NICHE SHIFT BY VIRGINIA OPOSSUM FOLLOWING REDUCTION OF A PUTATIVE COMPETITOR, THE RACCOON

Shauna M. Ginger, Eric C. Hellgren,* Maral A. Kasparian, Laurence P. Levesque, David M. Engle, and David M. Leslie, Jr.

Department of Zoology, Oklahoma State University, Stillwater, OK 74078 (SMG, ECH, MAK, LPL)
Oklahoma Cooperative Fish and Wildlife Research Unit, United States Geological Survey, Biological Resources Division, 404 Life Sciences West, Oklahoma State University, Stillwater, OK 74078 (SMG, MAK, LPL, DML)
Department of Plant and Soil Sciences, Oklahoma State University, Stillwater, OK 74078 (DME)

Increases in mesopredator populations due to habitat fragmentation may have cascading effects on prey (e.g., songbirds) and may increase competitive interactions within the guild. We compared micro- and macrohabitat selection of the Virginia opossum (*Didelphis virginiana*) between areas with and without removal of the raccoon (*Procyon lotor*), a putative competitor, in a fragmented habitat in north-central Oklahoma. Live trapping conducted in 1998–2001 resulted in 482 total captures of opossums. Vegetation was sampled in summer (April–August) around trapsites associated with 235 of those captures. Ordination analyses indicated that opossums shifted microhabitat use toward eastern red cedar (*Juniperus virginiana*) forest when density of raccoons was reduced. Geographic Information Systems analyses at the habitat-patch scale revealed no differences in habitat selection after raccoon reduction. Niche breadths were high for both species, but niche overlap varied by time and treatment. Overlap of habitat patches between raccoons captured preremoval and opossums captured postremoval was high, suggesting a shift in habitat selection. The niche shift by opossums and change in niche overlap between raccoons and opossums supported our competition hypothesis. We acknowledge our lack of replication, but note that our work represents the 1st report of experimental manipulation coupled with work at multiple scales to examine competitive relationships between these key mesopredators.

Key words: competition, *Didelphis virginiana*, habitat fragmentation, mesopredator, niche, Oklahoma, ordination, *Procyon lotor*

Habitat manipulation alters composition and structure of animal communities, and the most important and large-scale cause of habitat manipulation is expansion and intensification of land use by humans (Andren 1994). An increase in mesopredator populations is a potential consequence of habitat manipulation and fragmentation (Oehler and Litvaitis 1996). Mesopredators, also termed mesocarnivores, are medium-sized (1–15 kg) mammalian carnivores and omnivores. Buskirk (1999) summarized characteristics and importance of these species: they are notable for their diversity of taxa, form, and function and are ecologically vital because they affect behaviors and demography of prey, cycle nutrients by scavenging carrion, affect plant fitness (and possibly landscape patterns) through dispersal and predation of seeds, complete or interrupt life cycles of pathogens or parasites of other animals, and influence distributions and abundances of nonprey vertebrates, including each other.

* Correspondent: ehellgr@okstate.edu

Food abundance, habitat structure, interference competition, and humans, especially via trapping and habitat manipulation, can structure mesopredator communities (Buskirk 1999). Theoretically, competitive interactions among mesopredators will increase as their populations increase. Because many of these species are not strictly carnivores, probability of overlapping use of habitats (Shirer and Fitch 1970) and foods increases. Such interactions can compress the niche (Kormondy 1996) of each species below limits of its physiology or morphology (Begon et al. 1990). Niche space can be reduced under the influence of another carnivore species, and the proposed order by Buskirk (1999) for this narrowing is home-range displacement, microhabitat avoidance, and prey shifting.

A removal experiment is an effective way to study competitive interactions, due to its controlled nature (Connell 1975). These experiments provide more compelling evidence for competition than synecological studies among sympatric species but are lacking for mid- to large-sized mammals (Gurevitch et al. 1992; Schoener 1983). Henke and Bryant (1999) removed a top predator, the coyote (*Canis latrans*), in western Texas, and studied subsequent effects on the faunal community but did not directly assess competition. Most studies of carnivore synecology have identified potential patterns in interspecific competition, such as those between coyotes and bobcats (*Felis rufus*—Litvaitis 1981; Litvaitis and Harrison 1989; Major and Sherburne 1987), coyotes and foxes (Cypher 1993; Cypher and Spencer 1998; Theberge and Wedeles 1989; White et al. 1995), and sympatric desert carnivores (Bothma et al. 1984). Prey partitioning, both spatially (Litvaitis 1981) and temporally (Bothma et al. 1984), negative correlations with relative abundance (Litvaitis and Harrison 1989), and interference competition (Fedriani et al. 2000; White et al. 1995) have been observed.

Removal experiments provide a means of measuring and testing hypotheses about

niches and habitat selection (Keddy 1989). If a competing species is removed and habitat segregation results from interspecific interactions, then other species should demonstrate competitive release characterized by a shift in habitat selection (Löfgren 1995). We performed a removal study with Virginia opossums (*Didelphis virginiana*) and raccoons (*Procyon lotor*) to test the hypothesis that competition existed between the 2 species. These species co-occur throughout much of their distribution and associated habitats, have similar omnivorous food habits, and display similar resource use (Gardner 1982; Kaufman 1982; Kissell and Kennedy 1992; Lotze and Anderson 1979; Shirer and Fitch 1970). Food habits have been investigated for comparative purposes without determining interspecific interactions (Hamilton 1951; Stieglitz and Klimstra 1962; Wood 1954), although an increase in the potential for interspecific interactions that may lead to exploitative or interference competition does occur with species that consume similar prey items (Ladine 1997). Previous work on ecological relationships of these 2 species has found only minor evidence of competition in terms of habitat use (Kissell and Kennedy 1992; Ladine 1995), although direct interference in the form of the killing of opossums by raccoons in enclosure experiments has been observed (Stuewer 1943).

We chose to investigate opossum habitat selection upon removal of the raccoon, because although the 2 species are similar in terms of habitat use, opossums have a more *r*-selected life history (Seidensticker et al. 1987) and we expected that they may respond quickly to removal of a potential competitor. We predicted that raccoon removal would result in a shift in opossum habitat selection manifested either in niche expansion or by greater use of habitats formerly shared with raccoons.

