EFFECT OF RACCOON REMOVAL ON OPOSSUM HABITAT USE AT MULTIPLE SCALES IN A FRAGMENTED CROSS TIMBERS ECOREGION

By

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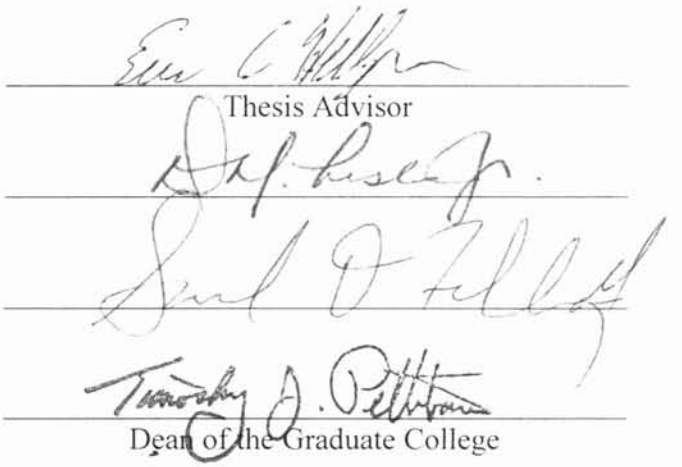

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Preface and Acknowledgments

The purpose of this study was to assess competition between raccoons and Virginia opossums on a fragmented area and to describe aspects of habitat niche for opossums with and without sympatric raccoons at multiple scales. Activity of the top predator in this system, the coyote, also is addressed.

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INTRODUCTION

Habitat manipulation alters composition and structure of animal communities, and the most important and large-scale cause of habitat manipulation is the expansion and intensification of human land use (Andren 1994). Concern over human alterations of landscapes on natural diversity has led to study of effects of these alterations on wildlife populations and communities. Increased interest in wildlife as an economic resource (Eltringham 1984) also warrants an evaluation of habitat management impacts on animal populations.

A widespread increase in mesocarnivore populations is one consequence of habitat manipulation and fragmentation. Mesocarnivores are medium-sized (1-15 kg) carnivores and omnivores. There are 2 opposing explanations for the cause of this increase. In 1 view, absence of top carnivore predators allows for direct expansion of smaller predator populations (Palomares et al. 1995). This phenomenon has been coined "mesopredator release" (Soulé et al. 1988). Conversely, increased heterogeneity due to habitat manipulation may favor generalist predators, such as raccoons (*Procyon lotor*) and foxes (*Vulpes* spp., *Urocyon* spp.), over larger, more specialized predators like lynx (*Felis lynx*) or gray wolf (*Canis lupus*) that need large continuous areas to survive. Vegetation management can increase foraging opportunities, efficiency, and ultimately, density of generalist predators (Litvaitis and Villafuerte 1996). In some cases, habitat differences may provide a stronger explanation to differences in predator densities than intraguild predation/mesopredator release. Nevertheless, increases in mesopredator populations can impact many aspects of an ecosystem (Estes 1996), from decreasing population densities of smaller vertebrate prey (Crooks and Soulé 1999) to indirectly

causing important top-down changes in vegetation structure and species diversity (Asquith et al. 1997). Indeed, smaller carnivores may cause greater problems for some rare species than larger carnivores (Goodrich and Buskirk 1995).

Although the mesopredator release hypothesis remains controversial (but with little critical evaluation; Litvaitis and Villafuerte 1996), mesopredator release has been implicated in the decline and extinction of prey species. Crooks and Soulé (1999) demonstrated that the decline and disappearance of the coyote (*Canis latrans*) in a landscape fragmented by development was associated with elevated numbers and activity of mesopredators (including opossum and raccoon), which in turn exerted strong predation pressure on native bird species. Mesopredator abundance (mostly raccoons) and predation on artificial bird nests were related positively in an experimental study in Michigan (Rogers and Caro 1998). Results from a natural experiment in the same area showed higher bird nest success in the presence than in the absence of the top carnivore, the coyote. In a lynx (*Felis pardina*)-mongoose (*Herpestes ichneumon*)-rabbit (*Oryctolagus cuniculus*) system in the Iberian Mediterranean ecosystem of southwestern Spain, Palomares et al. (1995) demonstrated that the absence of lynx resulted in decreased rabbit numbers due to increased mongoose numbers. Analysis of a mathematical model of a prey-mesopredator-superpredator system, with and without control of meso- and superpredators, showed that the mesopredator release process exists and can lead to prey extinction (Courchamp et al. 1999). Henke and Bryant (1999) found an increase in mammalian mesopredators and decrease in richness and diversity of rodent species within 9 months of removing coyotes in a short-grass prairie ecosystem in western Texas.

Numerous opportunities exist for interspecific relationships, most notably competition, among mesocarnivores that use similar habitats. Because many of these species are not strictly carnivores, capacity for sympatric use of habitats (Shirer and Fitch 1970) and foods increases. Such interactions generally 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. The role of competition in determining community structure has received much attention (Busch and Kravetz 1992), and interspecific competition has a prominent structural role in mesocarnivore communities, perhaps more so than in herbivore communities (Buskirk 1999). The greater the resource overlap, the greater the potential for interspecific competition (Schoener 1983). Habitat segregation generally is considered a major factor in allowing several species to coexist (Hairston et al. 1960; Keddy 1989; Löfgren 1995; Pianka 1981; Shoener 1974), although Schoener (1974) suggested that food, time, and habitat were 3 major niche dimensions along which potential competitors partitioned resources.

A removal experiment is an effective way to study competitive interactions, due to its controlled nature (Connell 1975). Such experiments answer questions about factors impacting species abundance and distribution. Furthermore, this type of experiment provides a means of measuring and testing hypotheses about niches and habitat selection (Keddy 1989). If a competing species is removed and habitat segregation depends on interspecific interactions, then the other species should demonstrate a competitive release characterized by a shift in habitat selection (Löfgren 1995).

Objectives and Hypotheses

My objective was to describe aspects of habitat niche for Virginia opossum (*Didelphis virginiana*) with and at a reduced density of sympatric raccoons (*Procyon lotor*) in the Cross Timbers ecoregion in Oklahoma at microhabitat (trap site) and macrohabitat (habitat patch and landscape) scales. I hypothesized that competition exists between raccoons and opossums. Under this hypothesis, two major habitat shifts are possible. I predicted that raccoon removal could result in either 1) a decrease in opossum niche breadth on raccoon removal pastures and decrease in niche overlap for control raccoons and removal-site opossums, or 2) an increase in opossum niche breadth on raccoon removal pastures and increase in niche overlap for control raccoons and removal-site opossums. If raccoons are excluding opossums from 1 preferable habitat by forcing them to select more general habitats, then number 1 should hold true. If raccoons are forcing opossums into specific, less desirable, habitats rather than more general and preferable habitats, then number 2 should hold true. Either way, a shift in habitat by opossums should occur. If neither prediction holds, then I will conclude that competition between raccoons and opossums is not occurring.

Literature Review

Opossum Biology

The Virginia opossum is the only member of the family Didelphidae found north of Mexico, and its range stretches from northwestern Costa Rica, through much of the United States, to southern Ontario and British Columbia, Canada (Gardner 1982,

Seidensticker et al. 1987). Virginia opossums grow throughout life; adults range in size from < 1 kg to 6 kg, depending on sex and time of year, with males usually larger and heavier than females (Seidensticker et al. 1987). The skull is characterized by a small braincase. Pelage and skin coloration vary from region to region, with northern populations having a gray appearance from thick white underfur with dark brown to black terminal ends, interspersed with mostly white and sometimes black-tipped guard hairs. The black phase is more common in southern populations (McManus 1974; Seidensticker et al. 1987).

The opossum is as far toward the *r*-end of the *r/K*-selection continuum as morphology and physiology allow among mammals (Seidensticker et al. 1987). Males have a permanently descended scrotum and a bifurcated penis with no baculum. The females have 2 uteri connected to a median vagina by 2 lateral vaginae, which receive sperm. Typically, there are 13 teats symmetrically arranged, with 1 in the center, in a well-developed, fur-lined marsupium (Gardner 1982; Gillette 1980; McManus 1974; Seidensticker et al. 1987). The marsupium may have evolved in response to selection pressures to allow females to forage with a "movable nest" (Seidensticker et al. 1987). The breeding season, defined as the period from first estrus to the time the last young-of-the-year are weaned (Reynolds 1945), usually begins in late December or early January in southern populations and extends through November. Gestation is among the shortest found in mammals, averaging 12.5–13 days (Nowak 1991), and young grow while attached to teats for 95–105 days before weaning. Mean litter sizes are 6.6–8.5 young that survive to weaning (Seidensticker et al. 1987). Females can have 2 litters in a season, with litter size determined by number of functional teats and number of young

reaching the pouch (Gardner 1982; Gillette 1980; McManus 1974; Seidensticker et al. 1987).

High mortality and rapid population turnover are characteristic of the Virginia opossum (Gardner 1982; Gehrt et al. 1997; Hunsaker 1977; VanDruff 1971). These characteristics make it a suitable model species to examine responses to manipulation of potential competitors. Because of their *r*-selected life history, they may respond rapidly to manipulation, if at all. Opossums typically live only 1 year post-weaning (Gardner 1982; Gehrt et al. 1997; Gillette 1980; Lay 1942; McManus 1974; Seidensticker et al. 1987). Weather, nutrition, and disease were the major causes of natural death suggested by Hunsaker (1977). Natural enemies include hawks, great horned owls *(Bubo virginianus*), domestic dogs (*Canis familiaris*), coyotes, red foxes (*Vulpes vulpes*), raccoons, bobcats (*Felis rufus*), and large snakes (Gardner 1982; Hunsaker 1977). Gardner (1982) reported greatest mortality occurring from human activities such as hunting, trapping, and roadkills.

Home Range and Population Dynamics of Opossums and Raccoons

Home range is the area frequented by a particular animal and where the animal spends most of its time (Feldhamer et al. 1999). It differs from a territory in that it may overlap with home ranges of others and is not defended. Home ranges within species vary according to factors such as sex, age, and food availability. Animals prefer landscapes that offer a high frequency of resource encounters that are necessary for survival. Within its home range, an individual will make finer-scale use of land based on factors such as food availability and competitive interactions (Pedlar et al. 1997).

Home ranges of opossum vary by sex, season, and habitat. Lay (1942) concluded that home-range size was 4.7–17.5 ha. Using an elliptical home-range model, Verts (1963) derived ranges of about 12.5 ha in Texas and 13.4 ha in Kansas. He also reported that home ranges were larger in cultivated areas than wooded areas, suggesting animals were compensating for possible resource shortages by increasing their movements. Shirer and Fitch (1970) reported an average circular home range of 120 ha in Kansas. Activity ranges reported by VanDruff (1971) ranged from 4 ha for a juvenile female to > 40.5 ha for a large adult male. Home ranges of 5–10 ha were reported by Seidensticker et al. (1987) in Virginia. Males had larger home ranges than females during nonwinter months, and both sexes reduced range size in winter months. Recently, mean home ranges of 114 ha for males and 57 ha for females were reported in Kansas (Gipson and Kamler 2001).

Kaufmann (1982) summarized home-range sizes of raccoons from previous studies and stated that most values ranged from 79 to 707 ha, with a maximum of 3,200 ha. Wild raccoons transplanted to unfamiliar territory showed no evidence of homing ability (Kaufmann 1982), although transplanted raccoons are known to disperse long distances before establishing new home ranges (Rosatte and MacInnes 1989; Tabatabai and Kennedy 1989; Wright 1977). Rural and urban raccoons translocated in Illinois showed high daily movement rates for 2 weeks postrelease before establishing new home ranges. Some dispersed distances >20 km, with most dispersing 3.8–9.1 km (Mosillo et al. 1999).

Density of mesocarnivores varies with habitat, and raccoons and opossums use a variety of habitats (Gardner 1982; Kaufmann 1982). Shirer and Fitch (1970) found that

opossums were more abundant in coniferous stands, and raccoons had greater population densities near water and in upland hardwoods. Highest densities of opossums occur in temperate woodlands with numerous streams, and lowest densities occur in cultivated habitats. Lay (1942) estimated 62.5 opossums/km^2 in a coastal pine-hardwood forest in eastern Texas. Verts (1963) estimated opossum density of 3.9 animals/km^2 in cultivated farmland in Illinois. The population in the Montezuma National Wildlife Refuge wetland in New York was estimated to be 14.3 opossums/km^2 (VanDruff 1971). In a Virginia forest mosaic, Stout and Sonenshine (1974) reported a density of 4.9 opossums/km^2. A density of 6.4 opossums/km^2 was reported in mixed upland and lowland habitats in western Tennessee (Leberg et al. 1983). Kissell and Kennedy (1992) found densities of 10.1 animals/km^2 at a site composed of 68% hardwoods and 2.2 animals/km^2 at a site composed of nearly 100% hardwoods in Tennessee. Gehrt et al. (1997) found densities of 1–7 opossums/km^2 in a predominantly mesquite- and chaparral-mixed grass habitat with riparian woodland patches. In central Oklahoma, densities were estimated at 3.9–12.8 opossums/km^2, with lower values in summer and higher values in spring (Levesque 2001).

Population dynamics of Virginia opossums follow a fairly predictable annual cycle. Lowest numbers are seen in the winter and early spring when only reproductive adults, mainly from the previous year's cohort, are present. Populations peak in autumn when second-litter young become independent (Gardner 1982; Seidensticker et al. 1987).

Typical raccoon densities are 5–20 animals/km^2 (Kaufmann 1982; Kissell and Kennedy 1992; VanDruff 1971), with higher nonurban densities reported in bottomlands and marshes (Kaufmann 1982). Urban (1970) reported a density of 17.4 raccoons/km^2 on

a managed waterfowl marsh in Ohio. The density in the Montezuma National Wildlife Refuge wetland was 8 raccoons/km^2 (VanDruff 1971). Kissell and Kennedy (1992) found densities of 1 raccoon/km^2 at a site composed of 68% hardwoods and 3 raccoons/km^2 at a site composed of nearly 100% hardwoods in Tennessee. Near Chicago, Illinois, densities were 36.6–72.6 raccoons/km^2 in urban areas and 8.1–14.6 raccoons/km^2 in rural areas (Hatten 2000). In central Oklahoma, raccoon densities were 8.6–15.3/km^2, with higher values in summer and lower values in spring (Levesque 2001).

Habitat Selection by Opossums and Raccoons

Most ecologists maintain that interspecific competition plays a significant role in population regulation, therefore directly affecting structure of biological communities (Kormondy 1996). The literature on interspecific interactions of opossums and raccoons is limited. The species cooccur throughout most of their geographic distribution and associated habitats, have similar food habits, and display similar resource use (Gardner 1982; Kaufmann 1982; Kissell and Kennedy 1992; Ladine 1995; Lotze and Anderson 1979; Shirer and Fitch 1970). Shirer and Fitch (1970) also reported that both species followed similar daily movements. Given these ecological similarities, it is surprising that studies focusing on the ecological relationships of these species have found only minor evidence of competition. Indeed, Kissell and Kennedy (1992) reported a positive but nonsignificant association between the species.

Opossums and raccoons prefer habitats that are associated with water, such as bottomland hardwoods and swamps (Kaufmann 1982; Kissell and Kennedy 1992; Sanderson 1987). Opossums use all habitats within their distribution, although lowest

numbers of opossums are found in residential, agricultural, and grassland habitats (Gardner 1982; Verts 1963). Stout and Sonenshine (1974) reported no evidence that opossum densities influenced habitat selection, although 75% of their captures were in forested vs. nonforested areas. Raccoons tend to have low densities in dry, upland woodlands, southern pine (*Pinus* spp.) forests, deserts, and high-mountain elevations, and they tend to avoid open terrain (Kaufmann 1982).

Concurrent use of habitats by these mesocarnivores may be attributed to dietary partitioning (Shirer and Fitch 1970; Wood 1954) or temporal partitioning of foraging (Ladine 1997). Many of the same foods are consumed by both species, but proportions vary between species and within species between regions (Gardner 1982; Kaufmann 1982; Sanderson 1987; Seidensticker et al. 1987; Stuewer 1943; Wood 1954). Virginia opossums are very opportunistic but are primarily insectivorous/omnivorous, feeding on arthropods, earthworms, mollusks, small vertebrates, and fruit (Seidensticker et al. 1987). Raccoons also are omnivorous and opportunistic, but in most habitats, plant foods are more important than animals in their diet. When animals are consumed, invertebrates are taken more than vertebrates (Kaufmann 1982).

Steuwer (1943) observed that high numbers of opossums did not tend to reduce the population of raccoons and no competition for den sites was observed. In fact, opossums were sometimes found sharing dens with raccoons (Steuwer 1943). Shirer and Fitch (1970) also found no apparent competition for dens. McKeever (1959) studied populations of opossums and raccoons in 6 vegetation types and demonstrated that abundance of both species was similar in all 6 habitats. Opossums preferred pine-hardwoods slightly more, whereas bottomland hardwoods were preferred more by

raccoons. Pine areas were selected least by both species.

Den site selection by opossums and raccoons has been thoroughly studied. For opossums, most dens tend to be located underground (Georgia—Allen 1985; Kansas—Fitch and Shirer 1970; New York—Hossler et al. 1994; Iowa—Wiseman and Hendrickson 1950). Raccoons use a variety of shelters for different purposes (e.g., seasonal resting sites, natal sites). Most commonly used are hollow tree dens, although ground dens and man-made shelters are also used, especially in areas where tree dens are scarce (summary—Kaufmann 1982; Illinois—Nixon et al. 2001; Michigan—Steuwer 1943).

