January 1996–December 1997. Raccoons on TWMA (0.78 ± 0.08, mean ± SD) maintained spaces with greater patch richness density ($t = –3.36$, $P = 0.022$) than raccoons on TC (0.70 ± 0.17; Table 1). Likewise, raccoons on TWMA (0.36 ± 0.27) maintained spaces with greater proportions of riparian habitat ($t = –1.76$, $P = 0.028$) than raccoons on TC (0.24 ± 0.15). However, mean size (ha) of riparian habitats was greater on TC ($t = 5.14$, $P < 0.001$; 19.6 ± 5.3) than TWMA (14.7 ± 3.3). Similarly, mean size (ha) of soft mast habitats was greater for raccoons on TC ($t = 4.54$, $P < 0.001$; 31.4 ± 25.1) than on TWMA (14.0 ± 4.9).

Discussion

The availability of critical resources (i.e., dens, foraging sites) influences space use and movements of raccoons (Gehrt and Fritzell 1998). Raccoons on TC maintain smaller home ranges and core use areas than raccoons on TWMA, and exhibit reduced movements within these spaces (Chamberlain et al. 2000). If space use is even partially a function of habitat quality (Sandell 1989), one may infer that habitat quality for raccoons is potentially greater on TC than TWMA, as suggested in Chamberlain et al. (2000). We sought to further explore patterns of habitat selection on TC and TWMA to examine mechanisms influencing raccoon behavior relative to differing forest management strategies. Our findings offer additional insight into previous works on these study areas, specifically that patch richness density (a measure of patch diversity) and landscape characteristics associated with specific habitat types (i.e., riparian zones) are important to raccoons in pine-dominated forest systems.

Raccoons are generalists, capable of exploiting a wide variety of habitats and prey (Kaufmann 1982). Selecting portions of the landscape with a richness of habitat patches should offer raccoons abundant foraging opportunities and provide necessary escape cover (Pedlar et al. 1997). It is likely that our observation that raccoons on TWMA maintained spaces with greater patch richness is a consequence of behavioral adaptations to selecting ecotones and areas with diverse habitats in addition to differences in forest management strategies between the study areas. The abundant ecotones associated with increased patch richness frequently contain abundant insects (Thomas et al. 1992), escape cover (Pedlar et al. 1997), and small mammals (Best 1983); all valuable resources for raccoons. Additionally, intensive forest management on TC created a landscape with reduced patch diversity; raccoons on TC inevitably inhabited a landscape with lower patch richness as a consequence of forest management practices.

Bottomland hardwoods and riparian habitats have long been recognized as providing quality raccoon habitat because of the availability of den sites and foraging resources (Kaufmann 1982, Leberg and Kennedy 1988) and previous work on our study areas noted the importance of these habitats to raccoons (Chamberlain et al. 2002, 2003). Although habitats classified as riparian in this study were selected by raccoons at multiple spatial scales on both study areas, plasticity of selection was greater for raccoons on TC (Chamberlain et al. 2002, 2003). In our study, raccoons on TWMA maintained spaces with greater proportions of riparian habitats, whereas raccoons on TC maintained spaces with greater mean size of these habitats. We offer that these differences resulted from landscape characteristics across the two areas. Riparian habitats on TWMA were contained within extensive bottomland hardwood drainages, in addition to pine-hardwood habitats along streams located throughout upland areas. Conversely, riparian habitats on TC were restricted entirely to SMZs and pine-hardwood stands adjacent to them. From a landscape perspective, riparian habitats were in greater abundance on TWMA. Raccoons on TWMA could therefore maintain spaces with numerous patches of riparian habitats available to them, whereas raccoons on TC were constrained in their selection for riparian habitats. Additionally, it is plausible that riparian habitats on TWMA were of higher quality relative to those on TC, particularly bottomland hardwood stands. The relatively narrow SMZs likely contained reduced availability of quality den sites and hard mast resources relative to more extensive bottomland drainages on TWMA, potentially requiring raccoons to select larger patches of riparian habitats on TC to fulfill life history requirements.