MATERIALS AND METHODS

Study area.—The Cross Timbers ecoregion, dominated by oak (*Quercus*) forest interspersed

with tallgrass prairie and invaded by eastern red-cedar (*Juniperus virginiana*), covers large parts of central Oklahoma and Texas. Livestock grazing is the primary economic use of the region because the area produces few economically valuable timber products (Stritzke et al. 1991). The Cross Timbers Experimental Range (CTER), located 11 km southwest of Stillwater, Payne County, Oklahoma (36°02′40″–36°04′20″N, 97°09′30″–97°11′39″W), encompasses 712 ha. The overstory is dominated by post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), and American elm (*Ulmus americana*) interspersed with eastern redcedar. Little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), grama grasses (*Bouteloua*), purpletop (*Tridens flavus*), ragweed (*Ambrosia*), and buckbrush (*Symphoricarpos orbiculatus*) are prevalent in the understory (Ewing et al. 1984).

Our study area was anthropogenically manipulated similar to the way the landscape is changing in the region. Beginning in 1983, combinations of prescribed fire and herbicides were applied to CTER to produce a mosaic of vegetation types. We investigated two 130-ha study areas on CTER blocked by major vegetation types, which were characterized as cedar forest, oak forest, grassland, and mixed brush. One area served as the control, and the other area served as the treatment, or raccoon removal area. Relative composition of these areas by vegetation type were 31.8% cedar, 33.8% oak, 28.8% grassland, and 5.3% mixed brush on the removal area and 18.4% cedar, 39.2% oak, 27.2% grassland, and 15.0% mixed brush on the control area. The areas were separated by 400 m and none of 31 radiocollared female opossums were located in both areas. Densities of the study species on the entire CTER in 1998–1999 ranged from 3.9 to 12.8/km² for opossums and 8.6 to 15.3/km² for raccoons (Levesque 2001).

Mesopredator trapping.—Trapping was conducted seasonally in 1998–1999 before raccoon removal (preremoval period), then bimonthly from January 2000 to January 2001 with raccoon removal (postremoval period). We trapped opossums and raccoons using wire-mesh traps (25 by 30 by 81 cm; Tomahawk Trap Company, Tomahawk, Wisconsin) baited with canned sardines. Traps were set in four 12-ha grids of 8 traps in each study area. Traps within grids were placed in 2 parallel rows of 3 traps 300-m apart

with traps spaced at 200-m intervals. The other 2 traps in the grid were placed 200-m apart between the 2 rows. We trapped the removal area for 10 consecutive days, followed immediately by a 10-day trapping session on the control area. We set 8 additional traps in a buffer area surrounding the treatment grids to reduce raccoon immigration into removal grids. Traps were baited with sardines and checked daily.

We chemically immobilized (8 mg/kg Telazol; Fort Dodge Animal Supply, Fort Dodge, Iowa), ear-tagged (Monel #4; National Band and Tag, Newport, Kentucky), and took morphological measurements on captured opossums and raccoons. We released animals on site, except for raccoons captured in the removal pastures in 2000–2001, which were translocated >10 km from the study area. During 2 years of study, Mosillo et al. (1999) reported that 13 of 15 raccoons translocated from rural areas in Illinois that survived to the end of the tracking period in each of 2 years moved <10 km from their release sites. Movements of translocated raccoons in other studies were often >10 km and occasionally >100 km (Wright 1977). However, no mention was made of directional movements or homing toward the original capture point. Wright (1977) reported that the direction of dispersal by translocated raccoons in Kentucky was random. We did not assume that raccoons could not return to the study area nor did we have the logistical means to translocate raccoons beyond the farthest movement distance recorded in previous studies. Our intent was to translocate raccoons far enough to reduce their probability of returning and to recapture and remove any individuals that returned.

Vegetation sampling.—Vegetation sampling was conducted in summer 1998, winter 2000, summer 2000, and winter 2001. For each trapsite, we sampled understory cover by the Daubenmire method (Bonham 1989) in a 1-m² plot at each trap site and in 1-m² plots 10 m from a trap site in northeast (45°), southeast (135°), southwest (225°), and northwest (315°) directions. Data included percentages of forb cover, grass cover, woody cover (≤0.5 m in height), bare ground, rock, hardwood leaf litter, and miscellaneous litter. To sample overstory and midstory cover, 4 canopy cover and 4 visual obstruction measurements were averaged from the five 1-m² plots at each trapsite using a densiometer (Bonham 1989) and 1-m board with alter-

nating 0.1-m dark and light blocks, respectively. Diameter breast height (DBH) of stems ≥5 cm DBH were measured and counts of coarse woody debris (≥10 cm DBH) recorded in a circular plot of 8.93-m radius (0.025 ha) centered at the trap site. Basal area (m^2/ha) was calculated for groups of tree species (eastern redcedar, oak, nonoak deciduous, and total) at each trapsite. We also recorded terrain position code (upland, midslope, bottomland) and aspect (direction of slope of terrain) for each trap site. Microhabitat variables were averaged by site for each sampled season.

Microhabitat analyses.—To test for microhabitat selection of opossums at CTER, we used a constrained ordination method, redundancy analysis, and an unconstrained ordination method, partial principal components analysis, with CANOCO 4.0 (ter Braak and Šmilauer 1998). Vegetation data were centered and standardized because we used different sampling measurements for these variables. We used continuous and categorical variables. Total opossum captures were calculated per trapsite per month, with data from April to August used for the summer 1998 period, and from May and July for summer 2000. Captures from 1999 and winter 1998 could not be used due to lack of corresponding vegetation data.

We conducted a redundancy analysis to determine if removal and control areas had different microhabitat composition within and between years, which might have allowed differential trap selection by opossums. In redundancy analysis, the ordination of species or response variables (in our case, microvegetation) was constrained so that sample scores were linear combinations of environmental or explanatory variables (in our case, control as compared with removal—Legendre and Legendre 1998; Økland et al. 1999). Constrained ordinations corresponded roughly to regressions; both response and explanatory variables could have been multivariate (Spitzer et al. 1997). Redundancy analysis can explicitly investigate and statistically test relationships between species and environmental variables (Verschuren et al. 2000). A distribution-free Monte Carlo permutation test ($n = 999$ permutations) was used to provide significance values for the constrained axis. For these and other analyses, we chose $P < 0.05$ as indicating significance, and we report *P*-values between 0.05 and 0.10 as approaching significance

and worthy of note (Robinson and Wainer 2002).

