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DISTRIBUTION AND OCCURRENCE OF CARNIVORES IN THE OKLAHOMA PANHANDLE

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A Dissertation APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

BY

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For teaching me how to learn

To

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ABSTRACT

Carnivores were sampled in the Oklahoma panhandle from October 1995 to February 1997 using aluminum, baited tracking plates and infra-red triggered cameras. Carnivore distributions on regional, landscape and local scales were examined using traditional univariate statistical techniques. A model of carnivore distribution in the panhandle was also developed using remotely sensed Advanced Very High Resolution Radiometer (AVHRR) data and logistic regression.

Five carnivore species representing three families were detected sufficiently to permit analysis. Carnivores were, in general, not distributed evenly over regional, landscape and local scales in the panhandle environment. Carnivores were also found to impact each others distributions both locally and at landscape level scales. Logistic regression modeling determined that carnivore distributions and canid distributions in particular, could be modeled according to their affiliations with remotely sensed Normalized Difference Vegetation Index data (NDVI) in the Oklahoma panhandle. This model provides a framework for predicting carnivore occurrence in habitats based upon remotely sensed vegetation spectral data.

CHAPTER 1

INTRODUCTION AND METHODS

INTRODUCTION

As a group, carnivores represent a unique set of mammals. The Order Carnivora is comprised of 11 families and approximately 271 species (Wilson and Reeder, 1993). Additionally, although most carnivores possess carnassial teeth, diets among carnivores can range from strict meat eaters or bone crushers to pure scavengers, very generalized omnivores or even primarily herbivores, as in the case of the giant panda (*Ailuropoda melanoleuca*) (Feldhamer et al., 1999). Such vast variation within such a relatively small group has naturally fostered a great deal of interest and research on the order. However, most research has focused on single carnivore species, their physiology, behavior, and/or ecology (Boness et al., 1998; Frank, 1996; Carbyn et al., 1995; Buskirk and McDonald, 1989; Koehler and Hornocker, 1989; Mills, 1989; Schaller et al., 1989; Seal et al., 1989). Some more recent studies (particularly ecological studies) have examined groups of carnivores, carnivore guilds, or relationships (both systematic and ecological) between closely related carnivores (Bueno, 1996; Waser, 1996; Buskirk et al., 1994; Murray et al., 1994; Dayan et al., 1989; Gorman and Trowbridge, 1989; McNab, 1989; Sunquist and Sunquist, 1989). However, few studies have examined naturally occurring carnivore assemblages in specific environments.

Another recent trend in ecological studies has been to focus on the impact of landscape level features on the distributions of organisms (Brown, 1995; Edwards et al., 1994; Miller et al., 1994; Stone and Roberts, 1990). Contemporary ecological research has often been aimed at determining which dynamics, outside of local processes, explain species/group distributions and patterns (Marquet, 1994; Gaisler et al., 1991).

In Oklahoma, few comprehensive investigations of carnivores have ever been undertaken (Kilgore, 1969; Glass, 1956). Most of the information on carnivores in the state has occurred in conjunction with and ancillary to projects focused on other vertebrates (Peoples and DeMaso, 1996; Shackford and Tyler, 1991; Shackford et al., 1989). This study had five objectives. The first objective was to survey the swift fox (*Vulpes velox*) in the Oklahoma panhandle. Particular emphasis was placed upon the efficiency of detection and survey techniques as well as the specific status of the swift fox across the entire panhandle and between panhandle habitats. Habitats were identified primarily by vegetation, geological/hydrological features, and/or land use. Presently, there exist four broadly classified types of habitat in the Oklahoma panhandle: mesa, riparian areas, grassland/range, and agriculture. Determining if and how swift foxes differentially utilized these unique habitats was an important focus of this project.

The second objective was to determine the distributions of all other detected carnivores across the Oklahoma panhandle and between the major habitats. Historically, the Oklahoma panhandle has supported a diverse carnivore community. Carnivores from the region include 17 species in five families (Caire et al., 1989) (Table 1-1). Four species, gray fox (*Urocyon cinereoargenteus*), western spotted skunk (*Spilogale gracilis*), hog-nosed skunk (*Conepatus mesoleucus*), and ringtail (*Bassariscus astutus*), are thought to be restricted to a small mesa physiographic region in the northwesternmost corner of the Oklahoma panhandle (Caire et al., 1989). The others are more widely distributed and may be found throughout the panhandle. Examining patterns of carnivore distributions and habitat use were also central themes of this project.

The third objective was to examine whether carnivore distributions and habitat affinities were influenced by the distributions or presence of other carnivore species. Specifically, do different carnivore species (particularly closely related carnivore species) in the Oklahoma panhandle occur together regionally, or in specific habitats, more or less than would be expected by chance? In this way, I could examine not only the effects of large scale factors such as habitat on carnivore distributions, but also how local processes influence where carnivores occur. This approach has provided for a better, more comprehensive understanding of carnivore interactions and distributions in the Oklahoma panhandle.

The fourth objective of this study was to examine carnivore occurrence at black-tailed prairie dog (*Cynomys ludovicianus*) towns in the Oklahoma panhandle. Specifically, I intended to determine which carnivores were present at black-tailed prairie dog towns in this region and if any particular carnivore taxa occurred more often at black-tailed prairie dog towns than they occurred in surrounding habitats. Patterns of specific carnivore occurrence at black-tailed prairie dog towns were also examined in relation to the presence of other carnivores. This objective was intended to provide a better understanding of the role, if any, that black-tailed prairie dogs play in structuring local and regional carnivore assemblages.

The fifth and final objective was to create a model describing carnivore occurrence in the panhandle based upon vegetative spectral reflectance data. Using remotely sensed satellite imagery of panhandle vegetation, it was hoped that a predictive model could be developed describing a pattern between vegetation and carnivore occurrence. A model of this type would be valuable towards a variety of management and ecological applications.

Study Area

The Oklahoma panhandle is a strip of land approximately 267 km long (east - west) and 55 km wide (north - south) adjacent to the northwesternmost part of the body of the state. The panhandle region is comprised of three counties, each of about equal size. The counties (from east to west) are Beaver County (470,172 hectares), Texas County (527,855 hectares), and Cimarron County (475,506 hectares).

Historically, the panhandle consisted primarily of shortgrass prairie (Duck and Fletcher, 1943) and was dominated by blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), and prairie three-awn (*Aristida oligantha*). Prairie dog towns also covered much of the panhandle, occurring in all habitat types (Shackford and Tyler, 1991; Shackford et al., 1989). Presently, the panhandle landscape has been altered. While the historical habitat types persist, their quality and quantity has changed. The grassland, mesa, and riparian areas are now grazed by domestic cattle. The severity of this grazing varies among habitats and locations (pers. obs.). Prairie-dog towns have been reduced in number and size due to the combined effects of periodic plague (*Yersinia pestis*) episodes and concentrated eradication efforts. Agricultural areas, present since at least 1893, cover substantial areas. These extensive monocultures have had a profound impact on the composition of the vegetation in the panhandle.

The four major habitats differed significantly and were relatively easy to distinguish. The mesa habitat, which occurs in the panhandle's extreme northwest corner, extends into and can be found more extensively in New Mexico and Colorado. In

Oklahoma, the mesa encompasses approximately 74,290 ha of land and is the only single, continuous habitat in the panhandle. Mesa habitat is dominated by sagebrush (*Artemisia filifolia*), juniper (*Juniperus scopulorum*), and two-needle pine (*Pinus edulis*). Large, conspicuous riparian areas are also evident in the panhandle. Four major riparian corridors, along with their associated tributaries, drainages and soils, run predominantly west-east through the Oklahoma panhandle and are dominated by large eastern cottonwoods (*Populus deltoides*), shrubs, and taller grasses. Typically, these areas contained water sometime during the year, but were usually also dry at times. Riparian areas accounted for approximately 133,881 ha of land in the panhandle. Grassland or range areas are the third predominant habitat type in the Oklahoma panhandle. These areas are dominated by a variety of native and introduced grass species from 0.1 - 0.75 meters high. The overall composition of grassland/range areas was highly variable across the panhandle. Grassland/range areas accounted for approximately 844,292 ha of land in the panhandle. The final major habitat type, agriculture, has come to prevail across several parts of the panhandle. Agricultural land was defined as any plowed and/or planted field, any field with central pivot irrigation, or any bare or stubble field. The dominant agricultural crops in the panhandle are wheat, winter wheat, corn, sorghum, and milo. Agricultural land encompassed approximately 421,053 ha of land in the panhandle. Agricultural areas can be extensive and uniform, as such, they cannot be ignored as potential habitat for Oklahoma carnivores.

MATERIALS AND METHODS

Presence and distribution of carnivores was determined primarily through the use of baited tracking plates at pre-established tracking stations, and supplemented with infra-red photography (Figure 1-1). Tracking plates were made of sheets of stainless 26 gauge steel approximately one square meter in size and sprayed with a mixture of carpenter's chalk and isopropyl alcohol (G.M. Fellers, Biological Resources Division, USGS, pers. comm.). The alcohol served as a dispersant and the mixture resulted in a thick, uniform coating of chalk on the plate after the alcohol evaporated. These materials were selected over traditional sand tracking techniques for two reasons. First, tracks in the chalk tended to persist longer and were clearer than tracks in sand under the typical high wind conditions of the panhandle. Second, plate and chalk stations were easier to establish and less expensive to operate repetitively than sand stations. Each plate had a one-inch (2.5 cm) hole drilled through its center, allowing it to be placed directly over a stake that permanently marked the tracking station (Shaughnessy, in press). Canned mackerel and beef scraps were then placed in the center of each plate or on the stake to serve as bait (Shaughnessy, in press). The plates were checked for tracks and recovered after three nights (Paveglio and Clifton, 1988; Orloff et al., 1986; Pocatello Supply Depot progress report, 1981; Hatcher, 1978; Egoscue, 1956).

Ninety permanent tracking stations were established throughout the panhandle according to a stratified design (Figure 1-2). Tracking stations were distributed first according to county size. Stations were then distributed across habitats proportionally based upon estimates of the total habitat area covered in the panhandle. Stations were also established near county and state lines due to the availability of well-maintained roads at these areas as well as the foreknowledge that swift fox populations occurred in states adjacent to the panhandle. At this stage, prairie dog towns were also identified as habitat features and included in the distribution of tracking stations as a subset of the total number of tracking plates distributed in any particular habitat.

Total area covered by prairie dog towns in the Oklahoma panhandle was small (approximately 5,862 ha; Shackford et al. 1989), so treating them as a major habitat and allocating independent tracking stations to them was not appropriate. Instead, active prairie dog towns within particular habitats were selected as locations for tracking stations within that habitat. These stations functioned as habitat stations for the broader scale habitat affinity questions and as prairie dog town stations for smaller scale comparisons. These stations were also paired with stations in adjacent, similar habitats to facilitate comparisons between prairie dog town areas and non-prairie dog town areas. Efforts were made to keep the location of the paired site within 15 kilometers of the prairie dog town site in order to maintain local habitat consistencies. In order to ensure adequate pairings, the total number of prairie dog town sites selected for tracking station locations was independent of the amount of area actually covered by prairie dog towns. In this way, the assignment of prairie dog town stations were not subject to the constraints of proportional sampling that the other habitats were held to. Prairie dog town track-plate data are included in the broader scale analyses as data representing the habitat where the prairie dog town occurred.

The minimum number of permanent tracking stations established in any habitat was 12 in each of the mesa and riparian habitats. The most stations (43) were placed in range/grassland habitat (Shaughnessy, in press). Four carnivore tracking surveys, covering each season of the year, were completed in the Oklahoma panhandle from January 1995 to February 1997.

Infra-red triggered cameras were also used in order to detect and verify carnivore presence. The infra-red triggered cameras consisted of an infra-red detection unit connected to a camera housing and automatic shutter release (Shaughnessy, in press). A standard auto-focus, auto-wind, compact camera was placed in the camera housing and attached to an automatic shutter release. The camera units were set at tracking plate stations so that the infra-red trigger and the camera were aimed at the center of the station (Figure 1-1). The infra-red triggers were set to a 3 minute delay in order to allow the camera sufficient time to advance the film between exposures.

Ten infra-red triggered cameras operated during each sampling trip at tracking stations (Shaughnessy, in press). Cameras were placed at stations based upon the prior tracking history of the station and a qualitative judgement of the potential of the habitat to produce carnivore detections. Cameras were also placed at stations that appeared to be in areas of high carnivore densities or high quality carnivore habitat that had not tracked carnivores to that point (Shaughnessy, in press). These priorities were based upon the assumption that panhandle carnivores were territorial; if a carnivore was detected at a tracking station during one sampling session, it was likely to revisit the station during the second sampling session. While cameras were useful for novel detections of carnivores, the cameras functioned primarily for verifying carnivore tracks at tracking plates.

Spotlighting surveys were conducted opportunistically during the first two tracking sessions. Habitats were chosen for spotlighting according to the relative proportion of area they covered in the panhandle (similar to the assignment of tracking stations within habitats). The procedure for spotlighting surveys required that an 8.0 km stretch of road within the desired habitat be selected. At the beginning of the survey route a predator call would be used, attempting to attract carnivores. The audible range of the predator calls was approximately 1.6 km. After 15 minutes, the spotlight was used to identify and record any carnivores that responded to the call. If no carnivores were present, the call was used again, and the procedure repeated. Once this procedure was repeated at least twice, the investigator would drive 1.6 km on the transect and repeat the calling process. This pattern continued along the length of the 8.0 km transect. Spotlighting was also used primarily for verification of carnivore presence in areas that had already tracked carnivores.

Table 1-1. Carnivores of the Oklahoma panhandle (from Shackford and Tyler, 1991; Caire et al., 1989); Bold indicates a threatened, endangered or protected species; *indicates carnivores detected during the course of this study. No differentiation was made between Western and Eastern Spotted Skunks.

Scientific Name	Common Name	Prairie Dog Town Associate
Family Mustelidae		
*Taxidea taxus**	Badger	Yes
Mustela nigripes	**Black-footed ferret**	Yes
Mustela frenata	Long-tailed weasel	------
*Mephitis mephitis**	Striped skunk	------
*Spilogale putorius**	Eastern spotted skunk	------
*Spilogale gracilis**	Western spotted skunk	------
Conepatus mesoleucus	**Hog-nosed skunk**	------
Family Canidae		
Vulpes velox*	**Swift fox**	Yes
Vulpes vulpes	Red fox	------
Urocyon cinereoargenteus	Gray fox	------
*Canis latrans**	Coyote	Yes
Canis lupus	**Wolf**	------
Family Felidae		
*Lynx rufus**	Bobcat	------
Felis concolor	Cougar	------
Family Procyonidae		
*Procyon lotor**	Raccoon	------
Bassariscus astutus	Ringtail	------
Family Ursidae		
Ursus americanus	Black bear	------

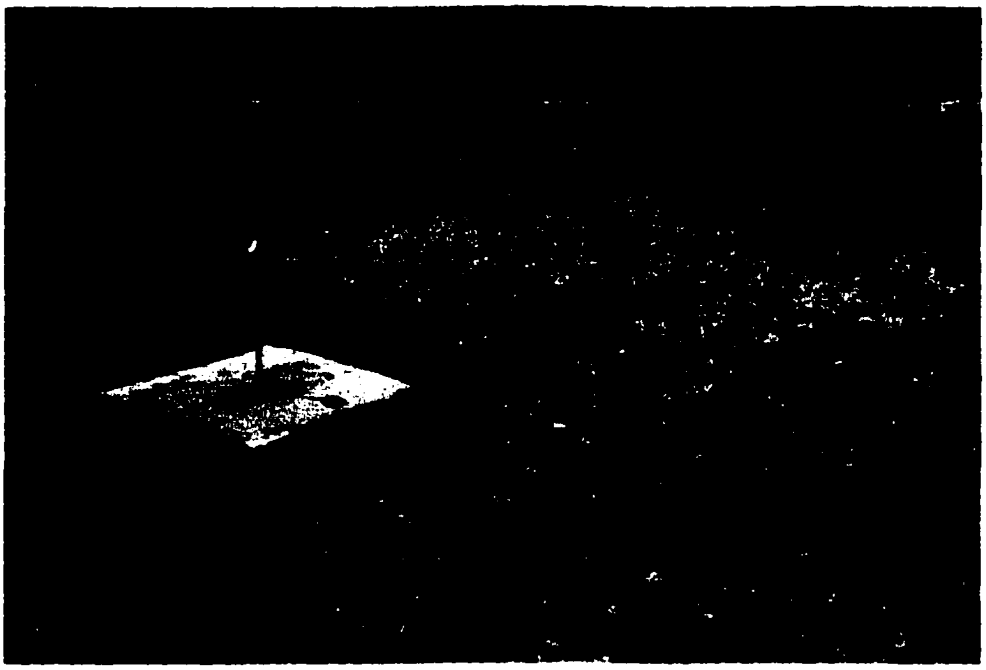


Figure 1-1. Tracking plate and infrared triggered camera station for carnivore detection in the Oklahoma panhandle, 1995-1997.

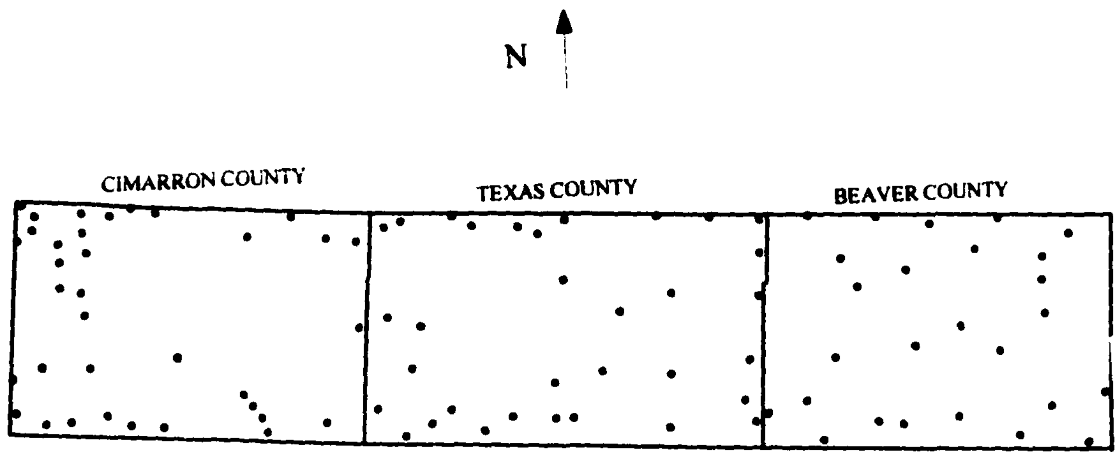


Figure 1-2. Carnivore tracking station locations in the Oklahoma panhandle, 1995-1997.

CHAPTER 2

THE SWIFT FOX

BACKGROUND

The first records of swift fox (*Vulpes velox*) in Oklahoma date from 1888, when a specimen was obtained from what is now the Oklahoma panhandle (Caire et al., 1989). Historically, the swift fox was reported to range throughout the Oklahoma panhandle and Woodward County in northwestern Oklahoma (Caire et al., 1989).

The most comprehensive and recent study of swift foxes in Oklahoma was completed by Kilgore (1969). He examined denning habits, breeding and reproduction, food preferences, and parasites of swift foxes in Beaver County, from 1965 to 1966. Since 1969, most studies of the Oklahoma swift fox population have been completed in conjunction with swift fox investigations in neighboring states (e.g. Zumbaugh and Choate, 1985). The U.S. Fish and Wildlife Service's decision to include the swift fox as a candidate species for federal listing under the Endangered Species Act (Federal Register, 1995) prompted renewed interest in the distribution of swift foxes in Oklahoma.

Three primary objectives were identified as the focus of the swift fox study in Oklahoma. The first objective was to evaluate the efficacy of scent-post surveys, spotlighting, and infra-red triggered cameras as carnivore detection techniques. Since few recent studies have been conducted on swift fox, there was no single preferred technique for investigating this particular carnivore. A determination of which techniques worked best in Oklahoma seemed vital to the success of the project. The second objective was to determine the current range of the swift fox in Oklahoma. Again, no recent range or population estimations existed for the swift fox in Oklahoma prior to 1989 (Caire et al., 1989). The most recent estimations of swift fox range and population status in Oklahoma were based upon data collected from neighboring states and from foxes collected in Oklahoma prior to 1970. A current status for the species in Oklahoma needed to be determined. The third objective was to investigate habitat affinities of the swift fox.

MATERIALS AND METHODS

Field methods used to determine carnivore presence in the Oklahoma panhandle were consistent throughout this study. Statistical methods varied slightly between different treatments.

Statistical methods

The three counties of the panhandle divide the panhandle conveniently into west, central, and east sections. Using these divisions, I performed a chi-square goodness of fit test on the swift fox tracking plate survey data to determine if swift fox were distributed evenly among the west, central, and eastern extremes of the panhandle. I computed expected frequencies for the test based on sampling effort conducted in each county.