Soft mast producing plant species serve as important food items for raccoons throughout the annual cycle (Johnson 1970). Raccoons on TC consistently maintained spaces with larger patch sizes of habitats providing soft mast resources, likely a consequence of foraging opportunities provided within these habitats and their distribution across the landscape. Forest management on TC commonly produced clearcuts ≥50 ha, whereas clearcuts of this size were not present on TWMA. Consequently, sizes of habitat patches producing soft mast resources were considerably larger on TC, particularly for early successional environments. Furthermore, lack of prescribed burning on TC in mature pine habitats resulted in understory conditions dominated by woody species producing soft mast (Chamberlain 1999). Raccoons on TC selected these pine habitats at multiple spatial scales during all seasons (Chamberlain et al. 2002).

Management Implications

The structure of a landscape affects numerous ecological processes, such as species interactions and animal distribution (Dunning et al. 1992). Increasing intensity of forest management on private and public lands has important implications to wildlife because this management tends to result in increasing forest patch size and reduced stand rotations and landscape complexity (i.e., more simple edges). As plantation acreage increases throughout the southeastern United States, land managers constantly seek to determine how forest management affects wildlife populations. Specifically, considerable research has recently focused on how mesocarnivores and other predators respond to landscape patterns and subsequent effects of these responses on predation (Chalfoun et al. 2002, Kuehl and Clark 2002, Thompson et al. 2002) although relationships between intensive forest management and mesocarnivore behavior are not well understood. Forest management practices that manipulate landscape patterns such as edge, patch diversity, and habitat structure all inevitably affect mesocarnivore behavior and therefore predation rates on a host of wildlife species. Forest managers have the ability to manipulate these landscape characteristics in a predictable fashion.

Thompson (2002) noted that ecological patterns at all spatial scales (regional, landscape, micro-scale, etc.) are often influenced by scales larger than the one under consideration and multiple spatial scales may be viewed as a hierarchy where larger scales constrain patterns and processes at smaller scales (Allen and Starr 1982). Our findings, when coupled with earlier findings by Chamberlain et al. (2000, 2002, 2003), indicate that habitat and landscape features at numerous spatial scales are important influences on raccoon behavior. Therefore, we recommend managers use multi-scale perspectives when planning forest management, recognizing that intended outcomes may be constrained by processes operating at broader spatial scales.

Analyses similar to ours offer land managers opportunities to refine management programs and improve effectiveness and efficiency of broad-scale management plans. For example, U.S. Department of Agriculture/Wildlife Services currently is conducting large-scale programs directed at reducing rabies in raccoon populations across a variety of landscapes. By developing models to predict raccoon distribution and use patterns using landscape characteristics, managers could determine portions of the landscape most likely to contain raccoons and direct management actions to those specific sites. We recommend future research evaluate the applicability and effectiveness of using landscape analyses to refine management programs targeted across broad geographic scales.

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Literature Cited

Allen, A. W., Y. K. Bernal, and R. J. Moulton. 1996. Pine plantations and wildlife in the southeastern United States: an assessment of impacts and opportunities. U.S. Department of the Interior Information and Technical Report, National Biological Service, Washington, D.C.

Allen, T. F. H. and T. B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois.

Best, L. B. 1983. Bird use of fencerows, implications of contemporary fencerow management practices. Wildlife Society Bulletin 11:343–347.

Bowman, J. L., D. R. Wood, F. J. Vilella, B. D. Leopold, L. W. Burger Jr., and K. D. Godwin. 1999. Effects of red-cockaded woodpecker management on vegetative composition and structure and subsequent impacts on game species. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 53:220–234.

Chalfoun, A. D., F. R. Thompson, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306–318.

Chamberlain, M. J. 1999. Ecological relationships among bobcats, coyotes, gray fox, and raccoons, and their interactions with wild turkey hens. Dissertation, Mississippi State University, Mississippi State, Mississippi, USA.

_____, L. M. Conner, and B. D. Leopold. 2002. Seasonal habitat selection by raccoons *(Procyon lotor)* in intensively managed pine forests of central Mississippi. American Midland Naturalist 147:102–108.

_____, _____, _____, and K. M. Hodges. 2003. Space use and multi-scale habitat selection of adult raccoons in central Mississippi. Journal of Wildlife Management 67:334–340.

_____, B. D. Leopold, K. M. Hodges, and J. E. G. Burton. 2000. Space use and movements of raccoons in two forested ecosystems. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 54:391–399.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.

