POPULATION CHARACTERISTICS OF THE VIRGINIA OPOSSUM IN THE CROSS TIMBERS EXPERIMENTAL RANGE DURING RACCOON REMOVAL

By

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CHAPTER I

POPULATION CHARACTERISTICS OF THE VIRGINIA OPOSSUM IN THE CROSS TIMBERS EXPERIMENTAL RANGE DURING RACCOON REMOVAL

ABSTRACT

Mesocarnivore populations are increasing as a result of habitat fragmentation and elimination of keystone predators. An increase of mesopredators such as raccoons (*Procyon lotor*) and the Virginia opossum (*Didelphis virginiana*) may change competitive interactions at this trophic level. To assess whether raccoons compete with opossums, I conducted a 1-year raccoon-removal study on 8, 32.4-ha pastures at the Cross Timbers Experimental Range (CTER), Oklahoma. Forty-five individual opossums were captured in 158 captures in raccoon-removal pastures, and 53 individual opossums were captured in 145 captures in non-removal pastures in 5,010 trap-nights during the study. Twenty-two individual raccoons were captured in 28 captures in raccoon-removal pastures, and 38 individual raccoons were captured in 72 captures in non-removal pastures during the study. Three raccoons removed from raccoon-removal pastures were recaptured and removed 3 times. The capture rate for raccoons was greater ($P = 0.015$) in non-removal pastures compared to raccoon-removal pastures. Opossum capture rates varied by a treatment-month interaction ($P = 0.008$), with higher capture rates in non-removal areas for most of the study. Opossum population estimates and density did not vary by treatment. Opossum survival rates varied by sex and season but not by treatment according to modeling of opossum survival in program MARK. The annual survival rate of female opossums estimated by the Kaplan-Meier procedure was greater ($P = 0.05$) in

non-removal pastures than in removal pastures. Average litter size and body mass did not vary between treatments. My study failed to demonstrate apparent changes in opossum population parameters in response to raccoon removal. Habitat partitioning, prey switching by opossum predators, food supply, study scale, and environmental and demographic stochasticity may have masked effects of interspecific competition on the population dynamics of opossums on the study site.

INTRODUCTION

Biotic communities are composed of various species that may compete for a limited resource, thereby altering the population dynamics of one or both species (Milne 1961, Krebs 1994). There are two types of competition. Exploitative competition occurs when organisms utilize the same resource that is limited in supply. Interference competition occurs when organisms seeking a resource harm one another, possibly through direct conflict (Milne 1961, Case and Gilpin 1974, Schoener 1983).

Human activities, such as hunting and habitat destruction, have eliminated large, keystone predators such as the mountain lion (*Felis concolor*) and grizzly bear (*Ursus arctos*) in certain habitats. A reduction of mammalian megapredators may increase populations of small- and medium-sized mammalian carnivores (mesocarnivores) that otherwise would have been limited by predation or competition. The term keystone species can be defined as a species whose ecological role is disproportionately large relative to its abundance in an ecosystem (Power et al. 1996, Estes 1996).

The loss of megacarnivores can shift community structure whereby lower trophic levels move to the top, and increase population size, a phenomena known as (Hunter and Price 1992) mesopredator release (Litvaitis and Villafuerte 1995, Palomares et al. 1995).

A coyote (*Canis latrans*) removal study in western Texas demonstrated an increase in mesocarnivore populations after the first year of coyote removal (Henke and Bryant 1999). Mesocarnivores such as bobcat (*Felis rufus*), striped skunk (*Mephitis mephitis*), gray fox (*Urocyon cinereoargenteus*), and badger (*Taxidea taxus*) became more common on removal areas and remained absent on non-removal sites. Because they removed only 50% of the coyote population, Henke and Bryant (1999) suggested that mesocarnivore populations would have shown greater increases with local extinction of the coyote.

Exact causes of mesopredator release are controversial. Litvaitis and Villafuerte (1995) suggested increases in mesopredator populations are merely correlated with the severe reduction of keystone predators. They proposed increased habitat fragmentation and increased foraging opportunities, rather than reduction of megacarnivore populations, are the causes of increased mesocarnivore populations.

The widespread increase of mesocarnivores in their natural communities makes it important to establish mesocarnivore roles in community processes such as competition and predation. Comparative studies among mesocarnivores, such as raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), and striped skunks (Shirer and Fitch 1970, Kissell and Kennedy 1992, Ladine 1997), have addressed ecological relationships between the species. However, manipulative experiments designed to explore competition among mesocarnivores and their roles in a community have not been reported. Manipulation of the natural system by adding or removing individuals is necessary to understand whether resources are partitioned and competition is involved in structuring a community (Schoener 1974).

Most removal experiments examining community processes among mammals have used rodents as their target species (Grant 1969, Cameron 1977, Gliwicz 1981). Rodent removal experiments monitored changes in population size, survival, reproduction, body weight, spatial segregation and microhabitat association. For example, removal of swamp rats (*Rattus lutreolus*) led to an increase in the abundance of the eastern chestnut mouse (*Pseudomys gracilicaudatus*) and expansion of habitat range to microhabitats that were previously occupied by *R. lutreolus* (Higgs and Fox 1993). Habitat expansion by *P. gracilicaudatus* suggests it occupied inferior habitats due to exclusion pressures from the larger *R. lutreolus* (Higgs and Fox 1993).

Studies examining interspecific relationships among mammalian carnivores have focused on spatial organization and community structures as a function of a putative competitor. Intraguild predation, as a form of interference competition, also can play a role in these relationships. Voigt and Earle (1983) and Major and Sherburne (1987) found that coyote groups excluded red foxes (*Vulpes vulpes*) from core areas of their home ranges. Coyotes and San Joaquin kit foxes (*Vulpes macrotis mutica*) used similar food sources, potentially increasing exploitative competition during years of low prey abundance. Although both predators eat leporids and dipodomids, coyotes prefer leporids. Because kit foxes are also a prey species of coyotes, kit fox mortality has been attributed to interference competition (Cypher and Spencer 1998) and density-dependent predation by coyotes (White and Garrott 1999).

Opossums and raccoons occur in similar habitat types throughout their range. They consume similar prey items, thereby increasing the potential for interspecific interactions that may lead to exploitative and interference competition (Ladine 1997).

Individuals of both species have been captured in the same location, indicating spatial overlap (Shirer and Fitch 1970, Kissell and Kennedy 1992, Ladine 1995). Habitat-use overlap of opossums and raccoons has been recorded as high as 94.7% (Kissell and Kennedy 1992). High degrees of tolerance between the two species have been documented, including simultaneous den sharing (Shirer and Fitch 1970). Although tolerance may be exhibited by shared resource use, there is evidence of interspecific competition or avoidance behavior between the species. Ladine (1995) found that raccoons and opossums used available habitat during different hours based on the absence of dual species captures at double-trap sites. The presence of large raccoons may force opossums to forage at different times (Ladine 1997). Stuewer (1943) demonstrated a predator-prey relationship between *P. lotor* and *D. virginiana* in several small enclosure experiments, where raccoons killed and partially consumed opossums. Although the opossum is not a preferred prey item of the raccoon, Stuewer's experiments indicate that predation of opossums by raccoons can occur.

My objectives were to assess the effects of raccoon removal on opossum population characteristics by estimating opossum capture rates, population size, density, survival rate, reproductive output, changes in body mass, and age and sex ratios at the Cross Timbers Experimental Range in Oklahoma. Under the hypothesis that raccoons and opossums compete, I predicted that the following would occur:

1. The capture rate would be higher for opossums living in raccoon-removal pastures because more traps would be available for the capture of opossums when raccoons are removed.

2. Greater population estimates and density of opossums would be evident in raccoon-removal pastures because decreased competition for food and space in these pastures would facilitate opossum access to better food sources. Therefore, opossums could increase reproductive rate, survival rate, body mass and overall fitness.
3. Reproductively active females would produce male-biased litters in raccoon-removal pastures, evident by higher numbers of juvenile males captured there (Trivers and Willard 1973). Females from raccoon-removal pastures would have the competitive advantage of obtaining higher-quality foods than their raccoon-competing counterparts once raccoons were removed. Parental investment in offspring would be greatest for the sex that contributes the largest reproductive return. Opossum females produce male-biased litters when provisioned with food (Austad and Sunquist 1986, Hardy 1997).

STUDY AREA

CTER is located 11 km southwest of Stillwater, Payne County, Oklahoma (36°02'40" to 36°04'20"N, 97°09'30" to 97°11'39"W). It has been studied since 1982 to determine the effects of different methods of rangeland management on vegetation (Ewing et al 1984, Engle et al. 1991, Stritkze et al. 1991), livestock production and wildlife. It is composed of 22 32.4-ha pastures totaling 712 ha. CTER pastures were assigned different treatment regimes within 4 randomly located replicates of 5 experimental treatments (Table I.1). Four distinct habitat types exist at CTER as a result of the treatments that differentially influenced conifer and deciduous tress and shrubs (D. M. Engle, Department of Plant and Soil Sciences, Oklahoma State University, personal communication). The habitat types were classified by Levesque (2001) redcedar forest, derived grassland, mixed-brush community, and mature oak forest.

METHODS

Experimental Design and Field Methods

The study site was composed of 4 raccoon-removal and 4 non-removal pastures (Figure I.1). Two sets of 4 pastures each were composed of a replicate block of habitats (i.e., non-removal and raccoon-removal pastures included the same 4 habitats). I trapped animals using Tomahawk live traps (Tomahawk Trapping Company, Tomahawk, Wisconsin, USA) baited with sardines. Trapping was conducted bimonthly from January 2000 to January 2001 for 10-day periods. Trapping grids for all pastures were arranged in a 3 x 5 grid containing 8 traps. Traps were placed 100 m from the edges of pastures, 300-m apart along 2 parallel transects spaced at 200-m intervals and 2 interior traps were placed diagonally at 180 m from the corners (Figure I.2). I placed eight traps between non-removal and treatment pastures as buffers to minimize raccoon immigration from non-removal pastures to treatment pastures. I checked traps daily and re-baited every 5 days and as needed during the 10-day trapping sessions.

Captured mesocarnivores were immobilized chemically with telazol (tiletamine hydrochloride and zolazepam hydrochloride; A. H. Robins Company, Richmond, Virginia, USA) at 8.0-mg/kg body weight. All individuals were tagged in both ears with numbered, brass Ketchum Tambra ear tags (Nasco, Fort Atkinson, Wisconsin, USA). Individuals were sexed, weighed to the nearest kg with a spring scale (Chatillon Scale Company, New York, New York, USA) and raccoons and opossums were aged (juvenile, adult). Morphological measurements were measured to the nearest 0.1 mm with flexible tape. Age was assessed using individual body mass to indicate whether the opossum was a juvenile or an adult. I considered opossum individuals weighing ≤ 0.9 kg to be juvenile (young-of-the-year) and opossum individuals weighing > 0.9 kg to be adults. Large young-of-the-year caught in November may have been classified as adults. Raccoons weighing ≤ 4.0 kg were classified as juveniles and individuals weighing > 4.0 kg were considered adults. Reproductive condition of female opossums was assessed by examining the development of the marsupium and determining the number of offspring. I did not determine sex of juveniles within the marsupium. Female opossums in all pastures weighing ≥ 0.9 kg were fitted with a radiocollar. Female opossums were radio-located from January 2000 to June 2001 on a weekly basis by triangulation from roads and pasture edges and by homing.

Once handling procedures were completed, I released opossums at their point of capture on treatment pastures. Initial captures of animals within a trap session were treated as unique captures. Animals recaptured within the 10-day trapping session were considered recaptures. I transferred raccoons from raccoon-removal pastures by truck and released them to a remote, forested location approximately 11 km east of the raccoon-removal sites. A 4-lane highway separated the release site and CTER. Three raccoons originally removed from raccoon-removal pastures were recaptured in raccoon-removal pastures, and removed again.