Additionally, analyses of swift fox distributions across the entire panhandle were conducted by further categorizing plates according to their location with respect to large scale panhandle habitat features. Track plates were placed into one of seven categories based upon geological/hydrological features of the panhandle and habitat similarities, irrespective of county boundaries. This permitted evaluation of how swift fox detections might vary across the entire panhandle, independent of county lines.

To examine swift fox distributions between habitats, I conducted a chi-square goodness of fit test designed to test the null hypothesis that no differences existed between swift fox occurrences among the four habitats. Once again, counts of swift fox from the tracking stations were used for this analysis.

Pseudoreplication of detection data was a potential problem in the analysis of the track plate data. In order to account for the potential that some detections between sampling periods were of the same individuals, county and habitat chi-square analyses were conducted two ways. First, all detections were considered novel detections, regardless of when or where they occurred, and analyzed using chi-square. In this approach, the actual detections were the statistical measurement. The second approach counted plates only once for each species detection, regardless of how many times the plate was visited by that species over the course of the entire study. In this approach, the tracking plate (whether or not it ever recorded a track, regardless of how many tracks it recorded) was the unit of statistical measurement. The second approach is a more conservative analysis of the data, and while it does not completely control for the possibility of pseudoreplication in the data, it lessens its effect. The outcomes of both analyses are compared.

RESULTS

Sampling Effort

Sampling effort for the swift fox project in Oklahoma is presented in Table 2-1. We recorded 850 functional plate nights during the study (Table 2-1). Plate nights per county ranged from a low of 263 in Beaver County to 296 in Cimarron County (Table 2-1). Plate nights in habitats ranged from 136 in the mesa to 376 in range areas (Table 2-1).

Track plates

Tracking plates had distinct advantages over other survey methods. First, tracking plates required less effort than other methods examined. One person could set 40 plates per day, depending on weather conditions. Second, operating plates was inexpensive after the initial purchase of the plates, stakes and sprayer. Costs for alcohol, bait and carpenter's chalk per sampling session were typically under $100.00 (not including mileage costs). We could also detect visits of multiple species even after bait had been taken. Carnivores frequently defecated on tracking plates, leaving further evidence of their presence and identity. Finally, carpenter's chalk sprayed on plates typically yielded clear, distinct tracks that were, in most cases, readily identifiable.

The principal disadvantage of tracking plates was that rain usually destroyed tracks. One sampling period was severely affected by rain. A second disadvantage of tracking plates was that we could not distinguish between individuals of the same carnivore species. This resulted in the statistical problem of pseudoreplication of the data, since one individual could potentially be responsible for tracks at a particular tracking plate during multiple sampling sessions.

Cameras

Infra-red triggered cameras enabled us to verify the presence of swift fox at stations and provided a photographic record of carnivore visitation (Figure 2-1). Cameras could detect swift foxes that visited tracking stations but did not step on tracking plates. Cameras also functioned properly in the rain. During periods of rain, data from tracking stations that had infra-red triggered cameras could be salvaged even though rain had washed the track evidence away. A third advantage of the cameras was detection of multiple individuals of the same species at a single plate. Two individuals could be recorded together at a tracking station on the same exposure, verifying multiple visits at a tracking station.

The major disadvantage of the cameras was cost. Each camera unit, including infra-red trigger unit and compact camera, cost approximately $190.00. Film, batteries, and film processing for each sampling session cost approximately $25.00 per camera. The cost of operating the cameras for the duration of the study was approximately $1000.00. Using cameras we were able to detect two carnivores (one swift fox and one bobcat) which were not detected using the tracking plates. Clearly, cameras would not have been cost effective if used solely for novel detections. Cameras were also insensitive to endotherm size, thus even mice would trigger the shutter switch. A mouse sitting on the tracking plate, eating the bait, had the potential to expose several frames of film before leaving. However, as a track verification tool, we felt the cost of cameras was offset by confirmation of track identifications.

Cameras also malfunctioned frequently. Problems with the cameras included drained batteries, improper film advancement, and poor exposures.

Spotlight surveys

The obvious advantage to the spotlighting surveys was the visual records of carnivores in the habitat being investigated. Any carnivore observed during spotlighting could be recorded as positively occurring in the particular habitat. Spotlighting was the least expensive method used in our determination of swift fox occurrence.

Spotlighting was also the least effective method used for detecting swift fox. No foxes were detected through the spotlighting efforts. This may be attributable, at least in part, to the numbers of observers present during spotlighting surveys. During most spotlighting sessions, only one observer was present and no carnivores were detected during any of these sessions. However, during a spotlighting session with three observers, multiple (6) coyotes were detected and one bobcat (*Lynx rufus*) was detected. Clearly, spotlighting effectiveness increased with the number of people present. For this reason, spotlighting was considered an ineffective use of time and was discontinued after the second survey session.

Analyses

The chi-square analysis of swift fox distributions among counties (detections) was significant ($\chi^2 = 29.61$, df = 2, $p < 0.001$). Swift fox occurrence was higher than expected in Cimarron County and less than expected in both Texas and Beaver Counties (Figure 2-2). When analyzed using the more conservative plate approach, differences in swift fox detections across counties remained significant (χ^2=9.228, df = 2, $p < 0.01$). Swift fox detections were also not distributed evenly across the seven large scale habitat designations ($\chi^2 = 24.18$, df = 6, $p < 0.001$), supporting the results of the county based chi-square analysis.

Swift foxes were not detected in habitats in proportion to survey effort ($\chi^2 = 12.51$, df = 3, $p < 0.01$). Swift foxes occurred more frequently than expected in the mesa habitat and less frequently than expected in the riparian habitat (Figure 2-3). In range and agricultural habitats, swift foxes occurred slightly less often than expected (Figure 2-3).

Habitat differences in swift fox distribution using the more conservative approach, however, were not significant ($\chi^2 = 2.77$, df = 3, $0.50 > p > 0.25$). Power analysis was conducted on the data in this approach. Power for this test was low (w = .3557, U=3, Power = .3279).

DISCUSSION

Sampling effort between track plates, cameras, and spotlighting was not even. Within two sampling sessions though, the effectiveness of the various methods had become apparent. While one person could set and operate numerous track plates at one time, one person could conduct only two or three spotlighting sessions per night. Track plates also produced far more evidence (per unit effort) of carnivores than spotlighting during the first two sampling sessions. As a result, spotlighting was discontinued after the second sampling session.

Furthermore, carnivores tend to scent mark areas they visit, particularly when there is some new structure in that area (e.g., a scent station stake). Some carnivores are also curious about new scents. As a result, if a carnivore marked a scent station stake or plate, that plate was in effect "rebaited" (Conner et al., 1983). Due to this behavior, track plates were probably able to remain operational even after the bait had been taken.

Cameras were effective at detecting and recording carnivores, but their cost prohibited their widespread use in the panhandle. Track plates were as effective at carnivore detection, but more could be operated at one time and at lower cost than the cameras. Consequently, track plates were determined to be the most effective method overall for detection of swift foxes and other carnivores in the Oklahoma panhandle.

Additionally, cameras might have been helpful in identifying individuals at tracking plates during different sampling sessions, thereby addressing issues of track plate pseudoreplication. However, cameras were not used repetitively at the same sites because priority was given to the track verification ability of cameras. As a result, cameras were not useful in addressing issues of pseudoreplication at tracking plates.

Three primary areas of the Oklahoma panhandle support swift fox (Figure 2-4). The highest concentrations of swift fox appear to be in the westernmost part of the panhandle (Cimarron County), with very regular detections in the mesa region of that county (extreme northwestern portion). Fewer detections of swift fox occurred in both southern Texas and southern Beaver counties, suggesting lower densities. Swift foxes were detected infrequently in other areas of Texas and Beaver counties (Figure 2-4).

Cimarron County, in the western third of the panhandle, is the least human-populated county. The mesa area, in particular, supports a very low human population. This translates to larger tracts of unbroken range and possibly higher quality range than in the other two counties. Agriculture is also a very small component of land use in Cimarron County. Swift fox were not detected as often in agricultural areas. Land use in Texas County is primarily agriculture. Additionally, Texas County has recently undergone major growth in commercial pig farming and agriculture. This might explain the low numbers of swift fox detections in this county. The extreme southern portion of Texas County, however, remains committed to cattle production, which encourages range management practices. This land use pattern may explain why swift foxes were much less common in the northern sections of Texas County. Swift foxes were detected in Beaver County slightly more often than in Texas County, but still much less often than in Cimarron County. Beaver County land use is not skewed towards agriculture as much as Texas County, but still has a much larger agricultural component than Cimarron County.

Comparisons of habitat data during this project assumed that swift foxes (and coyotes) were equally detectable in all habitats. This assumption has been questioned by some authors because habitat biases that could affect detectability generally persist over time, and can not be controlled by replication (Sargeant et al., 1998). The habitat classifications during this project, however, were considered to be defined broadly enough to minimize the impact of any detection biases associated with more specific habitat types.

The analysis of swift fox occurrence in habitats suggests that swift fox are more common in some habitats than others. In contrast, when track plates were used as the detection unit, instead of individual detections, the results were not significant. Power analysis suggests that this statistical test lacked sufficient power to confidently retain the null hypothesis (Thomas and Juanes, 1996). However, this analysis was also the more conservative of the two analyses and reduced (but did not eliminate) the pseudoreplicative effect of possible multiple detections at a single plate over the course of the study. As a result, while habitat interpretations of these data are still valuable based upon the results of the first approach, interpretations should be viewed with caution due to the ambiguous results of the second approach.

Swift foxes occurred regularly in range and were detected more often than expected in mesa areas. Swift foxes occurred in agricultural areas slightly less often than expected. Swift fox were rare in riparian areas (Figure 2-3).

Mesa areas are apparently good habitats for swift foxes. The mesa was the only habitat which produced consistent swift fox detections. Coyotes were rarely detected in mesa habitat. Agricultural areas may be a substandard habitat for swift foxes. Swift foxes were not consistently detected in agricultural areas. Riparian areas apparently do not support swift fox populations. This may be due to a preference for these areas by coyotes.

SUMMARY

The most effective method for detecting swift fox and other carnivores in the Oklahoma panhandle was baited tracking plates placed at permanent tracking stations and coated with isopropyl alcohol and chalk. The least effective method was spotlighting. Infra-red triggered cameras were valuable for verifying track identifications but were not cost effective or reliable enough to serve as an independent detection technique.

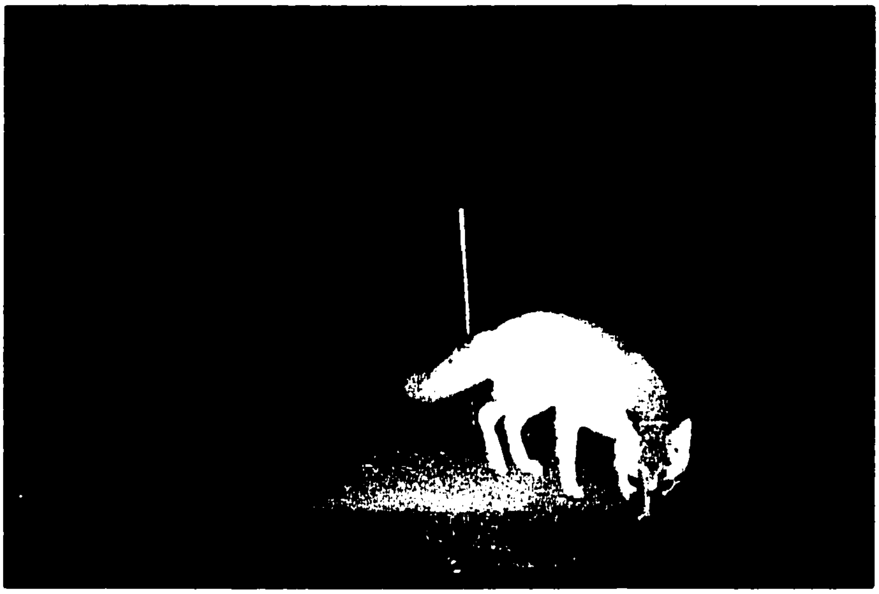
Swift fox were not evenly or randomly distributed throughout the Oklahoma panhandle. Swift fox occurred most often in the extreme western section of the panhandle (Cimarron County), particularly in the mesa region. Secondary concentrations of swift fox occurred in both southern Texas and southern Beaver counties.

Swift fox were not evenly distributed among habitats. Swift fox seemed to prefer the mesa habitat and avoided riparian areas. Swift fox also occurred in range and agricultural areas. However, relative numbers of occurrence in these habitats seemed to suggest that swift fox prefer range areas over agricultural areas.

Table 2-1. Number of functional-plate nights[1], by county and habitat type, used to determine distribution of Swift Foxes in the Oklahoma panhandle, 1995 - 1997.

	Cimarron Co.	Texas Co.	Beaver Co.	Total	# Plates
Range	104	132	140	376	41
Mesa	136	0	0	136	14
Agriculture	13	108	80	201	21
Riparian	43	51	43	137	14
Total	296	291	263	850	90
# Plates	31	33	26	90	

[1] Number of operational track plates/number of nights the plates were set up



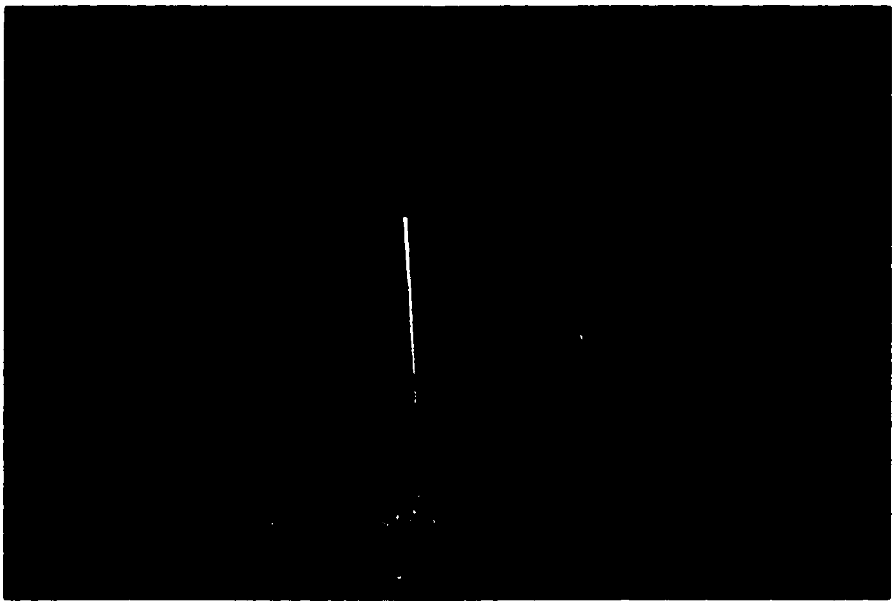


Figure 2-1. Infrared triggered camera photos of a swift fox (*Vulpes velox*) visiting a tracking station in the Oklahoma Panhandle.

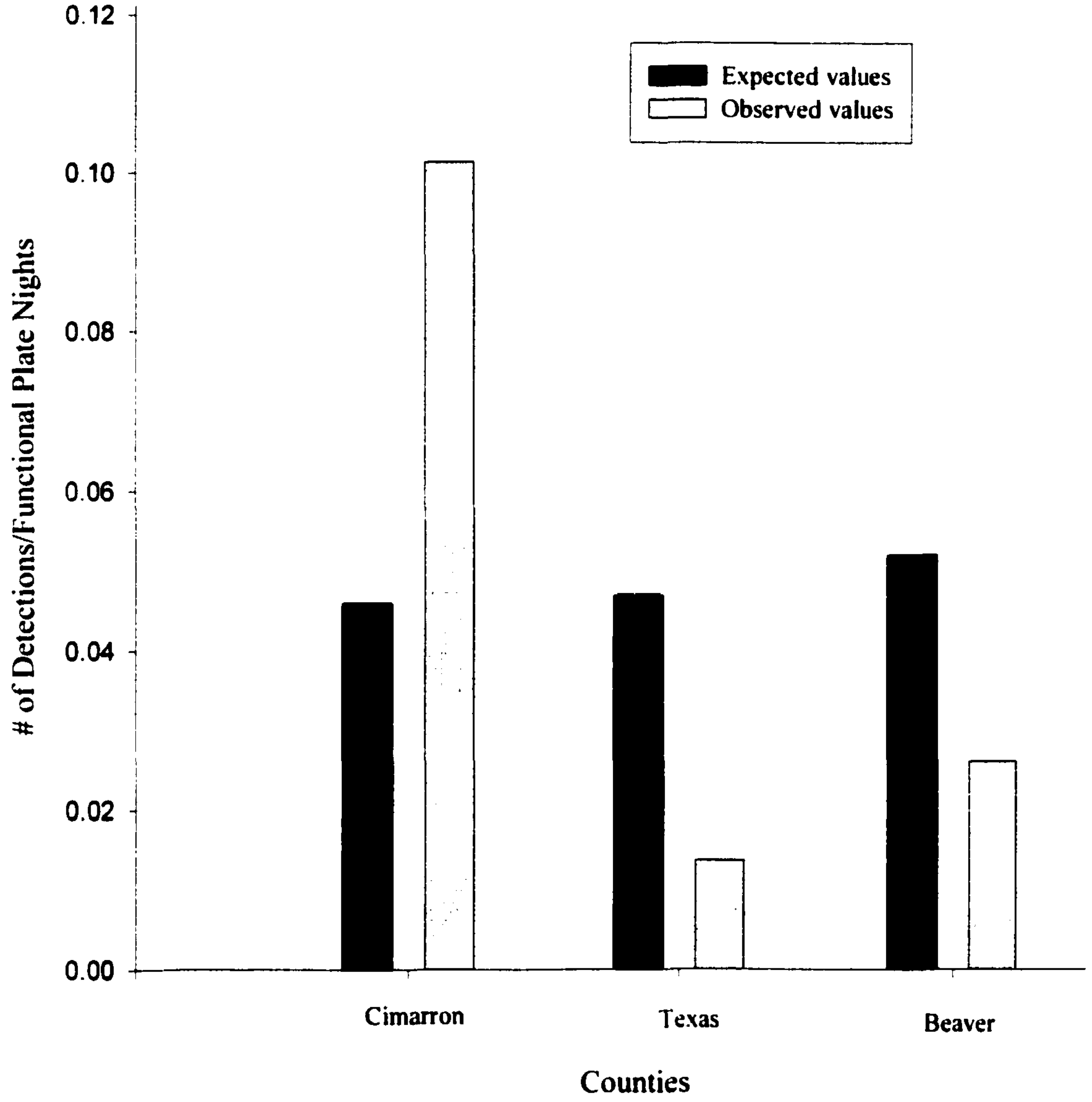


Figure 2-2. Results of Chi-square analysis for swift fox occurrence in counties located in the panhandle of Oklahoma, 1995 - 1997 ($p < 0.05$).

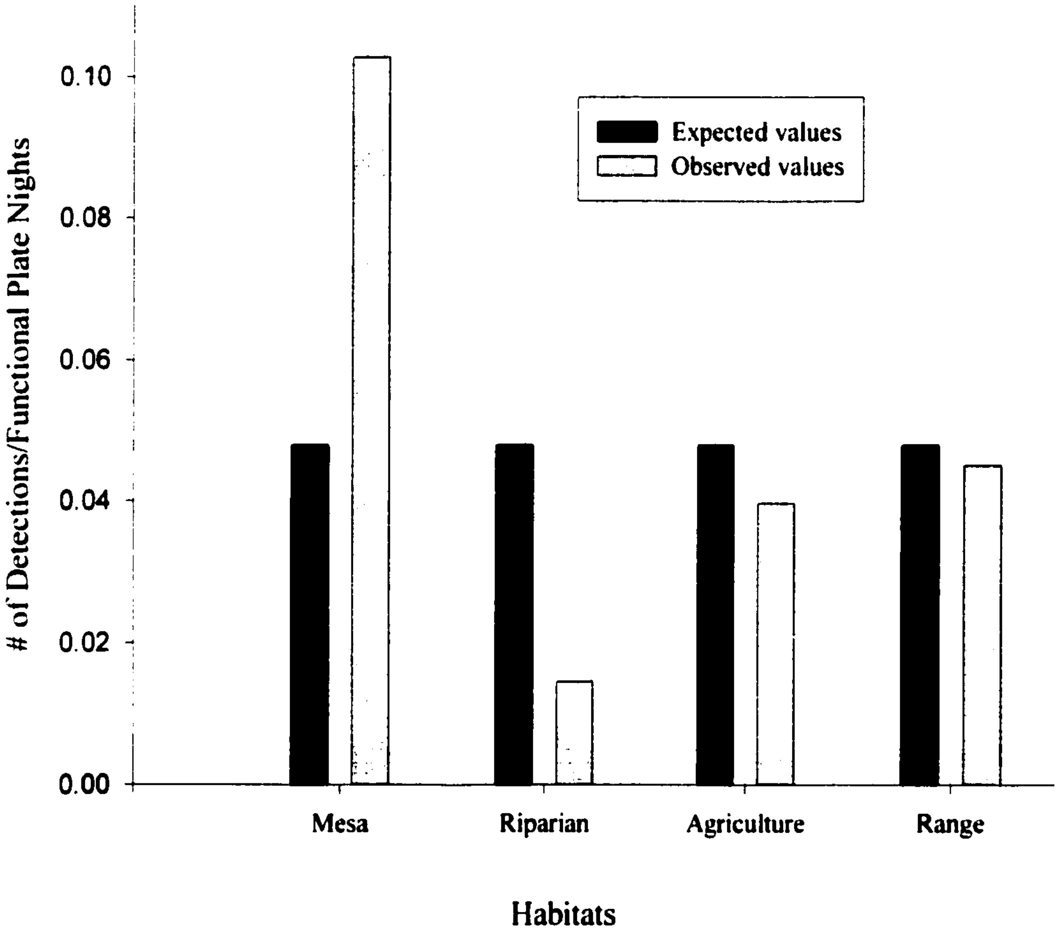


Figure 2-3. Results of chi-square analysis of swift fox occurrence across panhandle habitats in Oklahoma, 1995 - 1997 ($p < 0.05$).