Dijak, W. D. and F. R. Thompson. 2002. Landscape and edge effects on the distribution of mammalian predators in Missouri. Journal of Wildlife Management 64:209–216.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169–175.

Elkie, P. C., R. S. Rempel, and A. P. Carr. 1999. Patch analyst user's manual: a tool for quantifying landscape structure. TM-002. Ontario Ministry of Natural Resources, Northwest Science and Technology, Ontario, Canada.

Fritzell, E. K. 1978. Habitat use by prairie raccoons during the waterfowl breeding season. Journal of Wildlife Management 42:118–127.

Gehring, T. M. and R. K. Swihart. 2003. Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biological Conservation 109:283–295.

Gehrt, S. D. and E. K. Fritzell. 1998. Resource distribution, female home range dispersion, and male spatial interactions: group structure in a solitary carnivore. Animal Behavior 55:1211–1227.

Henner, C. M., M. J. Chamberlain, B. D. Leopold, and L. W. Burger, Jr. 2004. A multi-resolution assessment of raccoon den selection. Journal of Wildlife Management. 68:179–187.

Hoffmann, C. O. and J. L. Gottschang. 1977. Numbers, distribution, and movements of a raccoon population in a suburban residential community. Journal of Mammalogy 58:623–636.

Ims, R. A. 1995. Movement patterns related to spatial structures. Pages 85–109 *in* L. Hansson, L. Fahrig, and G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman and Hall, London, UK.

Johnson, A. S. 1970. Biology of the raccoon (*Procyon lotor various* Nelson and Goldman). Alabama Agricultural Experiment Station Bulletin Number 402.

Kaufmann, J. H. 1982. Raccoons and allies. Pages 567–585 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America: biology, management, and economics. Johns Hopkins University Press, Baltimore, Maryland.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83: 530–544.

Kuehl, A. K. and W. R. Clark. 2002. Predator activity related to landscape features in northern Iowa. Journal of Wildlife Management 66:1224–1234.

Leberg, P. L. and M. L. Kennedy. 1988. Demography and habitat relationships of raccoons in western Tennessee. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 42:272–282.

Li, H. and J. F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology 75: 2446–2455.

McGarigal K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial patterns analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available online at www.umass.edu/landeco/research/fragstats/fragstats.html.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403–405.

Oehler J. D. and J. A. Litvaitis. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. Canadian Journal of Zoology 74:2070–2079.

O'Neill R. V., C. T. Hunsaker, S. P. Timmins, B. L. Jackson, K. B. Jones, K. H. Riitters, and J. D. Wickham. 1996. Scale problems in reporting landscape pattern at the regional scale. Landscape Ecology 11: 169–180.

Pedlar, J. H., L. Fahrig, and H. G. Merriam. 1997. Raccoon habitat use at 2 spatial scales. Journal of Wildlife Management 61:102–112.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164–182 *in* Carnivore behavior, ecology, and evolution. J. L. Gittleman, editor. Cornell University Press, Ithaca, New York.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Wiley. 2003. Effects of fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115:101–110.

Thomas, M. B., S. D. Wratten, and N. W. Sothern. 1992. Creation of "island" habitats in farmlands to manipulate populations of beneficial arthropods: predator densities and species composition. Journal of Applied Ecology 29:524–531.

Thompson, F. R. 2002. Principles of landscape ecology for conservation of wildlife and biodiversity. Pages 72–82 *in* J. G. Dickson, editor. Wildlife of Southern Forests: Habitat and Management. Hancock House Publishers, Blaine, Washington.

______, T. M. Donovan, R. M. DeGraaf, J. Faaborg, and S. K. Robinson. 2002. A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. Studies in Avian Biology 25:8–19.

Tischendorf, L. 2001. Can landscape indices predict ecological processes consistently? Landscape Ecology 16: 235–254.

Turner M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice: pattern and process. Springer-Verlag, New York.

White, J. C. and R. A. Garrott. 1990. Analysis of wildlife radio tracking data. Harcourt Brace Jovanovich, New York, New York.

Wynn, T. S., E. F. Songer, and G. A. Hurst. 1990. Telemetry data management: a GIS-based approach. Proceedings of the National Wild Turkey Symposium 6:144–148.