Microvegetation at trapsites with opossum captures in the control and removal areas in the summers of 1998 and 2000 were arranged in a biplot for comparison using partial principal components analysis (Gabriel 1971), with year as a covariate. Sites where opossums were captured in removal grids in 2000 were compared with the other 3 grid-season combinations as 1 class. The 2 most correlated variables as determined by the vegetative variable scores for the 2 most correlated principal components were chosen for significance testing in univariate analyses (*t*-tests) for opossum captures in 2000 (Mellink 1991 used similar methods).

Macrohabitat analyses.—A digitized black-and-white digital ortho-quarterquad from 1998 was used in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California) for macrohabitat analyses. Four habitat types (plus a pond category) were delineated based on vegetative composition and extensive ground reconnaissance (Levesque 2001). Those habitats were cedar forest (94 patches, $\bar{X} \pm SD = 1.67 \pm 3.35$ ha), deciduous forest (76 patches, 5.67 ± 13.45 ha), mixed cedar-deciduous forest (51 patches, 1.64 ± 3.20 ha), and grassland (60 patches, 6.18 ± 22.87 ha).

Individual trap sites were georeferenced using a hand-held global positioning system (GPS) and overlaid on the habitat coverage to determine the habitat patch in which each trap was located. Habitat availability at trapsites was determined as number of traps in each habitat class and compared with total captures for both opossums and raccoons using log-linear analysis (PROC CATMOD/CHISQ—SAS Institute Inc. 1990) for use–availability differentiation. Variables investigated included treatment (control, removal), species (opossum, raccoon), period (preremoval = May, July, October 1998–1999; postremoval = May, July, November 2000), selection (use or availability), habitat (cedar forest, deciduous forest, grassland, mixed forest), and all interactions. If a significant ($P < 0.05$) interaction between selection and habitat was observed, Bonferroni confidence intervals were calculated to determine which habitat types were used differently than their availability (Byers et al. 1984; Neu et al. 1974).

Niche breadth and overlap.—We used all captures of opossums or raccoons and the associ-

ated habitat patch of the successful trap sites from 1999 (preremoval—Levesque 2001) and 2000 (postremoval) for niche analyses. Niche breadth for macrohabitat use by opossums and raccoons was compared between treatments using Smith's measure of niche breadth (Krebs 1999), which takes into account resource availability:

$$FT = \sum_{j}^{n} (\sqrt{p_j a_j}),$$

where FT = niche breadth, p_j = proportion of individuals found in or using resource state j, a_j = proportion that resource j is of the total resources, and n = total number of possible resource states. Overlap in resource use between raccoons and opossums was calculated using Hurlbert's index, which allows resource states to vary in size (Krebs 1999):

$$L = \sum_{i}^{n} \left(\frac{p_{ij} p_{ik}}{a_i} \right),$$

where L = Hurlbert's measure of niche overlap between species j and k, p_{ij}, p_{ik} = proportional use of resource i of total resources used by species j or k, a_i = proportional amount or size of resource state i ($\Sigma a_i = 1.0$), and n = total number of possible resource states.

We compared L for opossums on the control area pre- and postremoval with L on removal pastures pre- and postremoval to assess changes in opossum resource use due to raccoon removal using Tukey's jackknife method (Sokal and Rohlf 1995) and a 1-tailed unpaired *t*-test. For that comparison, we assumed that niche overlap would decrease on the removal area over time. We also compared L between opossums and raccoons on the removal area before removal with overlap between opossums postremoval and raccoons preremoval to detect changes in niche overlap between the species when one was removed. To account for a possible year effect, we calculated L for opossums caught postremoval and raccoons caught preremoval in the control area. To account for a treatment-area effect, we calculated L for opossums and raccoons caught preremoval in the control and removal areas.

RESULTS

Trapping effort equaled 3,840 trap-nights in 1998–1999 before removal and 5,010

TABLE 1.—Capture data for opossums and raccoons on treatment areas at the Cross Timbers Experimental Range, Payne County, Oklahoma, before (1998–1999) and during (2000–2001) removal of raccoons. In the control area, raccoons and opossums were captured and released at the capture site; in the removal area, raccoons were removed from the capture site whereas opossums were released on site.

Species	Area	Preremoval		During removal	
		Individuals	Total captures	Individuals	Total captures
Opossum	Control	49	84	53	145
	Removal	50	95	45	158
Raccoon	Control	35	62	38	72
	Removal	23	25	22	28

trap-nights in 2000–2001 during removal, with 669 total captures of opossums and raccoons on the study areas (Table 1). Effort was split evenly between areas. Twenty-two raccoons were translocated (3 returned to the removal area and were trapped a 2nd time). Given the density of raccoons (8.6–15.3 animals/km²) across CTER (Levesque 2001), removing 22 individuals represented a large reduction (6.2 animals/km² removed). Three opossums (2 female, 1 male) were trapped in both areas in 1998–1999, and 9 (5 female, 4 male) in 2000–2001. Although 4 raccoons (2 female, 2 male) were trapped in both areas in 1998–1999, none were captured in both areas during the experimental phase (2000–2001) of the project.

We do not report statistical comparisons of capture rates of raccoons between the 2 areas because, although we had 4 grids in each area, these grids were not independent relative to raccoon ranging behavior. Capture rates on control grids were qualitatively higher both before and during raccoon removal (Fig. 1). However, this difference appeared to increase during the removal phase after May 2000 (Fig. 1). Capture rates and estimated densities of opossums on the 2 areas were not affected by treat-
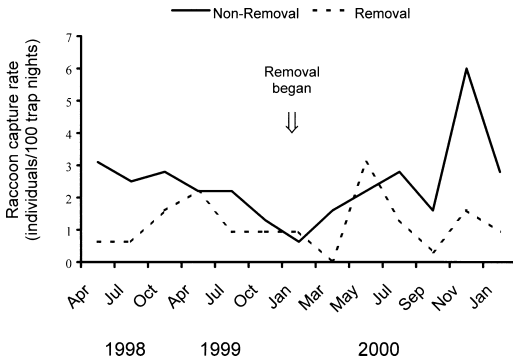
FIG. 1.—Capture rates of raccoons on control and removal areas (average of 4 trapping grids/area), Cross Timbers Experimental Range, Payne County, Oklahoma (1998–2001). Removal of raccoons began in January 2000.

ment (6.95 opossums/km^2 on the removal area, 6.83/km^2 on the removal area; Kasparian 2002).