Analysis

Capture rates (unique captures/100 trap nights) within pastures (n = 4/treatment) were compared between treatments by repeated-measures ANOVA separately for opossums and raccoons. I calculated opossum population estimates (± 95% C. I.) for each pasture during each trapping period using Chapman's version of the Lincoln-Petersen estimate for closed populations (Lancia et al. 1994). Population estimates were compared between pastures for 6 trap intervals (7 trap sessions) using a Z-test with a critical value of $Z_{0.002} = 2.86$. I used the following formula to calculate density:

$$D = N / A$$

where N is the population estimate for opossums in either non-removal or treatment pastures, and A is the total effective trapping area (sum of pasture areas plus buffer). A buffer equal to the radius of a 27.4-ha circle (average size of home range of an adult female; S. M. Ginger, Department of Zoology, OSU, unpublished data) was added to the area of the 4 raccoon-removal and non-removal pastures, respectively (Wilson and Anderson 1985).

I calculated annual survival rates for raccoon-removal and non-removal pastures using telemetry data on radio-collared opossums with the Kaplan-Meier staggered-entry procedure pooled across years (Pollock et al. 1989). I was unable to identify if female opossums had died or dropped collars because transmitters did not emit mortality signals. If consecutive locations were in the same general vicinity for > 3 weeks, I located the animal or collar to determine fate. I recorded the censored date (i.e., the time when a female opossum was removed from the number of females at risk) as the last date when an active signal was recorded. During the winter months, some females used the same dens for 2 to 3 months. If after 3 months, I could no longer locate a signal, I assumed the last date that denned females were at risk was the last signal reading 3 months earlier. Because the fates of 16 females were unknown, I conducted 2 separate analyses to estimate minimum and maximum survival for both treatments (Heisey and Fuller 1985, White and Garrott 1990). For maximum annual survival, I considered females that had dropped their collars or were missing (i.e., those whose signals had not been heard for ≥ 3 month) as alive. For minimum annual survival, I made the same assumptions about female fates, except that I considered missing females dead.

The Cormack-Jolly-Seber (CJS) live-recaptures model in Program MARK (White and Burnham 1999) was used to estimate apparent survival (Φ) and capture probability (p) of individual opossums from mark-recapture data. Apparent survival is a combination of resident survival and emigration. The 4 assumptions of the CJS model were that (1) marks were not lost or overlooked; (2) samples were instantaneous and releases were made soon after the sample; (3) all animals in the population at the time of the ith sample had equal capture probability; (4) all marked animals in the population immediately after the ith sample had equal survival until the (I + 1)-th sample (Pollock et al. 1989). I assumed populations of animals within each area to be closed within a 10-day sampling period.

The most general model coded survival as a function of sex, treatment, and season (breeding season [March – July] vs non-breeding season [August – February]) and capture probability as a function of season (winter [January – March 2000 and November 2000 – January 2001] vs non-winter [May – September 2000]). I denoted this model as Φ (sex*season*treatment), p (season). To further investigate the effects of sex, treatment, and season on these parameters, I tested reduced-parameter models. The minimum Δ Akaike's Information Criteria value (ΔAICc; Burnham and Anderson 1998) was used to identify and rank parsimonious models. A goodness-of-fit test using a parametric bootstrap approach was used to accommodate any lack of fit in the analysis. Models were ranked and averaged using AICc weights to show apparent survival by sex for each treatment (Burnham and Anderson 1998).

I compared litter size between areas using the Student's t-test. Proportion of adult females with litters was compared between treatments using Chi-square analysis. Average body mass was compared between treatments by repeated-measures ANOVA. Sex ratio and age structure (juveniles:adults) of opossums were compared between areas and among months using log-linear modeling to assess effects of raccoon removal (PROC CATMOD, SAS Institute 1996). All statistical analyses were considered significant at $P \leq 0.05$, and actual P-values are reported.

RESULTS

Capture Rate, Population Size and Density

Forty-five individual opossums were captured in 158 captures in raccoon-removal pastures, and 53 individual opossums were captured in 145 captures in non-removal pastures in 5,010 trap-nights during the study. Twenty-two individual raccoons were captured in 28 captures in raccoon-removal pastures, and 38 individual raccoons were captured in 72 captures in non-removal pastures during the study. Three raccoons removed from raccoon-removal pastures were recaptured and removed 3 times. The capture rate for raccoons was greater in non-removal than raccoon-removal pastures ($F_{1,14} = 7.78$, $P = 0.015$, Figure I.3). Capture rate varied by month ($F_{6,31.8} = 2.75$, $P = 0.03$); however, there was no month*treatment interaction ($F_{6,31.8} = 1.73$, $P = 0.15$). Overall mean ($\pm$ S. E.) capture rates were 2.68 ± 0.37 and 1.16 ± 0.37 unique individuals/100 trap nights for non-removal and raccoon-removal pastures, respectively.

The capture rate for opossums interacted between treatment and month ($F_{1,11}$ = 3.41, $P = 0.09$, Figure I.4) or treatment ($F_{6, 32.9} = 3.59$, $P = 0.008$). Opossum capture rates did not vary by month ($F_{6, 32.9} = 1.48$, $P = 0.22$). Overall mean (± S. E.) capture rates were 4.24 ± 0.60 and 2.77 ± 0.60 unique individuals/100 trap nights for non-removal and raccoon-removal pastures, respectively, and were greater in control pastures from March to November.

Population estimates for opossums between treatments did not vary for all months ($P > 0.05$) except September (Figure I.5), when opossum abundance was higher on non-removal pastures. The effective trapping area around the raccoon-removal and non-removal pastures totaled 3.54 km^2 and 3.22 km^2, respectively. Density estimates (across months) averaged 10.5/ km^2 for raccoon-removal pastures and 10.8/ km^2 for non-removal pastures (Figure I.6).

Survival

Thirty-one females were radio-collared in the study (non-removal pastures [$_{nr}$], n_{nr} = 16; raccoon-removal pastures [$_r$], $n_r = 15$). Nine females ($n_{nr} = 2$; $n_r = 7$) were discovered dead, 6 ($n_{nr} = 5$; $n_r = 1$) collars were recovered without opossums present and assumed to be alive until last active signal (i.e., dropped collar), and 16 individuals were censored by the date of last active signal because of lost contact (Table I.2). Maximum annual survival rate was greater ($\chi^2_1 = 0.69$, $P = 0.049$) in non-removal (0.73; 95% CI = 0.45 – 1.00; Figure I.7) than raccoon-removal pastures (0.39; 95% CI = 0.09 – 0.69). Minimum annual survival rate was similar ($\chi^2_1 = 0.71$, $P = 0.47$) in non-removal (0.16; 0.00 – 0.32) and raccoon-removal pastures (0.17; 0.00 – 0.36).

The model that ranked highest by ΔAIC was parameterized for variation in male survival between seasons without treatment effects, constant female survival, and variation in recapture probability between seasons (Φ[males*season], *p*[winter]; model A, Table I.3). Under model A, 2-month survival rates for male opossums was 0.77 ± 0.11 and 0.29 ± 0.10 during the non-breeding and breeding seasons, respectively. Female opossums had a 2-month survival rate of 0.64 ± 0.07. These interval rates translate to annual survival of 0.030 for males and 0.069 for females. Recapture probability was 0.37 ± 0.09 during winter and 0.63 ± 0.08 during non-winter. Two additional models described the data (Table I.2, ΔAIC < 2.0; Burnham and Anderson 1998). Model B indicated that female opossum survival was a function of treatment (2-month rates: raccoon-removal = 0.61 ± 0.11; non-removal pastures = 0.67 ± 0.09), whereas model C suggested that male opossum survival varied by season and treatment (Table I.3). All other models contributed little to explaining the data (i.e., ΔAICc ≥ 2.95; Table I.3). Model averaging highlighted the differences in male survival between seasons and the lack of treatment differences (Table I.4).

Reproduction

Litter size averaged 7.8 ± 1.3 (n = 17) in non-removal and 5.8 ± 3.9 (n = 10) in raccoon-removal pastures, and did not vary by treatment ($t_{26} = 0.62$, $P = 0.52$). Young were found in marsupium during March, May and July of this study. Proportion of females with litters did not differ ($\chi^2_1 = 0.41$, $P > 0.05$) between raccoon-removal (0.43; n = 23) and non-removal (0.46; n = 37) pastures.

Body Mass

Adult opossums body mass did not differ ($F_{1,109} = 3.51$, $P = 0.06$, Figure I.8) between raccoon-removal (1.8 ± 0.1 kg) and non-removal pastures (1.7 ± 0.1 kg). Adult body mass did not vary by month ($F_{6,109} = 1.79$, $P = 0.11$) nor by month*treatment ($F_{6,109} = 0.59$, $P = 0.74$). Juvenile body mass did not vary ($F_{1,24} = 0.01$, $P = 0.9$) between non-removal (0.7 ± 0.1 kg) and raccoon-removal pastures (0.7 ± 0.1 kg).

Sex Ratio and Age Structure

Sex ratio did not vary by treatment ($\chi^2_1 = 1.85$, $P = 0.17$, Figure I.9), and there was no month*treatment interaction ($\chi^2_1 = 7.32$, $P = 0.29$); however, sex ratios varied by month ($\chi^2_1 = 12.75$, $P = 0.05$), with more females than males captured from July 2000 to January 2001. Sex ratios for adult or juvenile males to females did not vary by treatment ($\chi^2_1 = 1.77$, $P = 0.18$; $\chi^2_1 = 1.56$, $P = 0.21$), respectively. Juveniles were caught in July ($n_{nr} = 5$; $n_r = 5$), only juvenile females were caught in both pasture types in September ($n_{nr} = 5$; $n_r = 2$), and 3 juveniles (1F:2M) were captured only in non-removal pastures in November. Adult opossums were captured more often and in higher numbers than juveniles (Figure I.10). Age ratio did not vary by treatment ($\chi^2_1 = 0.03$, $P = 0.87$) and by month*treatment ($\chi^2_1 = 2.03$, $P = 0.36$), but did have a month*age interaction ($\chi^2_1 = 7.85$, $P = 0.02$). This interaction was clear in the variation in age ratio by month (Figure I.10), with no juveniles captured in the January – May period.

DISCUSSION

Predictions supporting the hypothesis of interspecific competition between raccoons and opossums were not supported in this 1-year study. Capture rates of opossums were not higher in raccoon-removal pastures than non-removal pastures for most of the study as predicted. Apparently, the removal of raccoons did not create opportunities for capturing more individual opossums; indeed, the reverse occurred during most of the study. Greater capture rates in non-removal pastures could be explained by a larger number of opossums in non-removal pastures than raccoon-removal pastures. However, population and density estimates for each treatment were quite close except for September 2000. Opossum densities calculated for treatment and non-removal pastures fell within the range reported by other opossum ecology studies ($1.1/km^2$ to $12.3/km^2$; Fitch and Sandidge 1953, Seidensticker et al. 1987, Kissell and Kennedy 1992, Gehrt et al. 1997) and similar to previous estimates on CTER (3.9-$17/\ km^2$; Levesque 2001).

Survival of adult opossums also was not affected by raccoon removal, although maximum estimates of female survival using telemetry data were higher on non-removal pastures. However, I believe that minimum survival estimates, which were based on the assumption that missing animals were dead, were more accurate because of low opossum survival in the wild (Gardner 1982). Annual opossum survival rates for this study were similar to previous estimates at CTER (0.01; Levesque 2001). Survival of opossums in other areas also is uniformly low. In Kansas, Gipson and Kamler (2001) reported annual survival rates for adult opossums ranging from 17% to 25%. Gehrt et al. (1997) found that 4% of the captured population survived $\geq$ 12 months past initial capture in Texas. Gillette (1980) reported total mortality for 92 adult opossums over 1 year. Lay (1942) had only 1 opossum in 56 that lived > 11 months post-capture. Llewellyn and Dale (1964) estimated the oldest male opossum to be 3-years old and the oldest female opossum to be 27-months old when last trapped in their study.