Niche Breadth and Overlap

An ideal experiment to assess interspecific competition is to manipulate abundance of ≥1 of the species in question (Schoener 1983). Removals are manipulations that offer important opportunities to study the role of competition between species. Experiments of this kind have been performed most notably on rodent communities, examining responses in microhabitat selection (Löfgren 1995; Stroh and Fleharty 1988; Turner and Grant 1987), macrohabitat use (Scott and Dueser 1992), temporal activity patterns (Cameron et al. 1979; Mueller and Mueller 1979), demographics (Busch and Kravetz 1992; Cameron 1977), and movement (Cameron and Kincaid 1982). Removal experiments have been performed on other taxa; studies reviewed by Connell (1975) show habitat shifts after removal of 1 competitor in competing interspecific populations of ants, salamanders, and birds.

Removal experiments on guilds of larger species can explore effects of bottom-

up and top-down forces in structuring communities. For example, Henke and Bryant (1999) demonstrated that removal of coyotes, the top extant predator in a western Texas ecosystem, influenced faunal community structure by increasing relative abundance of microherbivores and mesocarnivores. Banks et al. (1998) demonstrated that removal of red fox in Australia caused large increases in densities of European rabbits, although subsequent fox reintroduction only suppressed rabbit populations at low densities (Banks 2000). However, removal studies addressing competition of sympatric mesocarnivores have not been reported previously. Field experiments of this nature are rare because it is difficult to change abundance of larger mammals that are highly mobile (Connell 1975). Studies on niche overlap among mammalian carnivores may shed some light on competitive interactions.

Among sympatric carnivores, patterns of interspecific competition have been identified. Prey species are partitioned by carnivore body size, and in regions where similarly sized carnivores coexist and resources are limited, temporal or spatial divisions of habitat, or prey specialization, may occur (Litvaitis and Harrison 1989). For example, niche relationships in sympatric populations of bobcats and coyotes were the topic of several studies in the 1980s. In Oklahoma, Litvaitis (1981) found evidence of diet partitioning. Coyotes consumed prey associated with savanna and prairie, whereas bobcats consumed prey common to woodlands. In an expanding coyote population in Maine, Litvaitis and Harrison (1989) found a negative correlation between relative abundance of the 2 species, which suggested a population response to exploitative competition but also suggested that coyotes would never completely displace bobcats due to the bobcat's superior ability to obtain prey in dense vegetation. Examination of

interspecific relationships of coyotes, bobcats, and red foxes in Maine showed no evidence of competition between bobcats and red foxes (Major and Sherburne 1987). Although coyote and bobcat use of food and habitat overlapped, no supporting data for interference competition were obtained, although interference competition between coyotes and red foxes was inferred from spatial segregation.

Several studies have inferred competition between coyotes and smaller canids. Cypher and Spencer (1998) found that exploitative and interference competition probably occurred between coyotes and San Joaquin kit foxes (*Vulpes macrotis mutica*), but some other feature, such as food availability, may have been the primary factor affecting fluctuations in abundance. They suggested that habitat partitioning resulting in spatial segregation reduced both exploitative and interference competition. This phenomenon also has been reported between coyotes and red foxes (Theberge and Wedeles 1989) and coyotes and gray foxes (*Urocyon cinareoargenteus*—Cypher 1993). In another study of coyotes and San Joaquin kit foxes, resource overlap contributed to competition for resources, but the authors suggested this was reduced by coyotes killing the smaller foxes (interference competition). Kit foxes, in turn, were able to coexist due to resource partitioning, year-round use of dens to avoid agonistic encounters, and high reproductive potential (White et al. 1995).

A study of 4 sympatric carnivores in the Namib Desert revealed that separation in diet, space, and activity times reduced competition and made coexistence possible, even in an area of unpredictable rainfall (Bothma et al. 1984). For example, the aardwolf (*Proteles cristatus*) and bat-eared fox (*Otocyon megalotis*) exclusively consumed insects but were separated by species preference. Cape foxes (*Vulpes chama*) and black-backed

jackals (*Canis mesomelas*) used a spectrum of food types but were separated temporally in the same area. In general, the 4 species were separated temporally but not spatially.

These niche-overlap studies suggest that resource partitioning allows sympatric coexistence. In areas where this is ineffective, such as in Maine where an expanding coyote population appeared to displace the red fox population (Major and Sherburne 1987), competition ultimately may have resulted in exclusion by the dominant species or both species coexisting at reduced densities. Competition may be stronger when interference is involved, such as with coyotes and kit foxes, as opposed to just resource overlap. Removal studies provide more compelling evidence than synecological studies for competition among sympatric species.

Study Area

The Cross Timbers ecoregion covers large parts of central Oklahoma and Texas (Fig. 1). 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, OK (36°02'40" to 36°04'20"N, 97°09'30" to 97°11'39"W), has been used since 1983 to study response of livestock, wildlife (Boren et al. 1993; Lochmiller et al. 1991; McMurry et al. 1993, 1994, 1996; Schultz et al. 1992ab; Soper et al. 1993) and vegetation (Engle et al. 1991; Stritkze et al. 1991) to various vegetation-management techniques. Climate is continental with an average frost-free growing period of 204 days from April to October. Mean annual temperature is 15°C and ranges from an average daily minimum of –4.3°C in January to an average daily maximum of 34°C in August.

Average annual precipitation is 831 mm (Myers 1982; National Oceanic and Atmospheric Administration 1999).

Upland forest habitats were dominated by post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), American elm (*Ulmus americana*), and eastern redcedar (*Juniperus virginiana* L.), in the overstory, interspersed with a mosaic of tallgrass prairie. Understory was composed of eastern redcedar, American elm, redbud (*Cercis canadensis*), and rough-leaf dogwood (*Cornus drummondii*). Herbaceous ground cover was dominated by little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), rosette panicgrass (*Panicum oligosanthes*), and western ragweed (*Ambrosia psilostachya*—Ewing et al. 1984).

European land-use of CTER started in the 1930s with homesteading and cultivation of crops such as cotton (Ewing et al. 1984). The CTER encompassed 712 ha divided into 22, 32.4-ha pastures, each measuring 400 m by 800 m. Beginning in 1983, 5 experimental conditions were applied to 4 randomly located replicate pastures to produce a mosaic of vegetation types (Table 1, Fig. 2). The treatments were tebuthiuron (*N*-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-*N,N'*-dimethylurea; Dow Elanco, Indianapolis, Indiana, USA) applied aerially at 2.2kg/ha in March 1983; tebuthiuron with late-spring prescribed fire (annually 1985-87, every 3 years 1990-present); triclopyr ([(3,5,6-trichloro-2-pyridinyl)oxy]acetic acid, Dow Elanco) applied aerially at 2.2kg/ha in June 1983; triclopyr with prescribed fire (annually 1985-87, every 3 years 1990-present) and 2,4-D and picloram; and control (no herbicides or burning). The triclopyr-alone treatment also had prescribed fire starting in 1996 on a 3-year cycle. Prescribed fires were conducted by the Oklahoma State University Research Range Fire Crew in late

March to early April using strip-headfires timed to coincide with initial green-up of warm season grasses and leaf expansion of oaks and buckbrush. Conditions during burns were about 18°C, wind speed >10 kph, and relative humidity between 30-50%. In 1985, burning was limited primarily to grassland sites due to fine fuel load. By 1986, some brush areas burned (mainly shallow savannah sites), and by 1987 about 25% of brush areas in the triclopyr-treated pastures and > 50% of brush areas in the tebuthiuron-treated pastures burned (D.M. Engle, pers. comm..).

Tebuthiuron, a soil-applied herbicide absorbed through the root system, resulted in die-off of the mature oak (*Quercus* spp.) forest and most of the other woody species except for eastern redcedar (Stritzke et al. 1991). Triclopyr is a foliar-applied herbicide absorbed through the leaf surface that caused die-off of mature overstory oak but not other woody species. When either herbicide is combined with a spring headfire regime, remaining woody species are reduced (Engle et al. 1991; Stritzke et al. 1991).

Treatments resulted in heterogeneous study pastures dominated by 4 major habitat types: eastern redcedar forest in tebuthiuron pastures, derived grassland in tebuthiuron-with-fire and triclopyr-with-fire pastures, a mixed-brush community in triclopyr-with-recent-fire pastures, and mature oak forest in untreated pastures (Table 1). Habitat types were classified based on vegetation composition in pastures observed in a 1998 aerial black-and-white photograph (scale 1:4,875) and extensive ground reconnaissance (Fig. 2, Levesque 2001). All experimental pastures were grazed by yearling cattle; stocking was adjusted annually to meet a goal of 50% use of annual forage production (Stritzke et al. 1991). No prescribed fires were conducted during the present study (Jan 2000-Jan 2001).

METHODS

Two 130-ha study areas, each composed of a block of 4 pastures corresponding to 4 different management prescriptions, were investigated. Study areas were blocked by soil types and cover prior to vegetation management. For final selection, the 4 pastures of each study area had to be connected and the 2 study areas had to be separated by at least on pasture. One block served as the control area, and the other block was the treatment, or raccoon-removal, area (Fig. 3).

Trapping

Animals were trapped using Tomahawk (Tomahawk Trap Company, Tomahawk, Wisconsin, USA) wire-mesh traps (25 x 30 x 81 cm) baited with canned sardines. Trapping was conducted bimonthly from January 2000 to January 2001. Removal pastures were trapped for 10 consecutive days, followed immediately by a 10-day trapping session on the control pastures. Trapping grids were set up in a grid of 8 traps/pasture (Fig. 4). Traps were located 100 m from the edges of pastures to diminish edge effects. Traps were located 300 m apart along parallel transects spaced at 200-m intervals, with 2 interior plots located 180 m diagonally from the corners. Eight additional traps were set in the buffer area surrounding the treatment pastures to reduce raccoon immigration from buffer pastures into removal pastures. Traps were monitored daily.

All captured opossums or raccoons were immobilized with Telazol (tiletamine

hydrochloride and zolazepam hydrochloride; Fort Dodge Animal Supply, Fort Dodge, Iowa, USA) at 8 mg/kg estimated body mass, ear-tagged with brass Ketchum Tambra tags (Nasco, Fort Atkinson, Wisconsin, USA), sexed, aged (adult, juvenile), and weighed with a spring scale (Chatillon Scale Company, New York, New York, USA). Raccoons captured in removal pastures were translocated >10 km from the study area across a 4-lane highway. Raccoons captured in the control area were released at the site of capture. Captured female opossums > 0.9 kg were fitted with radiocollars. Rectal temperature, heart rate, and respiration were monitored and recorded to ensure animal safety. If an animal had been captured previously during the current 10-day trapping session, it was released after species, ear-tag number, and location were recorded and status of the radio collar (if any) was checked. Nontarget species (e.g., gray fox and striped skunk [*Mephitis mephitis*]) were immobilized, marked, and released. Other non-target species (e.g., armadillos [*Dasypus novemcinctus*], box turtles [*Terrapene* spp.], woodrats [*Neotoma floridanus*], and others) were released without handling. Procedures for trapping and handling followed Institutional Animal Care and Use Committee protocol AS-50-719 at Oklahoma State University.

Radiotracking

Radiotracking began March 2000 and continued through May 2001. Diurnal den sites were located by homing in on the signal on foot with a portable receiver (model T4; Telonics, Mesa, Arizona, USA) and H-antenna. Den locations were recorded using a hand-held GPS unit. Data were later differentially corrected to <2 m accuracy (Pathfinder 2.10; Trimble Navigation Limited, Sunnyvale, California, USA). Den sites

were marked for future reference and described (e.g., den type, aspect, dimensions, etc.). Den type was classified as in the ground, in a tree, or underneath a standing tree at ground level. Dens also were described as being riparian (being <1 m from or located in a riparian feature) or non-riparian.

Nocturnal locations were established through triangulation using the same portable receiver and antenna. A set route (approximately 8 km) through CTER was driven and signals for all radiocollared animals were checked, mostly at defined telemetry stations. Route starting points and starting times varied. When a signal was detected, ≥ 2 bearings were taken for each radio-collared animal within a 20-minute time span. Triangulations for each animal were taken >28 hours apart and at all hours of the night. Typically, CTER was scanned 1-3 times weekly for signals, but often only once during trapping sessions. Bearings were converted into UTM locations using Locate II (Nams 1990).

To test telemetry's bias and error, 19 radiocollars were placed at various locations at varying times of the year for each researcher (myself and M. A. Kasparian). Collar locations were recorded using a GPS and differentially corrected for accuracy. At least 3 bearings were taken for each hidden collar. Bearings were loaded into Locate II and the UTM location of the 3 best bearings (based on angle, distance, signal strength [from field notes], and intersection) was recorded for each collar. These bearings were compared with the true bearings from each location, and the mean and *SD* degree of error was determined for each researcher. Mean distance between true and estimated collar locations also was determined for each researcher.

For each triangulation, if the error polygon generated in Locate II was greater

than 75% of the average patch size of the study pastures (> 3.8 ha), then that triangulation was not used in further analyses. Average patch size was determined by adding a 300-m buffer around all 8 study pastures, then averaging areas of generated inclusive patches using the Patch Analyst extension (Elkie et al. 1999) in ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA, USA). Small patches dominated CTER, so a conservation measure of 75% was used in analyses.

Vegetation Sampling

Vegetation sampling was conducted during winter 2000, summer 2000, and winter 2001. At each trap site, understory cover was sampled by Daubenmire cover classes (Bonham 1989) in a 1-m^2 plot at each trap site and in 1-m^2 plots 10 m from the trap site in northeast (45°), southeast (135°), southwest (225°), and northwest (315°) directions (Fig. 5). Data included percent cover of forb, grass, woody vegetation (≤0.5 m in height), bare ground, rock, hardwood leaf litter, moss, and miscellaneous litter (e.g., eastern redcedar duff, twigs). To sample overstory and midstory cover, 4 canopy cover and 4 visual obstruction measurements were taken and averaged from each 1-m^2 plot at each trap site using a densiometer (Bonham 1989) and 1-m board with alternating 0.1-m dark and light blocks, respectively. Tree condition (live, snag, standing stump) and diameter breast height (dbh) of stems ≥ 5 cm were measured and counts of coarse woody debris (≥ 10cm dbh) recorded in an 8.93-m-radius circular plot (0.025 ha) centered at the trap site (Fig. 5). Basal area (m^2/ha) was calculated for each group of tree species (eastern redcedar, oak, nonoak deciduous, and total) for each trap site. Terrain position code (lower, mid or upper slope) and aspect were recorded for each trap site.

Microhabitat variables were averaged for each trap site for each sampled season.

Microhabitat Analyses

I used constrained ordination method redundancy analysis (RDA) and partial principal components analysis (pPCA), an unconstrained ordination method, with CANOCO 4.0 (ter Braak and Šmilauer 1998) to evaluate opossum microhabitat selection at CTER. Due to different sampling measurements for the 31 variables, vegetation data were centered and standardized. I used both continuous and categorical variables (Table 2). Total opossum captures were calculated per trap site per month, with January and March sessions combined for winter 2000, May and July sessions combined for summer 2000, and November and January sessions combined for winter 2001.

I conducted an RDA to determine if the removal and control pastures had different microhabitat composition between removal and control pastures within seasons, which might allow for differential trap selection by opossums. In RDA, the ordination of species or response variables (i.e., microvegetation) is constrained so that the resulting ordination vectors are linear combinations of the environmental or explanatory variables (i.e., control vs removal—Legendre and Legendre 1998; Økland et al. 1999). Constrained ordinations correspond roughly to regressions; both response and explanatory variables can be multivariate (Spitzer et al. 1997). RDA can explicitly investigate and statistically test relationships between species and environmental variables (Verschuren et al. 2000). A distribution-free Monte Carlo permutation test (999 permutations) was used to provide significance values for the constrained axis.

Microhabitat data at trap sites with opossum captures in the control and removal

were arranged in a biplot for comparison using pPCA (Gabriel 1971). Seasons were covariables. The 4 most correlated vegetation variables as indicated by the variable scores for the first 2 principal components were chosen for significance testing in univariate analyses (see Mellink 1991 for similar methods). I compared microhabitat characteristics between successful and unsuccessful traps using a 3-way analysis of variance (ANOVA). The model incorporated season, treatment, and opossum presence/absence as main effects and all interactions (PROC MIXED; SAS Institute Inc. 1990).

Macrohabitat Analyses

A digitized black and white 1998 digital ortho-quarterquad was used in ArcView 3.2 for macrohabitat analyses. The 10 original habitat types delineated based on vegetation composition (Levesque 2001) were reduced to 4 major habitat types (plus a pond category) for analyses (Table 3, Figs. 2 and 6).

Trapping.—Individual trap sites were "georeferenced" using a hand-held GPS and overlaid on the habitat coverage to determine the habitat patch in which each trap was located. Habitat trap availability 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. Pretreatment data from identical trapping sessions conducted in 1998–1999 (Levesque 2001) also were used. 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 following Neu et al. (1974) and Byers et al. (1984) to determine which habitat types were used differently than their availability.

To investigate trap selection at a larger scale, 100-m buffers were created around each trap point in ArcView. Buffers of this size were chosen to investigate a larger scale around each trap site without areas overlapping. This buffered theme was subsequently intersected with the habitat theme for each trap site (Fig. 7) and then split into 64 separate themes, one for each buffered trap site. Using the Patch Analyst extension in ArcView, landscape metrics were generated for each buffered trap. Six landscape variables were used in the analysis: number of patches, patch-size coefficient of variance, total edge, mean shape index, mean patch fractal dimension, and Shannon's diversity index. Variables were chosen based on the high amount of landscape variation they explained (Ritters et al. 1995). Using a backwards stepwise regression in StatView 5.0.1 (SAS Institute Inc. 1998) and opossum captures as the dependent variable, a model was created for each treatment group (control and removal) pooled across seasons with corresponding significant landscape variables.