Microhabitat.—Redundancy analyses of microhabitat vegetation showed no difference in composition between removal and control sites in 2000 ($P = 0.28$) but approached a difference in 1998 ($P = 0.09$). Comparisons of removal and control pastures between years indicated microhabitat changes ($P = 0.001$) in both areas from 1998 to 2000.

The first 4 principal components of the partial principal components analysis explained 43.6% of the variance in the microhabitat. The 1st axis, explaining 18.8% of the variance, represented a gradient from grassland to forest (Fig. 2), whereas the 2nd axis, explaining 9.8% of the variance, defined a gradient from xeric upland to mesic lowland. The 3rd axis, explaining 8.8% of the variance, represented a gradient from cedar forest to deciduous forest.

Opossum captures in the removal area in 1998 (preremoval) and the control area in 2000 were most correlated with the 1st axis ($r = 0.19$ and 0.22, respectively). Opossum captures in the 1998 control and 2000 removal groups were most correlated with the 3rd axis (-0.15, 0.33). Therefore, these axes were used in the biplot. A niche ex-

pansion toward cedar forest upon raccoon removal was indicated (Fig. 2). Means for the site scores on the removal area shifted (axis 1 = -0.14, axis 3 = 0.13) and standard deviations increased (axis 1 = 1.27, axis 3 = 1.33) in 2000 compared with site scores for the nonremoval area (axis 1 = 0.05, $SD = 0.90$; axis 3 = -0.04, 0.87).

The 2 most correlated microhabitat variables for the 1st axis (percentage leaf litter, percentage grass cover) and 3rd axis (number of cedar trees, cedar basal area) were chosen to compare opossum selection differences between areas in 2000. Percentage leaf litter ($P = 0.014$), percentage grass cover ($P = 0.056$), and number of cedar trees ($P = 0.078$) differed between opossums caught in removal and control areas. Opossums in the removal area in 2000 were captured in sites characterized by lower percentage cover of hardwood leaf litter (18.1% ± 26.2% removal compared with 38.1% ± 7.2% control), higher percentage grass cover (37.4% ± 32.0% compared with 24.3% ± 4.4%), and greater number of eastern redcedar trees (11.5 ± 9.4 compared with 7.9 ± 7.5; Fig. 2). This analysis, combined with the partial principal components analysis results, implied a shift in microhabitat selection by opossums following reduction of raccoon density.

Macrohabitat.—For the 1998–2000 comparisons of trap captures with habitat patch, there were no significant 3-, 4-, or 5-way interactions and no significant year or treatment effects for either species, so years and treatments were combined and analyzed for each species separately. For opossums, an interaction between use–availability and habitat type was found ($P = 0.002$), with deciduous forest preferred and grassland avoided after Bonferroni correction (Fig. 3a). For raccoons, that interaction approached significance ($P = 0.061$), with deciduous forest avoided after Bonferroni correction (Fig. 3b).