Lower survival by male opossums during the breeding season than females was consistent with the semelparous life-history strategy of other carnivorous marsupials. Male opossums are semelparous because they do not invest in any parental care for their young, instead expending energy on mating. Female opossums bear complete responsibility for raising offspring in their marsupium. Post-mating male mortality has been examined in several dasyurids (Inns 1976, Wilson and Bourne 1984, Lee and Cockburn 1985, Oakwood et al. 2001). For example, *A. stuartii* males are preoccupied with mating during a short breeding period and die immediately thereafter (Lee and Cockburn 1985). Post-mating mortality has been associated with intestinal bleeding, liver necrosis, increased parasite loads and pathogenic infections most likely due to microorganism invasion earlier in the marsupial's life. *A. stuartii* males showed suppressed immune and inflammatory responses during and post-mating (Lee and Cockburn 1985).

Opossums at CTER have a longer mating period than *A. stuartii*, and adult male *D. virginiana* survive to mate once or twice but die shortly after mating. Perhaps survival of male opossums during the breeding season at CTER was hampered by weakened immune response, as evident by poor physical condition. Male opossums at CTER exhibited hair loss, damaged or broken appendages, high parasite loads (e.g., ticks), and unhealed wounds when captured during the first (Jan- Mar) and second (May-Jul) breeding periods (M. A. Kasparian, personal observation). The increased ratio of females to males in late summer (Figure I.9) was consistent with high male breeding mortality.

Female reproductive rates, based on the proportion of females with young in the marsupium and litter size, did not change between treatment and non-removal pastures.

The opossum-breeding season in Oklahoma extends from 1 February to 1 September (Reynolds 1945, Gardner 1982, Seidensticker et al. 1987, Levesque 2001). Across the geographic range, opossum litter sizes average 6.8-8.9 young per litter (Lay 1942, Fitch and Sandridge 1953, and Gardner 1982) and can be produced up to 3 times a year (Reynolds 1945, Llewellyn and Dale 1964). Litter sizes for this study fall within the reported range.

Sex ratios in mammals are hypothesized to vary according to the amount of parental investment in resource allocation (Trivers and Willard 1973). Parental investment in offspring will be highest for the sex that will contribute the largest reproductive return. In the case of the opossum, females produce male-biased litters when provisioned with food (Austad and Sunquist 1986, Hardy 1997). In environments where food was not provisioned to opossums, researchers have consistently trapped slightly more males than females (Reynolds 1945, Llewellyn and Dale 1964, Edmunds et al. 1978), suggesting reproductively active females could be producing male-biased litters.

Gardner (1982) stated that opossum litters might consist of equal numbers of males and females at birth, but become male-dominated once offspring have been weaned. Opossum sex ratios may be explained by the First-Cohort Advantage Hypothesis (Wright et al. 1995), where adult females produce larger and male-biased first litters, allowing these male offspring greater opportunities for reproduction upon maturity. Larger male offspring have higher reproductive success than females and small males. Adult females should produce more female-biased litters and smaller males in the second cohort to decrease mate competition for males from the first cohort (Wright et al.

1995). If male offspring from both cohorts survive at least one year, then the opossum population will be male-biased.

Few juveniles of either sex were caught in my study and of those caught most were female. However, because I did not assess sex of juveniles within the marsupium, I cannot conclude, based on juvenile captures alone, that CTER litters were biased for females or that treatment had an effect on opossum sex ratio.

There may be a lack of competition between raccoons and opossums at CTER due to differential habitat selection, prey switching by predators, biotic and abiotic factors and demographic stochasticity. S. M. Ginger (2002) analyzed habitat selection based on total trap captures at CTER and concluded that opossums were found more often in deciduous oak forests (approximately 42% of total captures) whereas raccoons were captured more often in cedar forests. Ladine (1995) noted that raccoons and opossums were trapped at different hours based on double trap sites. Ladine's finding suggested a reduced chance of interspecific interactions if the two species were not foraging at the same time of day. If raccoons and opossums are not being captured in similar habitats as predicted and if they foraged at different times, it may explain why competition between these two mesocarnivore populations at CTER was not evident.

A reduction in the raccoon population may tend to increase predation on opossums by other predators. Known predators of both raccoons and opossum such as owls, coyotes, and bobcats (Seidensticker et al. 1987) are present at CTER. Prey switching by these carnivores may have occurred in raccoon-removal pastures, and increased predator impact on the opossum population. My data on survival were ambiguous relative to this scenario.

The study pastures were not regulated for immigration and emigration of individuals of either species and the duration of the study was short. Physical barriers, such as enclosures, were not used to prevent animal movement into or out of all pastures. Opossum emigration from raccoon-removal sites may have occurred concurrently with experimental manipulation of the system, further decreasing opossum population size in raccoon-removal pastures. If barriers were placed to prevent animal movement and the field season extended another year, additional raccoon removal may have increased the opossum population in raccoon-removal pastures.

Other abiotic and biotic factors that influence animal populations were not assessed in this study. Factors influencing opossum population dynamics include food quality and availability, the presence/absence of water near dens, and climate. Climate was similar between the 2 areas, and was unlikely to have influenced area comparisons. If habitat quality (e.g., food availability, abundance and water associations) influenced opossum population growth, perhaps it was lower in raccoon-removal pastures, such that even in the absence of raccoons, adult females in raccoon-removal areas could not convert food energy into offspring (Hossler et al. 1994). These factors may have differed for treatment and non-removal pastures. I did not assess food abundance and availability. I also was unable to assess the amount of water available to opossums because many of the creeks and pools in both pasture types were ephemeral. Knowing that opossums frequently associate den sites with water (Lay 1942, Reynolds 1945, Llewellyn and Dale 1964, Gardner 1982, Seidensticker et al. 1987), water may have been an influential component on population dynamics regardless of competition.

Demographic stochasticity, or the variation in survival and reproduction that occurs because a population has a finite number of individuals with different characteristics (Ackakaya et al. 1999), may have strong influences on an opossum population, especially in a small area during a short time interval. The populations of both study areas were only about 40 individuals, and about 50% of those were adult females in March and May (Figure I.8). High survival of a few large litters could easily affect population estimates over a 1-year study and override any potential effects of raccoon-removal on population dynamics.

Results could have been improved if several changes were made to this study. To ensure complete removal of raccoons, I would have trapped over a longer period of time in enclosed areas. Enclosures may have prevented opossum immigration and emigration from one pasture to the next, maintaining population closure. Trapping during a longer time frame (2-3 years) would have made population estimates more robust because of higher captures; opossum population changes may have been more easily attributed to either competitive release or demographic stochasticity. Extending the trapping period and trapping over a larger area with increased replicates would have resulted in more precise estimates of population parameters. Estimates of survival rates from radiotelemetry data would have been improved if collars were equipped with mortality signals to determine exact fate of female opossums.

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Table I.1. Past treatments (1983-1999) of Cross Timbers Experimental Range, Payne County, Oklahoma.

	Treatment regime			
Treatment	Herbicide	Burn	Mechanical	Current habitat[a]
1	Tebuthiuron 1983	None	None	Cedar forest
2	Tebuthiuron 1983; P+D[b] 1997	1985, 86 87, 90, 93, 96, 99	None	Derived grassland
3	Triclopyr 1983; 2,4-D 1988; P+D[b] 1994, 1997	1993, 96, 99	Bulldoze and windrow cedar pre-1996; saw cedar post-1996	Mixed-brush forest
4	Triclopyr 1983; 2,4-D 1988	1985-1997, 1990, 1993, 1996, 1999	None	Derived grassland
5	None	None	None	Oak forest

[a]D. M. Engle, Department of Plant and Soil Sciences, Oklahoma State University, personal communication

[b]picloram + 2,4-D

Table I.2. Fates of telemetered female opossums in non-removal and raccoon-removal pastures from January 2000 to January 2001, at Cross Timbers Experimental Range, Payne County, Oklahoma. NR = non-removal pastures; R = raccoon-removal pastures.

Opossum ID	Capture location	Radio days monitored	Fate of opossum at date censored
207	NR	164	Unknown[a]
321	NR	137	Unknown[b]
245	NR	233	Dead
246	NR	220	Unknown[a]
257	NR	0	Unknown[a]
260	NR	187	Unknown[b]
262	NR	391	Unknown[a]
263	NR	154	Unknown[b]
401	NR	35	Unknown[a]
367	NR	143	Unknown[a]
370	NR	153	Dead
371	NR	138	Unknown[a]
377	NR	145	Unknown[a]
385	NR	63	Unknown[a]
386	NR	43	Unknown[a]
389	NR	165	Unknown[a]

Table I.2. (Continued)

Opossum ID	Capture location	Radio days monitored	Fate of opossum at date censored
183	R	0	Unknown[a]
273	R	127	Dead
275	R	19	Unknown[a]
279	R	321	Dead
281	R	65	Dead
303	R	111	Dead
316	R	52	Unknown[b]
333	R	156	Dead
399	R	31	Unknown[a]
335	R	122	Dead
355	R	67	Dead
356	R	150	Unknown[a]
361	R	169	Unknown[a]
414	R	6	Unknown[a]
435	R	1	Unknown[a]

[a] Collar and female opossum were never located.

[b] Collar was recovered and opossum was considered alive until last active signal.

Table I. 3. Model parameters and ΔAICc values for models examining survival (Φ) and capture probabilities (p) for opossums in non-removal and raccoon-removal pastures from January 2000 to January 2001 at Cross Timbers Experimental Range, Payne County, Oklahoma.

Model	ΔAICc	AICc weights	Number of parameters	Deviance
A. Φ(males*season), p(season)[a]	0.00	0.589	5	98.024
B. Φ(males*season, females*trt), p(season)[b]	2.03	0.214	6	97.864
C. Φ(males*season*trt,), p(season)[c]	2.95	0.134	7	96.570
D. Φ(males*season*trt, females*trt), p(season)[d]	5.05	0.047	8	96.413
E. Φ(sex*season*trt,), p(season)[e]	8.25	0.009	10	95.003
F. Φ(sex*trt,), p(season)[f]	9.69	0.004	6	105.532

[a] Survival varies for males by season (breeding, non-breeding) and capture probability varies by season (winter, non-winter) for both males and females.

[b] Survival varies for males by season (breeding, non-breeding), for females by treatment, and capture probability varies by season (winter, non-winter) for both males and females.

[c] Survival varies for males by season (breeding, non-breeding) and treatment, and capture probability varies by season (winter, non-winter) for both males and females.

[d] Survival varies for males by season (breeding, non-breeding) and treatment, females by treatment, and capture probability varies by season (winter, non-winter) for both males and females.

[e] Survival varies for both males and females by season (breeding, non-breeding) and treatment, and capture probability varies by season (winter, non-winter) for both males and females for males and females.

[f] Survival varies for both males and females by treatment, and capture probability varies by season (winter, non-winter) for both males and females.

Table I.4. Estimates from model averaging for apparent survival of male and female opossums during 2-month intervals in non-removal and raccoon-removal pastures from January 2000 to January 2001 at Cross Timbers Experimental Range, Payne County, Oklahoma.

Sex/Treatment	Season	Weighted average	Standard error
Male/Removal	non-breeding[a]	0.787	0.110
Male/Non-removal	non-breeding	0.757	0.112
Male/Removal	breeding[b]	0.316	0.106
Male/Non-removal	breeding	0.289	0.100
Female/Removal		0.638	0.083
Female/Non-removal		0.651	0.076

[a] August-February

[b] March-July

Figure I.1. Design layout of Cross Timbers Experimental Range, Payne County, Oklahoma including location of pastures used in raccoon-removal study. Each 32-ha pasture is labeled with two numbers; the first number is the replicate and the second is the treatment regime (1-Tebuthiuron; 2-Tebuthiuron + Fire; 3-Triclopyr; 4-Triclopyr + Fire; 5-Non-removal).