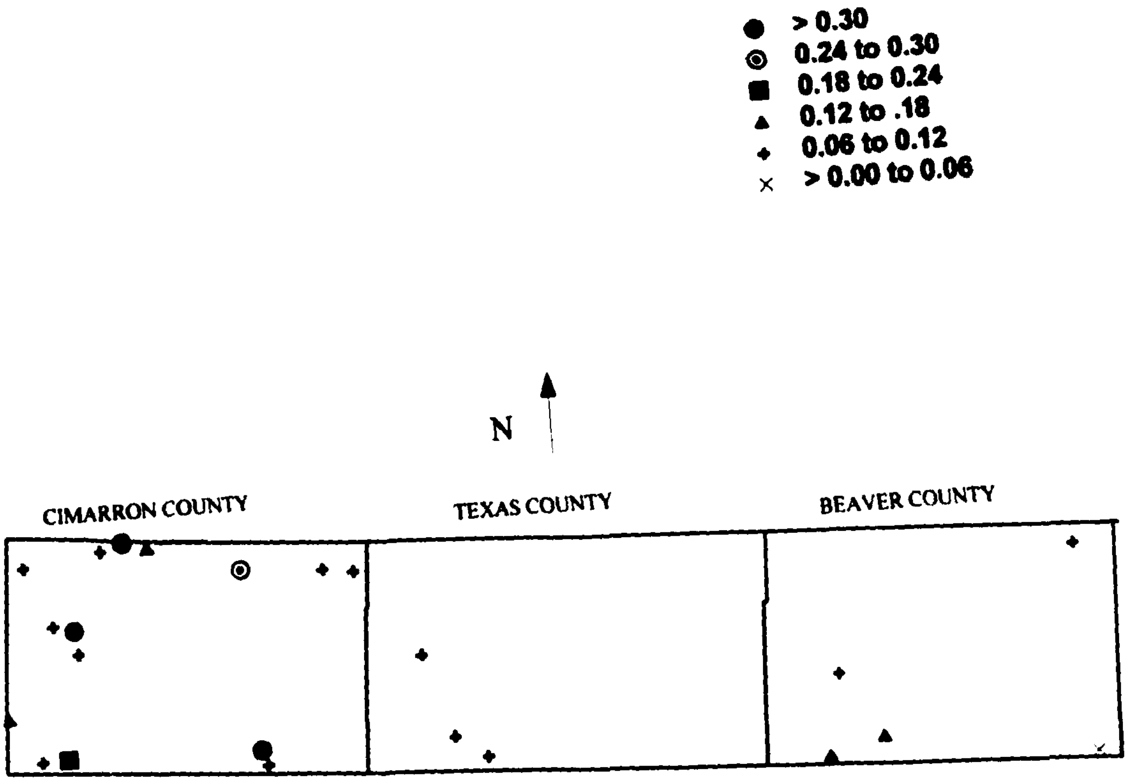


Figure 2-4. Swift fox detection profile in the Oklahoma panhandle, 1995-1997.

CHAPTER 3

CARNIVORES IN THE OKLAHOMA PANHANDLE

BACKGROUND

The carnivores represent 11 families and about 271 species (Wilson and Reeder, 1993). Significant morphological, behavioral, and physiological variation exists within the order Carnivora (Feldhamer et al., 1999). This variation has fostered a significant amount of primarily single species investigations (Boness et al., 1998; Frank, 1996; Carbyn et al., 1995; Buskirk and McDonald, 1989; Koehler and Hornocker, 1989; Mills, 1989; Schaller et al., 1989; Seal et al., 1989). Recent ecological and behavioral studies have focused more on groups of carnivores (Bueno, 1996; Waser, 1996; Buskirk et al., 1994; Murray et al., 1994; Dayan et al., 1989; Gorman and Trowbridge, 1989; McNab, 1989; Sunquist and Sunquist, 1989;). However, few studies have examined naturally occurring carnivore assemblages in specific environments.

In addition to the recent emphasis away from single species approaches and examining multiple carnivores or carnivore groups, additional interest has been directed towards larger scale ecological investigations in general (Brown, 1995; Edwards et al., 1994; Miller et al., 1994; Stone and Roberts, 1990). The ecological dynamics that transcend local process have also recently been found to contribute to explanations of species/group distributions and patterns (Marquet, 1994; Gaisler et al., 1991).

In Oklahoma, few comprehensive investigations of carnivores have been undertaken (Kilgore, 1969; Glass, 1956). Most of the information on carnivores in the state has occurred in conjunction with and ancillary to projects focused on other vertebrates (Peoples and DeMaso, 1996; Shackford and Tyler, 1991; Shackford et al., 1989). This study had three objectives. The first objective of this study was to survey comprehensively the carnivores of the Oklahoma panhandle. The Oklahoma panhandle has supported a diverse carnivore community. Carnivores reported from the panhandle region include 17 species in five families (Caire et al., 1989) (Table 1-1). Four species, gray fox (*Urocyon cinereoargenteus*), western spotted skunk (*Spilogale gracilis*), hog-nosed skunk (*Conepatus mesoleucus*), and ringtail (*Bassariscus astutus*), are thought to be restricted to a small mesa physiographic region in the northwesternmost corner of the Oklahoma panhandle (Caire et al., 1989). The others are more widely distributed and may be found throughout the panhandle.

The second objective was to determine the distributions of carnivores in the Oklahoma panhandle and to examine potential habitat affiliations of those carnivores. Presently, there exist four broadly classified types of habitat in the Oklahoma panhandle. The mesa habitat, which occurs in the panhandle's extreme northwest corner, extends into and can be found more extensively in New Mexico and Colorado. Mesa habitat is dominated by sagebrush (*Artemisia filifolia*), juniper (*Juniperus scopulorum*), and two-needle pinyon (*Pinus edulis*). Large, conspicuous riparian areas are also evident in the panhandle. Several riparian areas run predominantly west-east through the Oklahoma panhandle and are dominated by large eastern cottonwoods (*Populus deltoides*), shrubs, and taller grasses. Grassland, or range areas, are the third predominant habitat type in the Oklahoma panhandle. These areas are dominated by a variety of native and introduced grass species. Grassland/range areas all experience some degree of grazing by domestic cattle. The final major habitat type, agriculture, has come to prevail across several parts of the panhandle. The dominant crops in the panhandle are wheat, winter wheat, corn, sorghum, and milo. As these agricultural areas can be extensive and uniform, they cannot be ignored as potential habitat for Oklahoma carnivores.

The final objective was to examine whether carnivore distributions and habitat affinities were influenced by the distributions or presence of other carnivore species. Specifically, do different carnivore species (particularly closely related carnivore species) in the Oklahoma panhandle occur together regionally, or in specific habitats, more or less than would be expected by chance? In this way, I could examine not only the effects of large scale factors such as habitat on carnivore distributions, but also how local processes influence where carnivores occur. This approach has provided for a better, more comprehensive understanding of carnivore interactions and distributions in the Oklahoma panhandle.

MATERIALS AND METHODS

Field methods used to determine carnivore presence in the Oklahoma panhandle were consistent throughout this study. Statistical methods varied slightly between different treatments.

Statistical methods

Data were analyzed using chi-square analyses. The data were ordinal in nature and sample sizes were generally moderate. As such, the data did not lend itself easily to parametric statistical procedures. Chi-square, however, is a powerful and simple analysis that permits rigorous analysis of many types of data, particularly ordinal data (Zar, 1984).

Carnivore landscape distributions were analyzed through two separate chi-square analyses. First, data were compiled by detections within panhandle counties. The panhandle counties are conveniently oriented in-line from west to east and are of about equal in size. Chi-square was used to analyze these data according to their distributions across counties to determine if differences existed in gross distributions of carnivores across the panhandle. These data were analyzed for all carnivores, groups of carnivores based on taxonomic relationships, and for individual carnivore species.

Next, seven large scale, panhandle physiographic regions were delineated and tracking station affiliations to these regions were determined. These regions were designated independently of county lines within the panhandle. Regions were defined by riparian corridors, vegetation type and land use. Chi-square was used to analyze tracking data from these seven affiliations in order to define if and how carnivore detections varied across the entire panhandle, and to support the results of the county chi-square analyses.

A second series of tests analyzed carnivores in habitats. Data were compiled for the four major pre-defined habitat types, and chi-square analysis was used to determine if carnivore distributions and occurrences were random across these habitats. These analyses were performed for all carnivores, groups of carnivores, and all individual carnivore species.

Additionally, chi-square analyses were performed on the county and habitat data utilizing tracking stations only as the statistical unit. Multiple detections at a single station were not counted and the data were analyzed using only the criteria of whether a station ever tracked a carnivore or not. This approach reduced the overall size of the data set, but was applied to examine the difference between carnivore persistence over time in an area or habitat (multiple hit approach) and the general pattern of carnivore occurrence (each station only counted once regardless of multiple hits). Because the approach reduced the size of the data set, it was only applied to those analyses that were statistically significant under the multiple hit approach.

Finally, a third chi-square analysis was performed. A chi-square contingency table was used to analyze interspecific associations between carnivores within habitats. In particular, associations between taxonomically related carnivores were examined within Oklahoma panhandle habitats. This test was used to determine if carnivores within certain taxonomic groups were interacting with each other across the broader panhandle landscape. These interactions, if present, could then be used to explain overall patterns of carnivore occurrence within habitats. This analysis was completed for all carnivores, canids and mustelids.

Sample sizes during this project were not large. As a result, power analyses were conducted and reported on all non-significant chi-square results in order to determine the likelihood of the commission of Type II errors. Power values were computed using Cohen (1977) as a reference and evaluated as to their strength according to recent literature (Thomas and Juanes, 1996; Greenwood, 1993; Taylor and Gerrodette, 1993; Thompson and Neill, 1993). These values were used in the further interpretations of non-significant statistical results.

RESULTS

Six carnivores (no distinction was made between western and eastern spotted skunks) were detected in sufficient numbers to permit statistical analysis (Table 1-1). These carnivores represented three families (Canidae, Felidae, and Mustelidae) of the possible five families reported present in the Oklahoma panhandle.

Sampling Effort

Tracking plates were operated for 850 plate nights in the Oklahoma panhandle (Table 2-1). A plate night was defined as one tracking plate, baited and coated with chalk, set out for one night. Cimarron County recorded the most plate nights, while Beaver County accounted for the least number of plate nights (Table 2-1). The most tracking plate nights were in range/grassland areas and the fewest were in mesa and riparian areas (Table 2-1). These numbers reflect the proportions that habitats and counties occupy within the total area of the Oklahoma panhandle.

Analyses

The results of chi-square analysis of carnivore occurrences across counties was highly statistically significant ($\chi^2 = 34.16$, df = 2, $p \leq 0.001$) (Figure 3-1). Analysis of carnivore occurrence between the seven panhandle physiographic regions was not significant, however ($\chi^2 = 11.63$, df = 6, $p > 0.05$). This result was only marginally insignificant however ($\chi^2_{critical} = 12.59$), and power analysis for the test revealed that statistical power was relatively good ($U_{0.05} = 6$, $w = 0.321$, Power = 0.65). Chi-square analysis of carnivore distributions among habitats also revealed significant differences in the occurrence of carnivores in the habitats ($\chi^2 = 16.06$, df = 3, $p \leq 0.005$) (Figure 3-2). No differences were detected between counties or across habitats when chi-square was used to examine plates as single statistical units.

Two canid species were detected with sufficient regularity to permit analysis. The swift fox and the coyote were detected in all habitats and during all sampling periods. Analyses of swift fox in the Oklahoma panhandle are dealt with more extensively in Chapter two and in Shaughnessy (in press), yet, in all cases, swift fox distributions were significantly different from expected frequencies or occurrences. Chi-square analysis of swift fox distributions across counties was highly significant ($\chi^2 = 29.61$, df = 2, $p \leq 0.001$) (Figure 2-2). The chi-square analysis using only tracking plates as the statistical unit also supported this result ($\chi^2 = 9.228$, df = 2, $p \leq 0.01$). Analysis of detections across the seven physiographic panhandle regions was significant as well ($\chi^2 = 24.21$, df = 6, $p \leq 0.001$). Swift fox distributions among habitats were similarly uneven. Chi-square analysis showed significant differences in the numbers of detections of swift foxes between habitats ($\chi^2 = 12.51$, df = 3, $p \leq 0.01$) (Figure 2-3). Chi-square analysis of tracking plates as the statistical unit was not significant ($\chi^2 = 2.77$, df = 3, $p > 0.05$).

The analyses for coyotes yielded similar results. Coyotes were not evenly distributed between the three counties of the Oklahoma panhandle ($\chi^2 = 12.045$, df = 2, $p \leq 0.005$) (Figure 3-3). Using tracking plates as the statistical unit also supported this result ($\chi^2 = 11.65$, df = 2, $p \leq 0.005$). Coyotes were also not evenly distributed among the seven physiographic regions ($\chi^2 = 23.99$, df = 6, $p \leq 0.001$). Additionally, coyotes were not distributed evenly among the broadly defined habitats. Chi-square analysis revealed significant differences in coyote detections across the habitats ($\chi^2 = 25.90$, df = 3, $p \leq 0.001$) (Figure 3-4). This result also held true for the analysis of tracking plates only ($\chi^2 = 10.954$, df = 3, $p \leq 0.025$).

In general, the results were the same when the data for the two canid species were combined. The chi-square analysis indicated that canids were not evenly distributed across the three counties using either detections as the statistical unit ($\chi^2 = 24.43$, df = 2, $p \leq 0.001$) (Figure 3-5) or tracking plates as the statistical unit ($\chi^2 = 6.53$, df = 2, $p \leq 0.05$). Canids also were not evenly distributed across the broader physiographic regions ($\chi^2 = 16.70$, df = 6, $p \leq 0.025$). Canids were not evenly distributed among the major habitats of the panhandle either ($\chi^2 = 17.54$, df = 3, $p \leq 0.001$) (Figure 3-6). This result was not supported by the analysis using tracking plates as the statistical unit ($\chi^2 = 4.63$, df = 3, $p > 0.05$).

Three mustelid species were detected during the course of this study. The spotted skunk, striped skunk, and badger were detected with tracking plates and incidentally to varying degrees. The spotted skunk was detected most frequently. The chi-square analysis examining spotted skunk occurrence among counties revealed no significant differences in spotted skunk occurrences among the counties ($\chi^2 = 4.729$, df = 2, $p > 0.05$) (Figure 3-7). Power for this test was high ($U_{0.05} = 2$, w = 0.5962, Power = 0.75). Analysis of spotted skunk detections between the major physiographic regions agreed with the county analysis ($\chi^2 = 4.51$, df = 6, $p > 0.05$). Power for this test, though, was lower ($U_{0.05} = 6$, w = 0.4807, Power = 0.39). Similarly, chi-square analysis showed no significant differences in spotted skunk detections between major habitats ($\chi^2 = 3.17$, df =

3, $p > 0.05$) (Figure 3-8). Statistical power for this test was relatively high as well ($U_{0.05}$ = 3, w = 0.5821, Power = 0.70).

Chi-square analysis of badger detections between panhandle counties was also not significant. Badgers were not found to occur significantly differently between the counties ($\chi^2 = 4.54$, df = 2, $p > 0.05$) (Figure 3-9). Statistical power for this test was comparatively high ($U_{0.05}$ = 2, w = 0.6429, Power = 0.71). No physiographic analyses were conducted for badgers because badger detection data contained expected values less than one. Badgers also were not detected in any habitat more often then expected (χ^2 = 4.36, df = 3, $p > 0.05$) (Figure 3-10). Power for this test was marginal ($U_{0.05}$ = 3, w = 0.5379, Power = 0.54).

The final mustelid species examined was the striped skunk. In the analysis of striped skunk occurrences between counties, the results were not significant (χ^2 = .021, df = 2, $p > 0.05$) (Figure 3-11). Statistical power for this test was very low, however ($U_{0.05}$ = 2, w = 0.1414, Power = 0.02). Again, no physiographic analyses were conducted on striped skunks because of chi-square expected values of less than one. However, chi-square analysis did reveal that striped skunks were not detected evenly among habitats (χ^2 = 10.669, df = 3, $p \leq 0.025$) (Figure 3-12).

The mustelid data were grouped and analyzed to determine if any differences were manifested at the group level. The chi-square analysis of mustelid occurrences across counties showed that mustelids did occur evenly between counties, but results were only marginally insignificant ($\chi^2_{critical}$ = 5.991, χ^2 = 4.22, df = 2, $p > 0.05$) (Figure 3-13). Power for this test was low ($U_{0.05}$ = 2, w = 0.3209, Power = 0.43). Analysis of the physiographic regions supported this result ($\chi^2 = 3.948$, df = 6, $p > 0.05$). Power, again, was low for this test ($U_{0.05} = 6$, w = 0.3201, Power = 0.27). The chi-square analysis of mustelid occurrence between habitats revealed that mustelids did not occur evenly in all habitats ($\chi^2 = 9.934$, df = 3, $p \leq 0.025$) (Figure 3-14). This result was not supported using tracking plates as the statistical unit ($\chi^2 = 4.19$, df = 3, $p > 0.05$).

One felid was detected during this study, the bobcat. Chi-square analysis indicated that bobcats were occurring evenly between the counties and therefore across the panhandle in general ($\chi^2 = 3.804$, df = 2, $p > 0.05$) (Figure 3-15). Power for this test was relatively high ($U_{0.05} = 2$, w = 0.6165, Power = 0.61). Physiographic analysis was not conducted on bobcats because some chi-square expected values were less than one. Analysis of bobcat occurrence among habitats was also insignificant, but only just marginally so ($\chi^2_{critical} = 7.815$, $\chi^2 = 7.434$, df = 3, $p > 0.05$) (Figure 3-16). Statistical power for this test was low however ($U_{0.05} = 3$, w = 0.4472, Power = 0.32).

The final analyses of this project attempted to examine potential interspecific associations occurring between carnivores in the panhandle. These results may be used to understand patterns in occurrence and detections among panhandle habitats. Analyses were confined to carnivores within taxonomic groups at the family level based upon the assumption that more closely related carnivores are more likely to have a greater effect on one another. Chi-square contingency table analysis revealed that a significant interaction existed between the two canid species ($\chi^2 = 13.61$, df = 4, $p \leq 0.01$) (Figure 3-17). For mustelids, chi-square contingency table analysis revealed that no significant interactions were occurring between species ($\chi^2 = 7.5023$, df = 6, $p > 0.05$) (Figure 3-18). Statistical power for this test was marginal ($U_{0.05} = 5$, $w = 0.4351$, Power = 0.54).

DISCUSSION

Sampling effort was slightly uneven between the three panhandle counties (Table 2-1) and was more uneven among the panhandle habitats (Table 2-1). Discrepancies in sampling effort were by methodological design however, because land area covered by the counties and habitats was not equal between the counties and habitats. Differential sampling ensured that a county or habitat that occupied less area in the panhandle was not over sampled in terms of effort compared to any other county or habitat that occupied more panhandle land area. This approach worked well for habitats. The range/grassland areas, which occupy the most land area in the panhandle by far, received more sampling effort, proportional to its coverage (Table 2-1). The mesa and riparian areas, which occupy the least land area but are about equal in size, received almost identical sampling effort as well as the least sampling effort (Table 2-1). This approach also worked for counties, although not quite as accurately. Cimarron and Texas counties are the two larger counties in the panhandle and received the greatest amounts of effort (Table 2-1). However, Texas County is slightly larger than Cimarron County but received slightly less effort than Cimarron County (Table 2-1). This discrepancy may have been due to erratic precipitation events in the panhandle that occasionally washed tracking plates clean. Texas County plates may have been subjected to more precipitation events than Cimarron County plates. Beaver County, the smallest panhandle county, received the least amount of sampling effort in keeping with its relative smaller size (Table 2-1).