At the pasture level, landscape metrics were generated for each pasture and 5 landscape metrics (number of patches, patch size coefficient of variance, total edge, mean shape index, and mean patch fractal dimension) were used in a backwards stepwise regression in StatView with opossum captures as the dependent variable. A model indicating opossum preference of macro-landscape features was created with significant landscape variables.

The importance of permanent water sources also was investigated. The nearest distance from each trap point to a permanent water source (ponds or bottomland creeks visible on the habitat coverage) was calculated in ArcView. A regression between total opossum captures (across all seasons) at individual traps and distance of trap to water for removal and control areas was performed in StatView.

Telemetry.—I summarized number of telemetry locations and number of days tracked for each opossum (Appendix A). To determine if there were enough locations to perform home ranges, I ran a minimum convex polygon (MCP) bootstrap in ArcView using the Animal Movement extension (Hooge and Eichenlaub 1997) with 100 iterations and replacement. Two individuals (n = 54 and n = 20) were treated in this manner and both a 95% and 100% MCP were used. Graphs indicated that <15 locations would not accurately predict home-range size. Therefore, only those animals with >15 locations were used for home range analysis (n = 8). The Animal Movement extension was used to create 95% MCP home ranges for each individual female opossum.

I created a composite 95% MCP home range separately for the control and removal areas incorporating all telemetered locations of opossums because there were not enough locations per animal or enough animals to analyze habitat use differences between removal and control opossums using compositional analysis (Aebischer et al. 1993), in these areas. These 2 home ranges were intersected with the habitat map and spatially joined with the telemetered data in ArcView. The Patch Analyst extension in ArcView was used to determine habitat availability and to calculate spatial statistics on the composite ranges. A log-linear analysis (with selection, treatment, and habitat type as variables) and Bonferroni intervals were applied to the telemetry data to determine

differences in habitat selection between removal and control-site opossums at the home-range level.

Den use.—I used log-linear analyses to compare the number of dens (n = 77) in removal and control treatments by den type (ground, tree ground, tree), habitat patch (cedar, deciduous, grassland, mixed), vegetation treatment (control, tebuthiuron, tebuthiuron + fire, triclopyr + fire), and riparian location (riparian, nonriparian). Availability for habitat and vegetation treatment was determined in ArcView from a 100% MCP of all recorded opossum locations. For den type, availability was determined by dividing the total number of dens by three. Bonferonni intervals were used to determine selection where overall significance was obtained.

I used unpaired t-tests to compare removal and control areas for habitat patch area and perimeter around dens, and differences in distance of dens to nearest permanent water source, nearest fenceline, and nearest patch edge. Data were square-root transformed and an F-test performed to test for homogeneity of variances. A den selection model was created using the query builder and buffer tool in ArcView. The mean ± 1 *SD* for each of the 5 above variables were used to create a potential den selection model for CTER.

Overall habitat selection.—Nocturnal and diurnal opossum locations from radiotracking and trapping (n = 474) were combined to compare overall habitat use to availability by treatment using log-linear modeling. When overall significance was obtained, Bonferroni confidence intervals were calculated.

Niche Breadth and Overlap

I used all captures of opossums or raccoons and the associated habitat patch of the successful trap sites from 1999 (May, July, and October; preremoval—Levesque 2001) and 2000 (May, July, and November; postremoval) for niche calculation. Niche breadth in 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:

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

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 $\left(\sum a_i = 1.0 \right)$, and

n = total number of possible resource states.

I compared L for opossums on the control pastures 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 1-tailed

unpaired *t*-tests. I also compared *L* between opossums and raccoons on removal pastures 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, I calculated *L* for opossums caught postremoval and raccoons caught preremoval in the control pastures. To account for a treatment area effect, I calculated *L* for opossums and raccoons caught preremoval in the control and removal pastures.

RESULTS

Sampling effort equaled 5,010 trapnights. Ninety-eight opossums were captured 303 times (158 removal, 145 control), and 60 raccoons were captured 100 times (28 removal, 72 control), including buffer traps. Twenty-two raccoons were removed (3 were captured and removed twice). Capture rates of raccoons varied by month in both pastures ($F_{6,38.1} = 2.75$, $P = 0.03$), but rates were lower in removal pastures compared to control pastures ($F_{1,14} = 7.78$, $P = 0.02$, Fig. 8). Nontarget species captured included striped skunk (total captures = 36), box turtle (25), gray fox (15), armadillo (8), woodrat (8), cottontail (1—*Sylvilagus floridanus*) and roadrunner (1—*Geococcyx californianus*). No animals were adversely injured during capture or handling and no animals had to be resuscitated. Thirty-one female opossums were radiocollared (Appendix A).

Microhabitat

Redundancy analyses of microhabitat vegetation indicated a difference between removal and control areas for winter 2000 ($P = 0.02$), but no difference between areas for

summer 2000 ($P = 0.30$) or winter 2001 ($P = 0.19$). Therefore, winter 2000 data were not used in the pPCA because vegetation between control and removal pastures differed and because the removal was in an initial stage at that time. The first 4 principal components explained 47% of the variance in the microhabitat. The first axis, explaining 20.3% of the variance, represented a grassland to forest gradient, and the second, explaining 10.8% of the variance, a cedar forest to deciduous forest gradient (Fig. 9). Opossums in both the control and removal groups were most correlated with the first axis (0.23 control, 0.17 removal), followed by the second axis (-0.15, 0.15). A niche expansion toward cedar forest upon raccoon removal was indicated (Fig. 9). Removal site score standard deviations (Axis 1 = 1.08 *SD*, Axis 2 = 1.06) were larger for both axes than control site score standard deviations (Axis 1 = 0.91, Axis 2 = 0.94), further demonstrating a niche expansion. Of the 4 variables most correlated to the principal components in summer, % overhead density was lower at trap sites that captured opossums in the removal pastures ($P = 0.01$). Percent grass cover ($P = 0.06$) and number of cedar trees ($P = 0.08$) were higher in removal traps that captured opossums (Table 4). For the winter, microvegetation did not differ at successful traps between removal and control for any of the major microhabitat variables (Table 4).

Average cedar basal area ($F_{2,180} = 3.19$, $P = 0.04$) and number of nonoak deciduous trees ($F_{2,180} = 3.77$, $P = 0.03$) varied by the 3-way interaction of treatment, opossum presence/absence, and season. During the first winter, trap sites in the control without opossum captures had higher average cedar basal area (0.99 m^2/ha ± 0.19 *SD*) than in the summer (0.49 ± 0.12) or second winter (0.44 ± 0.14), but did not differ in the removal. In the second winter, trap sites without opossum captures in the control (7.30

trees ± 3.3 *SD*) had a greater number of deciduous nonoak trees than successful traps in the control (2.32 ± 0.87) or unsuccessful traps in the removal (1.38 ± 0.57), and a greater number of nonoak trees than unsuccessful traps in the control in summer 2000 (2.15 ± 1.41) or winter 2000 (2.75 ± 1.18). Differences between successful and unsuccessful traps for opossum captures, regardless of treatment or season, were reflected in several variables. Trap sites associated with opossum captures at CTER had the following relative to unsuccessful traps (Table 5): lower grass cover ($P = 0.001$), greater leaf litter cover ($P = 0.001$), greater overhead density ($P = 0.003$), more trees ($P = 0.02$), greater basal area ($P = 0.01$), greater number of oaks ($P = 0.01$), and higher oak basal area ($P = 0.03$). All of these variables are associated with cross timbers deciduous forest. When Bonferroni correction is applied (due to the relatedness of the variables), grass cover and leaf litter remain significant.

Macrohabitat

Trapping.—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 effect for either species, so years and locations were combined and analyzed for each species separately. For opossums, a significant interaction between use/availability and habitat type was found (P = 0.002), with deciduous forest preferred and grassland avoided after Bonferroni correction (Fig. 10a). For raccoons, this interaction approached significance (P = 0.061), with deciduous forest avoided after Bonferroni correction (Fig. 10b).

The stepwise regression of trap captures with the 6 landscape variables within

100-m of each trap site yielded a significant result for the removal treatment ($R^2 = 0.38$, $F_{31} = 8.94$, $P < 0.01$). The model was opossum captures = 4.22 + 0.004 (total edge) – 6.61 (Shannon's diversity index). In the removal area, opossums were more likely to be captured at traps that had higher edge and lower patch diversity. For the control area, patch-size coefficient of variance (PSCoV), which is a measure of the variability of patch sizes within the area of analysis, explained trap success ($R^2 = 0.13$, $F_{31} = 4.57$, $P = 0.04$). The model was opossum captures = 6.78 + -0.02 (PSCoV). As patch-size coefficient of variance increased, opossum captures decreased. According to these results, opossums used areas with lower variability in patch size in the presence of raccoons. This relationship, however, was weak with a low coefficient of determination.

The best multiple regression model for landscape metrics at the pasture level was opossum captures = 2.04 - 0.93 (number of patches) + 21.70 (mean shape index). The model was significant ($F_7 = 9.9$, $P = 0.02$) with high coefficient of determination ($R^2 = 0.80$). Opossums were caught more often in pastures with low numbers of patches that were complex in shape. Results from the regression of trap captures with nearest water source yielded no differences for control ($P = 0.38$) or removal ($P = 0.15$) sites.

Telemetry.—Thirty-one females were radiocollared from January 2000 to January 2001 (Appendix A), and 261 locations (114 diurnal and 147 nocturnal) were recorded from February 2000 to May 2001. The error of the telemetry system averaged 6.0° and 14.7° for the 2 investigators with an average distance of error of 47.2 and 77.9 m, respectively. Thirty-two nocturnal locations were removed from analysis due to large error polygons.

Home ranges for 8 female opossums used in these analyses ranged from 9.9 to

88.3 ha (27.4 ha ± 25.4 *SD*). Three home ranges were located in the removal area, and 5 were located mostly in the control area, with 1 female's home range nearly reaching a removal pasture (Fig. 11).

The 95% MCP for opossums in the removal area covered 188 ha using 106 telemetered locations, whereas the control opossums covered 170 ha using 112 telemetered locations (Fig. 12). There were no differences in habitat selection between control and removal areas ($P = 0.99$), so they were combined. A significant interaction between use/availability and habitat was found ($\chi^2_4 = 21.45$, $P < 0.001$), with deciduous forest preferred and grassland avoided after Bonferroni correction (Fig. 13).

Den use.—I located 77 dens, 7 of which were used twice (5 were used twice by the same animal and 2 by different animals). There were no interactions between treatment and den type ($P = 0.56$), habitat type ($P = 0.28$), vegetation treatment ($P = 0.11$), or riparian location ($P = 0.91$). The analyses were performed again with control and removal areas combined. An interaction between use/availability and den type ($P < 0.001$) indicated a preference for ground dens (Fig. 14a). An interaction between use/availability and habitat type ($P = 0.02$) indicated a preference for dens in deciduous forest and avoidance for dens in grassland (Fig. 14b). An interaction between use/availability and vegetation treatment was found ($P = 0.002$), but no preferences or avoidances were revealed after Bonferroni correction, although control pastures were used for den sites more than their availability (20.0% available, 33.3% used) and triclopyr + fire pastures (derived grassland) used less than their availability (46.7% available, 33.3% used).

Patch area ($P = 0.32$), patch perimeter ($P = 0.61$), distance to nearest water source

($P = 0.55$), distance to nearest fenceline ($P = 0.65$), and distance to nearest patch edge ($P = 0.60$) did not differ between den sites in removal and control areas. Distance to nearest fenceline had a significant variance difference, indicating that control den sites had higher variance in distance to fencelines. The 77 dens located by telemetry were overlaid on the den selection model to check the model's accuracy. The model fit 77% of the den sites, which were mostly located in deciduous and riparian areas (Fig. 15).

Overall habitat selection.—Opossums did not use habitat differentially by the control/removal treatment ($P = 0.20$), but used habitat nonrandomly across treatments ($P < 0.001$). Opossums preferred cedar forest, deciduous forest, and mixed forest, and avoided grasslands (Fig. 16).

Niche Breadth and Overlap

Both species, regardless of treatment, had large niche breadths (Table 6), but niche overlap varied. The difference in overlap between opossums captured in removal sites postremoval vs. preremoval (L = 1.04) and for control opossums in control sites for the same time periods ($L = 1.07$) approached significance ($t_{190} = 1.37$, $P = 0.086$). This result suggested that habitat use by opossum on removal sites shifted postremoval. Overlap of opossums and raccoons caught in removal sites preremoval was 1.07 and overlap of opossums caught postremoval with raccoons caught preremoval was 1.14 ($t_{109} = 0.52$, $P = 0.30$). In the control sites, overlap of opossums caught postremoval and raccoons caught preremoval was 0.91 (whereas it was 1.14 in removal areas for the same time periods), indicating fewer shared resources between the 2 species occurring in sympatry from 1 year to the next compared to the species occurring in allopatry after

removal (t_{167} = -1.61, P = 0.06). To control for area effects, overlap of opossums and raccoons caught preremoval in removal sites was not higher (L = 1.07, t_{89} = -0.84, P = 0.20) than overlap in control sites for the same time period (L = 0.92).

Discussion

Buskirk (1999) summarized characteristics and importance of mesocarnivores: 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. Some inflict harm on human economies and some are collected for fur, and in many places worldwide, these carnivores are the largest, most wilderness-dependent and ecologically important Carnivora that remain in anthropogenically disturbed landscapes. High densities of mesocarnivores and their subsequent top-down effects are 1 argument for restoring large carnivores to some regions (Noss 2001).

Major factors that structure mesocarnivore communities are food abundance, habitat structure, interference competition, and humans, especially via trapping and habitat manipulation (Buskirk 1999). Habitat structure and interspecific competition work together to interactively shape mesocarnivoran communities by meeting life requisites and mediating trophic and competitive relations.

Microhabitat

I demonstrated a shift in microhabitat selection on the basis of trap-site characteristics selected by opossums in reduced densities of its suspected competitor, the raccoon. Animals prefer landscapes that offer a greater chance of encountering resources that are necessary for survival. Within its home range at the landscape level, the animal makes 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 overlap at larger scales. The CTER study site was highly fragmented relative to the home range of opossums and may therefore allow such fine-scale selection of habitat.

Results from microhabitat analyses suggested that opossums and raccoons competed for resources at the microhabitat scale. In the control pastures, where raccoons and opossums cooccurred, opossums were captured in sites characteristic of deciduous forests of the Cross Timbers ecoregion. In areas of reduced densities of raccoons, however, opossums were more likely to select trap sites with characteristics associated with eastern redcedar forest. Levesque (2001) found that oak basal area (2.15 m^2/ha ± 0.42 *SE*) and nonoak basal area (0.65 ± 0.19) were higher at trap sites that captured opossums whereas cedar basal area was not different between successful and unsuccessful trap sites. Few microhabitat variables were associated with raccoon trap success, although a negative association of raccoons with average cedar basal area was noted. Additional studies of opossum habitat selection at a microhabitat scale have not been reported.

I speculate that reduced densities of the competitor caused a niche expansion, if

not a shift, to different type of habitat. The larger *SD* of removal axes supports this. Although the particular resource of interest (e.g., food or cover) causing this shift is unknown and additional studies focusing on aspects of fine-scale resource use should be addressed, Kasparian (2002) showed that eastern redcedar berries are consumed by opossums.

Macrohabitat

Analyses at scales greater than the trap-site level did not reveal effects of raccoon-removal on opossum habitat selection. However, differential habitat selection was revealed between species when treatments were combined. My data were fairly consistent with 1998–1999 CTER trapping data that showed opossums preferring oak and bottomland areas in the spring and raccoons using all habitats in accordance with availability (Levesque 2001). At the scale of 100-m, raccoon-removal effects were not clear, but less diverse patch types and sizes may be a potential factor in selection. At the pasture level, opossums were caught more often in pastures with fewer but more complex patches, regardless of treatment, which could not be tested due to small sample sizes. These results inferred an opossum need for a heterogeneous, but not overly patchy, landscape.

Opossums and raccoons are known to prefer areas associated with water (Kaufmann 1982; Kissell and Kennedy 1992; Sanderson 1987), however, I did not find distance to water and trap success to be related in either the control or removal pastures. If the two species were competing at this scale, I would expect the removal of the raccoon competitor to cause a shift towards water areas by opossum.

I conclude that den-site selection was not affected by removal of raccoons. Although female opossums rely heavily on den sites for their own survival, especially during winter, and survival of their young, I did not observe a shift in den-site selection upon removal of the potential competitor. Opossums in this Cross Timbers system selected ground dens in deciduous areas near permanent water and avoided selecting dens in open, grassland areas. Other studies also have found ground dens were used most often (Allen 1985; Fitch and Shirer 1970; Hossler et al. 1994; Wiseman and Hendrickson 1950), perhaps mainly due to greater availability.

Telemetry data revealed similar patterns of opossum habitat use as trapping data. Due to small sample size, home ranges could not be compared between opossums in removal and control areas. The large ranges generated by all telemetered points in each area also did not reveal removal differences. Combined, however, opossums selected deciduous forest and avoided grasslands. Overall habitat selection using all possible opossum locations also showed no selection due to treatment, but a general selection for all forested types and an avoidance of open, grassland areas.