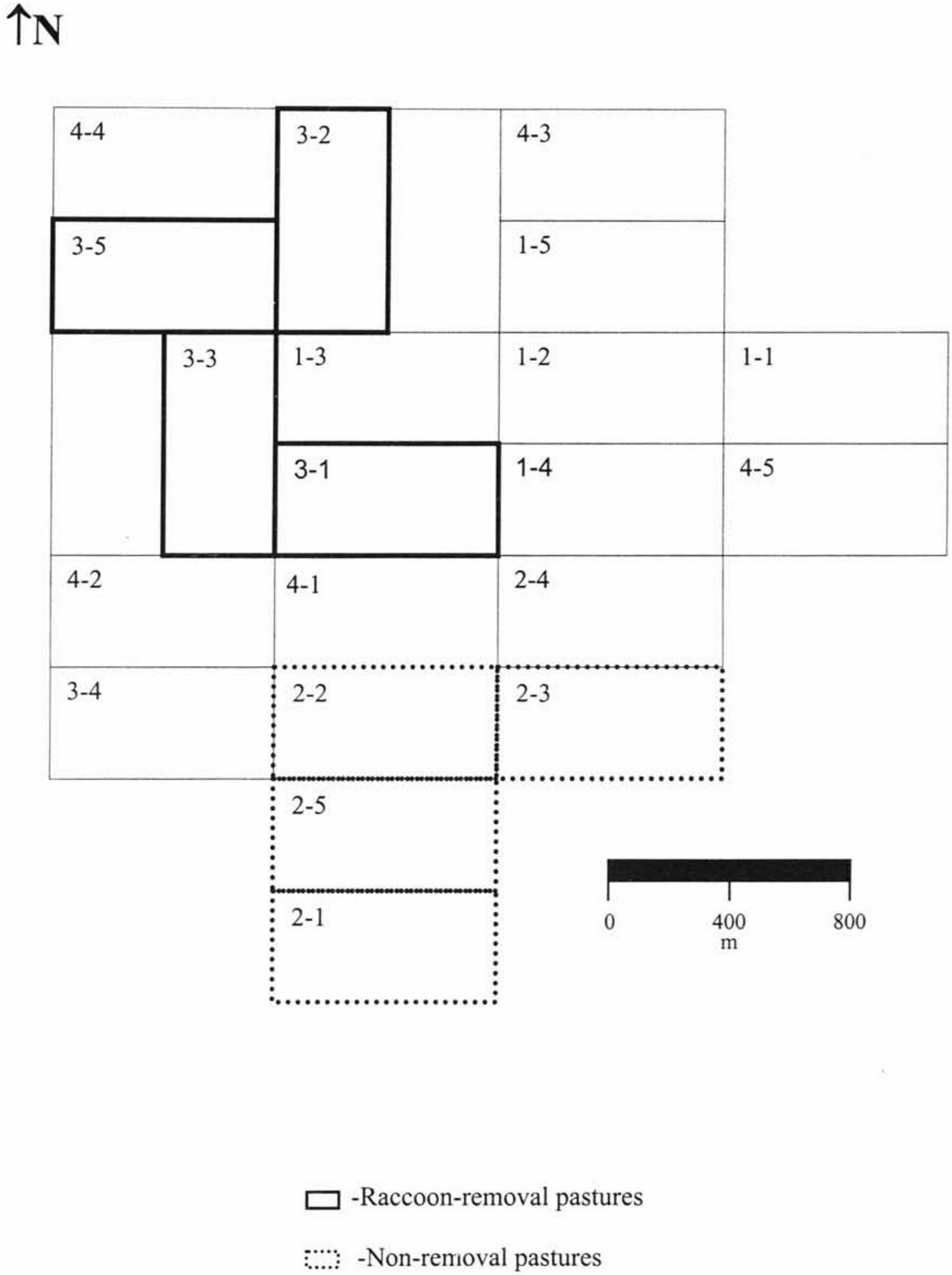

↑N
4-4
3-2
4-3
3-5
1-5
3-3
1-3
1-2
1-1
3-1
1-4
4-5
4-2
4-1
2-4
3-4
2-2
2-3
2-5
2-1
0
400
800
m
-Raccoon-removal pastures
-Non-removal pastures

Figure I.2. Design layout for trap placement in non-removal and treatment pastures at Cross Timbers Experimental Range, Payne County, Oklahoma.

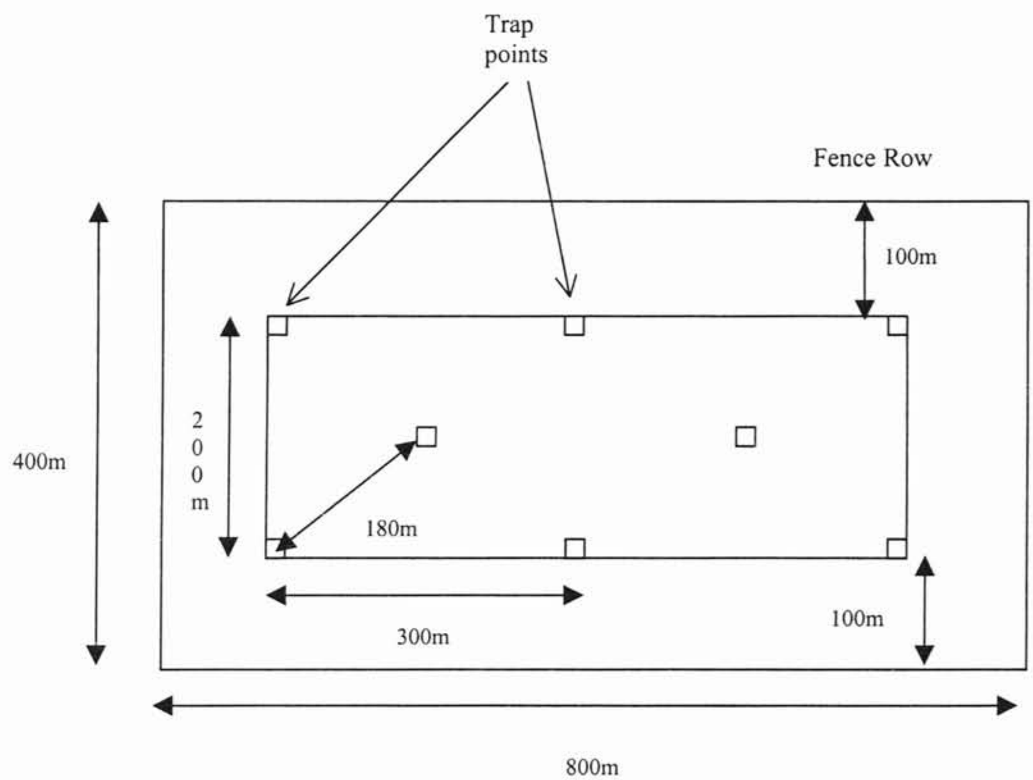
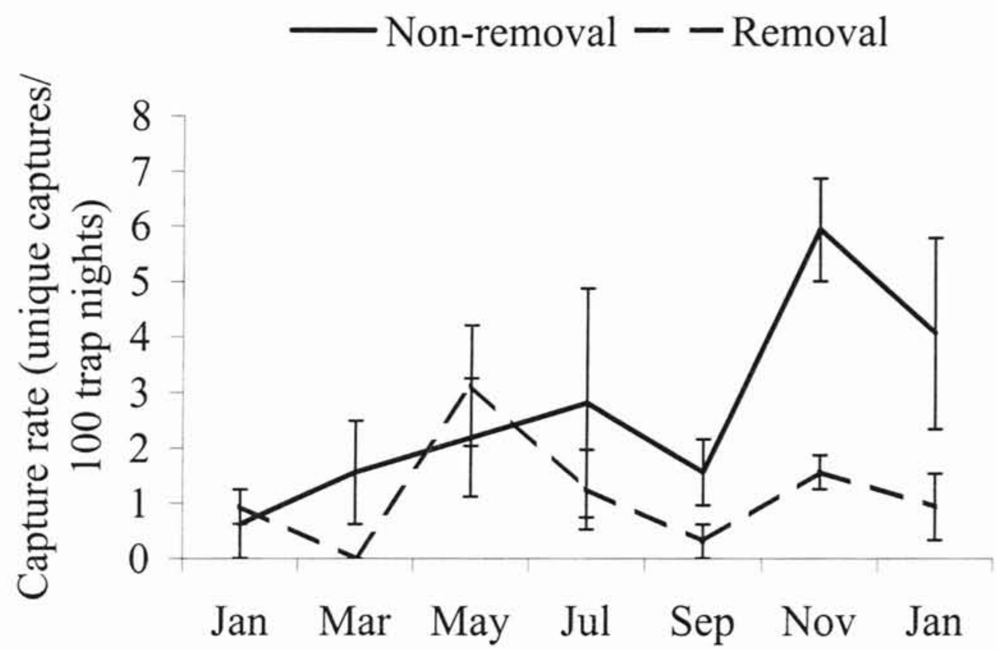
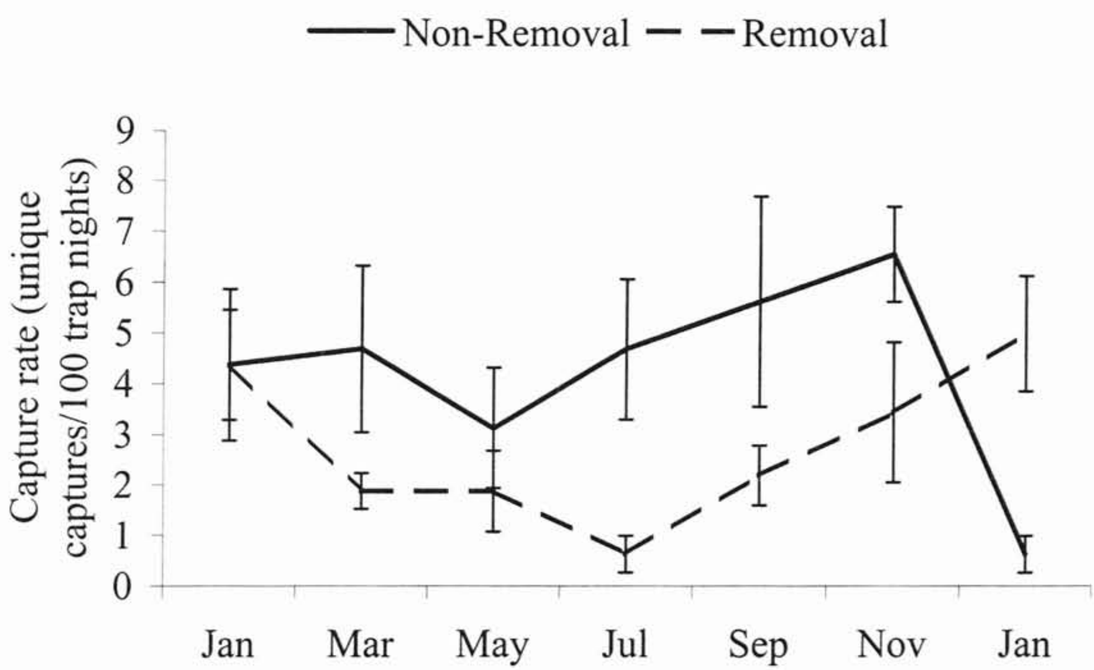

Trap
points
Fence Row
100m
400m
2
0
0
m
180m
300m
100m
800m

Figure I.3. Numbers of unique raccoon captures/100 trap nights in removal and non-removal pastures from January 2000 to January 2001, Cross Timbers Experimental Range, Payne County, Oklahoma. Bars represent standard error of the mean (n = 4 pastures/treatment).