Niche breadth and overlap.—Both species, regardless of treatment or period (1999 and 2000), had large niche breadths
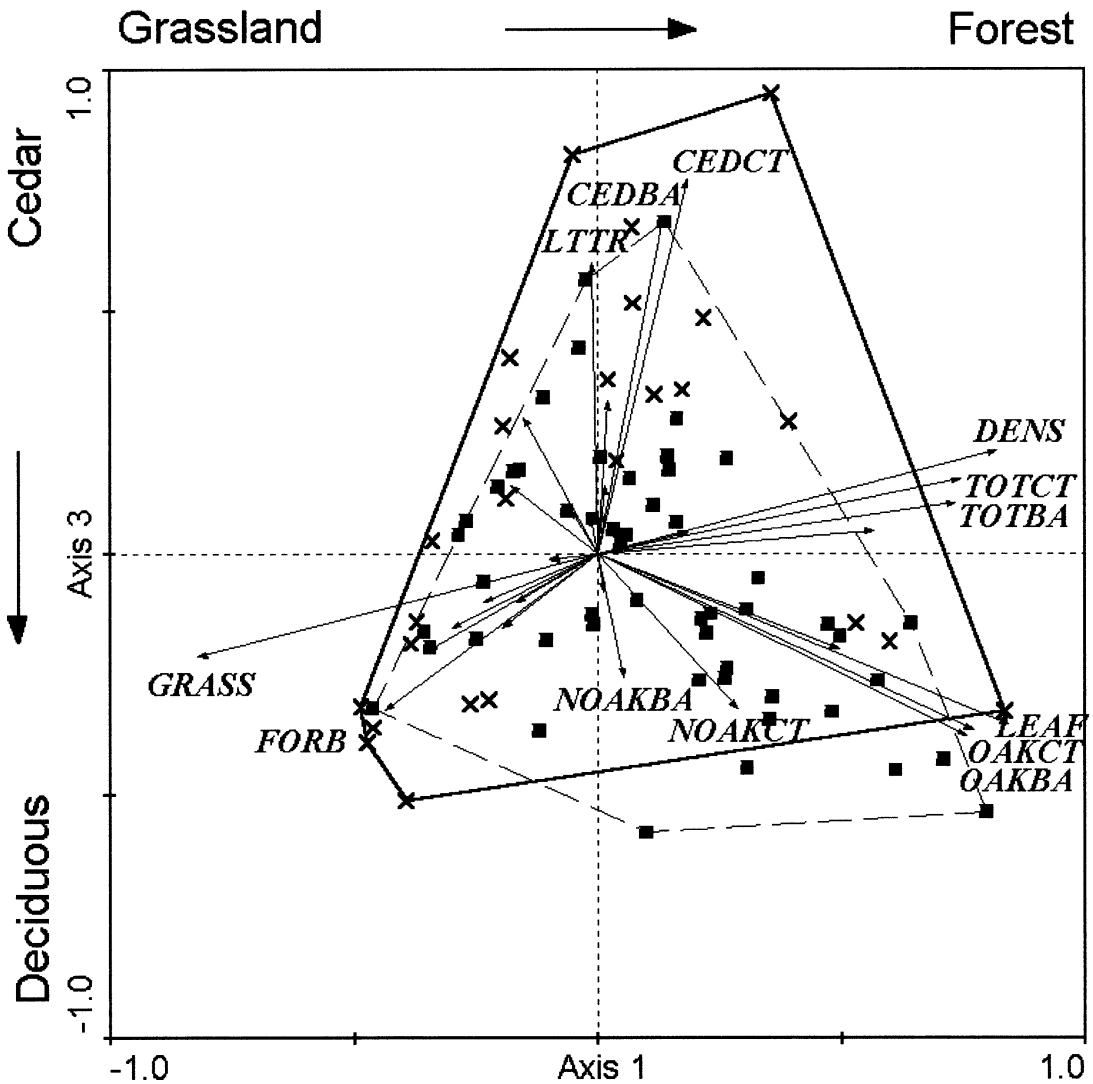
FIG. 2.—Biplot for 1st and 3rd principal component axes of scores for microhabitat vegetation and opossum capture samples in summers (April–August) 1998 and 2000 on Cross Timbers Experimental Range, Payne County, Oklahoma. Envelopes with solid lines and samples indicated by **x** represent trapsites with ≥1 captures in the removal area in 2000. Envelopes with dashed lines and samples indicated by ■ represent trapsites with ≥1 captures in the control area in 1998 and 2000 and the removal area (preremoval) in 1998. Abbreviations are as follows: GRASS = percentage grass cover; FORB = percentage forb cover; LTTR = percentage miscellaneous litter cover; CEDBA = basal area (m²/ha) of eastern redcedar; CEDCT = count for eastern redcedar in 0.025-ha plot; DENS = density of canopy cover (%); TOTCT = total trees present in 0.025-ha plot; TOTBA = total basal area (m²/ha) of trees; LEAF = percentage cover of hardwood leaf litter; OAKCT = count for oaks in 0.025-ha plot; OAKBA = basal area (m²/ha) of oaks; NOAKBA = basal area (m²/ha) of deciduous nonoaks; NOAKCT = count of deciduous nonoaks in 0.025-ha plot.
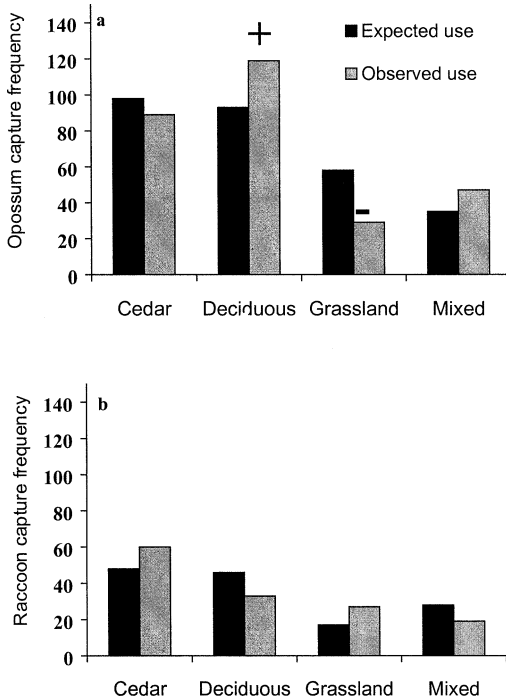
FIG. 3.—Habitat selection across all treatments for a) opossums ($n = 284$) and b) raccoons ($n = 139$) caught in 1998–1999 (May, July, October) and 2000 (May, July, November), Cross Timbers Experimental Range, Payne County, Oklahoma. Expected use based on total number captured and number of traps available in each habitat. The symbol $+$ indicates selection for and the symbol $-$ indicates avoidance of a particular habitat based on Bonferroni intervals (Neu et al. 1974).

TABLE 2.—Hurlbert's measure of niche overlap (L—Krebs 1999) of opossums and raccoons based on trapping data preremoval (1999) and postremoval (2000) at Cross Timbers Experimental Range, Payne County, Oklahoma. In control areas, raccoons and opossums were captured and released at the capture site; in removal areas, raccoons were removed from the capture site whereas opossums were released on site.

Area	Time periods[a]	
	Preremoval	Postremoval
Control	0.92 (0.13)[b]	0.91 (0.10)
Removal	1.07 (0.11)	1.14 (0.06)

[a] For measurement of niche overlap during the postremoval period, opossum habitat use was compared with habitat use by raccoons in the preremoval period to control for lack of data on raccoons in the removal area during the postremoval period.

[b] Jackknife SE given in parentheses.

ferences in overlap ($P > 0.20$ for all comparisons).

DISCUSSION

The niche shift by opossums and change in niche overlap between raccoons and opossums after raccoon reduction supported our competition hypothesis. We acknowledge our lack of replication, but note that our study represents the 1st report of experimental manipulation coupled with work at multiple scales to examine relationships between these key mesopredators. Given a longer study period and replication, these results may be more robust. We believe that removal of raccoons led to a real decrease in raccoon abundance and activity on the removal area, as evidenced by the decline in raccoon capture rates.

We demonstrated a shift in microhabitat selection on the basis of trap-site characteristics selected by opossums in an area of reduced density of raccoons. Analyses using vegetative data from winter 2001 (end of the removal period) revealed a similar difference in selection, but unlike summer, we did not have pretreatment data collected in winter to strengthen our inference (Ginger 2002). This shift was not coincident with a change in opossum density or cap-

(≥ 0.95), but niche overlap varied. The difference in overlap between opossums captured in removal sites postremoval compared with preremoval ($L = 1.04$) and for control opossums in control sites for the same time periods ($L = 1.07$) approached significance ($t_0 = 1.37$; *d.f.* $= 190$; $P = 0.086$). That result suggested that habitat use by opossums on removal sites shifted postremoval. Niche overlap of opossums and raccoons was higher ($t_7 = -1.61$; *d.f.* $= 167$; $P = 0.05$) on removal areas (1.14) than on control areas (0.91) during the postremoval period (Table 2). Other comparisons across time and area revealed no dif-

ture rates on the raccoon-removal area (Kasparian 2002).