In general, the additional chi-square analysis using tracking plates as the statistical unit did not affect data interpretation. Chi-square analyses using all detections as the statistical unit accounted for nine significant results. When tracking plates were analyzed as the statistical unit, four results were supported as significant. The more conservative (tracking plate only) approach does not take into account persistence of carnivores over time in a particular area or habitat or the strong affiliations and home ranges that carnivores exhibit and establish in particular areas (Herrmann, 1994; Zoellick and Smith, 1992; Sandell, 1989). Persistent home ranges are, by definition, established in preferred habitat (Feldhamer et al., 1999). These areas tend to be so preferred that when the resident carnivore is removed, a dominant conspecific usually moves into the area (Feldhamer, 1999). The repetitive occurrences of carnivores at particular tracking stations over time (two years) in the Oklahoma panhandle was determined to be due to being within the established home range or other preferred habitat of specific carnivores. As a result, interpretation of the data were made using the multiple detection approach so as not to overlook this behavior in determining habitat or locational preferences.

Carnivores were not distributed evenly across the Oklahoma panhandle in general, in counties, or in habitats. Carnivores, in general, were detected most often in Cimarron County and less often than expected in either Texas or Beaver counties (Figure 3-1). These data imply a gradual decline in carnivore occurrence from west to east in the Oklahoma panhandle. The physiographic analysis did not support this result though. When plates were grouped according to the very broad physiographic, panhandle-wide affiliations, carnivores exhibited even distributions over the entire panhandle. This result, however, was only marginally insignificant and power for this test, while relatively good, was not strong. It is likely that sample sizes were not sufficiently large for this approach to detect accurately true differences where the approach using only the three county categories did detect differences. As a result, it seems reasonable to conclude that carnivores do not occur evenly across the entire panhandle.

Carnivores also exhibited non-random trends in occurrence within specific habitats. Carnivores were detected more often then expected in the mesa and agricultural habitats (Figure 3-2). Carnivores were detected as often as expected in riparian areas, but were underrepresented in range/grassland areas (Figure 3-2). These patterns likely reflect trends in individual carnivore species.

Canids

Occurrence, distribution, and patterns in swift foxes over the course of this study are discussed more extensively in Chapter two and in Shaughnessy (in press). However, it is important to note that the swift fox was not detected in all counties or habitats equally. Swift foxes were detected more often in the westernmost parts of the Oklahoma panhandle and specifically in Cimarron County (Figure 2-2). Foxes were not detected as often as expected in either Texas or Beaver Counties (Figure 2-2). Additionally, swift foxes also demonstrated a clear preference for the westernmost physiographic regions of the panhandle (mesa and northwestern mesa/riparian) and were absent in the more centrally located regions of the panhandle (north/central agriculture and central mixed agriculture and range).

Swift foxes were detected most frequently in the mesa habitat, occurring more than twice as often as expected (Figure 2-3). In agriculture and range/grassland areas, foxes were detected about as often as expected (Figure 2-3). However, swift foxes were grossly under-represented in riparian areas of the panhandle (Figure 2-3).

Patterns in coyote occurrence in the panhandle were similarly uneven. Coyotes were detected most often in Texas County (Figure 3-3). They were only rarely detected in Beaver County and they were detected about as often as expected in Cimarron County (Figure 3-3). Coyotes detected in Cimarron County were detected outside of the mesa region. Physiographically, coyotes preferred the north/central agricultural region of the panhandle far above any other panhandle region. They also occurred regularly in the southwestern grassland region of the panhandle. Coyotes avoided the northwestern mesa/riparian region as well as the northeastern riparian/range area of the panhandle.

In habitats, coyotes preferred agricultural areas over all other areas. They were detected in agricultural areas more than twice as often as predicted (Figure 3-4). Coyotes were detected in riparian areas about as often as expected, but they apparently avoided mesa and range areas and were only recorded in these areas about half as much as expected (Figure 3-4). Given these habitat affinities for coyotes, it was not surprising that coyotes were detected most often in Texas County. Texas County is predominantly an agricultural county. Cimarron and Beaver counties are much less devoted to agricultural practices.

Canids as a group were also not distributed evenly across the panhandle, between counties or among macrohabitats. Canids were detected much more often than expected in Cimarron County and much less than expected in Beaver County (Figure 3-5). Canids displayed a decrease in occurrence from west to east in the Oklahoma panhandle. Canids also showed a preference towards the mesa and agricultural areas of the panhandle while exhibiting an aversion towards riparian and range areas (Figure 3-6). This result is probably due to the strong positive individual responses of swift foxes and coyotes towards each of these areas respectively.

Canid occurrences in the panhandle were determined to be governed at least in part by a strong interaction effect between the two species (Shaughnessy, in press). Where coyotes occurred in abundance, swift foxes were conspicuously absent (Figure 3-17). Swift foxes were present in abundance only in those areas where coyotes were detected infrequently, most notably the mesa region (Figure 3-17). This strongly negative interaction has been documented among other canid species (Dayan and Simberloff, 1996; Johnson et al., 1996; Peterson, 1995; Bailey, 1992; Thurber et al., 1992; Harrison et al., 1989; Sargeant et al., 1987; Carbyn, 1982; Rudzinski et al., 1982). Coyotes and other larger canids have been documented as significant sources of mortality for smaller canids, and swift foxes specifically in the prairie environment (Dayan and Simberloff, 1996; Johnson et al., 1996; Peterson, 1995; Bailey, 1992; Harrison et al., 1989; Sargeant et al., 1987; Carbyn, 1982; Rudzinski et al., 1982). This interaction between swift foxes and coyotes in the Oklahoma panhandle was, therefore, not surprising.

While the presence or absence of coyotes is certainly affecting swift fox habitat selection in the Oklahoma panhandle, the interaction is probably not the sole determining factor in swift fox distributions. Swift foxes tend to be highly sensitive to predation from many potential predators, not only larger canids (Egoscue, 1956, 1962, 1979). This susceptibility to predation also was inferred by the swift foxes heavy reliance on den sites and subterranean tunnels (Moehrenschlager et al., in press; Egoscue, 1962, 1979). Tall grass areas may inhibit the ability of the swift fox to detect predators because of the foxes small size (Allardyce, pers. comm.). Tall grass areas also may limit the ability of the fox to find a suitable escape route underground when confronted with a predator (Allardyce, pers. comm.). Swift foxes may be avoiding tall grass areas to facilitate predator detection and escape (Allardyce, pers. comm.).

The mesa areas are dominated by shorter grasses that the foxes may prefer because they allow them to detect predators more easily and locate escape routes underground. Additionally, agricultural areas are only seasonally planted and often left fallow, with only low ground plants covering them. Swift fox may be using agricultural areas because their normally low vegetation aids them in predator avoidance, and persisting in agricultural areas during the short periods of time when crops are tall. Conversely, range/grassland areas are often a mix of tall grass areas, short grass areas, and areas bare from overgrazing. The absence of coyotes in these areas (Figure 3-4) may be attractive to swift foxes, but the heterogeneous nature of the habitat, particularly the presence of tall grasses, may discourage selection of this habitat by swift foxes. This may explain the slightly depressed occurrence frequency of swift foxes in range/grassland areas (Figure 2-3). Finally, swift fox were grossly absent from riparian areas. These areas are often overgrown with tall grasses, shrubs, bushes, and trees. In addition, coyotes were found in riparian areas in abundance (Figure 3-4). It is not surprising then, that swift foxes were not selecting riparian areas.

Coyote occurrence patterns are not easily explained. Coyotes exhibited no aversion to riparian areas and an overwhelming preference for agricultural areas (Figure 3-4). Coyotes are among the largest terrestrial predators in the Oklahoma panhandle and were the largest carnivores detected during this study. Riparian areas often serve as travel corridors for a variety of panhandle vertebrates. Coyotes may be frequenting riparian areas to increase the probability of encountering potential prey. Agricultural areas may support higher numbers of small and medium sized mammals. Rodent populations may be higher in agricultural areas than in the surrounding grasslands due to the seasonal abundance of seed resources. Coyotes may prefer agricultural areas because of their potential for higher rodent resource bases.

Coyote habitat selection may also be influenced by human factors in the Oklahoma panhandle. Coyotes did not occur often in mesa or range/grassland areas (Figure 3-4). Much of the range/grassland and mesa areas of the panhandle are used for cattle production (Shaughnessy, in press). Coyotes are considered significant predators on livestock by the ranchers in the Oklahoma panhandle and substantial effort is invested in coyote control in the primary cattle production areas (Shaughnessy, in press). Coyote populations may be reduced in these areas due to these control efforts, and coyotes may be selectively avoiding these areas in response to the control efforts (Shaughnessy, in press).

An additional historical component may be at work in the dynamics of panhandle canid populations. The wolf (*Canis lupus*) historically occupied the Oklahoma panhandle (as well as the body of the state). Antagonistic interactions between coyotes and wolves are also well documented (Carbyn, 1982; Thurber et al., 1992; Peterson, 1995). It is possible that the wolf historically structured the panhandle canid community by eliminating coyotes from local areas and limiting their populations regionally. If this were the case, the interaction would have benefitted swift foxes and other smaller canids. With the removal of wolves though, coyote numbers have not only increased, but coyotes have invaded habitats that they were previously excluded from by wolves. As a result, it is likely that coyotes now eliminate swift foxes locally and swift foxes are only able to thrive and persist regionally in those habitats that coyotes do not prefer.

Mustelids

Of the three mustelid species that were detected during the course of this study, the spotted skunk was detected most often. Overall, spotted skunks were detected most often in Cimarron County and least often in Texas County (Figure 3-7). However, these differences were not statistically significant. Physiographically, spotted skunks also occurred evenly among all designated regions. While power for the physiographic test was low, power for the county test was high. Given that the two tests agreed, the probability of the commission of a Type II error seems remote. As a result, there was no regional bias in spotted skunk detections throughout the panhandle. In terms of habitat, spotted skunks preferred riparian areas overall, but also showed an affinity for agricultural areas (Figure 3-8). Spotted skunks were regularly present in range/grassland areas but apparently avoided the mesa area, which would help to explain patterns in their distribution across tracking stations in general. These differences were not significant however.

Badgers were detected regularly throughout the course of the study as well, but not with the frequency of spotted skunks. Badgers were detected much more often in Cimarron County than in any other panhandle county (Figure 3-9), however these differences were not significant. Power for this test was high as well, so although there were detection differences between counties, no regional preference existed. Badgers also exhibited unequal habitat preferences. Badgers were detected most often in agricultural areas (Figure 3-10). Badgers did not appear to avoid mesa or riparian areas either, but were under-represented in range/grassland areas (Figure 3-10). Again, however, these patterns were not statistically significant.

Striped skunks were detected least often over the course of this study. Striped skunks were distributed very evenly across the three panhandle counties (Figure 3-11). Statistical power was low though for this test, so these results should be interpreted with caution. However, striped skunks showed significant habitat preferences within the counties (Figure 3-12). Striped skunks markedly preferred riparian areas over all other panhandle habitats (Figure 3-12). They also occurred regularly in the mesa and agricultural areas, but were under represented in range/grassland areas.

Mustelids in general were distributed evenly across the entire panhandle, although power was low for this test. Due to the low power, results should again be interpreted with caution and trends in occurrences should be examined. Mustelids were detected more often in Cimarron County than in either Texas or Beaver counties (Figure 3-13). Mustelids were detected in Cimarron County twice as often as they were detected in

Texas County and nearly twice as often as they were detected in Beaver County (Figure 3-13). Mustelids did exhibit clear habitat preferences in the Oklahoma panhandle. Mustelids preferred riparian and agricultural areas over other habitats in the panhandle (Figure 3-14). They did not appear to avoid the mesa area, but did show a clear aversion to the range/grassland areas of the panhandle (Figure 3-14). Mustelids also did not demonstrate any significant intrafamily interactions (Figure 3-18).

Mustelid distribution patterns in the Oklahoma panhandle are more difficult to explain due to the lack of intrafamily interactions. Intraorder level interactions were present among all canids and mustelids though at significant levels throughout the panhandle ($\chi^2 = 31.58$, df = 12, $p \leq 0.005$). Mustelids tended to avoid those habitats which supported higher numbers of swift foxes, and were generally more abundant in areas with higher coyote occurrences. Antagonistic intraorder level interactions may be operating between swift foxes and mustelids in much the same way that these interactions structure swift fox/coyote distribution patterns. However, although swift foxes are generally larger than the mustelids, it would seem unlikely that the dynamics defining swift fox/coyote interactions and distributions completely account for the swift foxes/mustelid distributional differences. Due to the formidable defensive adaptations of skunks and the generally aggressive disposition of badgers, swift foxes are probably not as successful at excluding mustelids as coyotes are at excluding swift foxes. It seems more likely that mustelids, like coyotes, are selecting areas that may support larger small mammal and, in particular, rodent populations such as agricultural areas. Coyotes may not persecute mustelids as rigorously because of the greater disparity in their sizes as well as the ability of the mustelids to defend themselves aggressively.

Small canids tend to be more generalized in their food habits than larger canids (or mustelids) and are able to persist on a less strictly carnivorous diet (Johnson et al., 1996; Cutter, 1958). If coyotes exclude swift foxes from areas of high rodent densities, swift foxes should be able to persist in less optimal areas (in terms of rodent densities) by expanding their diet to include a wider variety of foods. Mustelids, by virtue of their defenses and smaller size, are probably not viewed by coyotes as being strong food resource competitors. Mustelids are also more strictly carnivorous than canids (Feldhamer et al., 1999). They would select areas with the highest prey bases available. This may explain the similar habitat selections by coyotes and mustelids, if agricultural areas do indeed support higher small mammal populations than surrounding habitats. Furthermore, if antagonistic intraorder interactions between swift foxes and mustelids do occur, then the local exclusion of swift fox from agricultural and riparian areas by coyotes would only strengthen the associations of mustelids to these areas.

Felids

The final carnivore detected during this study was the bobcat. Bobcats were only detected infrequently. Bobcats were distributed evenly among counties (Figure 3-15). Statistical power for this test was relatively good, but did not eliminate the possibility of a Type II error. As a result, bobcat occurrence trends are worth examining. Bobcats were detected more frequently in Cimarron County than in any other panhandle county (Figure 3-15). This was probably due to the relatively small human population in that county. Bobcats are among the carnivores most sensitive to human activity. Therefore, it was not surprising that bobcats were detected more in the county with the lowest human population. Bobcats also displayed even distributions among habitats, although this result was only marginally insignificant. Additionally, power for this test was low. It is therefore not unlikely that with larger sample sizes bobcats might show clearer habitat preferences. In the panhandle, bobcats did exhibit a slight preference for mesa and riparian habitats over range/grassland and agricultural habitats (Figure 3-16). It would be difficult to draw any further conclusions from these data because sample sizes were so small and could not be combined with other detected felids in order to make generalizations about the group.

SUMMARY

In general, carnivores were not distributed evenly throughout the panhandle or among habitats. Panhandle distributions may be indirectly related to human populations and activities. Carnivores were overwhelmingly detected more often in the western third of the panhandle (Cimarron County) and detections tended to decrease with eastward movement through the panhandle. Cimarron County is the least populated and developed county in the Oklahoma panhandle. Human populations steadily increase with eastward movement to Guymon, Oklahoma, which is located in the center of Texas County, in the very middle of the panhandle. Human populations then slightly decrease through Beaver County, which may also explain some of the far eastern distributional peaks in carnivore occurrences. Carnivore habitat preferences were often dependent upon the presence or absence of other carnivores and may also have been dependent upon relative densities of small mammals within habitats. However, more research in the form of small mammal surveys in the major panhandle habitats is needed to address this hypothesis properly.

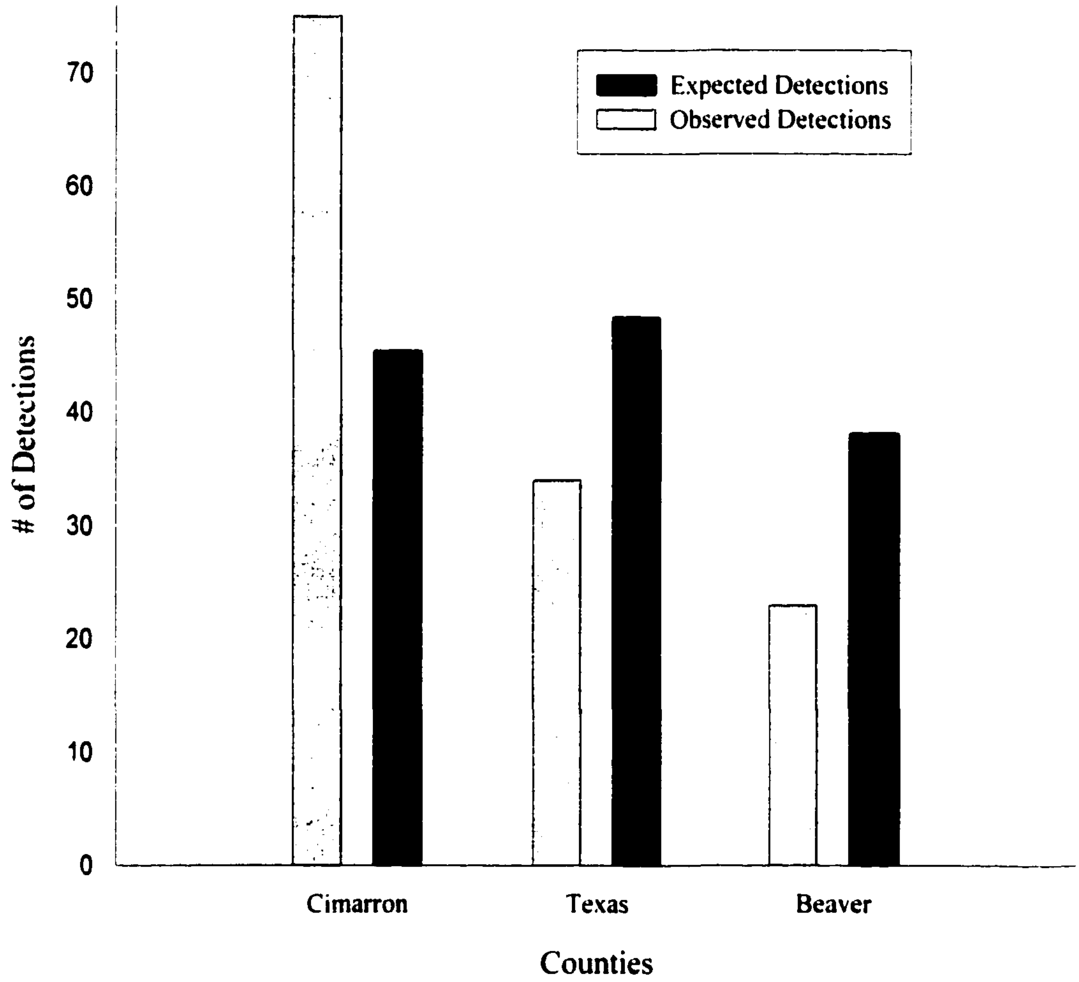


Figure 3-1. Carnivore detections across counties in the Oklahoma panhandle, 1995 - 1997 ($p < 0.05$).

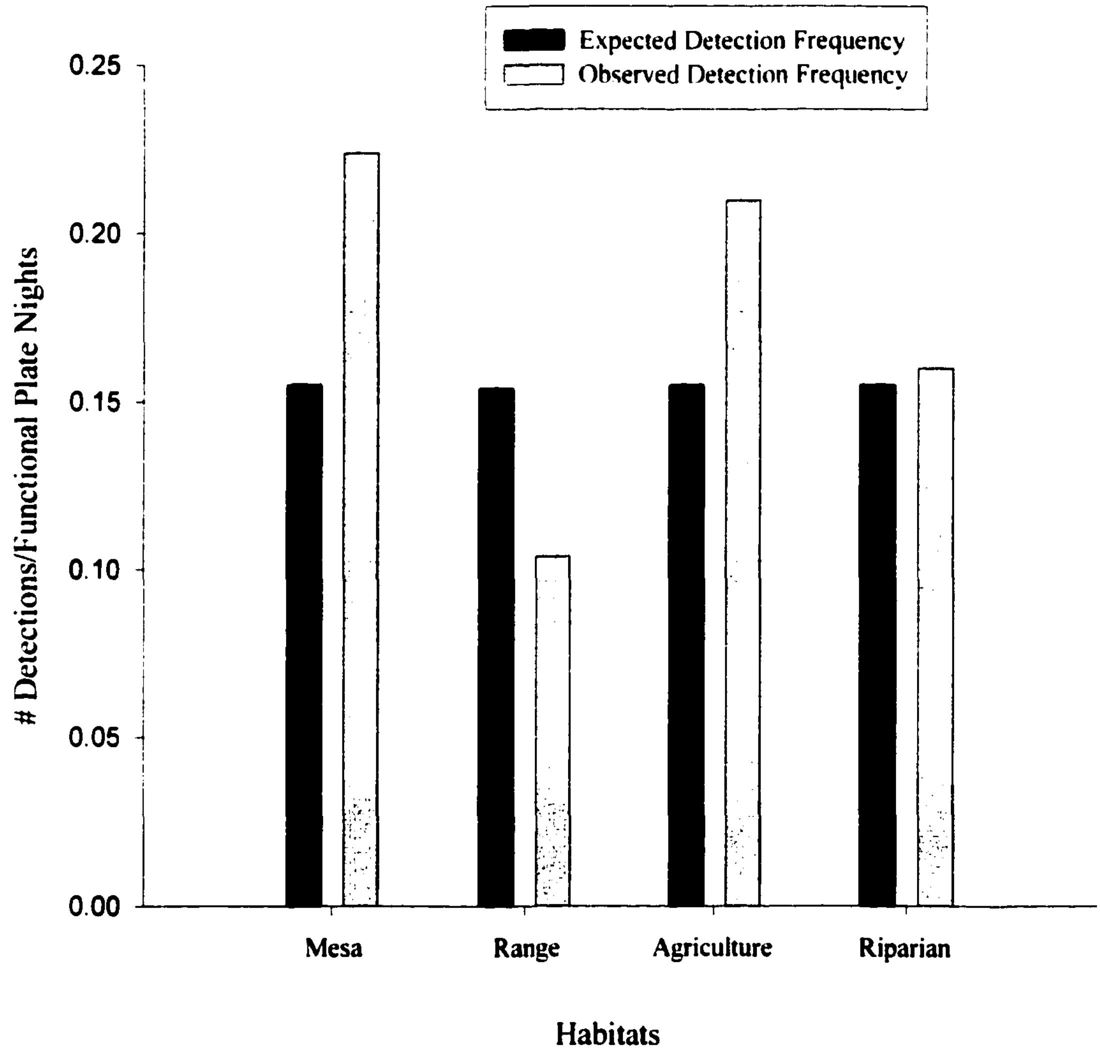


Figure 3-2. Carnivore occurrences among habitats in the Oklahoma panhandle, 1995 - 1997 ($p < 0.05$).