Non-removal
Removal
Capture rate (unique captures/
100 trap nights)
8
7
6
5
4
3
2
1
0
Jan
Mar
May
Jul
Sep
Nov
Jan

Figure I.4. Numbers of unique opossum captures/100 trap nights in removal and non-removal pastures from January 2000 to January 2001, Cross Timbers Experimental Range, Payne County, Oklahoma. Bars represent standard error of the mean (n = 4 pastures/treatment).



Non-Removal
Removal
Capture rate (unique captures/100 trap nights)
0
1
2
3
4
5
6
7
8
9
Jan
Mar
May
Jul
Sep
Nov
Jan

Figure 1.5. Lincoln-Petersen estimates of opossum populations in raccoon-removal and non-removal pastures from January 2000 to January 2001, Cross Timbers Experimental Range, Payne County, Oklahoma. Bars represent 95% confidence intervals.

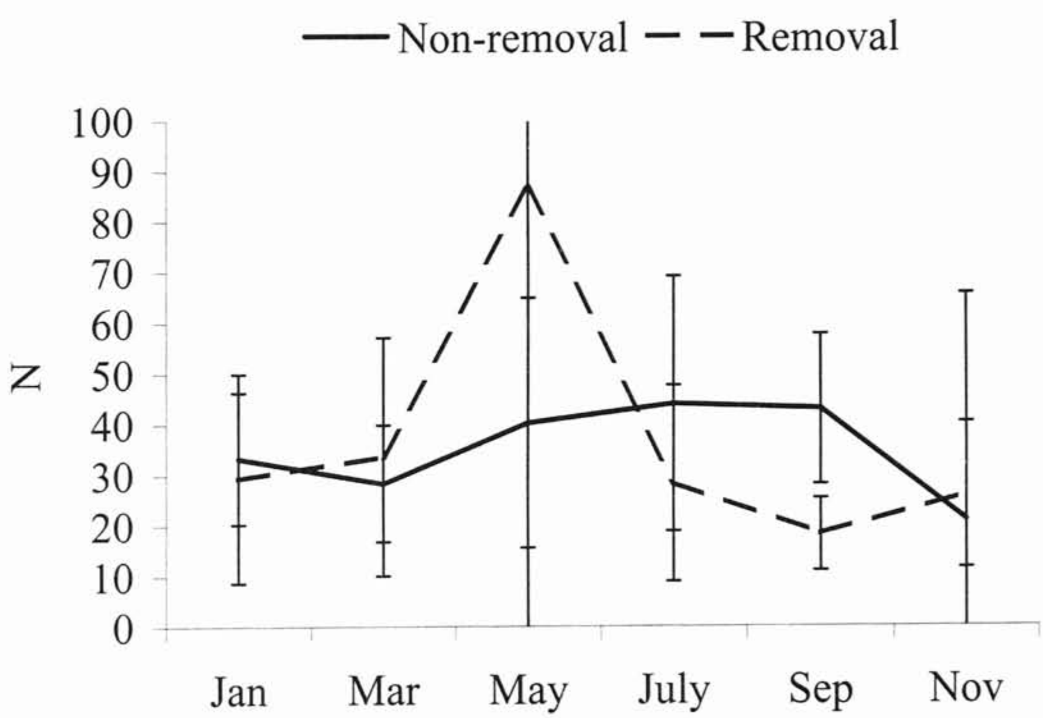

Non-removal
Removal
100
90
80
70
60
50
40
30
20
10
0
N
Jan
Mar
May
July
Sep
Nov

Figure 1.6. Density estimates of opossums in raccoon-removal and non-removal pastures from January 2000 to January 2001, Cross Timbers Experimental Range, Payne County, Oklahoma.

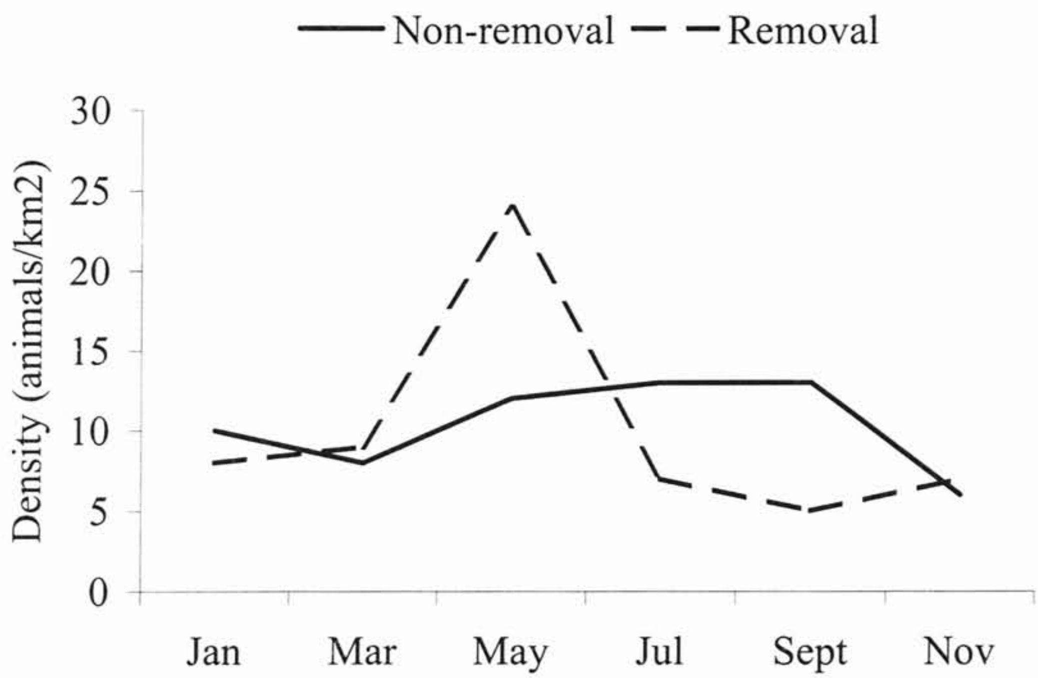
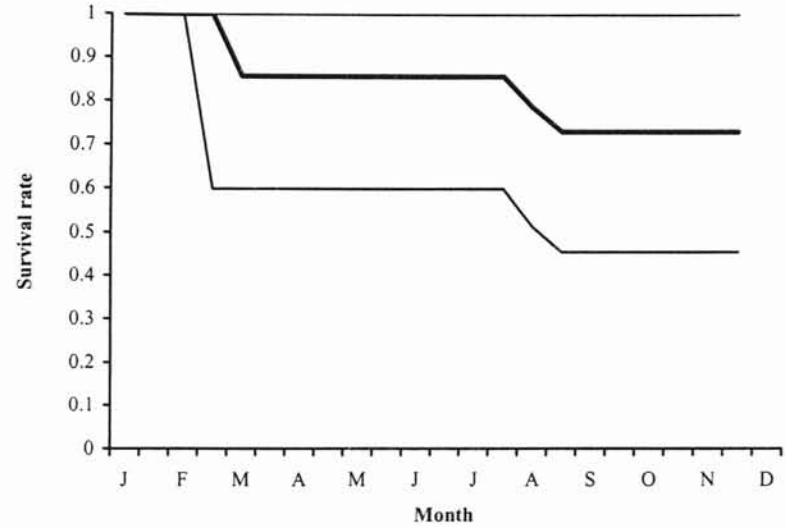

Non-removal
Removal
Density (animals/km2)
30
25
20
15
10
5
0
Jan
Mar
May
Jul
Sept
Nov

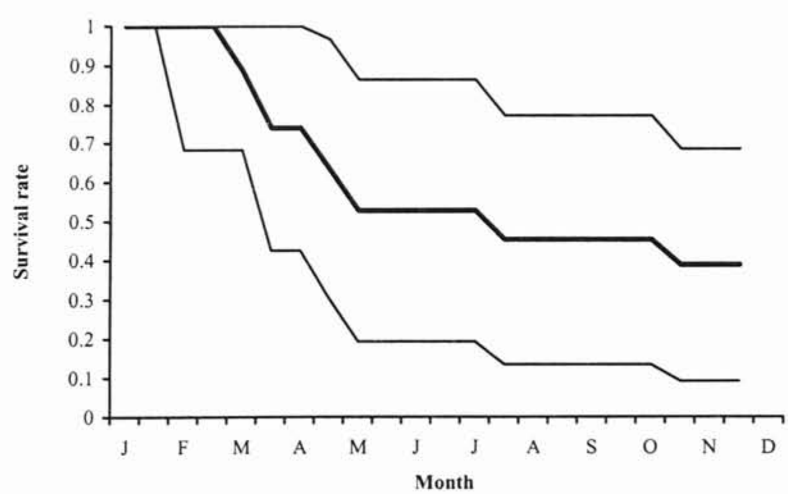
Figure 1.7. Maximum annual survival rate (± 95% C.I.) for adult female opossums in (a) non-removal and (b) raccoon-removal pastures from January 2000 to January 2001, Cross Timbers Experimental Range, Payne County, Oklahoma.

a)



Survival rate
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
J F M A M J J A S O N D
Month

b)



Survival rate
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
J F M A M J J A S O N D
Month

Figure 1.8. Average body mass of opossums captured in raccoon-removal and non-removal pastures from January 2000 to January 2001, Cross Timbers Experimental Range, Payne County, Oklahoma. Bars represent standard error of the mean.

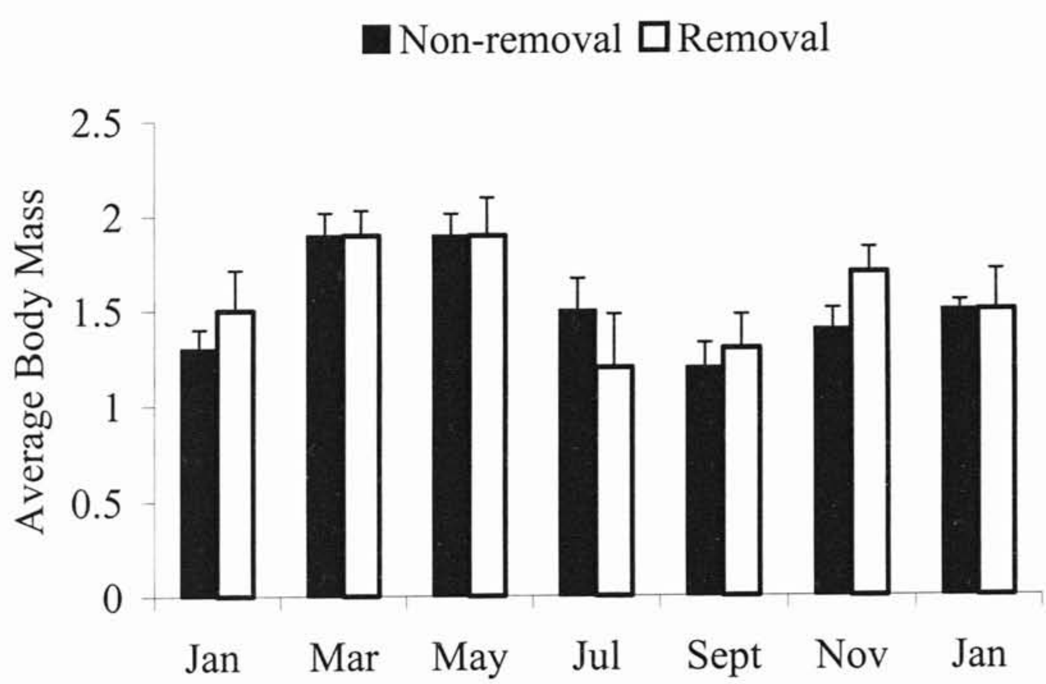

Non-removal
Removal
Average Body Mass
2.5
2
1.5
1
0.5
0
Jan
Mar
May
Jul
Sept
Nov
Jan

Figure 1.9. Sex ratio of adult opossums (females:males) by trapping period on non-removal and raccoon-removal pastures from January 2000 to January 2001, Cross Timbers Experimental Range, Payne County, Oklahoma. Total number of individuals used to produce ratio is above each bar.