Our results suggested that opossums and raccoons competed for resources at the microhabitat scale in CTER and that reduced densities of the competitor allowed a niche expansion by opossums. Animals prefer landscapes that offer a greater chance of encountering resources that are necessary for survival. Within a home range, animals make finer scale use of land based on factors such as food availability and competitive interactions (Pedlar et al. 1997). If such interactions are removed, resource use may shift. Schoener (1983) noted that greater niche overlap in food type or microhabitat implied a greater tendency to compete than to overlap at larger scales. The CTER study site was highly fragmented relative to the home range of opossums (mean home-range size = 27.4 ha compared with mean patch size = 3.5 ha ± 12.6 *SD*; Ginger 2002) and therefore may allow such fine-scale selection of habitat. In the control area, where raccoons and opossums co-occurred, opossums were captured in sites characteristic of deciduous forests of the Cross Timbers ecoregion (Fig. 2). Successful trap sites for opossums were characterized by greater percentage cover of hardwood leaf litter, overhead density, and oak basal area than unsuccessful traps (Ginger 2002; Levesque 2001). In areas with reduced densities of raccoons, however, opossums were more likely to select trap sites with characteristics associated with eastern redcedar forest. The particular resource (e.g., food or cover) causing this shift is unknown, and additional studies focusing on aspects of fine-scale resource use should be conducted.

Analyses at the habitat-patch scale did not reveal effects of raccoon removal on habitat selection by opossums. However, raccoons and opossums differentially selected habitat patches, perhaps due to differences in comparative home-range size, which is linked to body mass (Harestad and Bunnell 1979). Raccoons are larger in body mass (5 kg compared with 2 kg) and have larger home ranges (79–707 ha—summarized by Kaufman 1982) than opossums (4–114 ha—Gipson and Kamler 2001; Lay 1942; Seidensticker et al. 1987; VanDruff 1971; Verts 1963) in similar habitats. Raccoons also make long-range movements of several kilometers to temporary food sources (Fritzell 1978), whereas opossum movements are rarely >1 km (Gardner 1982; Seidensticker et al. 1987). Given differences in home-range size and movements, perhaps raccoons were more likely to encounter traps in a wider range of habitats than opossums. On CTER, raccoon captures were distributed fairly evenly across habitat types, whereas opossums were more likely to be caught in oak forest and less likely to be caught in grassland (Fig. 2). Although both species are known to prefer areas associated with water, trap success and distance to permanent water sources were not related in either control or removal areas (Ginger 2002). We suggest that opossums and raccoons are responding differently to the same scale of heterogeneity, but telemetric monitoring is necessary to fully evaluate comparative habitat selection by these species.

Increasingly, species–habitat relationships have been investigated at different spatial scales. Pedlar et al. (1997) suggested that effects could be found at a landscape scale for 1 species but at a local habitat level for others. Similar patterns also could be reflected across both scales if study species responded to local and landscape features. Relative abundances of raccoon and opossums were examined at 2 spatial scales in Missouri by Dijak and Thompson (2000). At a landscape scale, opossum abundance was related to latitude (associated with croplands), more heterogeneous landscapes, and high densities of riparian areas. Raccoons were more abundant in agricultural areas with high densities of streams than forested areas with low densities of streams (Dijak and Thompson 2000). At a local scale, opossum abundance showed no con-

sistent relationship to edge, whereas raccoons were more abundant in forest–agriculture and forest–riparian edges. Dijak and Thompson (2000) concluded that local features (e.g., distance to edge) and large-scale factors (e.g., landscape patterns in land use) may affect predator abundance and potentially affect predation rates of songbird nests. Pedlar et al. (1997) noted that microhabitat variables provided insight into the mechanism behind landscape patterns of raccoon activity.

Studies of ecological relationships between raccoons and opossums in Tennessee arrived at different conclusions regarding the influences of habitat and spatial scale. Kissell and Kennedy (1992) reported a nonsignificant positive association between opossums and raccoons. They suggested that habitat preferences by each species were independent of the occurrence of the other species. Conversely, Ladine (1995) found evidence of interactions between the 2 taxa for spatial attributes and habitat use. Individuals of both species were captured at the same location, indicating a significant amount of spatial overlap. However, opossums and raccoons used available habitat at different times during the day (based on time at capture), thus partitioning habitat temporally and reducing interspecific competition (Ladine 1997). Mean coefficients of association were negative at the microhabitat scale but positive at the macrohabitat scale, although results at both scales varied temporally. Interspecific interactions (inferences toward competition) were reflected most strongly from frequency of capture and vegetative data collected at the microhabitat scale, whereas association of species (presence or absence of individuals within a habitat) was reflected most accurately at the macrohabitat scale (Ladine 1995). Our findings were consistent with those of Ladine (1995), showing a niche shift by opossums at the microhabitat level (Fig. 2).

Niche breadths of both species were wide in our study for both species, as expected for generalist omnivores, and did not change with raccoon removal. However, when raccoons were removed, niche overlap for opossums in the raccoon-removal area between pre- and postremoval periods decreased relative to opossums in the control area. Overlap in habitat use between raccoons and opossums increased upon raccoon reduction compared with lack of a similar change in the control areas. These changes in overlap likely reflected the niche shift observed at the microhabitat level. The relationship between niche overlap and competition is complex (Holt 1987), poorly defined in the literature (Krebs 1999), and therefore our results should be interpreted as suggestive.

Competition between raccoons and opossums may be occurring on CTER as a result of mesopredator release and increased densities, given the high degree of habitat fragmentation on the area, a potentially reduced number of predators (Ginger 2002) and decreased overall harvest of the guild in the last 75 years (Novak et al. 1987). Further studies should be conducted to address effects of mesopredators on other animal populations, especially potential prey such as birds, in the Cross Timbers ecoregion. Increased fragmentation and lack of fire leads to invasion of eastern redcedar in the Cross Timbers, and oak forests and savannas are being drastically reduced in Oklahoma (Bidwell et al. 1996). These changes may lead to large-scale changes in vertebrate faunas.