These results indicate that scale may be relevant. Raccoons and opossums differentially selected habitat at a macrohabitat scale, perhaps due to differences in life-history traits. For example, raccoons are larger in body mass and home range. Due to the small patch sizes on CTER (3.5 ha ± 12.6 *SD*) and a large ranging behavior (average maximum 79–707 ha—Kaufmann 1982), raccoons may have an increased chance of encountering and being captured in more habitat types than opossums, whose home ranges are smaller (4.7–40.5 ha in wooded areas—Lay 1942; VanDruff 1971; 9.9–88.3 ha on CTER). Levesque (2001) reported that raccoons on CTER were distributed evenly

across habitats, whereas opossums were more prevalent in mixed-brush and oak forest habitats. Life history characteristics such as mentioned above may allow for this differential selection of habitat.

Niche Breadth and Overlap – Assessment of Competition

Niche breadths were very large in the present study (>0.95) and did not change with raccoon removal. However, when raccoons were removed, niche overlap for opossums in raccoon-removal pastures between pre- and postremoval periods decreased relative to opossums in control pastures. Overlap in habitat use between raccoons and opossums increased upon raccoon removal compared with lack of a similar change in the control areas. These changes in overlap likely reflect 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 should be interpreted with caution.

Removal studies provide more compelling evidence than synecological studies for competition among sympatric species but are lacking for mid- to large-sized mammals. Removals and resulting niche changes have been studied in rodents (Löfgren 1995) and nonmammalian taxa (Connell 1975, Paine 1969, 1974). Henke and Bryant (1999) removed a top predator, the coyote, in western Texas, and studied subsequent effects on the faunal community but did not look directly at competition. Most studies of carnivore synecology have identified potential patterns in interspecific competition, such as those found with coyotes and bobcats (Litvaitis 1981; Litvaitis and Harrison 1989; Major and Sherburne 1987), coyotes and several species of foxes (Cypher 1993; Cypher

and Spencer 1998; Theberge and Wedeles 1989; White et al. 1995), and sympatric desert carnivores (Bothma et al. 1984). Patterns identified included prey partitioning, both spatially (Litvaitis 1981) and temporally (Bothma et al. 1984), negative correlations with relative abundance (Litvaitis and Harrison 1989), and interference competition (White et al. 1995).

The niche shift by opossums and change in niche overlap between raccoons and opossums supported my competitive hypothesis, at least on a fine scale in this fragmented cross timbers area. Increasingly, wildlife studies investigate species-habitat relationships 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 the study species responded to local and landscape features. In this study, it appeared that opossums operated at a finer scale than raccoons.

Studies explicitly examining opossum habitat use at multiple scales have not been previously reported. However, raccoon and opossum relative abundances were examined at 2 spatial scales in Missouri by Dijak and Thompson (2000). Landscape and local scales were investigated to determine predator abundance. At a landscape scale (using scent station data), opossum abundance was related to latitude (associated with croplands), more heterogeneous landscapes, and high densities of riparian areas. My data also indicated a preference for complex-shaped patches at a macrohabitat scale and riparian areas for den sites (Fig. 15). 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 (using sooted-plate scent stations), opossum

abundance showed no consistent relationship to edge, whereas raccoons were more abundant in forest-agriculture and forest-riparian edges. The authors concluded that local features (such as distance to edge) and large-scale factors (such as landscape patterns in land use) may affect predator abundance and potentially affect songbird-nest predation rates.

Raccoon habitat use at 2 spatial scales was studied in rural areas of eastern Ontario by Pedlar et al. (1997). Activity was measured using tracking plates; landscape (1-km radius at each site) and local (10-m radius around each station) features were sampled. At a landscape scale, raccoons frequented areas with extensive agricultural edge and wooded remnants in areas with extensive corn cover. At a local scale, raccoons frequented areas associated with fencerows, den trees, and deciduous stands. Many of the patterns detected at the local scale were reflected at the landscape scale in this study, and the authors noted that microhabitat variables provided insight into the mechanism behind landscape patterns of raccoon activity.

Ecological relationships of these raccoons and opossums were studied recently in Tennessee by Kissell and Kennedy (1992) and Ladine (1995). They had different conclusions regarding habitat and spatial scale. Kissell and Kennedy (1992) studied the animals at 2 different sites, 1 heterogeneous and 1 homogeneous, and discovered a low, positive association between opossums and raccoons. At the heterogeneous site, raccoons used fewer habitats than opossum, suggesting that perhaps opossums were more generalist than raccoons. At the homogeneous site, both species used nearly equal amounts of available habitat. However, results suggested little spatial association between species because coefficients of association were not significant. The authors

suggested that habitat preferences by each species were independent of the occurrence of the other species.

Ladine (1995), in a long term study, 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. Cooccurrence of taxa appeared to be related to factors that resulted in reduced interactions of the species, including social behavior, food selection, habitat use, foraging patterns, and interspecific competition. For example, opossums and raccoons used available habitat during different time periods (based on time at capture), thus partitioning temporally availability of habitat and reducing interspecific competition (Ladine 1997). Coefficients of association differed at the micro- and macrohabitat scales, with a mean negative association of species at the smaller scale and a mean positive association at the larger scale. Results at both scales varied highly temporally. Interspecific interactions (inferences towards competition) were reflected most accurately from frequency of capture and vegetation data collected at the microhabitat scale, whereas association of species (presence-absence of individuals within a habitat) was reflected most accurately at the macrohabitat scale (Ladine 1995). My findings were consistent with those of Ladine (1995) by showing an opossum niche shift at the microhabitat level (Fig. 9).

Competition between raccoons and opossums at a microhabitat scale may be occurring on CTER as a result of mesopredator release and increased densities, given the high degree of habitat fragmentation, a reduced number of predators (e.g., coyotes [Appendix B], bobcats), and decreased overall harvest of this guild over the last 75 years (Novak et al. 1987). Given a longer study time and increased replication, these results

would be potentially more robust. 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). The present study area was anthropogenically manipulated but likely represents how the landscape is currently changing in the region.

Mesopredators act as surrogate top predators and the result is modified niche exploitation, altered diversity, and other ripple effects in the community (Terborgh et al. 1999). 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). Indeed, the problem of mammalian overabundance in areas of North America that are predator-free was the topic of a major symposium hosted by the Smithsonian Institution (McShea et al. 1997). In midwestern landscapes alone, predation of artificial nests is dominated by mammalian carnivores, 38% of which is from opossums and raccoons (Donovan et al. 1997). On CTER, studies by Schulz et al. (1992a, 1992b) showed that although total density and species diversity did not vary for breeding birds, overall avian assemblages varied among the derived habitats. Further studies should be conducted to address effects of mesocarnivores on other animal populations, especially potential prey such as birds, in the Cross Timbers ecoregion.

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

TABLE 1. --Timing of treatment regimes with resulting current major vegetation types at Cross Timbers Experimental Range, Payne County, Oklahoma (D. M. Engle, pers. comm.).

Treat-ment number	Herbicide	Broadcast burn	Individual tree burns	Mechanical treatment	Grazed treatment	Dominant vegetation type
1	Tebuthiuron 1983	None	None	None	SLS[a] 83-94; Beginning in 95 1/2 reps IES[b] and 1/2 reps SLS	Cedar Forest
2	Tebuthiuron 1983; P+D[c] 1997	1985-1987, 1990, 1993, 1996, 1999	1990, 1993, 1996	None	SLS 83-94; Beginning in 95 1/2 reps IES and 1/2 reps SLS	Derived Grassland
3	Triclopyr 1983; 2,4-D 1988; P+D[a] 1994	1993, 1996, 1999	1996	Bulldoze and windrow cedar pre-burn 1996; saw cedar post-burn 1996	SLS 83-91, Rest 92, SLS 93-94; Beginning in 95 1/2 reps IES and 1/2 reps SLS	Mixed-brush Community
4	Triclopyr 1983 2,4-D 1988	1985-1987, 1990, 1993, 1996, 1999	1990, 1993, 1996	None	SLS 83-91, Rest 92, SLS 93-94; Beginning in 95 1/2 reps IES and 1/2 reps SLS	Derived Grassland
5	None	None	None	None	SLS 83-94; Beginning in 95 1/2 reps IES and 1/2 reps SLS	Mature Oak Forest

[a] season-long stocking
[b] intensive-early stocking
[c] mixture of picloram and 2,4-D

TABLE 2.— Abbreviations and original units of measure for 31 microhabitat vegetation variables collected at mesocarnivore trapsites, Cross Timbers Experimental Range, Payne County, Oklahoma, 2000-2001. Percent cover, visual obstruction, and density of canopy cover measurements were averaged for each trap site.

Microhabitat Vegetation Variable	Abbreviation	Unit of Measure
% Grass cover	GRASS	%
% Herbaceous vegetation cover	FORB	%
% Woody vegetation cover (≤5 m height)	WOODY	%
% Moss cover	MOSS	%
% Bare ground cover	BARE	%
% Hardwood leaf litter	LEAF	%
% Rock cover	ROCK	%
% Miscellaneous litter (cedar litter, twigs, etc.)	LTTR	%
Visual obstruction (≤10 m height)	VISOB	%
Density of canopy cover	DENS	%
Coarse woody debris (≥10 cm dbh)	CWD	Count
Terrain position code	US, MS, LS	US = upper slopes, MS= mid-slopes, LS = lower slopes (categorical)
Aspect of slope of terrain	NONE, N, NW, W, SW, S, SE, E, NE	Cardinal direction (categorical)
Total basal area of eastern redcedar, oak, deciduous nonoak, and total trees present (≥5 cm dbh)	CEDARBA, OAKBA, NOAKBA, TOTBA	Site basal area (m^2/ha)
Tree count for eastern redcedar, oak, deciduous nonoak, and total trees present (≥5 cm dbh)	CEDARCT, OAKCT, NOAKCT, TOTCT	Site count

TABLE 3.--Criteria and description of original 10 and final 5 habitat delineations for digitized digital ortho-quarter quad of the Cross Timbers Experimental Range, Payne County, Oklahoma.

Original Habitat Classification[a]	% Cover Grassland	% Cover Oak Forest	% Cover Eastern Redcedar Forest	% Cover Non-Oak Forest	Final Habitat Classification	% Availability on CTER
Grassland	>75.0	<10.0	<10.0	<10.0	Grassland	35.5%
Grassland-Cedar	>50.0	<10.0	<50.0	<10.0	Grassland	
Cedar-Grassland	<50.0	<10.0	<50.0	<10.0	Cedar Forest	15.0%
Cedar Forest	<10.0	<10.0	>75.0	<10.0	Cedar Forest	
Oak Forest	<10.0	>75.0	<10.0	<10.0	Deciduous Forest	41.2%
Non-Oak Forest	<10.0	<10.0	<10.0	>75.0	Deciduous Forest	
Cedar-Oak Forest	<10.0	25.0-75.0	25.0-75.0	<10.0	Mixed Forest	8.0%
Cedar-Non-Oak	<10.0	<10.0	25.0-75.0	25.0-75.0	Mixed Forest	
Bottomland	Riparian Areas				Mixed Forest	
Pond	Ponds				Pond	0.3%

[a] Levesque 2001

TABLE 4.—Microhabitat vegetation characteristics of trap sites where opossums were captured in control or raccoon-removal areas by season on Cross Timbers Experimental Range, Payne County, Oklahoma, 2000-2001. Significant ($P < 0.05$) and marginally significant ($0.05 < P < 0.10$) values from 1-tailed t-tests are indicated by ** and *, respectively.

		Summer (May-Jul)			Winter (Nov-Jan)	
		Control		Removal	Control	Removal
Axis	Variable	$\bar{x}$ *SD*		$\bar{x}$ *SD*	$\bar{x}$ *SD*	$\bar{x}$ *SD*
1						
	% Grass	24.3 20.4	*	37.4 32.0	26.5 9.4	27.3 30.9
	% Density	79.3 22.7	**	55.8 37.7	66.9 26.0	55.7 35.9
	Total tree count (n)	19.1 10.6		17.6 12.6	17.2 11.1	18.9 13.8
	Basal area – all trees (m^2/ha)	11.5 5.5		10.6 8.4	11.0 5.8	12.1 9.5
2						
	% Other litter	26.0 17.6		25.6 21.9	24.5 15.0	20.2 19.0
	Oak count (n)	6.5 9.2		4.5 7.5	5.1 8.8	6.8 11.3
	Cedar count (n)	7.9 7.5	*	11.5 9.4	9.7 8.8	9.4 8.1
	Basal area – cedar (m^2/ha)	5.7 4.8		7.2 6.3	6.6 4.9	7.1 7.5

TABLE 5.— Microhabitat differences ($P < 0.03$) between successful and unsuccessful traps, Cross Timbers Experimental Range, Payne County, Oklahoma, 2000-2001.

	Successful Traps		Unsuccessful Traps	
Variable	$\bar{x}$	*SD*	$\bar{x}$	*SD*
% Grass	29.3	28.4	45.4	29.8
% Leaf litter	34.6	32.3	21.6	27.0
% Overhead density	62.3	31.6	45.5	31.9
Number of trees	18.8	12.0	15.2	11.8
Basal area	11.1	7.2	8.1	6.7
Number of oaks	6.0	9.3	3.1	6.2
Oak basal area	3.8	6.6	2.2	5.0

TABLE 6.— Smith's measure (Krebs 1999) of niche breadths of opossums and raccoons based on trapping data preremoval (1999) and postremoval (2000) at Cross Timbers Experimental Range, Payne County, Oklahoma.

	Control		Removal	
Treatment	Raccoon	Opossum	Raccoon	Opossum
Preremoval	0.953	0.987	0.949	0.997
Postremoval	0.974	0.983		0.981

FIG. 1. Potential natural distribution of the Cross Timbers forest type (7,909,700 ha). An estimated 129,500 ha remain (Küchler 1964).

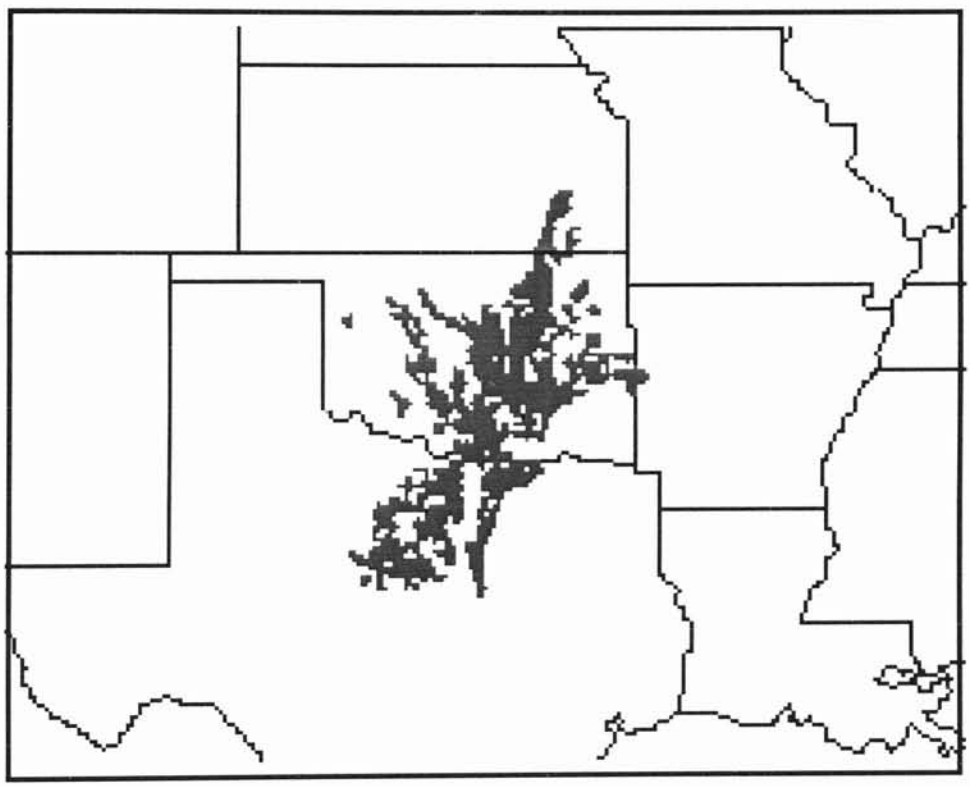


FIG. 2. Mosaic of vegetation types on Cross Timbers Experimental Range, Payne County, Oklahoma, produced by herbicide, burning, and grazing vegetation management. Pastures with an "R" and "C" are the removal and control sites used for this study.