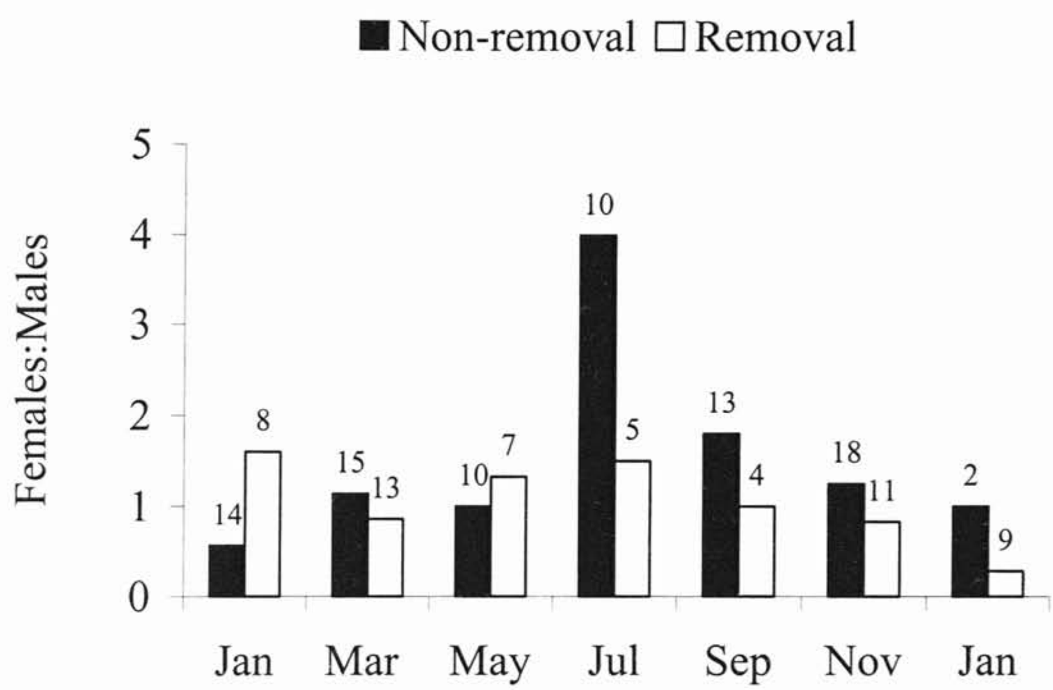
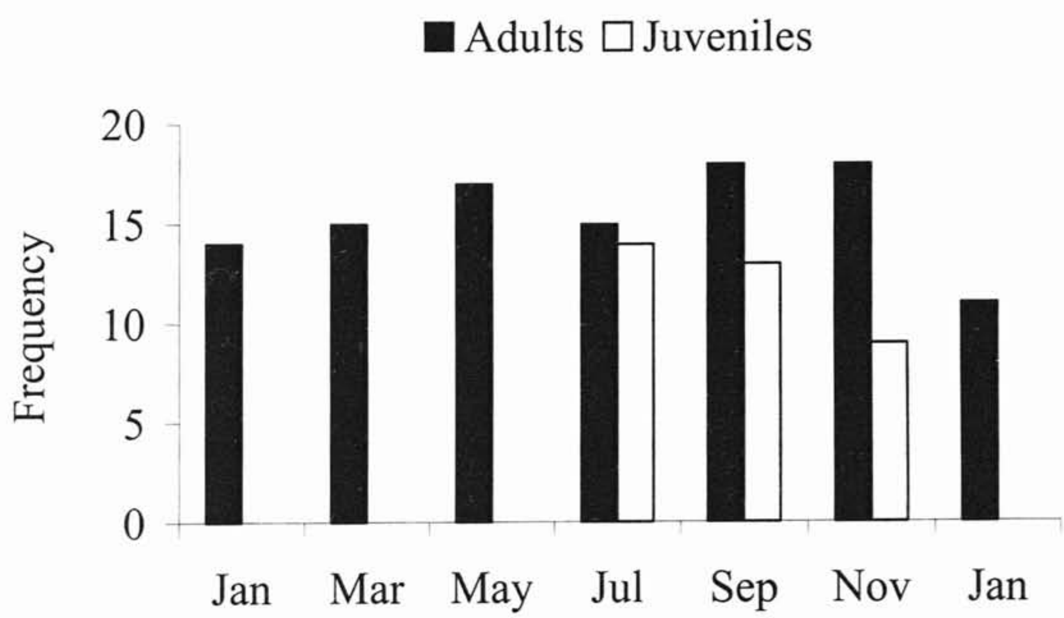

Non-removal
Removal
Females:Males
5
4
3
2
1
0
14
8
15
13
10
7
10
5
13
4
18
11
2
9
Jan
Mar
May
Jul
Sep
Nov
Jan

Figure I.10. Frequency of adult and juvenile opossums captured by trapping period on combined non-removal and raccoon-removal pastures, from January 2000 to January 2001, Cross Timbers Experimental Range, Payne County, Oklahoma.



Adults
Juveniles
Frequency
20
15
10
5
0
Jan
Mar
May
Jul
Sep
Nov
Jan

CHAPTER II

FOOD HABITS OF THE VIRGINIA OPOSSUM WITH AND WITHOUT RACCOON REMOVAL IN THE CROSS TIMBERS ECOSYSTEM, OKLAHOMA

ABSTRACT

Raccoons and opossums utilize similar habitats in the United States and share food preferences. I conducted a 1-year raccoon-removal study at the Cross Timbers Experimental Range, Stillwater, Oklahoma, and compared diets of opossums in non-removal and removal areas to assess the potential competitive influence of raccoons on opossum diets. A total of 75 scats were collected from 65 unique opossums captured in traps from non-removal (n = 28) and raccoon-removal (n = 47) pastures. Major food items were invertebrates, soft mast, grass and woody plant leaves. Principal component analysis with redundancy analysis revealed no difference in scat contents between treatments. Results from $\chi 2$ analysis suggested a lack of differences in major food items between opossum scats collected in non-removal and raccoon-removal pastures for the duration of the study. The lack of differences in diets of opossums in non-removal and raccoon-removal pastures suggests minimal interspecific food competition between raccoons and opossums at the spatial and temporal scale of this study. Interspecific competition for food may not occur at CTER because of differential habitat selection or diet partitioning between the two species.

INTRODUCTION

Food habit studies describe an animal's use of habitat and surrounding biota based on prey selection (Wood 1954). Studies examining interspecific competition in relation to food habits among rodents and marsupial carnivores of various sizes are common. Most studies have found larger species to competitively exclude smaller competitors through exploitative or interference competition (Jones and Barmuta 2000).

Interspecific interactions between three marsupial carnivores, Tasmanian devil (*Sarcophilus laniarius*), spotted-tailed quoll (*Dasyurus maculatus*) and eastern quoll (*D. viverrinus*), were examined in a Tasmanian study that determined niche differentiation based on diet overlap and morphological differences (Jones and Barmuta 2000). Eastern quolls were found more often in grassland habitats, whereas devils and spotted-tailed quolls preferred rainforest areas. The study concluded habitat partitioning between adult male spotted-tailed quolls and adult devils and between adult female spotted-tailed quolls and adult eastern quolls occurred when diets overlapped. Spotted-tailed quolls consumed greater amount of arboreal prey than the other 2 species. Food partitioning occurred between devils and spotted-tailed quolls because heavy-bodied devils lack climbing adaptations and are mostly terrestrial. Spotted-tailed quolls capitalized on arboreal prey by climbing trees with a well-developed hallux, whereas devils and eastern quolls remained close to the ground, ambushing their prey (Jones and Barmuta 2000).

Dickman (1986) reported interspecific competition for food type and size between *Antechinus stuartii* and *A. swainsonii* in Australia. He conducted a removal experiment removing the larger *A. swainsonii* from 2 out of 5 enclosures, keeping a non-removal enclosure where both species coexisted, and removing the smaller *A. stuartii* from 2 more enclosures. In a final step, he reintroduced the removed species from their respective enclosures to ensure that changes in resource shifts were due to removal effects rather than enclosure effects. Removal of *A. swainsonii* had clear effects on *A. stuartii*, but not the converse. Scats collected from traps revealed that *A. stuartii* ate a greater variety of prey sizes in the absence of *A. swainsonii*, switching its diet from arboreal prey (Aranea and Hemiptera) when the larger competitor was present to terrestrial prey (Isoptera larvae, Dermaptera, and Amphipoda).

The food habits of mesocarnivores, such as raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*), have been investigated for comparative purposes without determining interspecific interactions (Hamilton 1951, Wood 1954, Stieglitz and Klimstra 1962). Opossums and raccoons consume similar prey items, thereby increasing the potential for interspecific interactions that may lead to exploitative and/or interference competition (Ladine 1997). They occur in similar habitat types throughout their range and habitat-use overlap has been recorded as high as 95% (Kissell and Kennedy 1992). Ladine (1995) found that raccoons and opossums used available habitat during different hours based on the absence of dual species captures at double-trap sites. The presence of larger raccoons may force smaller opossums to forage at different times, suggesting competitive exclusion pressures for habitat use and potentially affecting opossum prey selection (Ladine 1997).

Several studies have determined that opossums and raccoons consume similar prey items, but have slight differences in preference. These studies analyzed scat and/or digestive tract (stomach, small intestine, and colon) contents for diet determination. Opossums are omnivorous, but prefer small-animal prey, such as insects (Lay 1942, Reynolds 1945, Wood 1951; Table II.1). Carrion, rodents, and other opossums are the most common mammalian prey (Sandidge 1953, Stieglitz and Klimstra 1962). Plants constitute a large portion of opossum diets (Lay 1942, Reynolds 1945, Wood 1954 and

Stieglitz and Klimstra 1962). Raccoons are also omnivorous generalists. Raccoons consume insects, but eat hard and soft plant matter more frequently (Hamilton 1951, Wood 1954). They prefer fruits such as grapes (*Vitis* spp.), apples (*Malus* spp.), and persimmons (*Diospyros* spp.), as well as acorns and corn (*Zea mays*). Aquatic invertebrates are consumed in greater numbers than vertebrates. Of the mammals eaten, rodents are most prevalent. Raccoons also eat bird and reptile (e.g., *Chelydra serpentina*, *Alligator mississippiensis*) eggs (Wood 1954, Kaufman 1982, Sanderson 1987).

Manipulation of the natural system by adding or removing individuals is necessary to understand whether resources are partitioned and competition is involved in structuring a community (Schoener 1974). To determine whether competition exists between raccoons and opossums, I conducted a raccoon-removal study to assess the effects of raccoon absence on opossum ecology at the Cross Timbers Experimental Range (CTER) in Payne County, Oklahoma. Specifically, the objectives of this paper were to identify changes in opossum diet following raccoon removal. I predicted opossums living in raccoon-removal sites would have better access to food of higher nutritive value because of release associated with removal of a larger, dominant competitor.

STUDY AREA

CTER is located 11 km southwest of Stillwater, Payne County, Oklahoma (36°02'40" to 36°04'20"N, 97°09'30" to 97°11'39"W). It has been studied since 1982 to determine the effects of different methods of rangeland management on vegetation (Ewing et al. 1984, Engle et al. 1991, Stritkze et al. 1991), livestock production and wildlife. It is composed of 22 32.4-ha pastures totaling 712 ha. CTER pastures were assigned different treatment regimes within 4 randomly located replicates of 5 experimental treatments (Table II.2). Four distinct habitat types exist at CTER as a result of the treatments that differentially influenced conifer and deciduous tress and shrubs (D. M. Engle, Department of Plant and Soil Sciences, Oklahoma State University, personal communication). The habitat types were classified by Levesque (2001) and are as follows: redcedar forest, derived grassland, mixed-brush community, and mature oak forest.