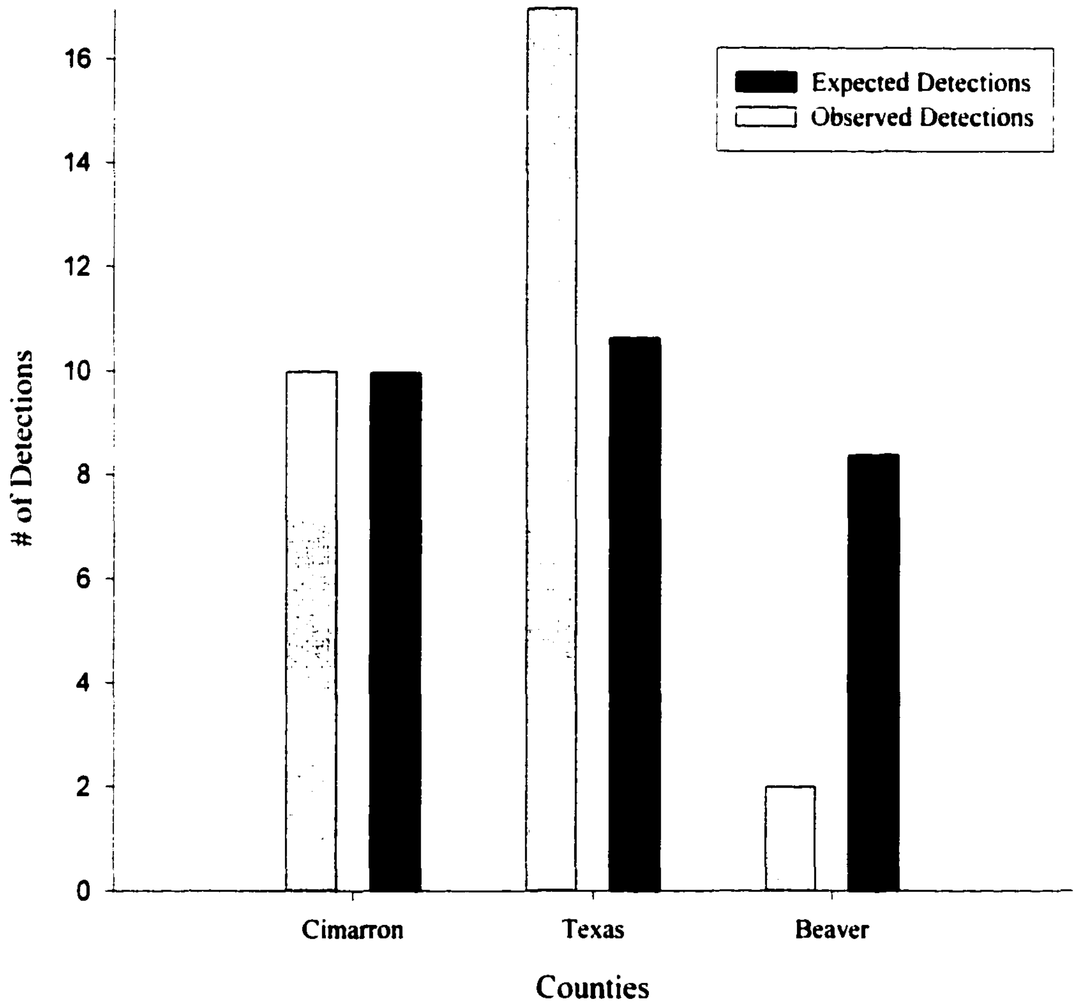


Figure 3-3. Coyote (*Canis latrans*) detections across counties in the Oklahoma panhandle, 1995 - 1997 ($p < 0.05$).

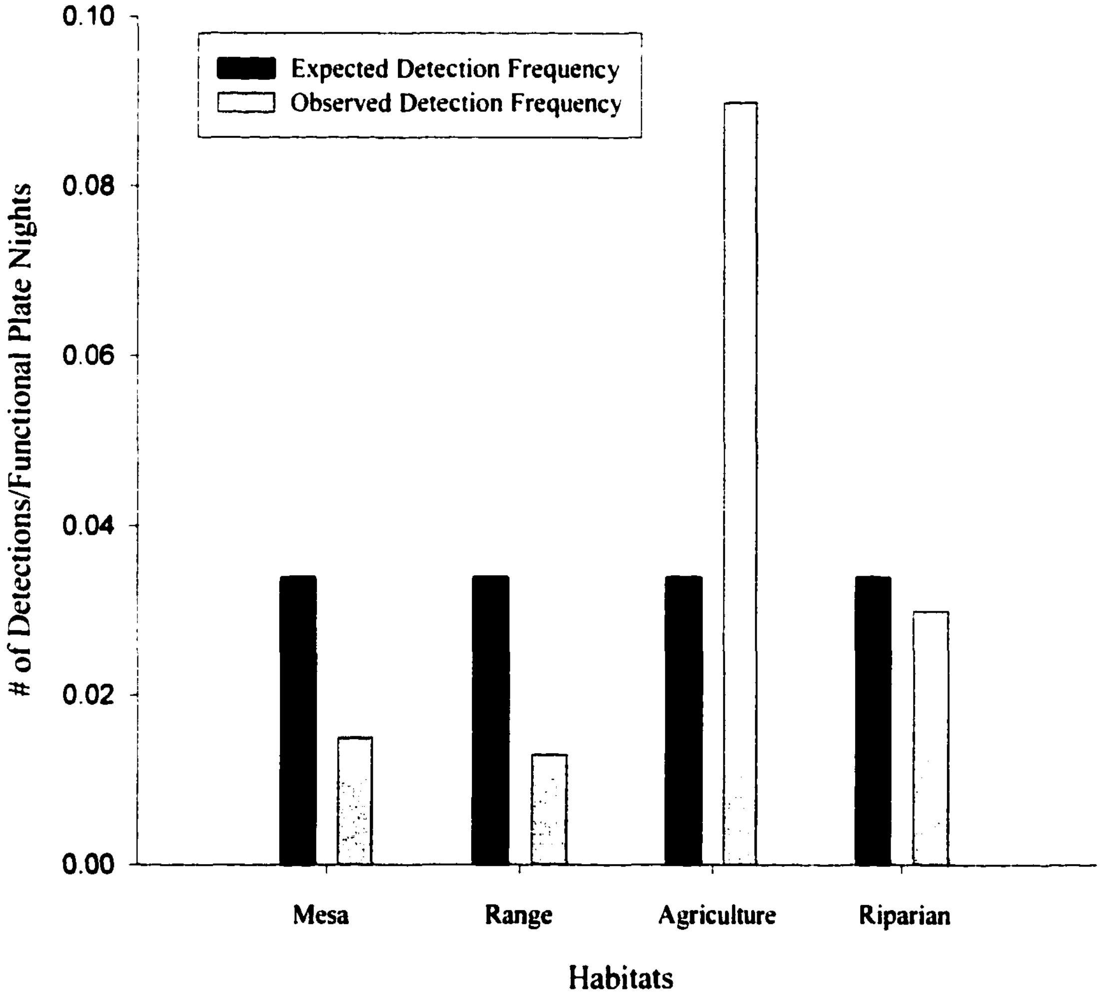


Figure 3-4. Coyote (*Canis latrans*) occurrences among habitats in the Oklahoma panhandle, 1995 - 1997 ($p < 0.05$).

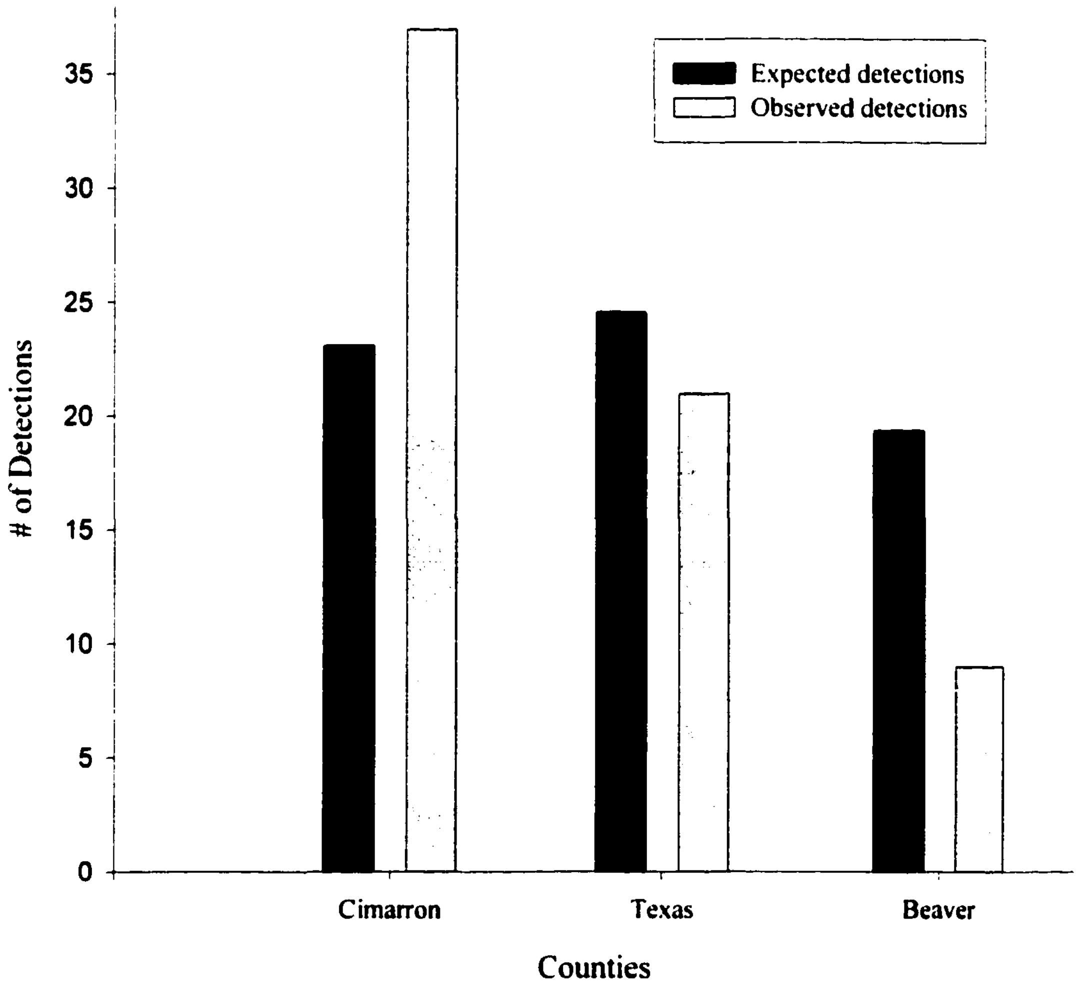


Figure 3-5. Detections of all canids among counties in the Oklahoma panhandle, 1995 - 1997 ($p < 0.001$).

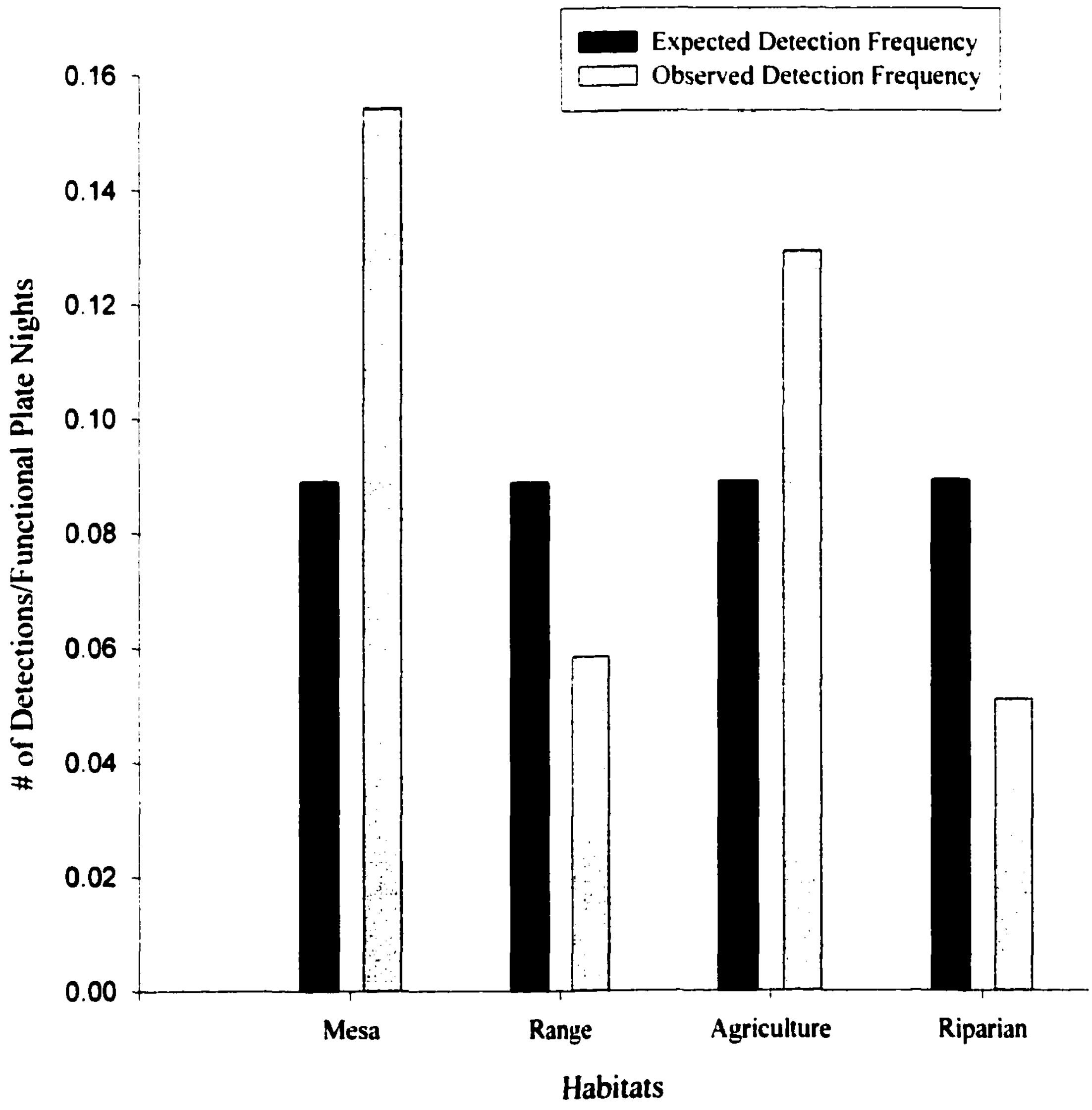


Figure 3-6. Detection frequencies of all canids in habitats of the Oklahoma panhandle, 1995 - 1997 (p < 0.001).

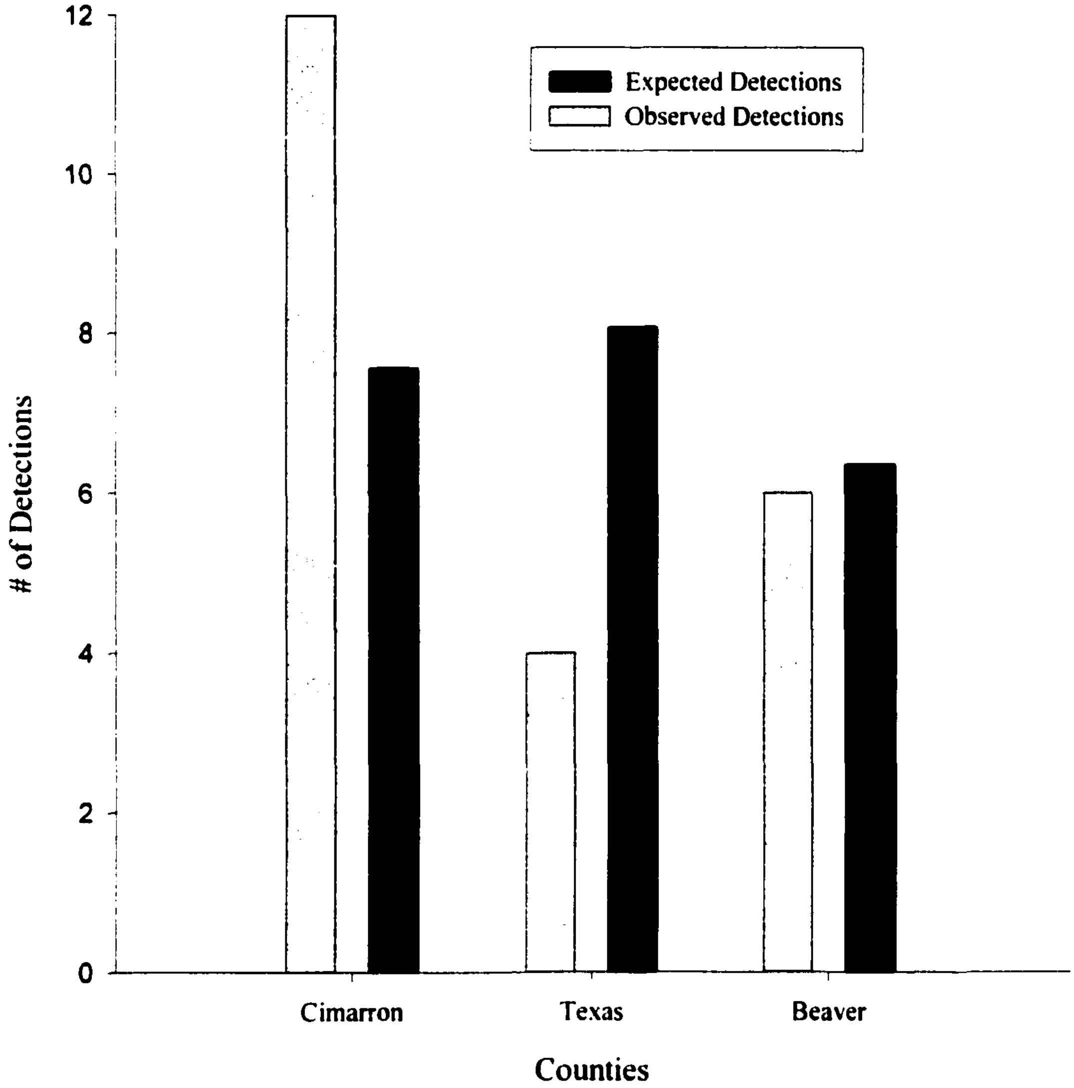


Figure 3-7. Spotted Skunk (*Spilogale putorius*) detections across Oklahoma panhandle counties, 1995 - 1997.