Increases in mesopredator populations, whether from mesopredator release (Palomares et al. 1995; Soulé et al. 1988) or increased landscape heterogeneity (Litvaitis and Villafuerte 1996; Oehler and Litvaitis 1996), can impact many aspects of an ecosystem (Estes 1996). Mesopredators can act as surrogate top predators and produce ripple effects in the plant and animal communities (Terborgh et al. 1999), such as by decreasing population densities of smaller vertebrate prey (Crooks and Soulé 1999) or indirectly causing important top-down

changes in vegetation structure and species diversity (Asquith et al. 1997). Mesopredator release has been implicated in driving some species to extinction (Courchamp et al. 1999), and there is mounting evidence of the phenomenon in several systems (Crooks and Soulé 1999; Goodrich and Buskirk 1995; Palomares et al. 1995; Rogers and Caro 1998; Sieving 1992; Soulé et al. 1988). We predict that, if increases in mesopredator abundance are real and continue, competitive relationships among these generalist species will become more evident.

ACKNOWLEDGMENTS

LITERATURE CITED

ANDREN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

ASQUITH, N. M., S. J. WRIGHT, AND M. J. CLAUSS. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology 78:941–946.

BEGON, M., J. L. HARPER, AND C. R. TOWNSEND. 1990. Ecology: individuals, populations, and communities. Blackwell Scientific Publications, Cambridge, Massachusetts.

BIDWELL, T. G., D. M. ENGLE, M. E. MOSELEY, AND R. E. MASTERS. 1996. Invasion of Oklahoma rangelands and forests by eastern redcedar and ashe juniper. Oklahoma State University Cooperative Extension Service Circular E- 947:1–4.

BONHAM, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, New York.

BOTHMA, J. DU-P., J. A. J. NEL, AND A. MACDONALD. 1984. Food niche separation between four sympatric Namib Desert carnivores. Journal of Zoology (London) 202:327–340.

BUSKIRK, S. W. 1999. Mesocarnivores of Yellowstone. Pp. 165–187 in Carnivores in ecosystems (T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, eds.). Yale University Press, London, United Kingdom.

BYERS, C. R., R. K. STEINHORST, AND P. R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization–availability data. Journal of Wildlife Management 48:1050–1053.

CONNELL, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pp. 460–490 in Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Harvard University Press, Cambridge, Massachusetts.

COURCHAMP, F., M. LANGLAIS, AND G. SUGIHARA. 1999. Cats protecting birds: modelling the mesopredator release effect. Journal of Animal Ecology 68:282–292.

CROOKS, K. R., AND M. E. SOULÉ. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

CYPHER, B. L. 1993. Food item use by three sympatric canids in southern Illinois. Transactions of the Illinois State Academy of Science 86:139–144.

CYPHER, B. L., AND K. A. SPENCER. 1998. Competitive interactions between coyotes and San Joaquin kit foxes. Journal of Mammalogy 79:204–214.

DIJAK, W. D., AND F. R. THOMPSON III. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. Journal of Wildlife Management 64:209–216.

ESTES, J. A. 1996. Predators and ecosystem management. Wildlife Society Bulletin 24:390–396.

EWING, A. L., J. F STRITZKE, AND J. D. KULBETH. 1984. Vegetation of the Cross Timbers Experimental Range, Payne County, Oklahoma. Research Report P-856, Agricultural Experiment Station, Oklahoma State University, Stillwater.

FEDRIANI, J. M., T. K. FULLER, R. M. SAUVAJOT, AND E. C. YORK. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

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

GABRIEL, K. R. 1971. The biplot display of matrices with application to principal component analysis. Biometrika 58:453–467.

GARDNER, A. L. 1982. Virginia opossum. Pp. 3–36 in Wild mammals of North America: biology, management, and economics (J. A Chapman and G. A. Feldhamer, eds.). John Hopkins University Press, Baltimore, Maryland.

GINGER, S. M. 2002. Effect of raccoon removal on

opossum habitat use at multiple scales in a fragmented Cross Timbers ecoregion. M.S. thesis, Oklahoma State University, Stillwater.

GIPSON, P. S., AND J. F. KAMLER. 2001. Survival and home ranges of opossums in northeastern Kansas. Southwestern Naturalist 46:178–182.

GOODRICH, J. M., AND S. W. BUSKIRK. 1995. Control of abundant native vertebrates for conservation of endangered species. Conservation Biology 9:1357–1364.

GUREVITCH, J., L. L. MORROW, A. WALLACE, AND J. S. WALSH. 1992. A meta-analysis of competition in field experiments. American Naturalist 140:539–572.

HAMILTON, W. J., JR. 1951. The food of the opossum in New York state. Journal of Wildlife Management 15:258–264.

HARESTAD, A. S., AND F. L. BUNNELL. 1979. Home-range and body weight—a reevaluation. Ecology 60: 389–402.

HENKE, S. E., AND F. C. BRYANT. 1999. Effects of coyote removal on the faunal community in western Texas. Journal of Wildlife Management 63:1066–1081.

HOLT, R. D. 1987. On the relationship between niche overlap and competition: the effect of incommensurable niche dimensions. Oikos 48:110–115.

KASPARIAN, M. A. 2002. Population characteristics of the Virginia opossum in the Cross Timbers Experimental Range during raccoon removal. M.S. thesis, Oklahoma State University, Stillwater.

KAUFMANN, J. 1982. Raccoons and allies. Pp. 567–585 in Wild mammals of North America: biology, management, and economics (J. A. Chapman and G. A. Feldhamer, eds.). John Hopkins University Press, Baltimore, Maryland.

KEDDY, P. A. 1989. Competition. Chapman & Hall, London, United Kingdom.

KISSELL, R. E., JR., AND M. L. KENNEDY. 1992. Ecological relationships of co-occurring populations of opossums (*Didelphis virginiana*) and raccoons (*Procyon lotor*) in Tennessee. Journal of Mammalogy 73: 808–813.

KORMONDY, E. J. 1996. Concepts of ecology. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

KREBS, C. J. 1999. Ecological methodology. 2nd ed. Addison-Wesley Educational Publishers, Menlo Park, California.

LADINE, T. A. 1995. Ecology of co-occurring populations of Virginia opossums (*Didelphis virginiana*) and raccoons (*Procyon lotor*). Ph.D. dissertation, University of Memphis, Memphis, Tennessee.

LADINE, T. A. 1997. Activity patterns of co-occurring populations of Virginia opossums (*Didelphis virginiana*) and raccoons (*Procyon lotor*). Mammalia 61: 345–354.