METHODS

Experimental Design and Methods

My study site was composed of 4 experimental and 4 non-removal pastures (Figure II.1). Each set of pastures was composed of a replicate block (i.e., non-removal and raccoon-removal pastures included the same 4 land management prescriptions). I trapped bi-monthly in both sets of pastures from January 2000 to January 2001 for 10-day periods. Animals were trapped using Tomahawk live traps (Tomahawk Trapping Company, Tomahawk, Wisconsin, USA) baited with sardines. Trapping grids for all pastures were arranged in a 3 x 5 grid containing 8 traps. Traps were placed 100 m from the edges of pastures, 300-m apart along parallel transects spaced at 200-m intervals, with 2 interior traps placed 180 m diagonally from the corners (Figure II.2; Levesque 2001). Eight traps were placed between non-removal and treatment pastures as buffers to minimize raccoon immigration from non-removal to raccoon-removal pastures. I checked traps daily and re-baited every 5 days and as needed during the 10-day trapping sessions. Once handling procedures were completed, I released opossums at their point of capture on treatment pastures. I transferred raccoons from removal pastures by truck and released them at a location, across a 4-lane highway, approximately 11km east of the removal sites.

I evaluated opossum diet from the collection and analysis of scat found at trap sites from both removal and non-removal pastures. I collected scats only from opossums caught in traps that had deposited scats. I assumed that opossums captured in a particular pasture fed in that pasture. Date of collection, animal identification number, sex, and location of collection (pasture type and trap site) were recorded. Scats collected from recaptured individuals on different days were considered separate samples. Collected scats were stored in a freezer until the end of each trapping period when I processed them for analysis. Raccoon scats were not collected because captured raccoons did not leave scats in traps.

I placed frozen scats in a sieve (USA Standard Testing Sieve, No. 30, Opening 600 mm Tyler equivalent, W.S. Tyler Incorporated, Mentor, Ohio 44060), soaked them in warm water to thaw and rinsed them again for further removal of soil particles. Wet, digested food items were air-dried in an oven at 60 °C for several hours until water had completely evaporated. Dried particles were separated with tweezers in a plastic petri dish, and then placed under a dissecting scope (50X magnification) for identification. I identified all prey items found, regardless of abundance per scat, and categorized them as mammal, bird, amphibian, reptile, invertebrate, plant mast (mast = fruit; soft and hard), leaf (grasses, woody plants [hardwoods and *Juniperus virginiana*], forbs), groom hair, root, or moss. Data was recorded for each scat as presence/absence of individual food categories.

Diet Composition

I used principal component analysis (PCA) and redundancy analysis (RDA; Gurnell 1996, Legendre and Legrendre 1998) using the program CONOCO (ter Braak and Smilauer 1988) for data analysis. For the PCA, I considered food items as species, scats as samples, and time (winter [January, March] 2000, summer [May, July] 2000, and winter [November 2000, January 2001) was used as a covariable.

Food Items

I summarized food items based on frequency of occurrence (Litvaitis et al. 1996) for scats collected in raccoon-removal and non-removal pastures. I used χ^2 analysis to compare distributions of food items in raccoon-removal and non-removal pastures during the entire study. Frequency of occurrence data were converted to proportional frequency to calculate Levins' index (Levins 1968):

$$B = (\sum p_i^2)^{-1}$$

where p_i is the proportional use of a food item relative to other food items. B ranges from 1 to n (n = total number of food item categories) and was used to calculate diversity of diets annually and seasonally for raccoon-removal and non-removal pastures. Diversity was standardized to a scale of 0.0 to 1.0 using Hurlbert's method (Krebs 1989):

$$B_s = (B-1)/(n-1)$$

where B = Levins' measure of diversity and n = number of food categories. Diversity indices and seasonal comparisons of percent occurrence were not statistically analyzed and are provided for descriptive purposes. A significance level of $\alpha = 0.05$ was chosen for all analyses.

RESULTS

A total of 75 scats were collected, with 47 and 28 scats collected in raccoon-removal and non-removal pastures, respectively. Scats were collected during every month for both treatments, except for non-removal pastures during January 2001 because opossums in those pastures left no scats.

Diet Composition

The RDA indicated no effect of raccoon removal on opossum diet ($P = 0.28$). The most important axis for the partial PCA graph (Figure II.3) was the first axis, with an eigenvalue of 0.18. Axis one explained 18% of the variation within the sample set. Invertebrates, plant soft mast, and woody plant leaves were negatively correlated with axis 1. Scats containing roots, moss and forb leaves were most likely to not contain woody plant leaves, invertebrates and plant soft mast. Scats with mammals and grass leaves were most likely to not contain plant hard mast, birds and groom hair. Scats from neither group had a strong relationship with either axis on this graph. Reptile and amphibian remains did not occur in scats.

Food Items and Diet Diversity

No frequency of occurrence of food categories varied between raccoon-removal and non-removal pastures ($\chi^2_{12} = 0.99$, $P > 0.05$; Table II.3). Levins' index for food diversity for scats across all seasons was $Br_s = 0.56$ and $Bc_s = 0.45$ in raccoon-removal and non-removal pastures, respectively. Food diversity was slightly higher for scats found in raccoon-removal pastures during winter and summer 2000 (Table II.4). The increase in soft mast was mainly due to a high occurrence of fruit from eastern red cedar. Percent occurrences of food items varied due to season (Table II.5).

DISCUSSION

Opossums at CTER consumed largely invertebrates (insects), soft mast (e.g., *J. virginiana*), and leaves from grasses and woody plants (*Quercus* spp). Occurrences for food items measured at CTER varied from other studies (Table II.1). Variation in percent occurrence was likely due to differences in habitat, food availability, timing of collection, or sample size. Mammal occurrence in CTER scats was similar to mammal occurrence in scats from central Missouri (Reynolds 1945) and Kansas (Sandidge 1953). Parts of CTER resemble the Post Oak Woods area of eastern Texas, where post oak (*Quercus stellata*) and black jack oak (*Quercus marilandica*) are the dominant tree species. Raccoon-removal scats had similar mammal occurrence as scats in eastern Texas (Wood 1954). Occurrence of mammals in CTER scats was most different from southern Illinois (Stieglitz and Klimstra 1962).

Invertebrate prey, such as insects, is very important in opossum diets. Occurrence of insects in CTER scats were most similar to scats collected in central Missouri (Reynolds 1945) and Kansas (Sandidge 1953), slightly lower than scats in southern Illinois (Stieglitz and Klimstra 1962), but least similar to opossum scats in eastern Texas (Wood 1954). Raccoon-removal scats closely resembled southern Illinois scats (Stieglitz and Klimstra 1962) in bird occurrence. CTER scats did not contain amphibians. Diet analysis studies in eastern Texas (Wood 1954) and southern Illinois (Steiglitz and Klimstra 1962) were the only studies to have amphibian occurrence and at a relatively low occurrence to other food items. Finally, plants were common in scats from all other studies. Opossum scats from CTER most resembled scats in central Missouri (Reynolds 1945) and east Texas (Wood 1954).

I had predicted that food items in opossum scats from raccoon-removal pastures should have varied from those in non-removal pastures due to competitive release. Levins' indices for raccoon-removal pastures were higher for all seasons except winter 2001, which had small samples. Raccoon-removal scats were slightly more diverse in food type rather than non-removal scats. However, these differences may be due to differences in food availability in non-removal and treatment groups, individual opossum preferences, and uneven sample sizes rather than competitive release.

Competition for food resources between raccoons and opossums may be minimized if they partition habitats. Opossum capture rates were higher in oak forest at CTER, whereas raccoons were more likely to be captured in cedar forests (Levesque 2001; S. M. Ginger, Department of Zoology, Oklahoma State University, unpublished data). Opossum scats from raccoon-removal pastures had a higher percent occurrence of cedar fruit. This finding coincides with analyses regarding microhabitat selection of opossums at CTER, where opossums occupied more cedar forest habitat during this study period in raccoon-removal pastures (S. M. Ginger, Department of Zoology, Oklahoma State University, unpublished data), and hints at a subtle diet shift in the absence of raccoons.

The lack of evidence for interspecific competition between raccoons and opossums at CTER would be better supported if food abundance and availability had been concurrently assessed on pastures in non-removal and raccoon-removal areas. Availability data would have allowed assessment of opossum diet selection, not merely use, in the 2 areas. In addition, the diversity of raccoon and opossum diets makes it more difficult to detect diet partitioning than in studies of obligate carnivores (Jones and Barmuta 2000).

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Table II.1. Opossum diets based on percent volume and occurrence of foods from previous diet analysis studies.

Food category	% Volume	% Occurrence	Reference	Collection Period
Mammals	7		Lay 1942	September
		28.2	Reynolds 1945	September - May
		33.3	Sandidge 1953	September - March
		14.9	Wood 1954	Annual
		76.3	Stieglitz and Klimstra 1962	August - February
Insects	45		Lay 1942	September
		87.6	Reynolds 1945	September - May
		86.7	Sandidge 1953	September - March
		25	Wood 1954	Annual
		93.1	Stieglitz and Klimstra 1962	August - February
Birds	4.3		Lay 1942	September
		8.9	Reynolds 1945	September - May
		21.7	Sandidge 1953	September - March
		3.8	Wood 1954	Annual
		19.1	Stieglitz and Klimstra 1962	August - February

Table II.1. (Continued).

Food category	% Volume	% Occurrence	Reference	Collection Period
Amphibians			Lay 1942	September
			Reynolds 1945	September - May
			Sandidge 1953	September - March
		7.4	Wood 1954	Annual
		5.3	Stieglitz and Klimstra 1962	August - February
Plants	33.4		Lay 1942	September
		63.3	Reynolds 1945	September - May
		13.3	Sandidge 1953	September - March
		44.8	Wood 1954	Annual
		100	Stieglitz and Klimstra 1962	August - February

Table II.2. Past treatments (1983-1999) of Cross Timbers Experimental Range, Payne County, Oklahoma.

	Treatment regime			
Treatment	Herbicide	Burn	Mechanical	Current habitat[a]
1	Tebuthiuron 1983	None	None	Cedar forest
2	Tebuthiuron 1983; P+D[b] 1997	1985, 86 87, 90, 93, 96, 99	None	Derived grassland
3	Triclopyr 1983; 2,4-D 1988; P+D[b] 1994, 1997	1993, 96, 99	Bulldoze and windrow cedar pre-1996; saw cedar post-1996	Mixed-brush forest
4	Triclopyr 1983; 2,4-D 1988	1985-1997, 1990, 1993, 1996, 1999	None	Derived grassland
5	None	None	None	Oak forest

[a]D. M. Engle, Department of Plant and Soil Sciences, Oklahoma State University, personal communication

[b]picloram + 2,4-D

Table II.3. Percent occurrence of food items in opossum scats from non-removal and raccoon- removal pastures in Cross Timbers Experimental Range, Payne County, Oklahoma, 2000-2001.

Food category		Raccoon-Removal (n = 47)	Non-removal (n = 28)	Overall (n = 75)
		%		
Animals				
	Mammals	15	43	25
	Birds	17	11	15
	Invertebrates	57	71	63
	Reptiles	0	0	0
	Amphibians	0	0	0
Fruit	Hard mast	11	14	12
	Soft mast	40	32	37
Herbaceous	Leaves-grass	64	64	64
	Leaves-forbs	17	11	15
	Leaves-woody	51	71	59
Other	Root	38	29	35
	Moss	2	0	1
	Groom hair	19	18	20

Table II.4. Levins's index (1968) for food diversity for opossum scats in non-removal and raccoon-removal pastures by season in Cross Timbers Experimental Range, Payne County, 2000-2001.