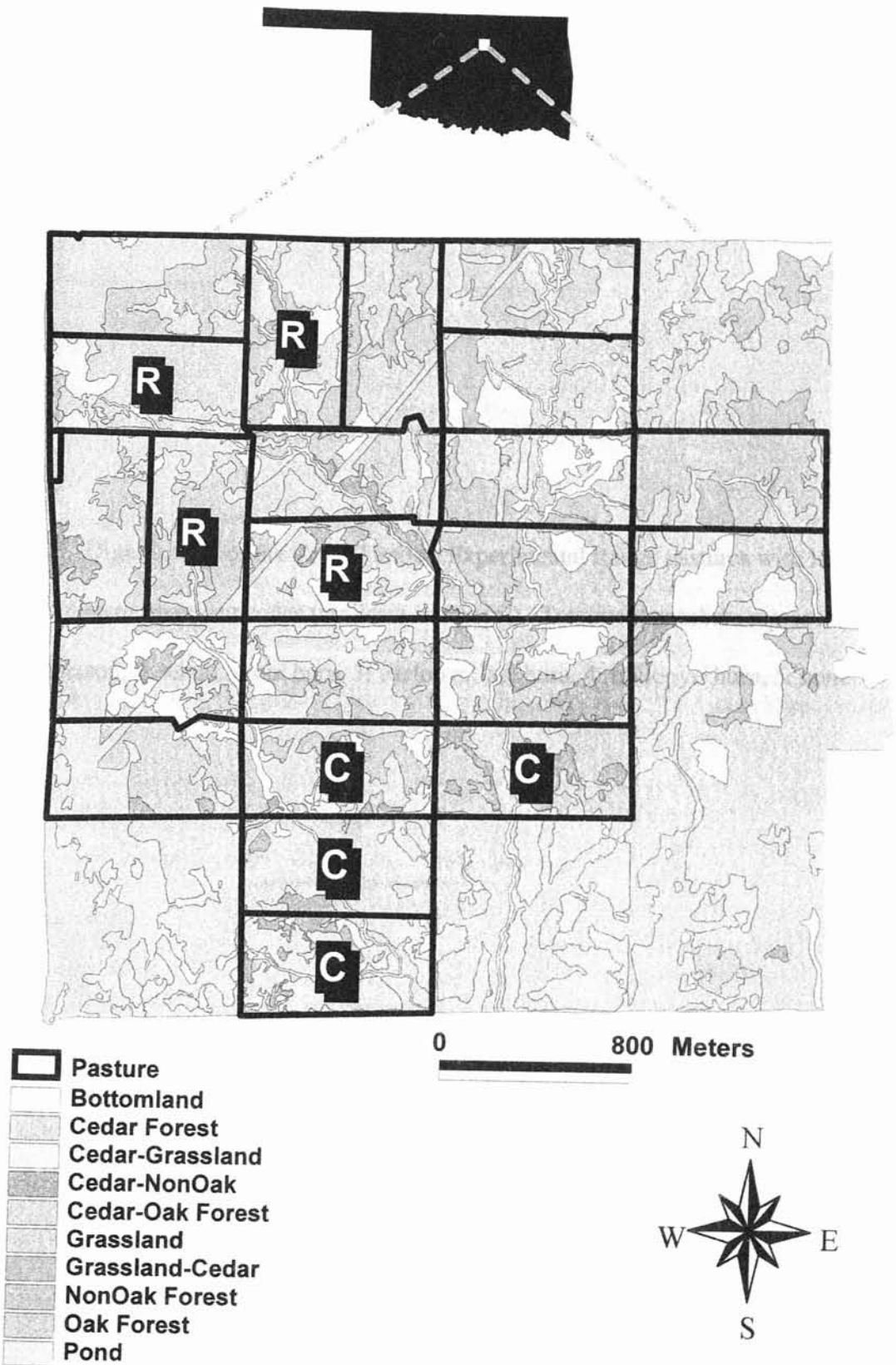
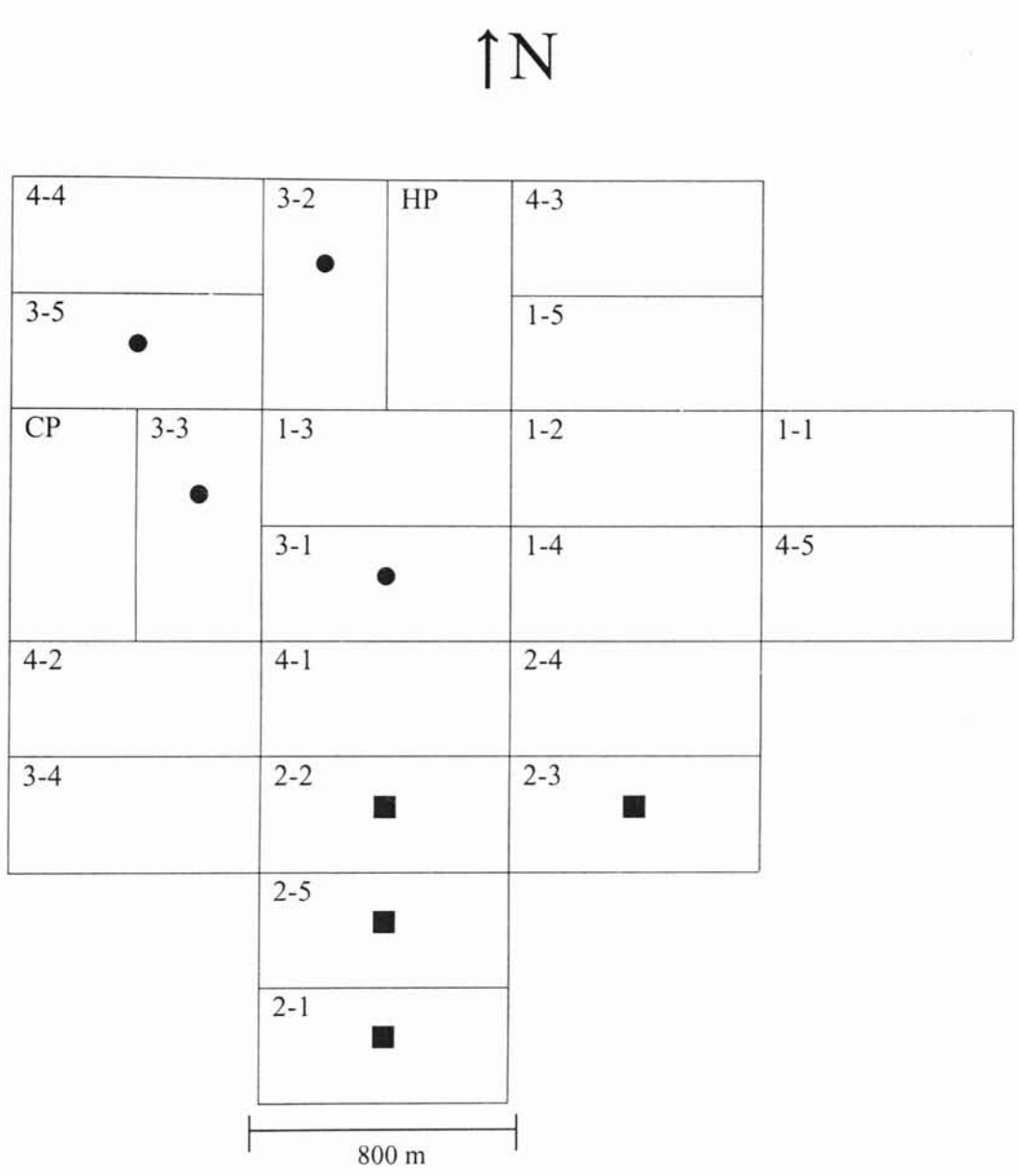

R
R
R
R
C
C
C
C
0
800 Meters
Pasture
Bottomland
Cedar Forest
Cedar-Grassland
Cedar-NonOak
Cedar-Oak Forest
Grassland
Grassland-Cedar
NonOak Forest
Oak Forest
Pond
N
W
E
S

FIG. 3. Organization of the Cross Timbers Experimental Range pastures with land management treatment codes (replicate-treatment). Treatment numbers represent: 1: tebuthiuron, 2: tebuthiuron/ burn, 3: triclopyr/ late burn, 4: triclopyr/ burn, 5: none.



CP = Corral Pasture
HP = Holding Pasture
● = raccoon-removal pastures
■ = control pastures
2-1 = replicate – treatment (1 = triclopyr, 2 = tebuthiuron + fire, 3 = triclopyr + late fire, 4 = triclopyr + fire, 5 = control)

FIG. 4. Example of grid layout for mesocarnivore trapping in each pasture in control and raccoon-removal areas on Cross Timbers Experimental Range, Payne County, Oklahoma.

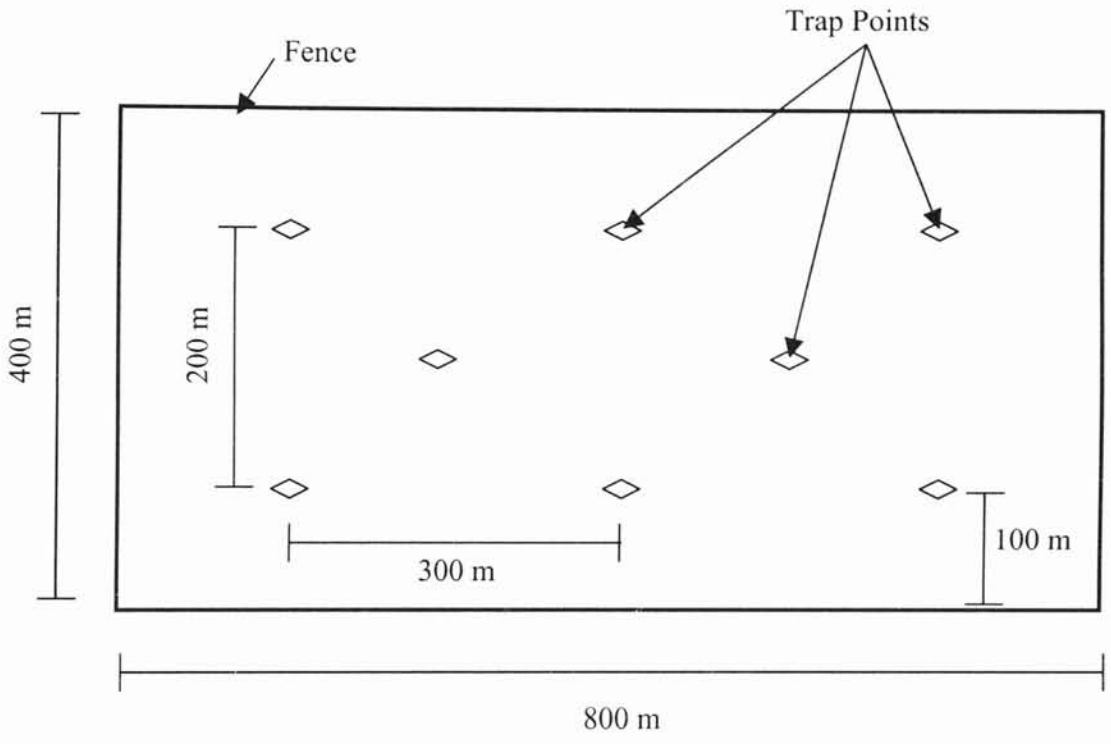

Trap Points
Fence
400 m
200 m
300 m
100 m
800 m

FIG. 5. Example of microvegetation sampling layout around trap sites on Cross Timbers Experimental Range, Payne County, Oklahoma.

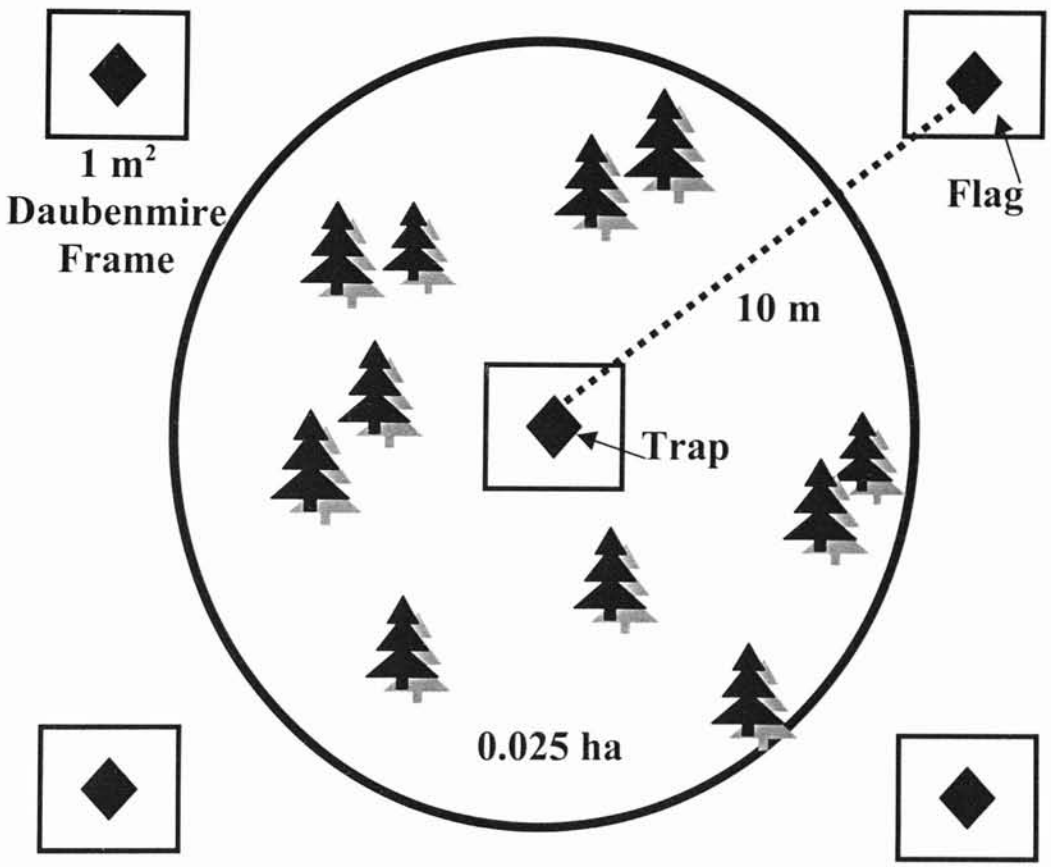

1 m²
Daubenmire
Frame
Flag
10 m
Trap
0.025 ha

FIG. 6. Map of Cross Timbers Experimental Range, Payne County, Oklahoma, with 4 major habitat types.

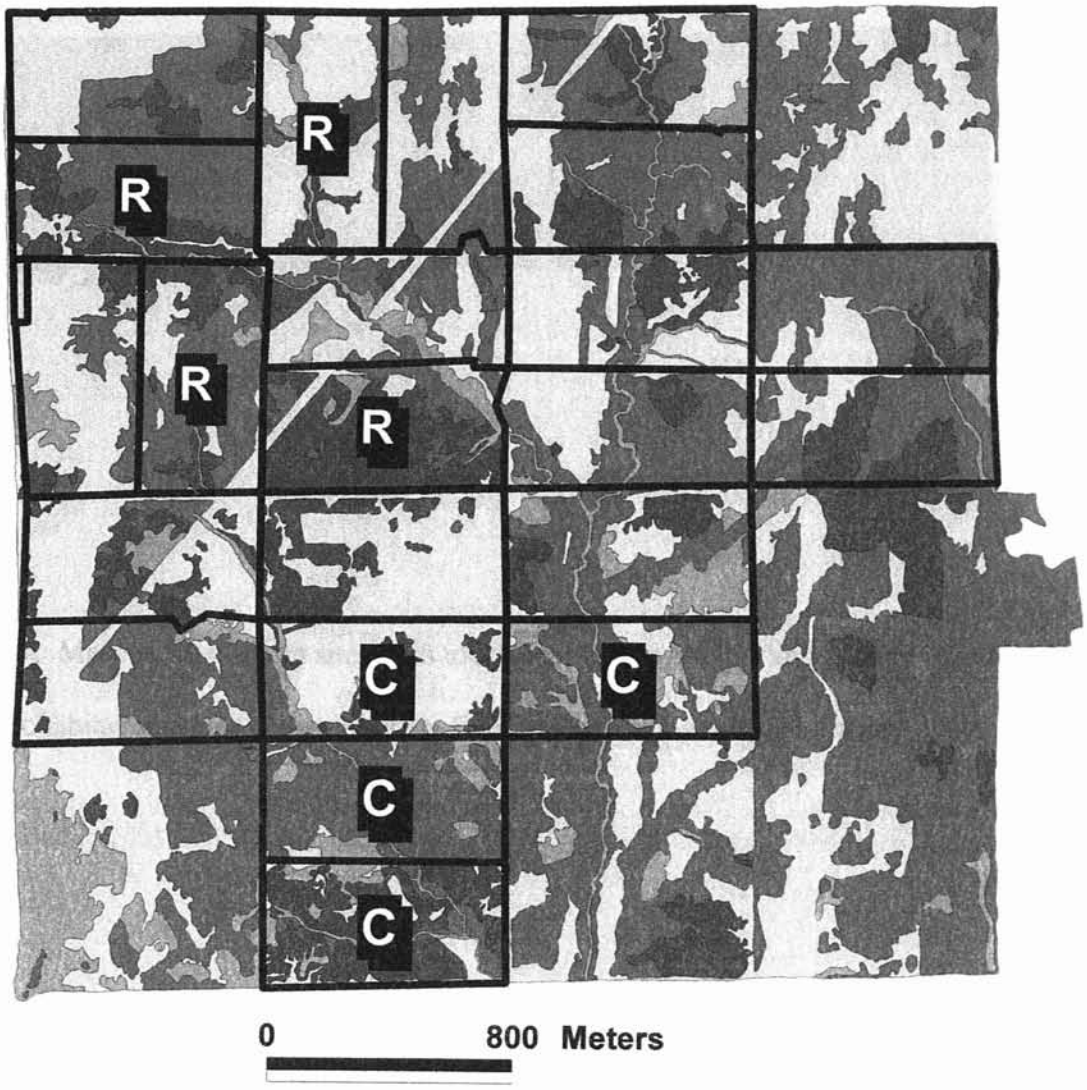

R
R
R
R
C
C
C
C
0
800 Meters
Cedar Forest
Deciduous Forest
Mixed Forest
Grassland
Pond
N
W
E
S

FIG. 7. Mesocarnivore trap sites with individual 100-m buffers and pastures used in macrohabitat analyses, Cross Timbers Experimental Range, Payne County, Oklahoma.