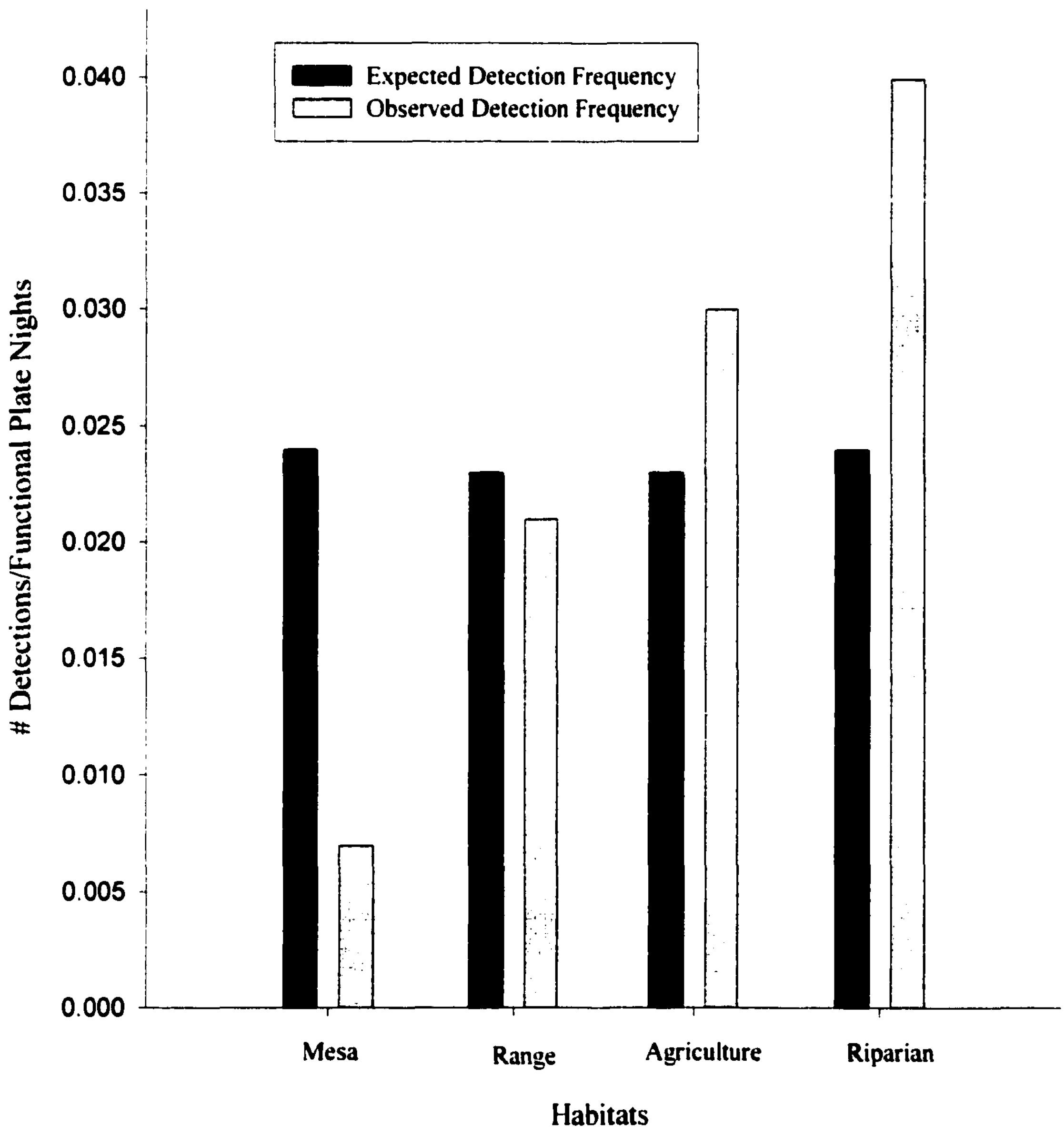


Figure 3-8. Spotted skunk (*Spilogale putorius*) occurrences across habitats in the Oklahoma panhandle, 1995 - 1997.

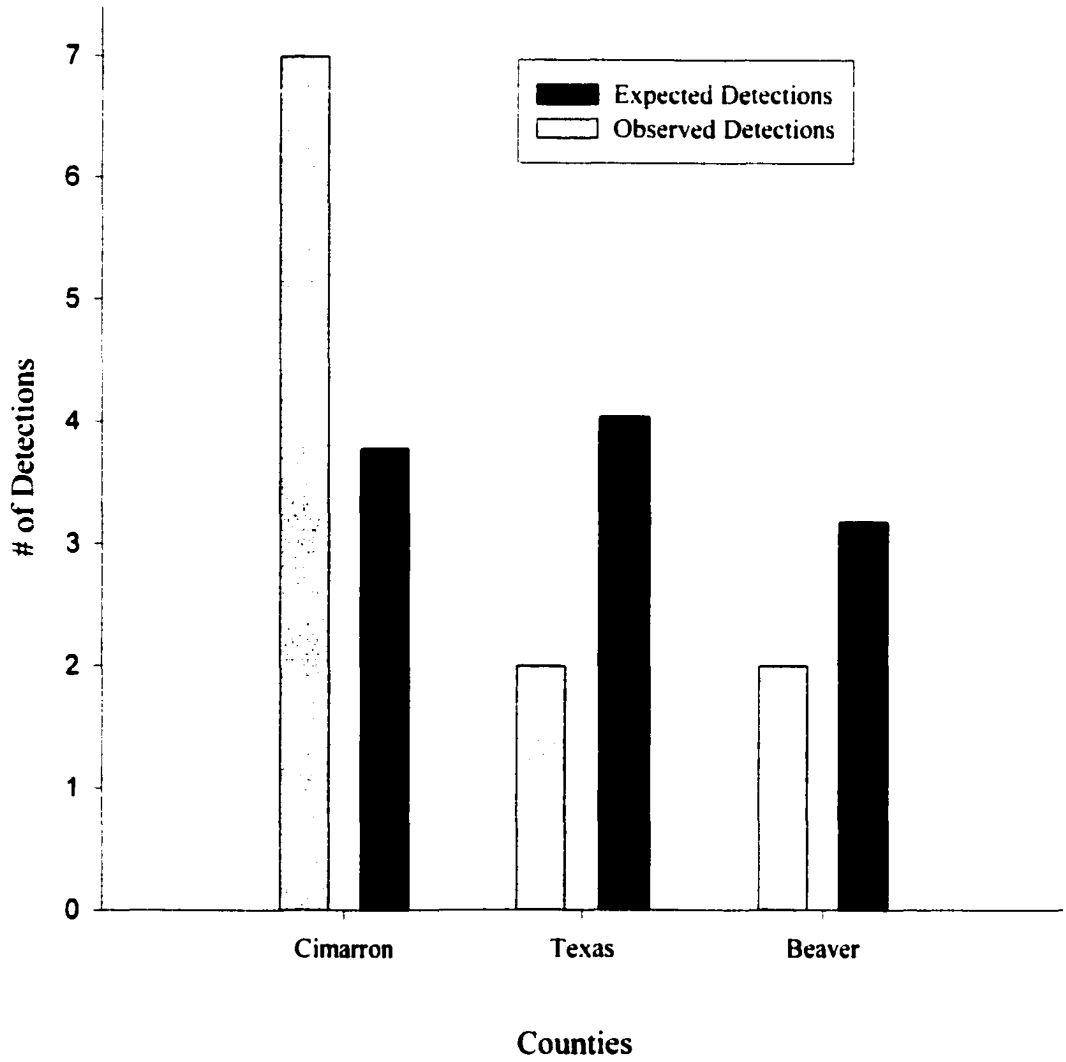


Figure 3-9. Badger (*Taxidea taxus*) detections across counties in the Oklahoma panhandle, 1995 - 1997.

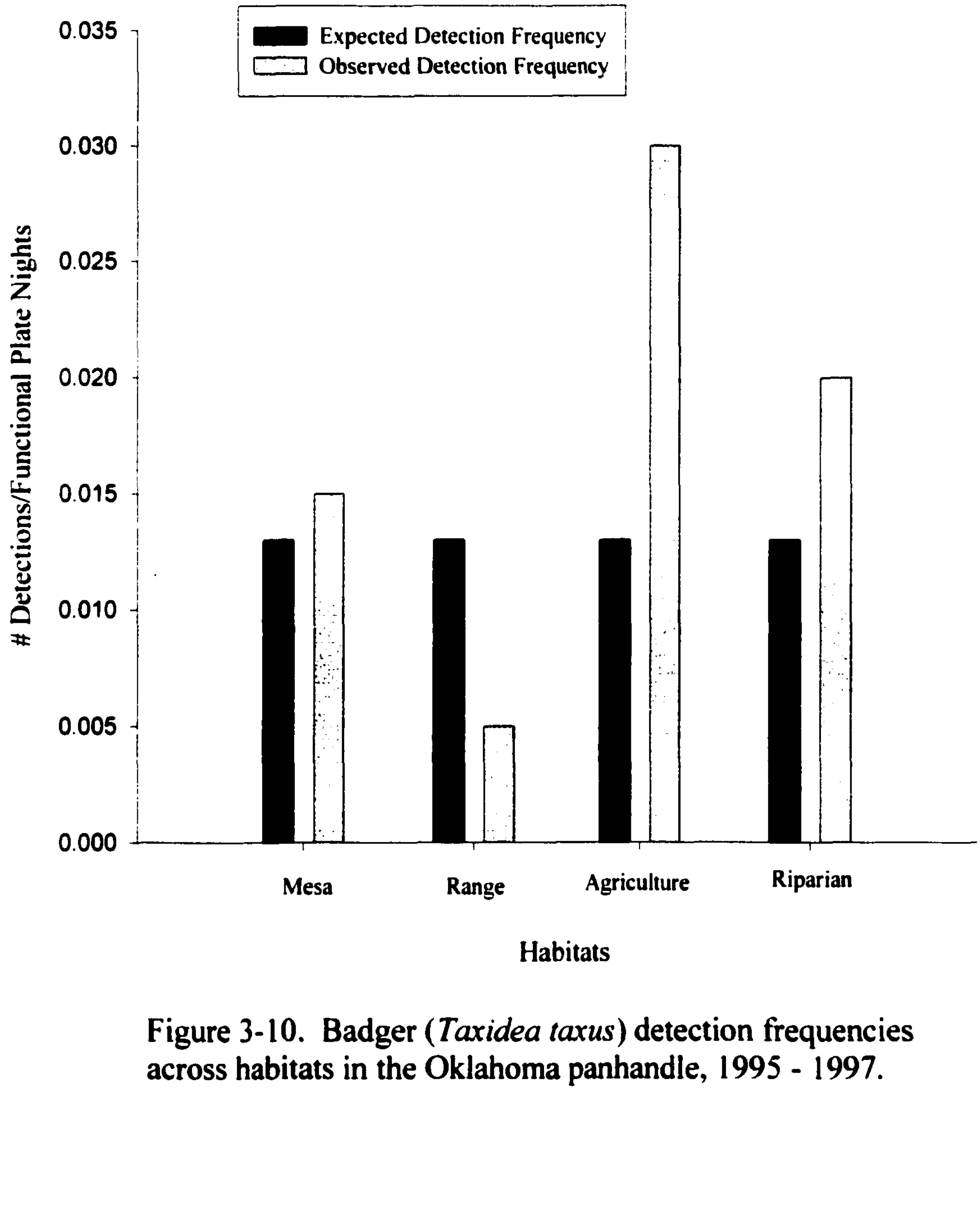


Figure 3-10. Badger (*Taxidea taxus*) detection frequencies across habitats in the Oklahoma panhandle, 1995 - 1997.

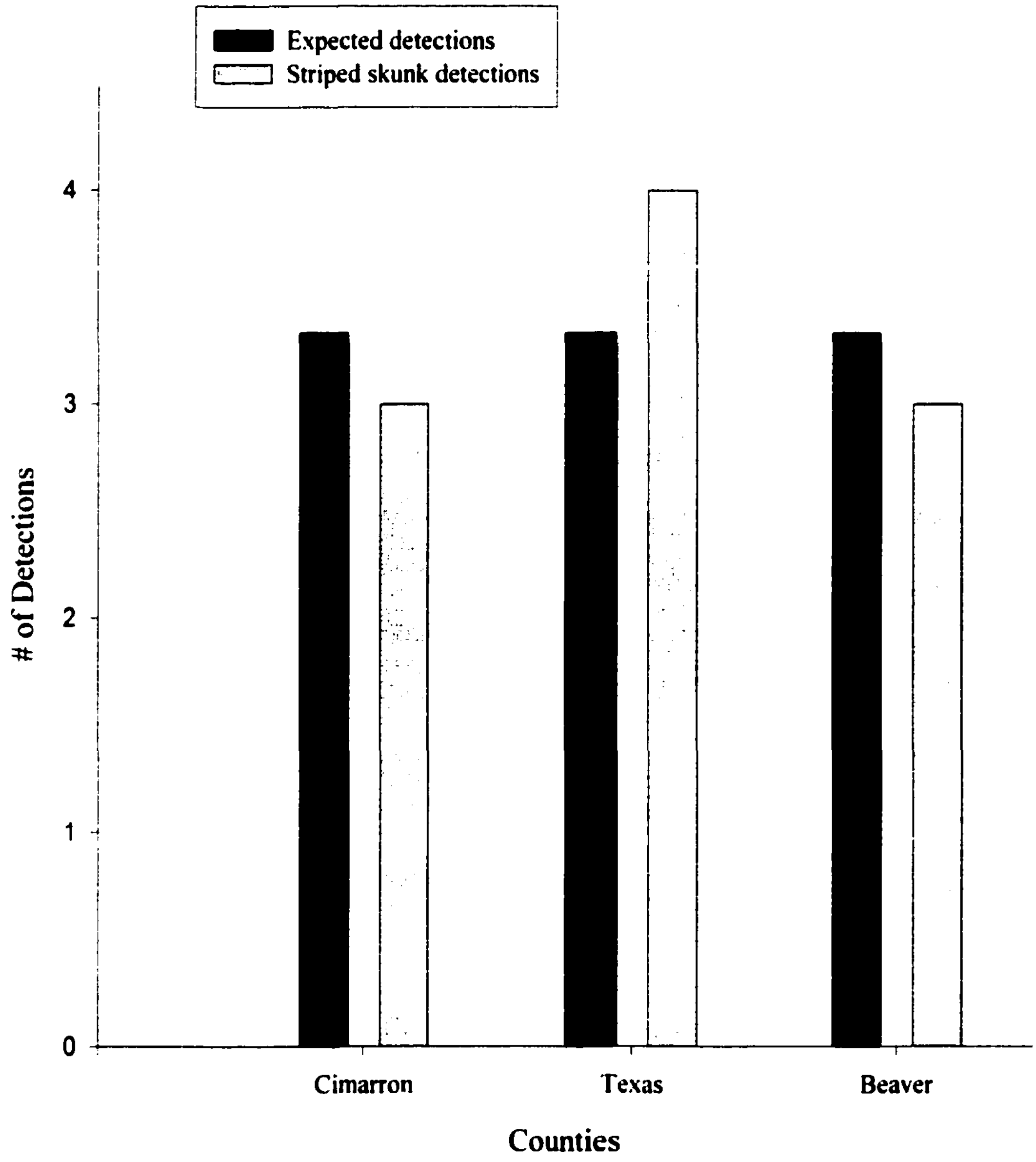


Figure 3-11. Striped skunk (*Mephitis mephitis*) detections across counties in the Oklahoma panhandle, 1995 - 1997.

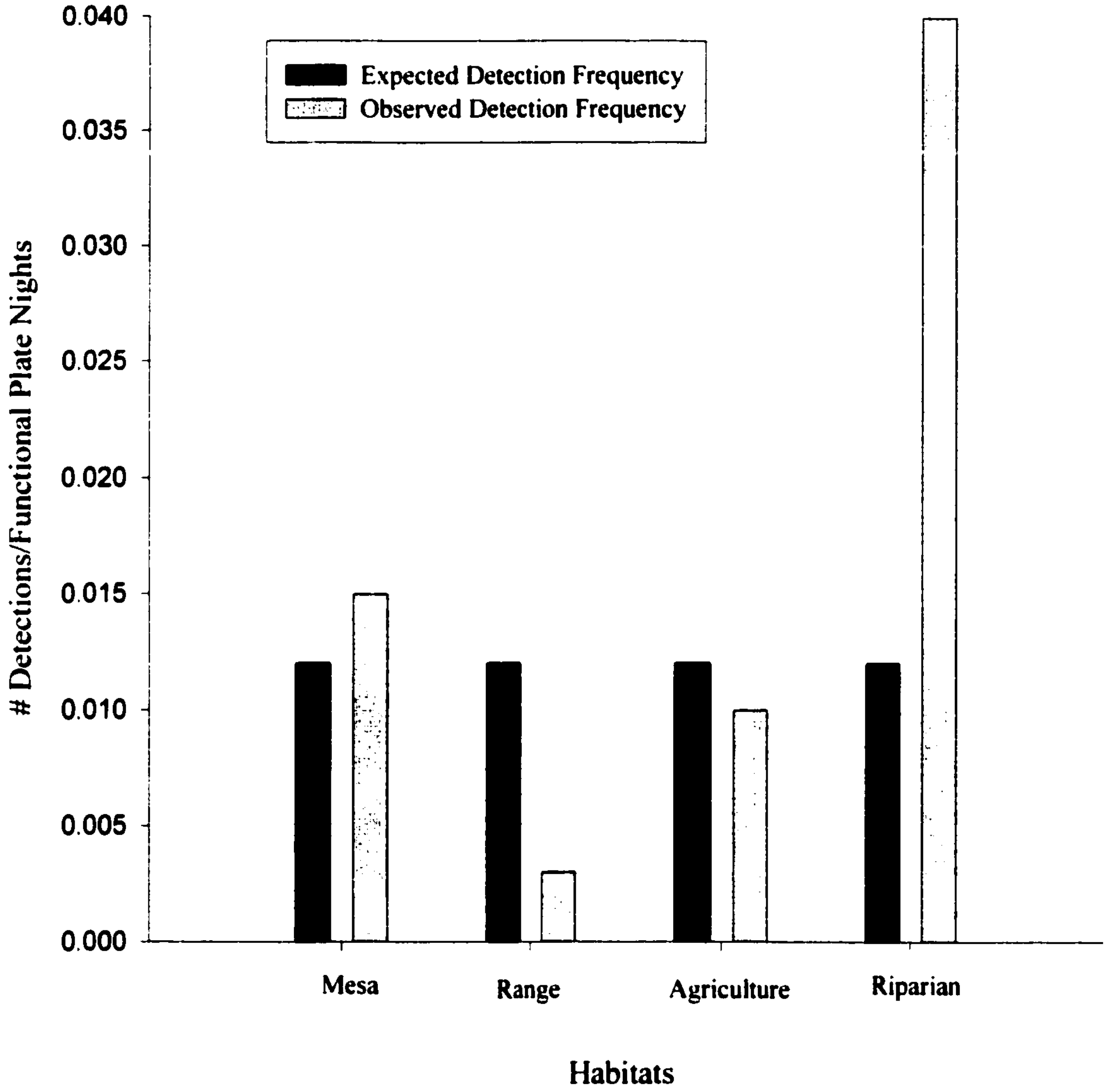


Figure 3-12. Detection frequency of striped skunks (*Mephitis mephitis*) across habitats in the Oklahoma panhandle, 1995 - 1997 ($p < 0.05$).

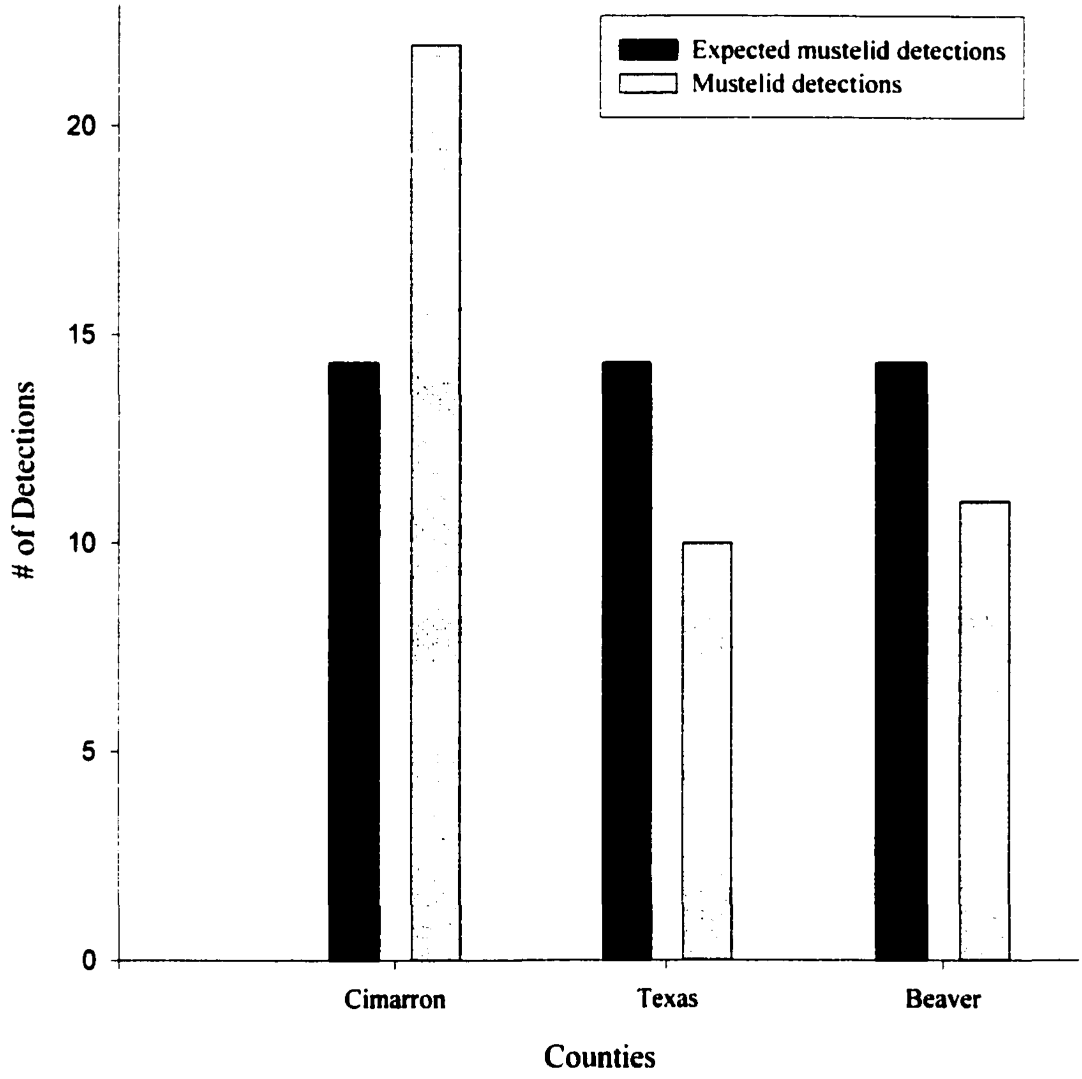


Figure 3-13. Detections of all mustelids across counties in the Oklahoma panhandle, 1995 - 1997.