Treatment	Winter 2000	Summer 2000	Winter 2001
Non-removal	0.44	0.36	0.29
Raccoon-Removal	0.49	0.43	0.26

Table II.5. Percent occurrence of food items in opossum scats, by season, from non-removal and raccoon- removal pastures in Cross Timbers Experimental Range, Payne County, Oklahoma, 2000-2001. R = Removal pastures, NR = Non-removal pastures

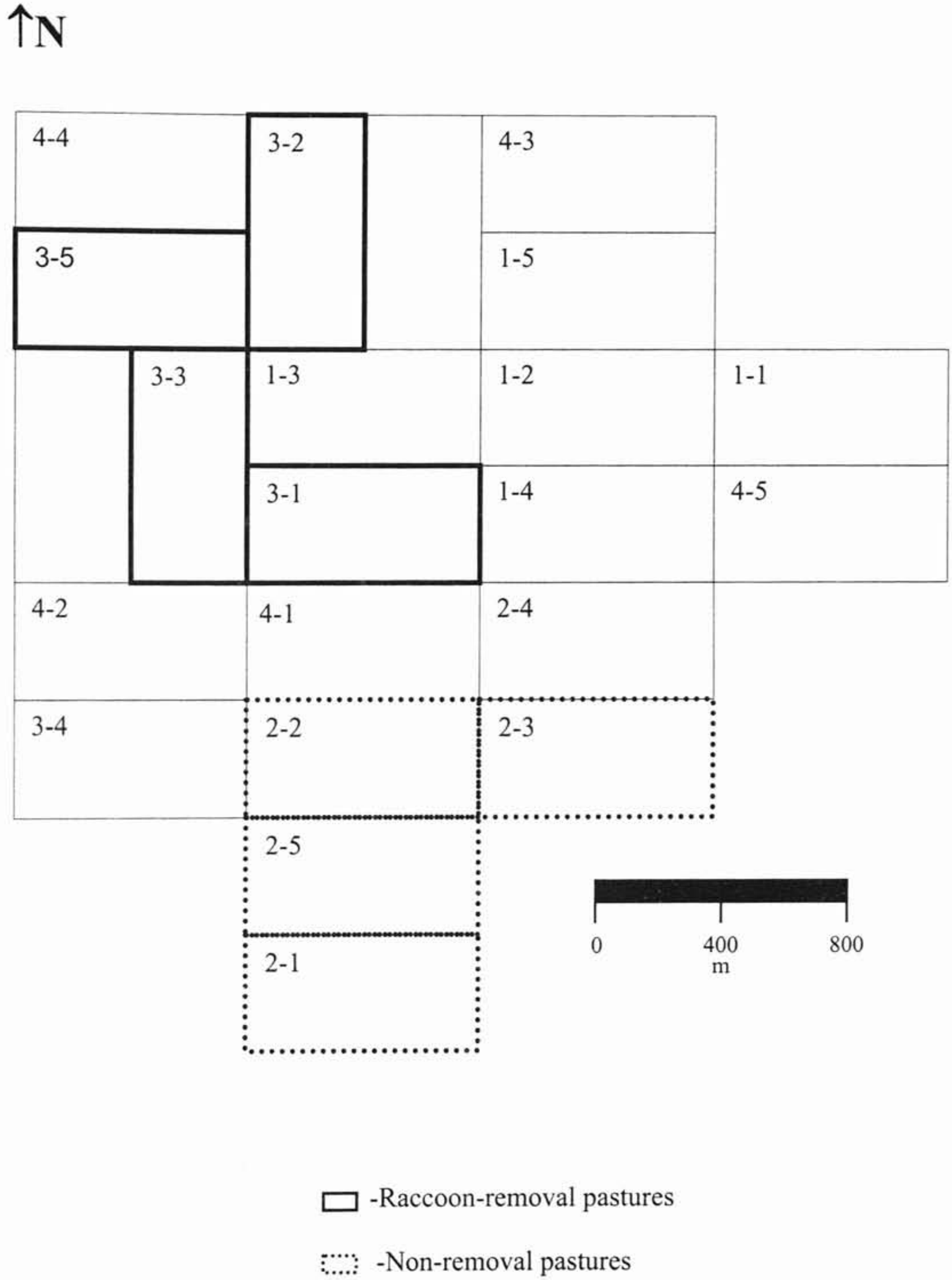
	Winter 2000[a]		Summer 2000[b]		Winter 2001[c]	
Food category	NR (n = 15)	R (n = 22)	NR (n = 10)	R (n = 11)	NR (n = 2)	R (n = 6)
Mammals	20%	33%	60%	18%	100%	0%
Birds	20%	33%	0%	9%	0%	33%
Invertebrates	93%	100%	60%	45%	0%	33%
Reptiles	0%	0%	0%	0%	0%	0%
Amphibians	0%	0%	0%	0%	0%	0%
Hard mast	27%	33%	0%	0%	0%	0%
Soft mast	33%	93%	40%	36%	0%	0%
Leaves-grass	87%	73%	20%	73%	100%	67%
Leaves-forbs	0%	0%	10%	18%	50%	33%
Leaves-woody	87%	100%	70%	36%	0%	0%
Root	20%	27%	20%	45%	100%	17%
Moss	0%	7%	0%	0%	0%	0%
Groom hair	33%	53%	0%	0%	50%	0%

[a]winter = January and March

[b]summer = May and July

[c]winter = November and January 2001

Figure II.1. Design layout of Cross Timbers Experimental Range, Payne County, Oklahoma including location of pastures used in raccoon-removal study. Each 32-ha pasture is labeled with two numbers; the first number is the replicate and the second is the treatment regime (1-Tebuthiuron; 2-Tebuthiuron + Fire; 3-Triclopyr; 4-Triclopyr + Fire; 5-Non-removal).



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-Non-removal pastures

Figure II.2. Design layout for trap placement in non-removal and treatment pastures at Cross Timbers Experimental Range, Payne County, Oklahoma.

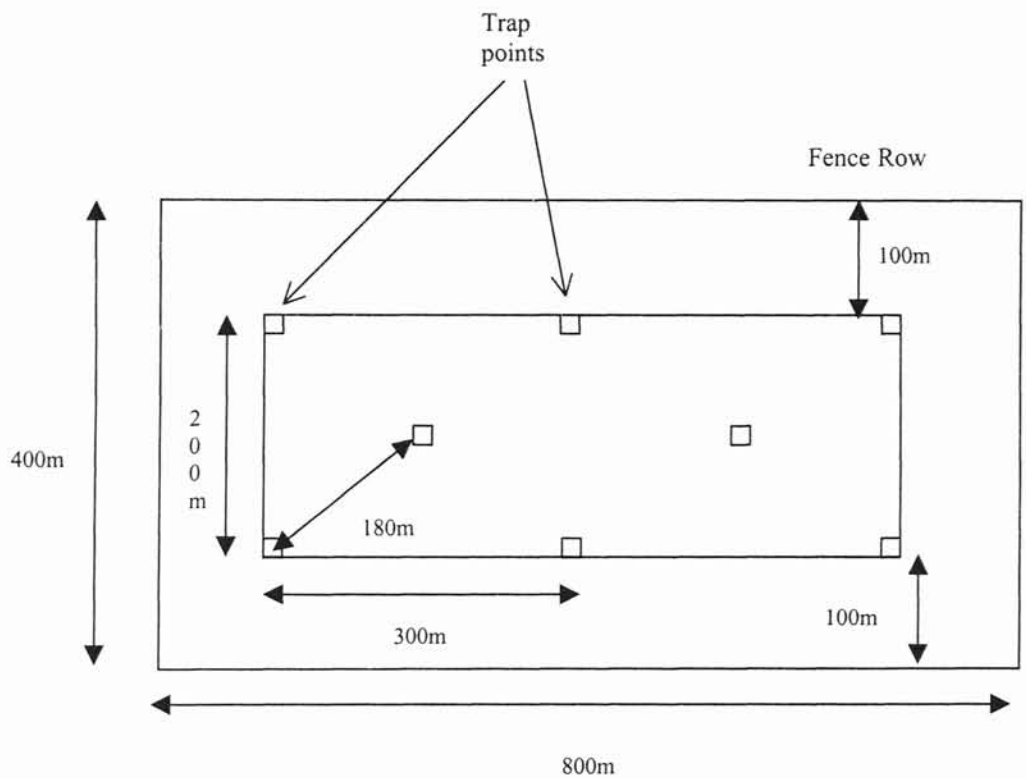
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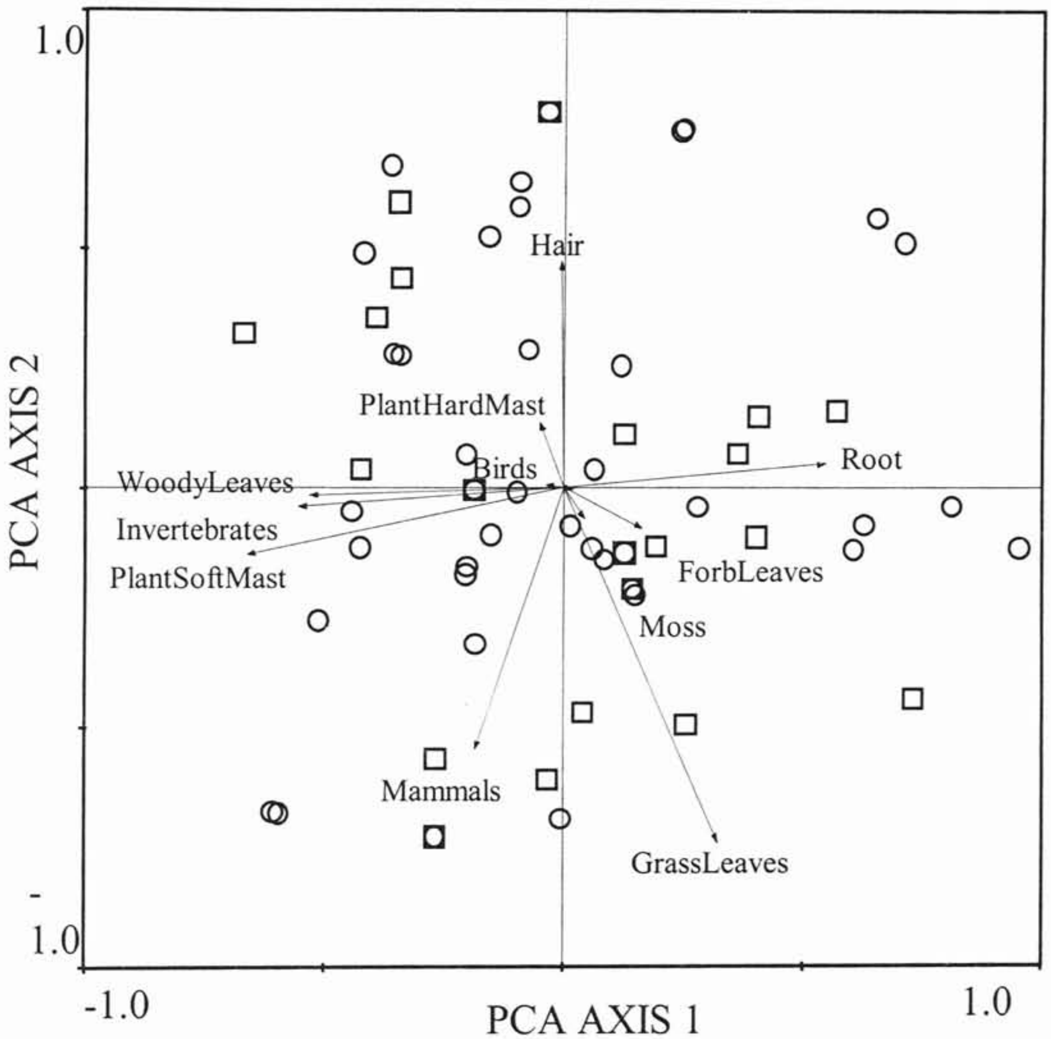
Figure II.3. Principal component analysis exploring relationships of food items found in opossum scat in non-removal and raccoon- removal pastures, Cross Timbers Experimental Range, Payne County, Oklahoma 2000-2001. Squares = removal scats; Circles = non-removal scats.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Invertebrates
PlantSoftMast
Root
ForbLeaves
Moss
Mammals
GrassLeaves