LAY, D. W. 1942. Ecology of the opossum in eastern Texas. Journal of Mammalogy 23:147–159.

LEGENDRE, P., AND L. LEGENDRE. 1998. Numerical ecology. 2nd ed. Elsevier Science B. V., Amsterdam, The Netherlands.

LEVESQUE, L. P. 2001. Effect of land-use manipulations on habitat associations and demography of mesocarnivores in the Cross Timbers ecoregion of Oklahoma. M.S. thesis, Oklahoma State University, Stillwater.

LITVAITIS, J. A. 1981. A comparison of coyote and bobcat food habits in the Wichita Mountains, Oklahoma. Proceedings of the Oklahoma Academy of Science 61:81–82.

LITVAITIS, J. A, AND D. J. HARRISON. 1989. Bobcat–coyote niche relationships during a period of coyote population increase. Canadian Journal of Zoology 67:1180–1188.

LITVAITIS, J. A., AND R. VILLAFUERTE. 1996. Intraguild predation, mesopredator release, and prey stability. Conservation Biology 10:676–677.

LÖFGREN, O. 1995. Niche expansion and increased maturation rate of *Clethrionomys glareolus* in the absence of competitors. Journal of Mammalogy 76: 1100–1112.

LOTZE, J.-H., AND S. ANDERSON. 1979. *Procyon lotor*. Mammalian Species 119:1–8.

MAJOR, J. T., AND J. A. SHERBURNE. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. Journal of Wildlife Management 51: 606–616.

MELLINK, E. 1991. Rodent communities associated with three traditional agroecosystems in the San Luis Potosi Plateau, Mexico. Agriculture, Ecosystems and Environment 33:363–375.

MOSILLO, M., E. J. HESKE, AND J. D. THOMPSON. 1999. Survival and movements of translocated raccoons in northcentral Illinois. Journal of Wildlife Management 63:278–286.

NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization–availability data. Journal of Wildlife Management 38:541–545.

NOVAK, M., J. A. BAKER, M. E. OBBARD, AND B. MALLOCH (EDS.). 1987. Wild furbearer management and conservation in North America. Ontario Trappers Association, Ontario, Canada.

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.

ØKLAND, R. H., K. RYDGREN, AND T. ØKLAND. 1999. Single-tree influence on understorey vegetation in a Norwegian boreal spruce forest. Oikos 87:488–498.

PALOMARES, F., P. GAONA, P. FERRERAS, AND M. DELIBES. 1995. Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. Conservation Biology 9:295–305.

PEDLAR, J. H., L. FAHRIG, AND H. G. MERRIAM. 1997. Raccoon habitat use at 2 spatial scales. Journal of Wildlife Management 61:102–112.

ROBINSON, D. H., AND H. WAINER. 2002. On the past and future of null hypothesis significance testing. Journal of Wildlife Management 66:263–271.

ROGERS, C. M., AND M. J. CARO. 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. Oecologia 116:227–233.

SAS INSTITUTE INC. 1990. SAS/STAT users guide, version 6. SAS Institute, Cary, North Carolina.

SCHOENER, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122:240–285.

SEIDENSTICKER, J., M. A. O'CONNELL, AND A. J. T.

JOHNSINGH. 1987. Virginia opossum. Pp. 246–261 in Wild furbearer management and conservation in North America (Novak, M., J. A. Baker, M. E. Obbard, and B. Malloch, eds.). Ontario Trappers Association, Ontario, Canada.

SHIRER, H. W., AND H. S. FITCH. 1970. Comparison from radiotracking of movements and denning habits of the raccoon, striped skunk, and opossum in northeastern Kansas. Journal of Mammalogy 51: 491–503.

SIEVING, K. E. 1992. Nest predation and differential insular extinction among selected forest birds of central Panama. Ecology 73:2310–2328.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. W. H. Freeman and Company, New York.

SOULÉ, M. E., D. T. BOLGER, A. C. ALBERTS, J. WRIGHT, M. SORICE, AND S. HILL. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75–92.

SPITZER, K., J. JAROŠ, J. HAVELKA, AND J. LEPŠ. 1997. Effects of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. Biological Conservation 80:9–15.

STIEGLITZ, W. O., AND W. D. KLIMSTRA. 1962. Dietary pattern of the Virginia opossum, *Didelphis virginianus* Kerr, late summer–winter, southern Illinois. Transactions of the Illinois Academy of Science 55: 198–208.

STRITZKE, J. F., D. M. ENGLE, AND F. T. MCCOLLUM. 1991. Vegetative management in the Cross Timbers: response of woody species to herbicides and burning. Weed Technology 5:400–405.

STUEWER, F. W. 1943. Raccoons: their habits and management in Michigan. Ecological Monographs 13: 203–257.

TERBORGH, J., ET AL. 1999. Pp. 30–64 in Continental conservation: scientific foundations of regional reserve networks (M. E. Soulé and J. Terborgh, eds.). Island Press, Washington, D.C.

TER BRAAK, C. J. F., AND P. ŠMILAUER. 1998. CANOCO for Windows, version 4.0. Centre for Biometry Wageningen, Wageningen, The Netherlands.

THEBERGE, J. B., AND C. H. R. WEDELES. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian Journal of Zoology 67:1285–1290.

VANDRUFF, L. W. 1971. The ecology of the raccoon and opossum, with emphasis on their role as waterfowl nest predators. Ph.D. dissertation, Cornell University, Ithaca, New York.

VERSCHUREN, D., J. TIBBY, K. SABBE, AND N. ROBERTS. 2000. Effects of depth, salinity, and substrate on the invertebrate community of a fluctuating tropical lake. Ecology 81:164–182.

VERTS, B. J. 1963. Movements and populations of opossums in a cultivated area. Journal of Wildlife Management 27:127–129.

WHITE, P. J., K. RALLS, AND C. A. VANDERBILT-WHITE. 1995. Overlap in habitat and food use between coyotes and San Joaquin kit foxes. Southwestern Naturalist 40:342–349.

WOOD, J. E. 1954. Food habits of furbearers in the upland post oak region of Texas. Journal of Mammalogy 35:406–414.

WRIGHT, G. A. 1977. Dispersal and survival of translocated raccoons in Kentucky. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 31:285–294.