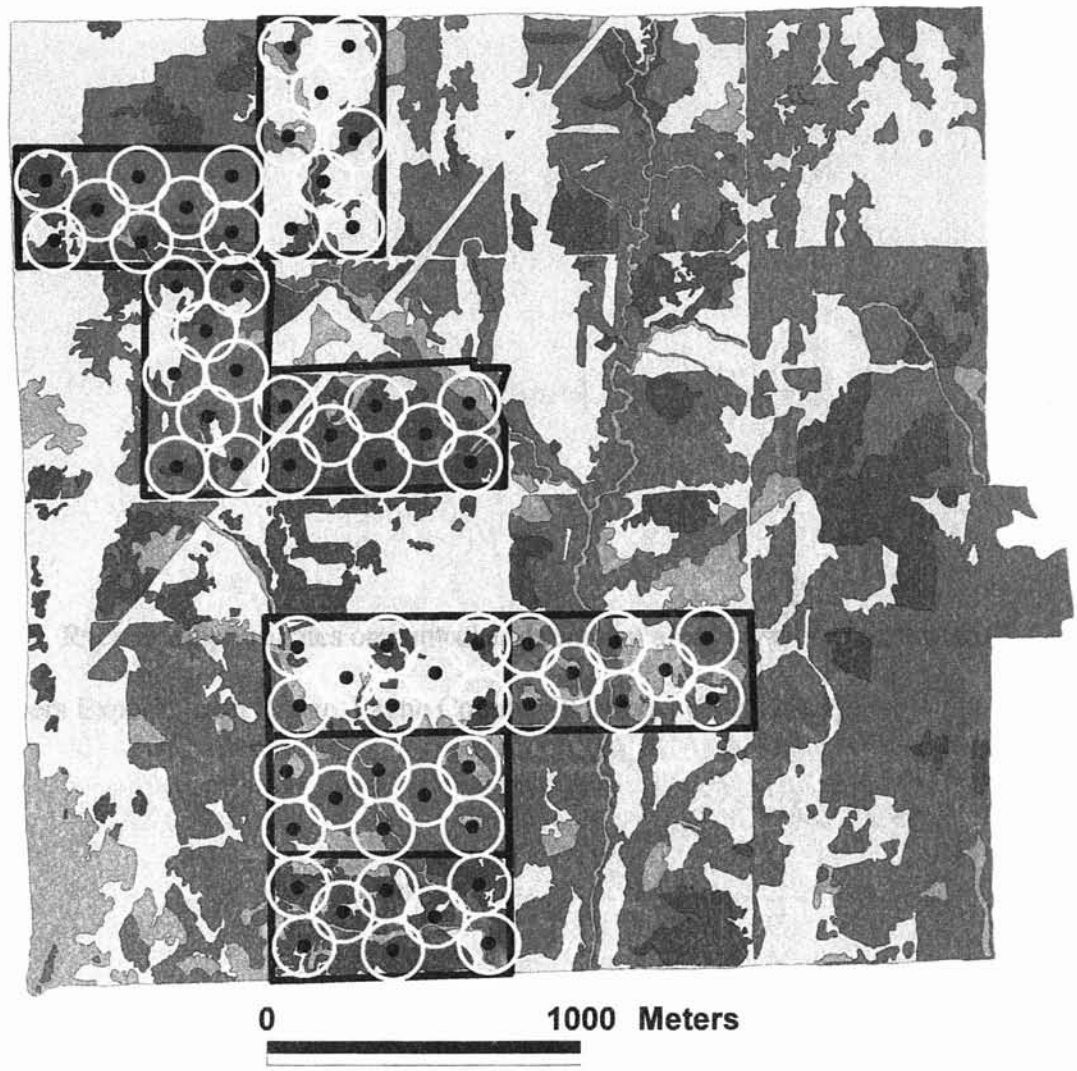

0
1000 Meters
Pasture
100 m buffer around trap
Cedar Forest
Deciduous Forest
Mixed Forest
Grassland
Pond
N
W
E
S

FIG. 8. Raccoon capture rates on control and removal areas (n = 4 replicates/ area), Cross Timbers Experimental Range, Payne County, Oklahoma (2000-2001).

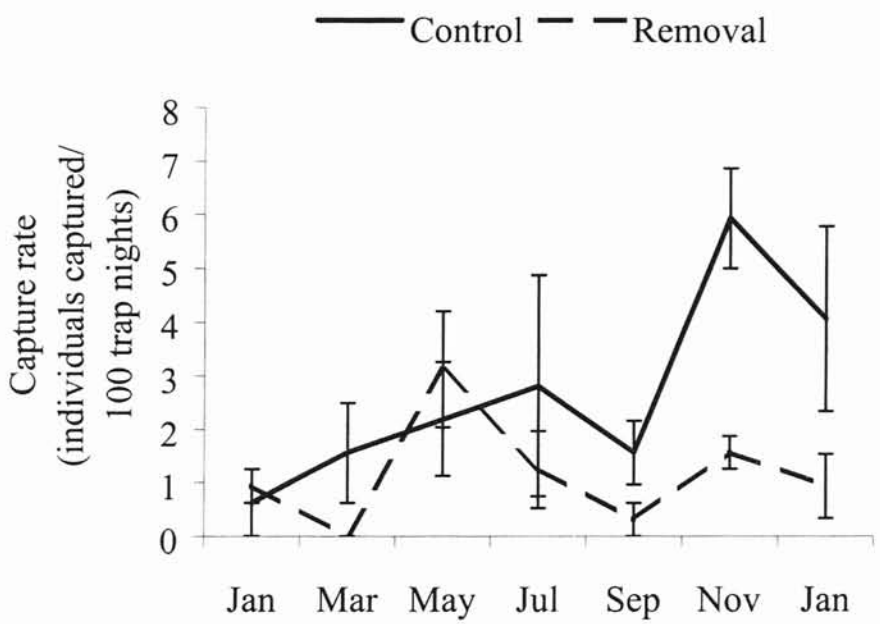

Control
Removal
Capture rate
(individuals captured/
100 trap nights)
8
7
6
5
4
3
2
1
0
Jan
Mar
May
Jul
Sep
Nov
Jan

FIG. 9. Biplot for first and second principal component axes of microhabitat vegetation and opossum capture sample scores, Cross Timbers Experimental Range, Payne County, Oklahoma, summer 2000 – winter 2001. Envelopes with ——— and samples with **x** represent trapsites ($n = 41$) with ≥1 captures in removal pastures. Envelopes with --- and samples with ■ represent trapsites ($n = 43$) with ≥1 captures in control pastures. Trapsites are weighted by number of captures. Only microhabitat variables with scores >0.58 are shown for clarity. See Table 2 for explanation of abbreviations.

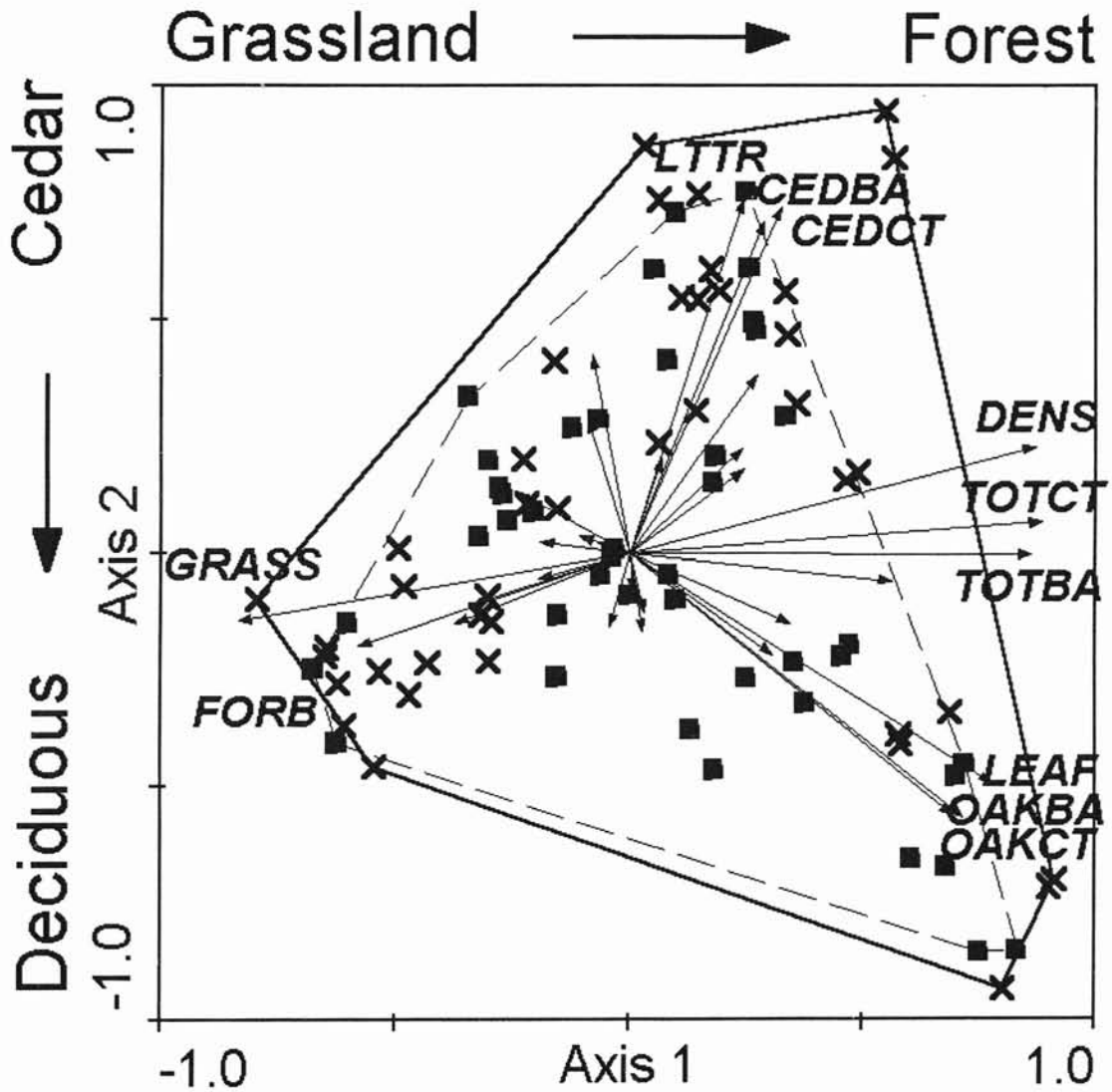

Grassland
Forest
Cedar
Deciduous
Axis 2
Axis 1
1.0
-1.0
-1.0
1.0
LTTR
CEDBA
CEDCT
DENS
TOTCT
TOTBA
GRASS
FORB
LEAF
OAKBA
OAKCT

FIG. 10. Habitat selection across all treatments for a) opossums (n = 284) and b) raccoons (n = 139) caught from 1998 to 1999 (May, July, October) and 2000 (May, July, November), Cross Timbers Experimental Range, Payne County, Oklahoma. Expected use based on the total number captured and the number of traps available in each habitat. A "+" indicates selection for and a "-" indicates avoidance of a particular habitat, as determined by Bonferroni intervals.

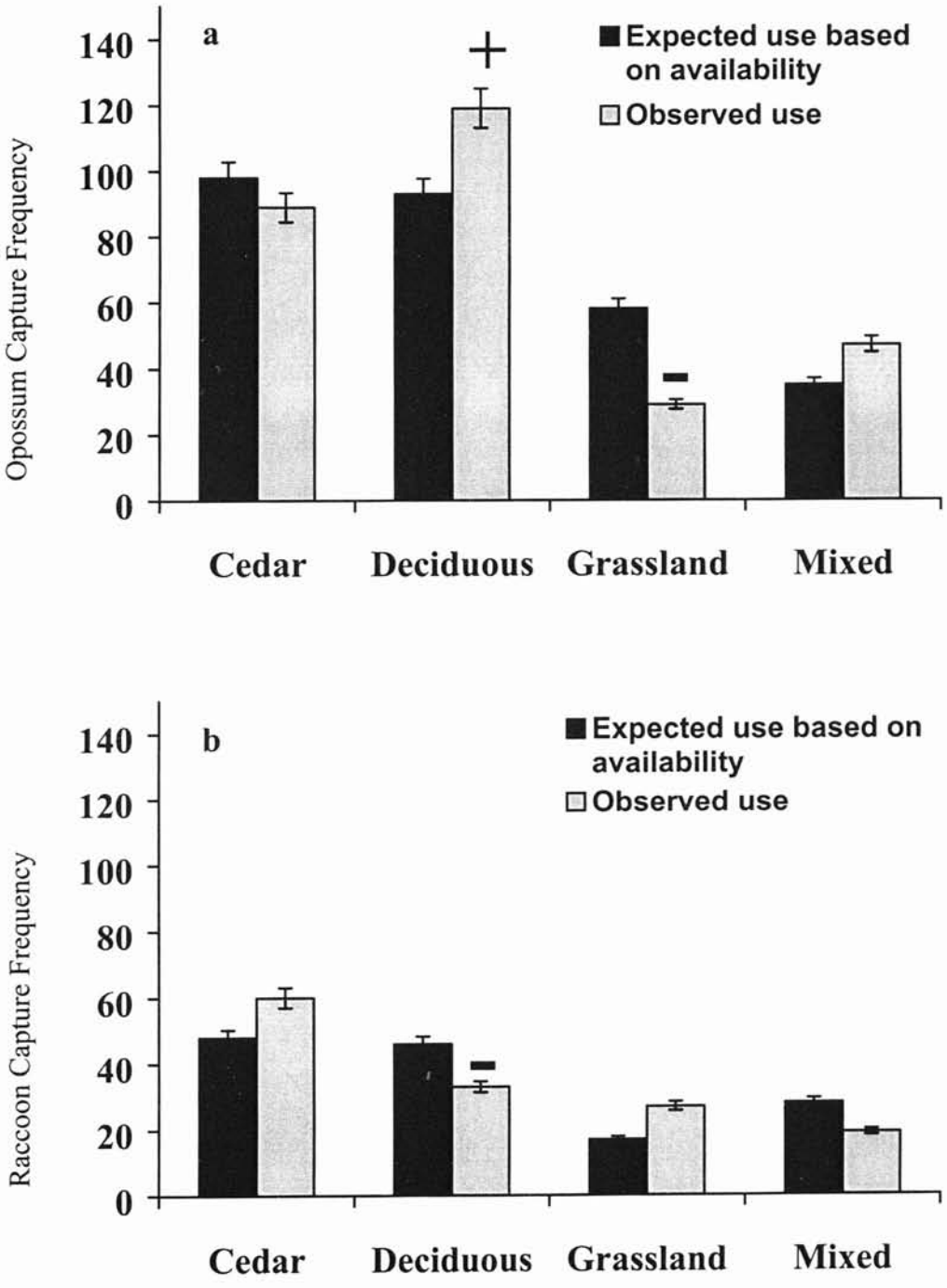

a
Expected use based on availability
Observed use
Opossum Capture Frequency
140
120
100
80
60
40
20
0
Cedar
Deciduous
Grassland
Mixed
b
Expected use based on availability
Observed use
Raccoon Capture Frequency
140
120
100
80
60
40
20
0
Cedar
Deciduous
Grassland
Mixed

FIG. 11. Home ranges (95% MCP) of individual female opossums on Cross Timbers Experimental Range, Payne County, Oklahoma.