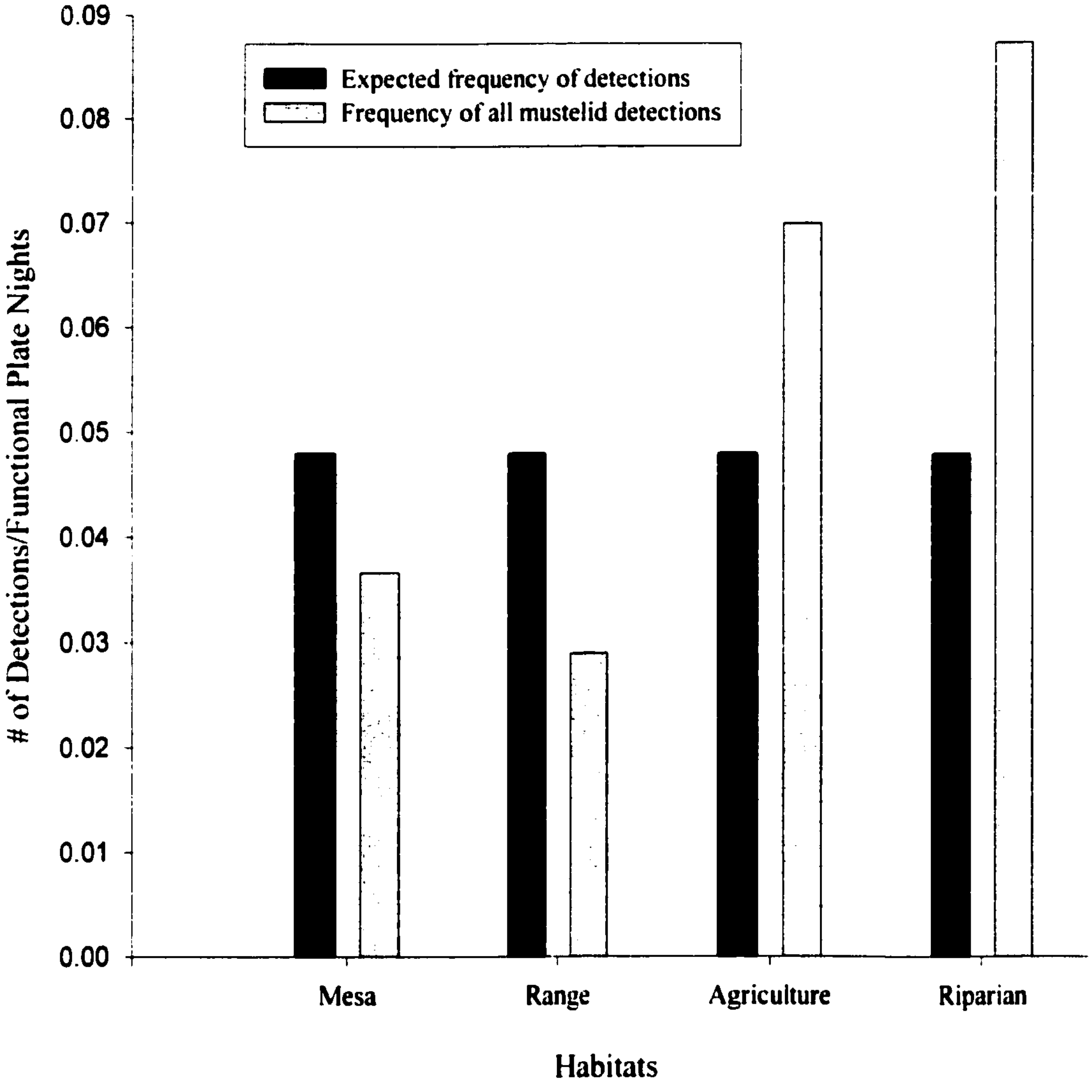


Figure 3-14. Detection frequency of all mustelids across habitats in the Oklahoma panhandle, 1995 - 1997 ($p < 0.025$).

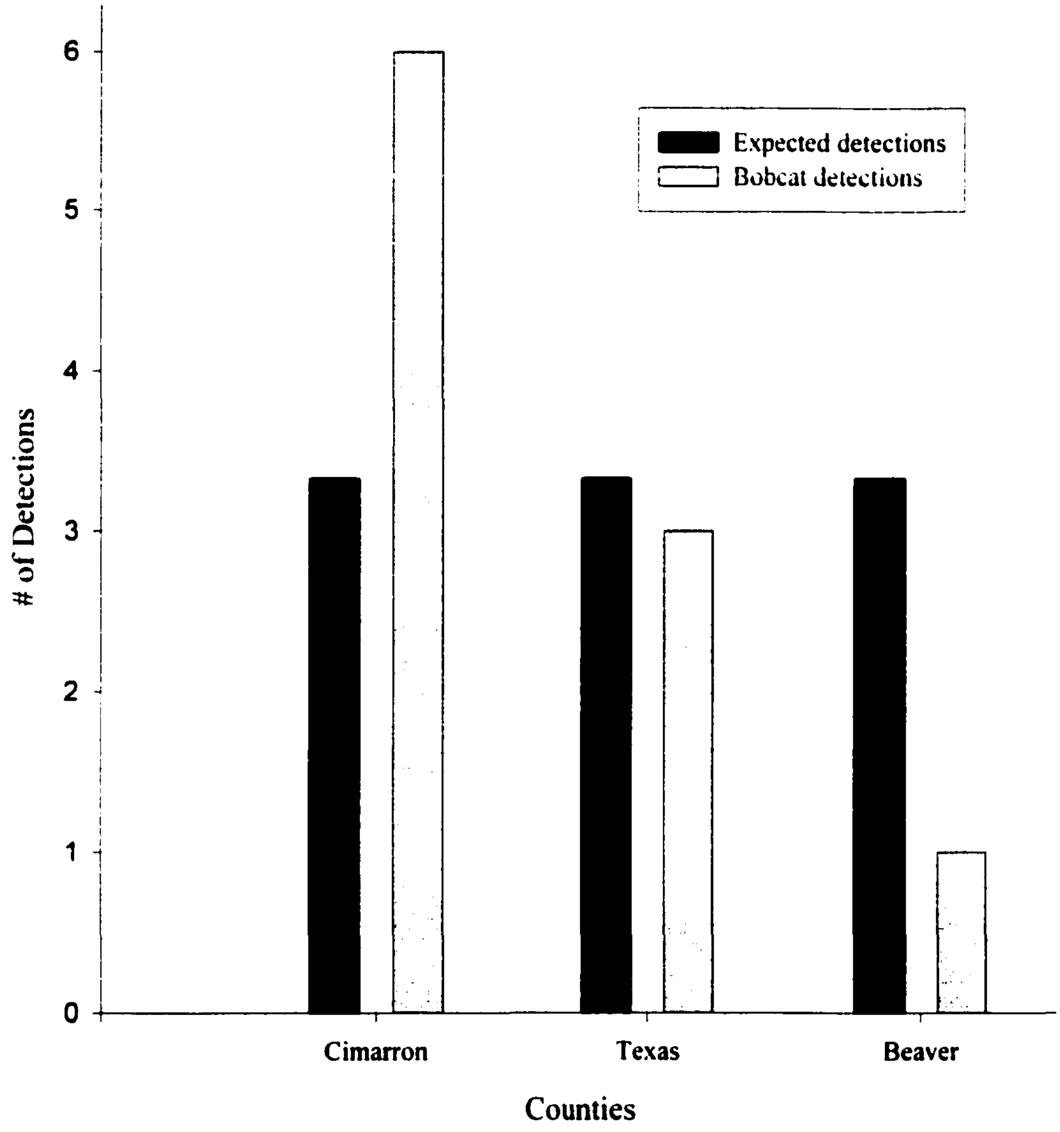


Figure 3-15. Bobcat (*Lynx rufus*) detections across counties in the Oklahoma panhandle, 1995 - 1997.

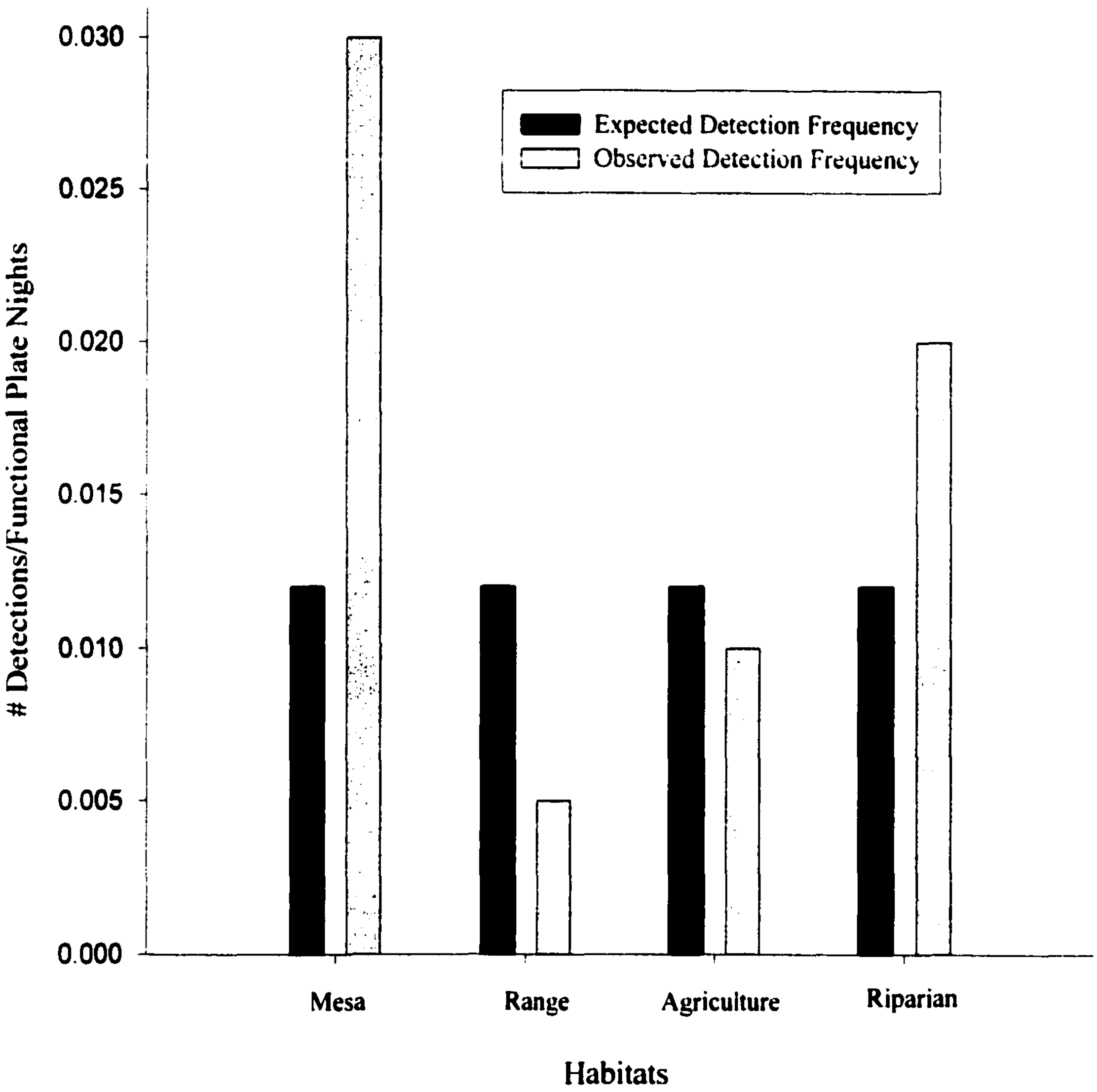


Figure 3-16. Bobcat (*Lynx rufus*) detection frequency across habitats in the Oklahoma panhandle, 1995 - 1997 ($p = 0.05$).

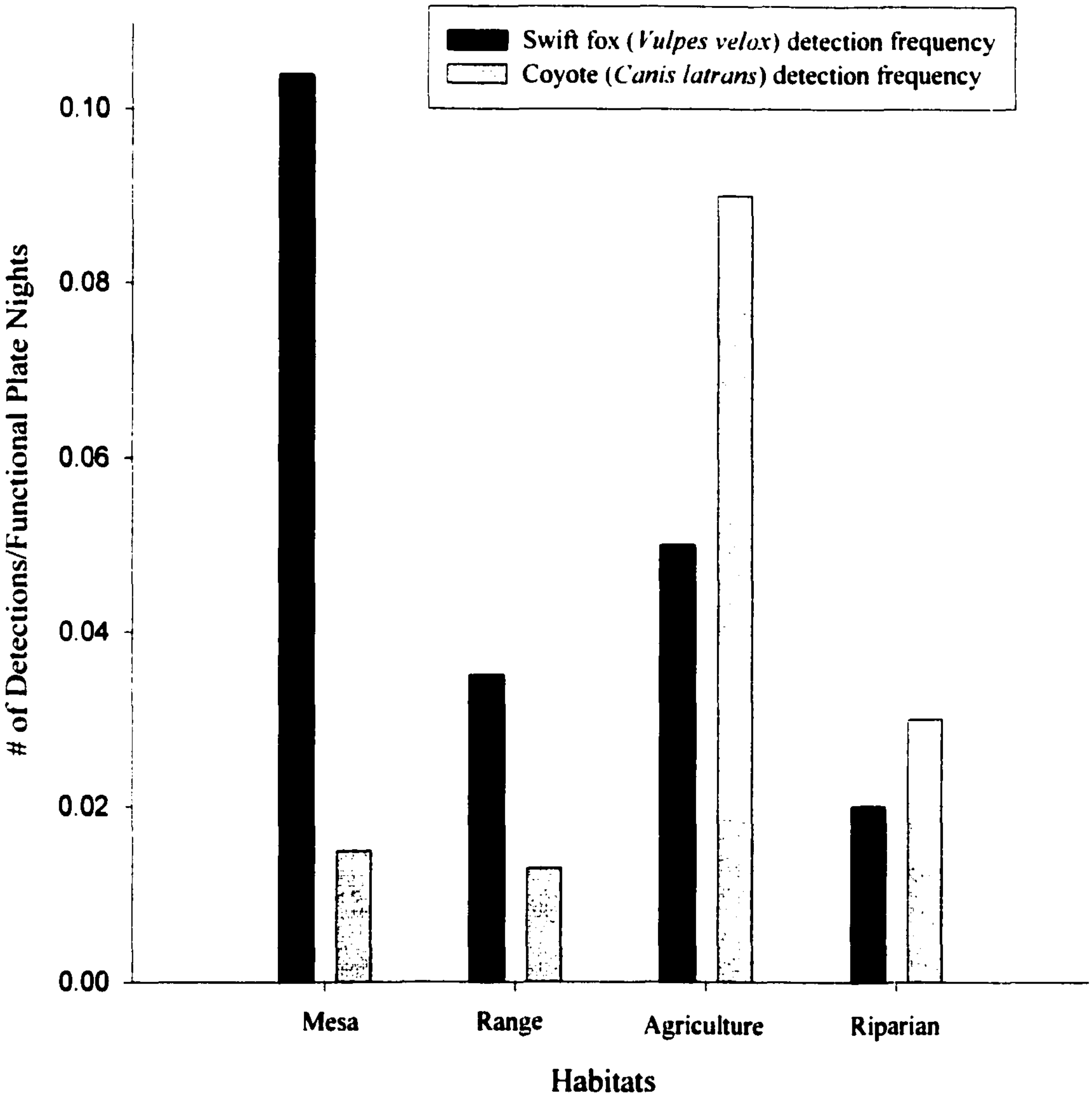


Figure 3-17. Detection frequencies of swift foxes (*Vulpes velox*) and coyotes (*Canis latrans*) in the Oklahoma panhandle, 1995 - 1997 ($p < 0.01$).

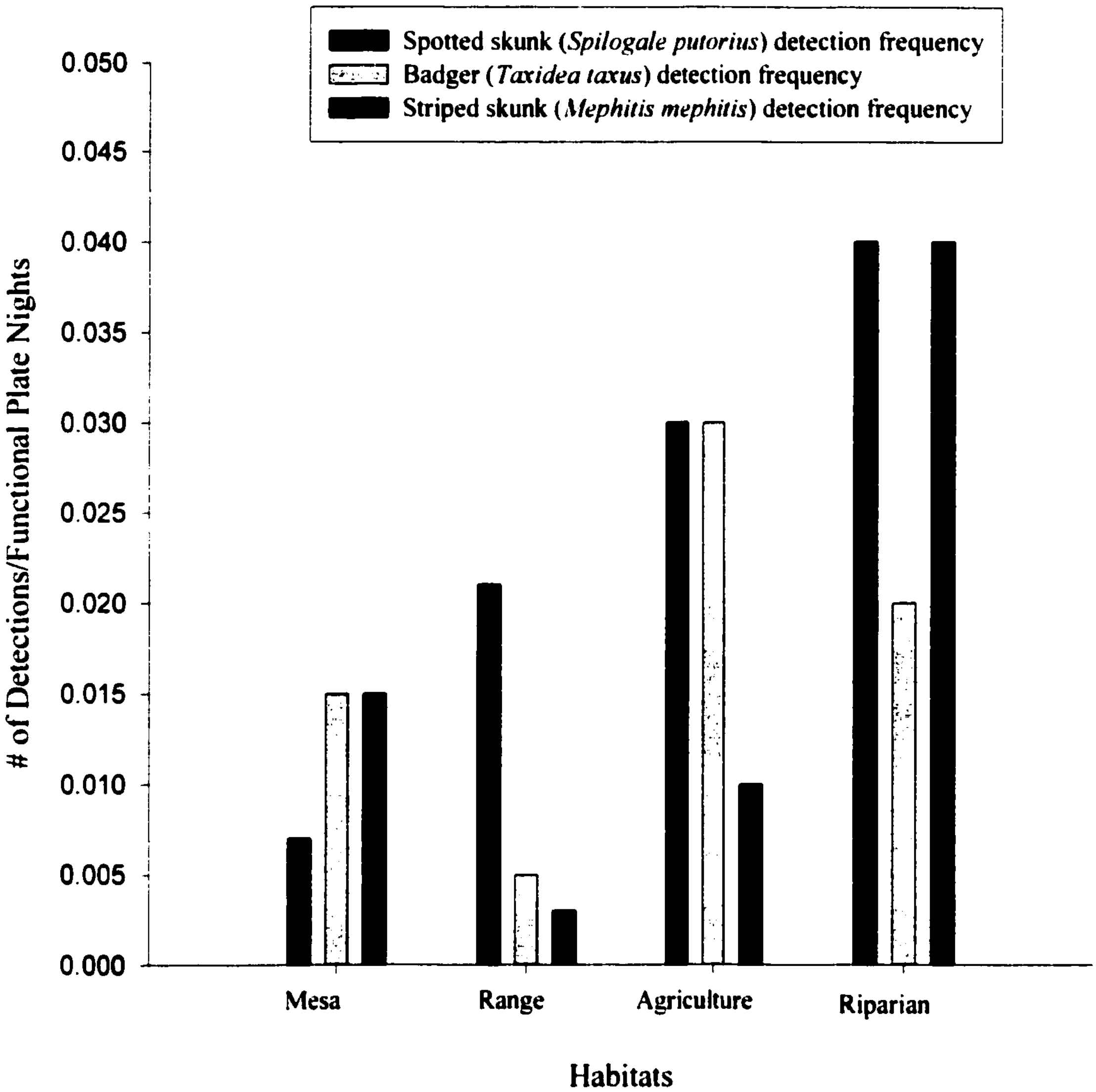


Figure 3-18. Detection frequencies of spotted skunks (*Spilogale putorius*), badgers (*Taxidea taxus*) and striped skunks (*Mephitis mephitis*) across habitats of the Oklahoma panhandle, 1995 - 1997.