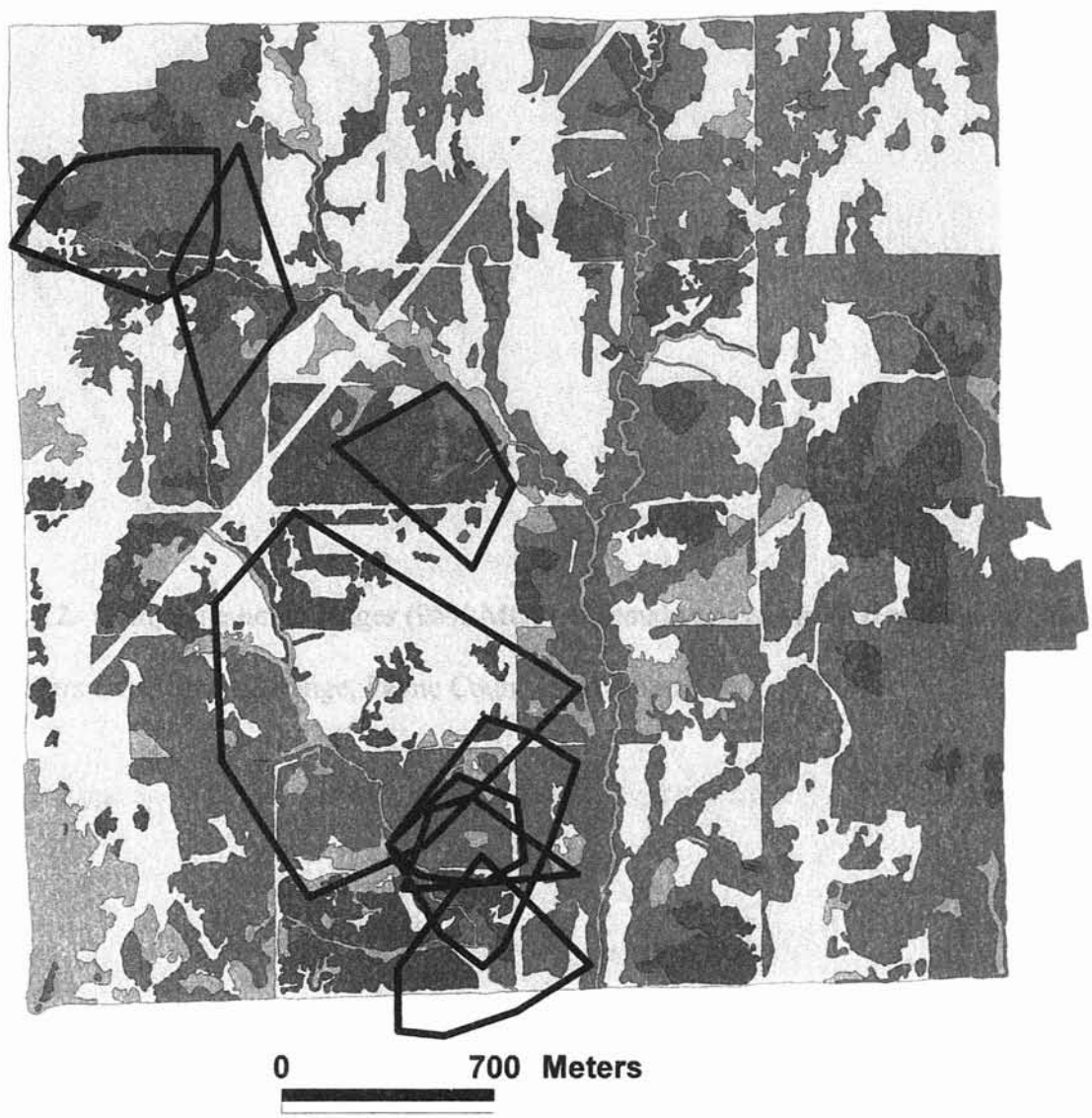

0
700 Meters
95% MCP home range
Cedar Forest
Deciduous Forest
Mixed Forest
Grassland
Pond
N
W
E
S

FIG. 12. Composite home ranges (95% MCP) of female opossums by treatment on Cross Timbers Experimental Range, Payne County, Oklahoma

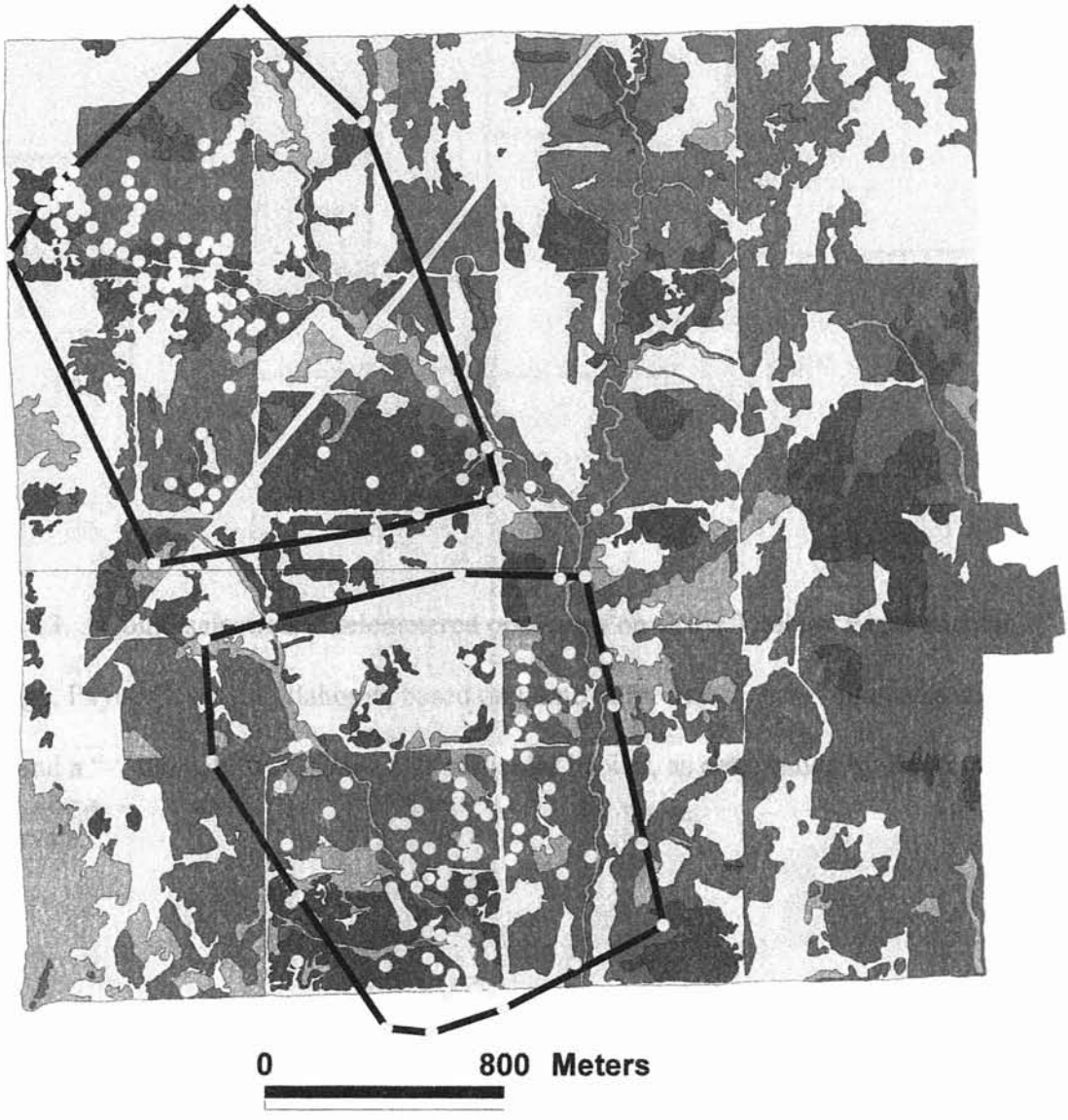

0
800 Meters
95% MCP composite range
Opossum locations
Cedar Forest
Deciduous Forest
Mixed Forest
Grassland
Pond
N
W
E
S

FIG. 13. Habitat selection of telemetered opossums on Cross Timbers Experimental Range, Payne County, Oklahoma, based on home range scale. A "+" indicates selection for and a "-" indicates avoidance of a particular habitat, as determined by Bonferroni intervals.

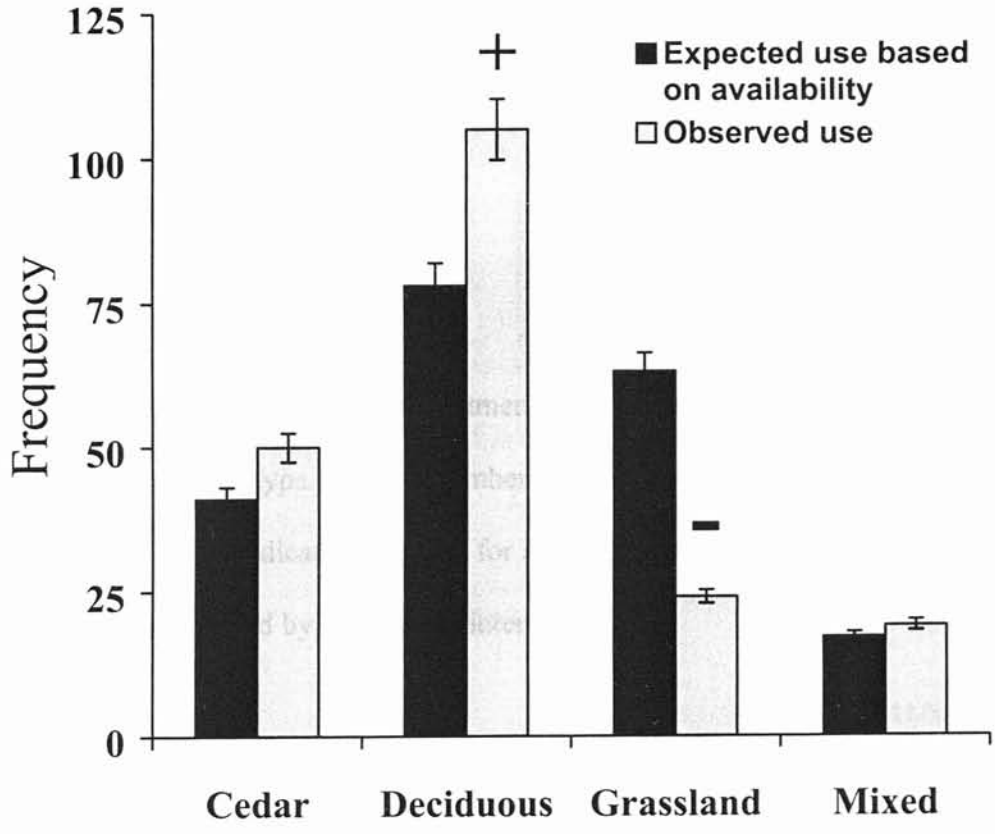
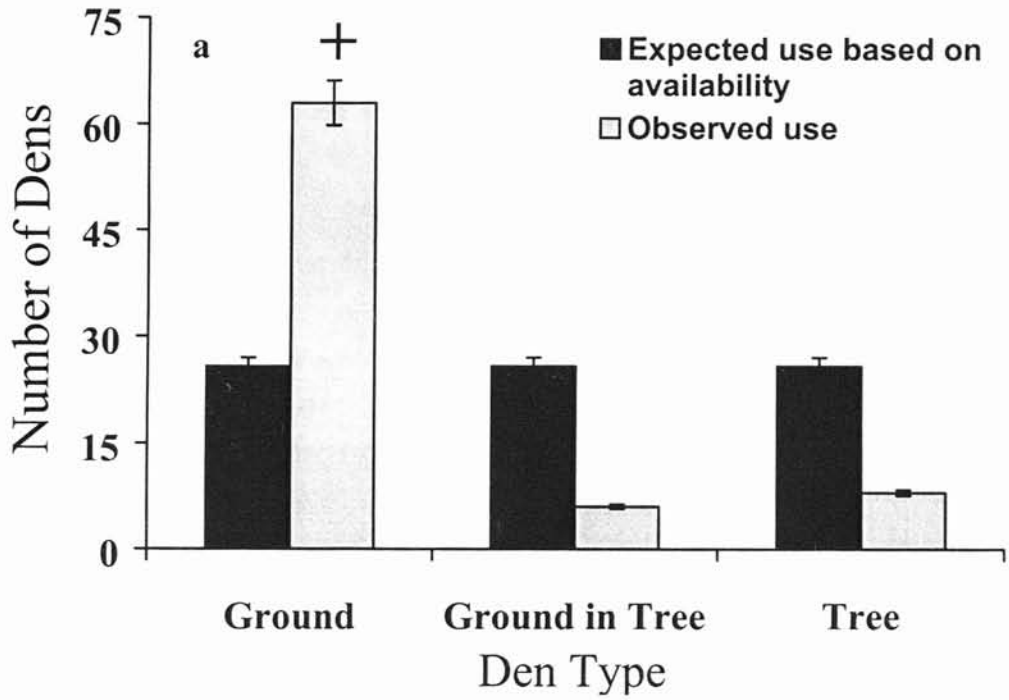

125
100
75
50
25
0
Frequency
Expected use based on availability
Observed use
+
-
Cedar
Deciduous
Grassland
Mixed

FIG. 14. Habitat selection across treatments for opossum den locations by a) den type and b) habitat patch type on Cross Timbers Experimental Range, Payne County, Oklahoma. A "+" indicates selection for and a "-" indicates avoidance of a particular habitat, as determined by Bonferroni intervals.


a
Expected use based on availability
Observed use
Number of Dens
75
60
45
30
15
0
Ground
Ground in Tree
Tree
Den Type

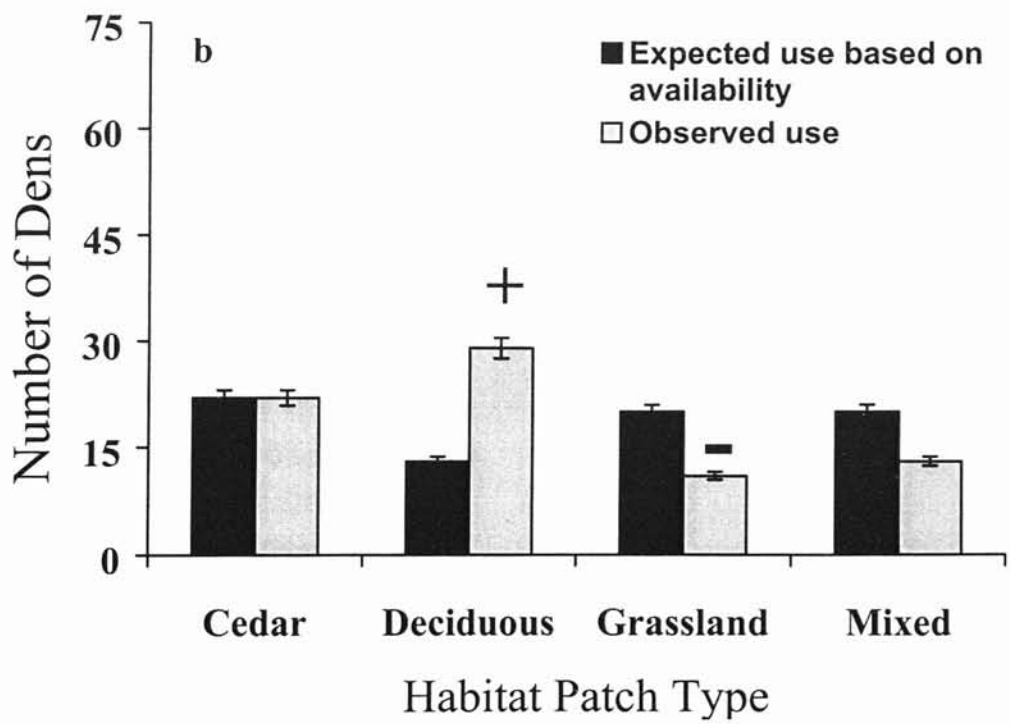

b
Expected use based on availability
Observed use
Number of Dens
75
60
45
30
15
0
Cedar
Deciduous
Grassland
Mixed
Habitat Patch Type

FIG. 15. Optimum den habitat of female opossums based on analyses of den selection data, Cross Timbers Experimental Range, Payne County, Oklahoma.

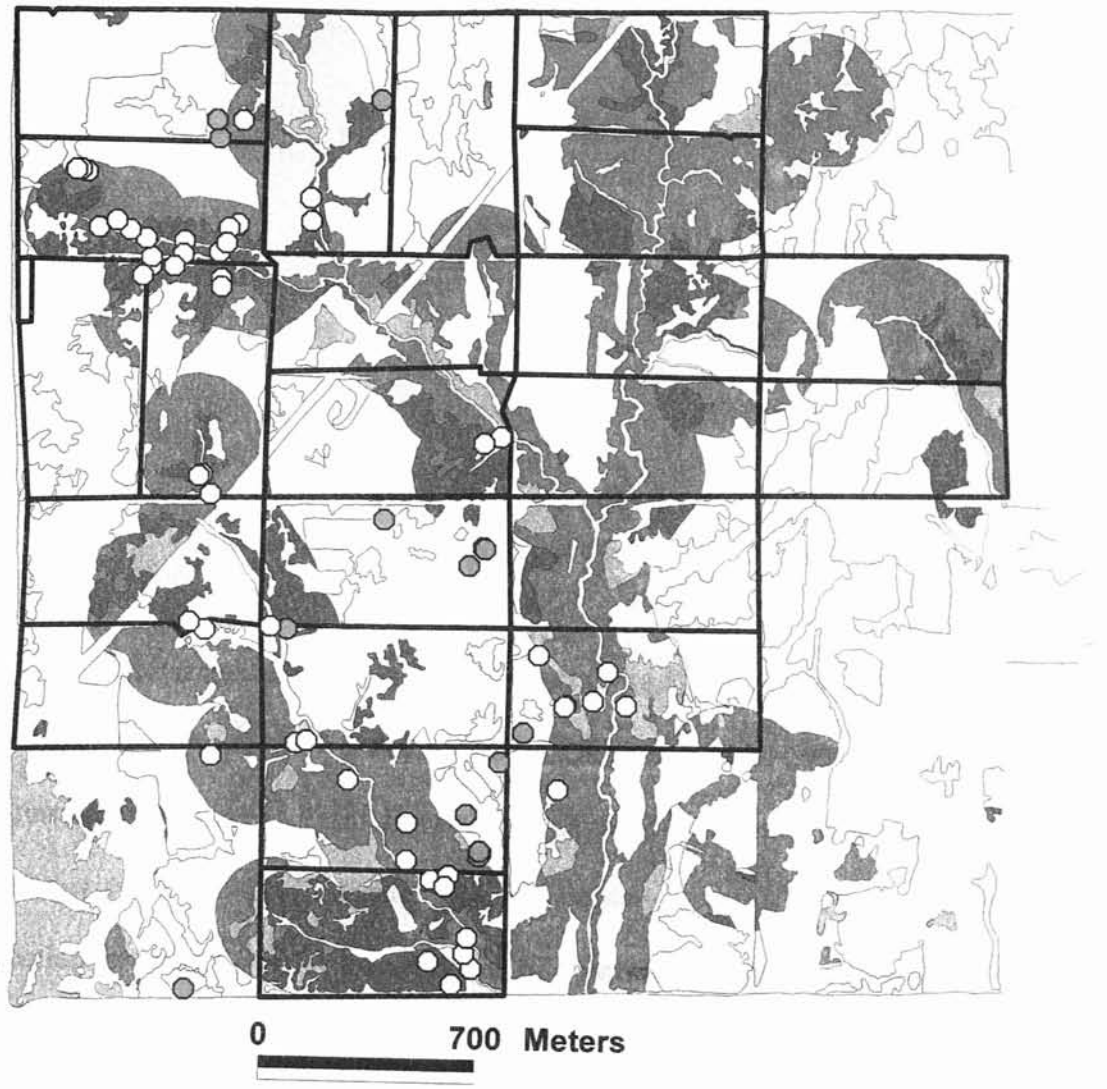
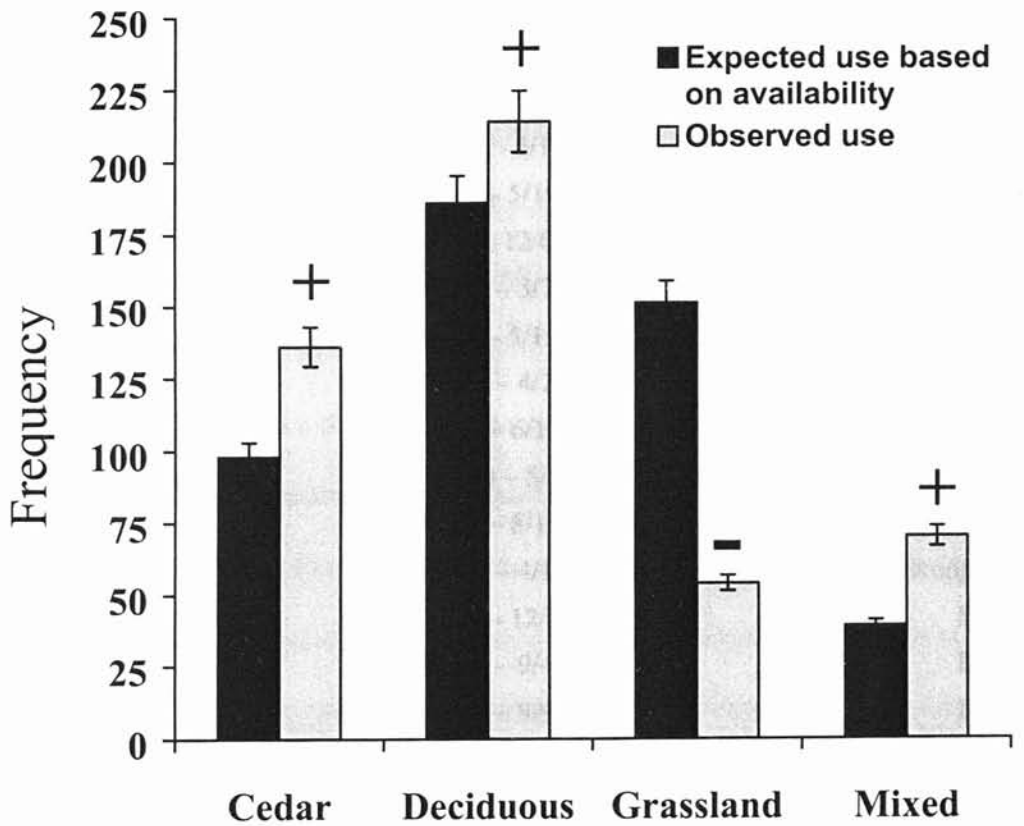

0
700 Meters
Dens in model
Dens not in model
Cedar Forest
Deciduous Forest
Mixed Forest
Grassland
Pond
N
W
E
S

FIG. 16. Habitat selection across all treatments for opossum (n = 474) locations on Cross Timbers Experimental Range, Payne County, Oklahoma, 2000-2001. Data are from telemetered and trap locations. Expected use is based on the total area available for each habitat within a 100% MCP created from all opossum locations. A "+" indicates selection for and a "-" indicates avoidance of a particular habitat, as determined by Bonferroni intervals.


250
225
200
175
150
125
100
75
50
25
0
Frequency
Expected use based on availability
Observed use
+
+
-
+
Cedar
Deciduous
Grassland
Mixed

APPENDIX A

Time monitored and fate as of 19 May 2001 of 31 radio-collared female opossums at CTER.

Opossum	Control or Removal Area	Period Monitored	# Telemetered locations	Fate
183	C	2/9/00 – 5/19/01	2	Signal lost
207	C	3/19/00 – 4/29/01	11	Dropped collar
245	C	2/7/00 – 10/16/00	23	Dead
246	C	3/14/00 – 5/19/01	10	Signal lost
257	C	2/11/00 - 5/19/01	1	Signal lost
260	C	3/15/00 - 5/19/01	9	Signal lost
262	C	2/7/00 - 5/19/01	10	Signal lost
263	C	2/2/00 – 12/03/00	9	Dropped collar
273	R	3/6/00 – 3/7/01	19	Dead
275	R	5/3/00 - 5/19/01	5	Signal lost
279	R	1/18/00 – 4/29/01	54	Dead
281	R	3/5/00 – 6/10/00	8	Dead
303	R	1/17/00 – 5/6/00	12	Dead
316	R	3/6/00 – 8/15/00	7	Dropped collar
321	R	3/9/00 – 4/1/01	8	Dropped collar
333	R	5/6/00 – 12/2/00	10	Dead
335	R	5/6/00 – 9/4/00	20	Dead
355	R	7/6/00 – 9/9/00	9	Dead
356	C	7/7/00 - 5/19/01	20	Signal lost
361	R	7/11/00 - 5/19/01	7	Signal lost
367	C	7/16/00 - 5/19/01	5	Signal lost
370	C	7/17/00 – 4/1/01	20	Dead
372	C	7/17/00 - 5/19/01	11	Signal lost
377	C	7/22/00 - 5/19/01	11	Signal lost
385	C	9/20/00 - 5/19/01	16	Signal lost
386	C	9/20/00 - 5/19/01	7	Signal lost
389	C	9/22/00 – 4/1/01	16	Collar dropped
399	R	11/1/00 – 4/29/01	13	Dead
401	R	11/1/00 - 5/19/01	5	Signal lost
414	C	1/18/01 - 5/19/01	2	Signal lost
435	R	1/14/01 – 5/19/01	2	Signal lost

APPENDIX B

Coyote activity on Cross Timbers Experimental Range (CTER), Payne County, Oklahoma, July – December 2001.

INTRODUCTION

The coyote (*Canis latrans*), considered a top predator in many areas (Gompper 2002; Wagner and Stoddart 1972) and present on the Cross Timbers Experimental Range (CTER), is known to prey on mesocarnivores (Bekoff 1977; Wooding et al. 1984; Chamberlain and Leopold 1999; Soulé et al. 1988). In light of my thesis research, investigation into the extent of coyote activity on CTER is warranted.

Scent stations have been used in monitoring presence and relative abundance of many mammalian species and were first used to determine relative abundance of red fox (*Vulpes vulpes*) and gray fox (*Urocyon cinareoargenteus*—Carroll et al. 1999). This method, although questioned for determining population sizes (Crawford et al. 1993; Sargeant et al. 1998), provides a cost-effective method for determining the relative abundance of medium-sized mammals such as coyotes, raccoons (*Procyon lotor*), and opossums (*Didelphis virginiana*—Carroll et al. 1999; Conner et al. 1983). Studies of coyotes have been most common, with work in the United States occurring in the southeast (Crawford et al. 1993; Main et al. 1999; Morrison et al. 1981), north (Sargeant et al. 1998), southwest (Windberg et al. 1997), and south central (Turkowski et al. 1983) regions.

The coyote is a native predator in Oklahoma (Freeman 1976). In the mid- to late-1970s, studies investigated coyote hybridization (Freeman 1976), socio-economic impact

(Mincolla 1977), diet (Holle 1977), and movement and habitat use (Litvaitis and Shaw 1980). Principal food items of coyotes were rodents, cattle, deer, lagomorphs, elk (*Cervus elaphus*), and armadillo (*Dasypus novemcinctus*), accounting for 80% by volume as collected in scats. Skunk (*Mephitis mephitis*) and raccoon were the only mesocarnivores found in 671 scats and each had a frequency of occurrence of 1%. Unidentified mammal hair, thought to be most likely of lagomorphs, occurred in 4% (Holle 1977). In most areas of the United States, small mammals and lagomorphs are the most commonly reported food items with mesocarnivores rarely reported (Bekoff 1977). My objective was to assess the extent of coyote presence on CTER to determine potential predation impacts on mesocarnivores.

METHODS

Methods were consistent with Linhart and Knowlton (1975) as modified by Roughton and Sweeny (1982), on a smaller scale. Due to the topography and arrangement of pastures on CTER, scent station locations were set up in a modified grid of 11 stations (Fig. 1). All stations were located along pasture fence lines, about 800 m from each other to minimize the possibility of multiple station visits by the same animal, and 400 m from roads or pastures surrounding CTER. For final placement of stations, topography often dictated exact site location. Stations were set on the side of the fence without cows, void of vegetation, and not in the direct path of a road or cattle trail, if possible. Stations were geographically located using a hand-held Trimble unit and differentially corrected (Pathfinder 2.10, Trimble Navigation Limited, Sunnyvale, California, USA).

In July 2001, each site was cleared of vegetation and a sand/mineral oil mixture (18 kg:0.5 L) spread out in a 1-m^2 circle. A fatty acid scent disk (FAS, Pocatello Supply Depot, Pocatello, Idaho, USA), a commercial attractant impregnated into a small plaster disk, was placed in the center. Disks were kept in airtight containers and removed with pliers. Knuckle impressions made in the medium aided in identification of stations considered inoperable by weather events.

The following day, stations were checked in the order they were set. A station was considered operable if the knuckle imprint remained intact. Prints of all species were recorded, along with relative number of tracks and size of a representative track (length x width in cm). Pictures often were taken with a measuring tape for scale. Other markings were recorded (e.g., scat, digging, disk moved or gone, etc.) Multiple tracks left by the same species were considered a single visit. The disk was removed (and later discarded) and the station covered with black landscaping cloth held down by bricks to prevent erosion. Stations were set up and checked once monthly from July to December 2001.

The scent-station index (SSI) for each species at each station was calculated by dividing the number of visits by each species by the number of operable stations, multiplied by 1000 (Carroll et al. 1999; Conner et al. 1983; Henke and Knowlton 1995). Analyses were used to evaluate coyote activity by habitat type and season (Summer = July, August, September; Fall/Winter = October, November, December) on CTER and whether visits to stations by coyotes were negatively or positively related to mesocarnivores on CTER. Habitat type was determined from a digitized black and white 1998 digital ortho-quarterquad in which 4 habitat types (oak forest, cedar forest, mixed

forest, grassland) were delineated in ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA, USA) based on vegetation composition. Five stations were located in deciduous patches, whereas 6 stations were located in grassland patches (Fig. 1).

RESULTS

Six months of sampling resulted in 66 operable station nights. Raccoons were the most common visitor (8), followed by striped skunks (5), coyotes (5), and gray fox (4). Other visitors included opossum (3), small birds (3), bobcat (1—*Lynx rufus*), feral cat (1—*Felis catus*), deer (1), turkey (1—*Meleagris gallopavo*) and 3 tracks recorded as unidentifiable mesocarnivores.

Mean SSI's varied by species and season (Table 1). Due to small sample sizes, statistical analyses were not utilized. All coyote visits occurred in the fall/winter portion of the study, with 60% occurring in December alone. All but one of these visits was at a station located in a grassland patch, and all visited stations were located on one of the outer pastures of CTER (Fig. 1). By contrast, mesocarnivores seemed to have no selection pattern in terms of habitat or station location.

DISCUSSION

Although sample size was low and sampling time relatively short, I can speculate that coyote activity is a factor on CTER, but may vary seasonally and spatially. Although mesocarnivores make up only small amount of the coyote diet, what may be important is coyote presence and potential interference competition. In southern

California, the presence of coyotes in fragments of chaparral habitat was correlated to a reduction in mid-sized predators (i.e., feral cats, opossums, and raccoons) and a subsequent increase in scrub-breeding birds (Crooks and Soulé 1999). Coyote presence had a particularly strong negative effect on opossum and raccoon abundance. Coyotes also may be killing smaller predators. This phenomenon has been reported with coyotes and San Joaquin kit foxes (*Vulpes macrotis mutica* —Cypher and Spencer 1998), coyotes and red foxes (Major and Sherburne 1987; Theberge and Wedeles 1989), and coyotes and gray foxes (Cypher 1993). Habitat fragmentation has increased in recent times, causing a decrease in large predators and an increase in mid-sized generalist carnivores, including the coyote. Interactions between coyotes and mesocarnivores such as raccoons and opossums are not well understood, but it is likely that coyotes are affecting their populations by interference or exploitative competition. As eastern redcedar (*Juniperus virginiana* L.) encroaches the Cross Timbers ecoregion (Bidwell et al. 1996), coyotes will be less likely to inhabit the thick, forested areas. This change may allow mesocarnivore populations to increase, which in turn could have deleterious effects upon their prey, especially bird populations (Crooks and Soulé 1999). Studies investigating the interactions of these mammalian species, and their potential top-down effects on prey populations in the Cross Timbers ecoregion, are needed.

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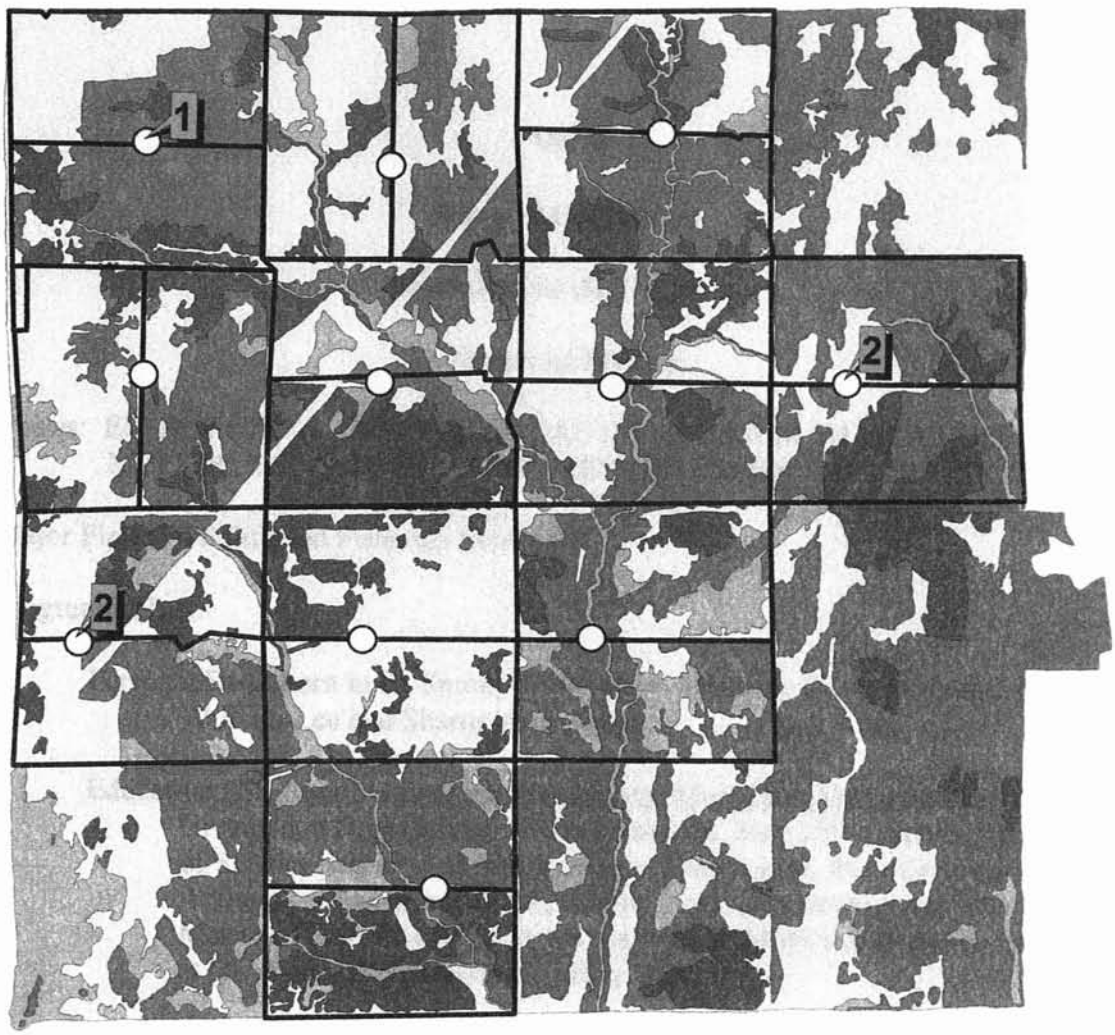
TABLE 1.—Total and seasonal mean scent station indices (SSI), Cross Timbers Experimental Range, Payne County, Oklahoma, July-December 2001.

Scent Station Index (SSI)	Coyote	Raccoon	Skunk	Gray Fox	Opossum	Birds
Overall SSI (*SD*)	75.8 (106.3)	121.2 (47.0)	75.7 (68.4)	60.6 (74.2)	45.5 (76.1)	45.5 (76.1)
Summer SSI (*SD*)	0	121.2 (52.5)	121.2 (52.5)	30.3 (52.5)	30.3 (52.5)	90.9 (90.9)
Fall/Winter SSI (*SD*)	151.5 (105.0)	121.2 (52.5)	30.3 (52.5)	90.9 (90.9)	60.6 (105.0)	0

FIG. 1.—Location of scent stations, habitat types, and coyote visits July-December 2001, Cross Timbers Experimental Range, Payne County, Oklahoma.


1
2
2
0
800 Meters
Scent station location
2
Number of coyote visits
Cedar Forest
Deciduous Forest
Mixed Forest
Grassland
Pond
N
W
E
S

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