CHAPTER 4

IMPACT OF BLACK-TAILED PRAIRIE DOG TOWNS (*CYNOMYS LUDOVICIANUS*) ON CARNIVORE DISTRIBUTIONS IN THE OKLAHOMA PANHANDLE

BACKGROUND

The ability of black-tailed prairie dogs (*Cynomys ludovicianus*) to alter the biotic and abiotic characteristics of their environment has been the focus of scientific attention over the last twenty years (Agnew et al., 1986; Coppcock et al., 1983; Clark et al., 1982; Garrett et al., 1982; O'Meila et al., 1982; Bonham and Lerwick, 1976). More recently, research has been directed to questions regarding what effects black-tailed prairie dog activities have on other prairie organisms (Barko, 1997; Miller et al., 1994; Sharps and Uresk, 1990; Whicker and Detling, 1988; Agnew et al., 1986; Clark et al., 1982; Knowles et al., 1982). Their ability to alter their environment has led to the suggestion that black-tailed prairie dogs may function as "keystone species" in the prairie ecosystem, creating patches of more suitable or even preferred habitat for other prairie organisms (Barko, 1997; Hoogland, 1995; Knowles and Knowles, 1994; Miller et al., 1994; Shackford and Tyler, 1991; Sharps and Uresk, 1990; Seal et al., 1989; Forrest et al., 1988; Clark et al., 1982). In Oklahoma, 48 species of vertebrates have been reported to be associates of black-tailed prairie dog towns; 22 of these species are considered rare and/or protected by federal or state legislation (Shackford and Tyler, 1991).

Since the turn of the century, black-tailed prairie dog populations have been in decline due to federal and private control practices (Miller et al., 1994). The area covered by black-tailed prairie dog towns in the central plains may have been reduced by as much as 99% since the turn of the century (Miller et al., 1994). The structure and arrangement of black-tailed prairie dog towns in the environment has changed as well. In the past, black-tailed prairie dog towns were typically large and continuous (Marsh, 1984). With the reduction in black-tailed prairie dog populations, towns have become increasingly fragmented, smaller, and isolated (Marsh, 1984). As a keystone species, the black-tailed prairie dog would be expected to have a disproportionate effect on species assemblages wherever they occur. This change in landscape dynamics could be expected to affect significantly those species associated with black-tailed prairie dog towns.

Populations of black-tailed prairie dogs have declined in Oklahoma, particularly in the region known as the panhandle (Shaw et al., 1991; Osborn and Allan, 1949). Populations in the panhandle are also unstable, only 39% of the black-tailed prairie dog towns mapped in 1967 had survived to 1989 (Shaw et al., 1991). During 1991, some of the largest black-tailed prairie dog towns in the panhandle were decimated by sylvatic plague (*Yersinia pestis*) (Shaw et al., 1991). This reduction of populations and town sizes has provided an increased incentive to study the relationships between black-tailed prairie dogs and their vertebrate associates.

Among the associates reported for black-tailed prairie dog towns, mammalian carnivores have the potential to be some of the most severely affected by decreases in population size and town area. As upper trophic level consumers, mammalian carnivores may depend upon prairie dogs and prairie dog towns as food sources, both for the prairie dogs themselves and for the small mammals and birds that they may attract (Hoogland, 1995; Sharps and Uresk, 1990; Forrest et al., 1988; Koford, 1958). Mammalian carnivores also may exploit prairie dog burrows as potential denning sites, particularly on the edges of prairie dog towns (Moehrenschlager et al., in press). Smaller carnivores may also depend upon the burrows of prairie dogs as escape routes when pursued by larger carnivores (Moehrenschlager et al., in press). The black-footed ferret (*Mustela nigripes*), a mammalian carnivore known to be highly associated with prairie dogs, suffered high losses when prairie dogs in Wyoming were exterminated by sylvatic plague (Seal et al., 1989; Forrest et al., 1988).

In Oklahoma, the three county panhandle region supports 17 mammalian carnivore species (14 extant, 3 historically) in 5 families (Caire et al., 1989). Four of these mammalian carnivores are reported to be associated with black-tailed prairie dog towns (Table 1-1)(Shackford and Tyler, 1991).

The purpose of this research was to examine carnivore occurrence at black-tailed prairie dog towns in the Oklahoma panhandle. I also investigated whether these carnivores occurred at black-tailed prairie dog towns more often than they occurred in the surrounding habitats. These questions were intended to provide a better understanding of the role of black-tailed prairie dogs in structuring local and regional carnivore assemblages.

MATERIALS AND METHODS

I determined the presence and distribution of carnivores using baited tracking plates at pre-established tracking stations applying the method described previously in Chapter 1. Of the ninety stations established throughout the panhandle, sixteen were established at prairie dog towns and sixteen were established at control sites located in habitats near to the prairie dog town stations. In almost all cases, control sites were located within about 15 km of tracking stations at prairie dog towns. In this way, it was reasonable to expect that any carnivores detected at one site had a reasonable chance at being detected at that sites' pair (Zoellick and Smith, 1992). In all cases, control sites were placed in habitats similar to or identical to that which the prairie dog town site occurred and control sites were paired with prairie dog town sites as part of the statistical design. Infra-red triggered cameras were used in conjunction with tracking plates to verify the carnivore tracks recorded on the tracking plates.

Statistical Analyses

Non-parametric statistics were used due to the ordinal nature of the data (two sample ranked test). All data for carnivores at prairie dog towns and paired sites were analyzed using a Wilcoxon Paired Sample test. This test was chosen because the sampling and statistical design had paired prairie dog towns with adjacent non-prairie dog town control sites prior to the initiation of data collection. It was felt that these a priori pairings appropriately linked the two sampling designations. As a result, the Wilcoxon Paired Sample test was determined to be the most rigorous and appropriate for these analyses.

The westernmost county in the Oklahoma panhandle (Cimarron) accounted for the most carnivore detections during all phases of this study. Because of this, two separate analyses were conducted; one analyzed data for the entire panhandle, and a second analyzed the data only for Cimarron County. The two analyses would help determine what effect, if any, the skewed detection frequencies had on data analyses and interpretation. All statistical tests were computed according to protocol described in Zar (1984).

RESULTS

Sampling effort at prairie dog towns and control sites is given in Table 4-1. Five carnivores species were detected at black-tailed prairie dog towns (*Vulpes velox*, *Canis latrans*, *Spilogale putorius*, *Taxidea taxus*, and *Lynx rufus*). Four of these carnivores were detected with enough frequency to permit individual analyses (*Vulpes velox*, *Canis latrans*, *Spilogale putorius*, and *Taxidea taxus*). The bobcat, *Lynx rufus*, was not detected often enough to permit individual analysis, but data on bobcats were included in analyses of all carnivores at prairie dog towns. Striped skunks, *Mephitis mephitis*, were detected in other areas during the course of this study, but no striped skunks were detected at prairie dog towns.

A total of 25 carnivore detections were recorded at prairie dog towns over the course of the study. Twenty-one detections were recorded at paired sites during this same period. Analysis using a Wilcoxon Paired Sample test revealed no significant differences between carnivore detections at prairie dog towns and non-prairie dog town paired sites ($n=11$; $T_{+} = 32.5$, $T_{-} = 30.5$; $p \geq 0.05$) (Figure 4-1).

Seventeen carnivore detections (in four species) were recorded at prairie dog town sites in Cimarron County only. Fourteen carnivore detections (in four species) were recorded at the Cimarron County paired sites. Again, the analysis using Wilcoxon Paired Sample tests revealed no significant differences in carnivore detections between prairie dog towns and their paired sites in Cimarron County ($n=5$; $T_{+} = 9$, $T_{-} = 5$; $p \geq 0.05$) (Figure 4-2).

Canids were analyzed as a group with respect to their occurrence at prairie dog towns and paired sites. Two canid species were detected during the course of this study (*Canis latrans* and *Vulpes velox*). Fifteen canid detections were recorded at prairie dog towns and 17 canid detections were recorded at paired sites. Wilcoxon Paired Sample analysis revealed no significant differences in detections of canids between prairie dog towns and paired sites ($n=10$; $T_{-} = 24$, $T_{+} = 31$; $p \geq 0.05$) (Figure 4-3).

Analysis of canid data for Cimarron County only also resulted in no significant differences in canid detections at prairie dog towns and paired sites ($n=5$; $T_{-} = 6$, $T_{+} = 9$; $p \geq 0.05$) (Figure 4-4). Ten canids had been detected at prairie dog towns while 11 canids were recorded at paired sites.

Individual species also were analyzed for differences in occurrence between prairie dog towns and non-prairie dog town sites. Coyote (*Canis latrans*) detections at prairie dog towns and paired sites were analyzed across the panhandle. No significant differences were found between coyote occurrences at prairie dog towns and at paired sites ($n=5$; $T_{-} = 13.52$, $T_{+} = 1.5$; $p \geq 0.05$) (Figure 4-4). However, nine coyotes were detected at prairie dog towns in contrast to only three detected at paired sites. Coyote occurrences at prairie dog towns and paired sites in Cimarron County only were not analyzed because the data set was too small and the distribution of the data across the panhandle was not as skewed.

Across the panhandle, six swift foxes were detected at prairie dog towns while 14 swift foxes were detected at paired sites (Figure 4-3). The Wilcoxon Paired Sample analysis of these data was marginally insignificant ($n=7$; $T = 5$; $p \geq 0.05$). When data for swift foxes detected in Cimarron County only were analyzed, however, the results were also marginally insignificant ($n=5$; $T = 4$; $p \geq 0.05$) (Figure 4-4). In Cimarron County, six swift foxes were detected at prairie dog towns as opposed to 10 swift fox detections at non-prairie dog town paired sites.

Mustelids were analyzed as a group as well. Across the Oklahoma panhandle, ten mustelids in two species were detected at prairie dog towns. Six mustelids in three species were detected at non-prairie dog town paired sites. Mustelids did not occur significantly more often at prairie dog towns across the panhandle than at the non-prairie dog town paired sites ($n=8$; $T_{+} = 25$, $T_{-} = 11$; $p \geq 0.05$) (Figure 4-5). In Cimarron County, mustelids were significantly associated with prairie dog towns ($n=4$; $T = 0$; $p \leq 0.05$) (Figure 4-6). Seven mustelids were detected at prairie dog towns in Cimarron County while only two mustelids were detected at Cimarron County paired sites.

The spotted skunk (*Spilogale putorius*) was the mustelid detected most often at prairie dog towns and paired sites. Spotted skunks were detected seven times at prairie dog town sites and five times at paired sites across the panhandle. Spotted skunks, however, were not significantly associated with either prairie dog towns or paired sites ($n=8$; $T = 7$; $p \geq 0.05$) (Figure 4-5). In Cimarron County, spotted skunks were again not significantly associated with either prairie dog towns or paired sites, although this result was only marginally insignificant ($n=4$; $T_{+} = 3$, $T_{-} = 0$; $p \geq 0.05$) (Figure 4-6). Four spotted skunks were detected at prairie dog towns in Cimarron County and only two were detected at paired sites.

The badger (*Taxidea taxus*) was the only other mustelid detected at prairie dog towns. No badgers were detected at paired sites and no badgers were detected outside of

Cimarron County. Three badgers were detected at prairie dog town sites in Cimarron County. Badgers were not determined to be significantly associated with either prairie dog towns or paired sites across the panhandle or in Cimarron County alone ($n=3$; $T_+ = 6$, $T_- = 0$; $p \geq 0.05$) (Figure 4-5 and Figure 4-6).

DISCUSSION

In general, the carnivore species detected during the course of this study did not show a significant affiliation with black-tailed prairie dog towns in the Oklahoma panhandle. Total numbers of carnivore detections at prairie dog towns and paired sites were very similar for the entire panhandle (Figure 4-1) and for Cimarron County as well, which was, in terms of total detections and frequency of detections, the county in which carnivores were most abundant (Figure 4-2).

There were variations among canids with respect to affiliation with prairie dog towns. The two canids detected during the study (the coyote and swift fox) showed divergent patterns in association with prairie dog towns. When combined, canids were not significantly associated with prairie dog towns either in Cimarron County alone or across the entire panhandle. Individually, however, certain trends were apparent. Coyotes, while not statistically significantly associated with prairie dog towns, did occur at prairie dog towns more often than at the paired sites in Cimarron County and the panhandle at large (Figure 4-3 and Figure 4-4).

In contrast, swift foxes occurred more often away from prairie dog towns in Cimarron County and across the entire panhandle (Figure 4-3 and Figure 4-4). Data for the entire panhandle and Cimarron County were only marginally insignificant, but a general trend in occurrence is apparent. These results would seem to be in conflict with the long held assumption that prairie dog towns are important resource areas for threatened species like the swift fox. In this case though, interspecific species interactions, which affect canid distributions in the prairie ecosystem, may be operating at prairie dog towns.

Interference competition, aggression and even predation have been documented between canids in many different ecosystems (Dayan and Simberloff, 1996; Johnson et al., 1996; Peterson, 1995; Bailey, 1992; Harrison et al., 1989; Sargeant et al., 1987; Carbyn, 1982; Rudzinski et al., 1982). Larger canids frequently harass, chase, and even kill smaller canids within their home ranges, presumably because the smaller canids are perceived as resource competitors. Larger canids often are able to exclude smaller canids from habitats at local scales but are not able to exclude smaller canids at landscape level scales (Peterson, 1995; Harrison et al., 1989; Sargeant et al., 1987; Carbyn, 1982). As a result, some resources or areas become unavailable to the smaller canids. Small canids persist in the environment by behaviorally avoiding those areas that are most likely to contain the larger canids (White and Ralls, 1993; Harrison et al., 1989; Sargeant et al., 1987; Carbyn, 1982). As a result of this avoidance, though, the ability to utilize favorable resource areas is often lost to the smaller canid. This interaction has been documented for red foxes and coyotes (Gese et al., 1996; Sargeant et al., 1987), coyotes and wolves (Carbyn, 1982), red foxes and arctic foxes (Bailey, 1992), and coyotes and swift foxes (White et al., 1995; White et al., 1994;).

It is possible that this dynamic is at work between swift foxes and coyotes in the Oklahoma panhandle at black-tailed prairie dog towns. Coyotes occurred more often at prairie dog towns than at paired sites. Prairie dog towns may be areas rich in resources that coyotes recognize and exploit. As a result, smaller canids, such as swift foxes, may perceive an increased risk of predation at prairie dog towns and therefore avoid them, confining their activity to areas with lower coyote densities. Support for this supposition also was available from data gathered in conjunction with another part of this study (Shaughnessy, in press) and in Chapter two. Across broader panhandle habitats, swift foxes were detected more frequently in range and mesa habitats (which most often contain prairie dog towns) (Shaughnessy, in press). Coyotes were detected infrequently in the broader range and mesa areas, away from the prairie dog towns (Shaughnessy, in press). Swift foxes in the Oklahoma panhandle appear to be foregoing prairie dog towns as resource areas in favor of the more "coyote depauperate" range and mesa habitats.

Mustelids also exhibited interesting occurrence patterns between prairie dog towns and paired sites. Mustelids were significantly associated with prairie dog towns in Cimarron County but were not significantly associated with prairie dog towns across the panhandle (Figure 4-5 and Figure 4-6). Three mustelids were detected during the course of this study, however, only two (badgers and spotted skunks) were detected at prairie dog towns. Striped skunks were not detected at the prairie dog town stations during any part of the study and were only detected once at a control site. Even with the poor representation of striped skunks, though, mustelids still exhibited a significant association with prairie dog towns in Cimarron County and a preference for prairie dog towns across the panhandle. However, no single mustelid species exhibited a significant association with either prairie dog towns or paired sites across the Oklahoma panhandle or in Cimarron County alone.

Both spotted skunks and badgers were detected more frequently at prairie dog towns. However, badgers were not detected at any paired sites during the course of this study. The occurrence of badgers exclusively at prairie dog towns appears to be the reason mustelids, in general, were determined to be significantly associated with these areas. Badgers have long been known to be associated with prairie dog towns and are, in fact, major predators of prairie dogs and ground squirrels (Caire et al., 1989).

Spotted skunks, however, also occurred at prairie dog towns in slightly disproportionate (although not significant) numbers (seven detections on towns, five detections at paired sites). This pattern could be due to the same dynamics that influence swift fox occurrences at prairie dog towns. Among canids in general, the intensities of interference interactions are often predicated by the size relationships between the canids (Ralls and White, 1995; Rudzinski et al., 1982). Canid species that are more similar in overall size tend to have more intense interactions, which often result in the death of the smaller canid. Canid species that demonstrate larger overall size differences usually have agonistic interactions with less severe consequences to the smaller canid. Wolves and coyotes tend to have very intense interactions (Peterson, 1995; Carbyn, 1982) while wolf and red fox interactions tend to be less severe (Peterson, 1995). Presumably the larger canid perceives much smaller canids as less important resource threats than canids that are closer in size.

This relationship may extend to other carnivores in different taxonomic groups at local scales. In the Oklahoma panhandle, carnivore size relationships (of all carnivores detected during this study) extend from the largest carnivore, the coyote, to the smallest carnivore, the spotted skunk. The swift fox is an intermediate sized carnivore. Absence of swift foxes at prairie dog towns may in fact create or otherwise make available more suitable habitat for carnivores smaller than the swift fox. Spotted skunks may not be perceived as competitors by coyotes given their large size difference (coyotes weigh between 9 and 25 kg, spotted skunks weigh only between 400 and 700 g; Caire et al., 1989). However, they may be perceived as competitors by swift fox (swift fox weigh between 2 and 4 kg; Caire et al., 1989). The same interactions that may be occurring between swift foxes and coyotes at prairie dog towns may also be occurring between swift foxes and spotted skunks off of prairie dog towns. Spotted skunks may be using and occurring at prairie dog towns more frequently in order to lessen agonistic interactions with similar-sized carnivores in non-prairie dog town areas.

Prairie dog towns appear to be important resource areas for carnivores in the Oklahoma panhandle. However, their overall importance and the strength of carnivore associations to prairie dog towns (particularly some rarer carnivores) may have been overstated or generalized in the past. Swift foxes are clearly able to persist in the Oklahoma panhandle in spite of their lower frequency of use and general avoidance of prairie dog towns due to the heightened coyote presence in these areas. Still, other carnivores are known to be highly tied to prairie dog towns (eg., black-footed ferret and badger).

Prairie dog towns in the plains ecosystem are undeniably unique areas. Their role in structuring, and influencing prairie communities has been the center of intense, recent scientific investigation. However, it is equally important not to overlook or underestimate other species interactions that may be as or more important in influencing organismal and, in this case, carnivore distributions in prairie environments. This research demonstrates that, while prairie dog towns do appear to be favored by some carnivores (coyotes and mustelids), other interactions (eg., interspecific interactions) may be working to determine the distributions of a rarer carnivore (the swift fox) in the Oklahoma panhandle.

Ultimately, the role of prairie dogs in the ecosystem of the Great Plains is dependent upon the definition of 'keystone species'. Keystone species is traditionally defined as a species whose presence or absence in an ecosystem overrides other interactions within the system and regulates the structure and dynamics of the entire community (Feldhamer et al., 1999). The role of prairie dogs as keystone species in the plains has recently been questioned by others (Barko et al., 1999; Stapp, 1998). With respect to carnivores in the Oklahoma panhandle, prairie dogs do not apparently exert an overriding influence on carnivore occurrence. At least one interaction (interspecific interactions) other than the presence of prairie dogs seems to be important in determining carnivore presence in the panhandle. As a result, the assignment of prairie dogs as keystone species in the plains environment may be premature or overstated as it relates to carnivores in the Oklahoma panhandle.

SUMMARY

Sixteen prairie dog towns and sixteen control sites were monitored for carnivores using baited tracking plates and infra-red triggered cameras during four sampling sessions between October 1995 and February 1997. Wilcoxon Paired Sample tests showed that carnivores, in general, did not exhibit preferences for either prairie dog towns or paired sites in the Oklahoma panhandle. Some carnivores did demonstrate patterns of occurrence away from prairie dog towns (swift foxes), while other carnivores displayed slight preferences for prairie dog towns (coyotes, and badgers). Mustelids, as a group, were detected significantly more often at prairie dog towns in Cimarron County. The results indicate that the designation of prairie dogs as keystone species in the prairie environment may be overstated or unwarranted.

Table 4-1. Sampling effort at prairie dog towns in the Oklahoma panhandle, 1995 - 1997.

	Cimarron Co.	Texas Co.	Beaver Co.	Total
Prairie Dog Town	53	60	50	163
Paired Sites	51	54	50	155

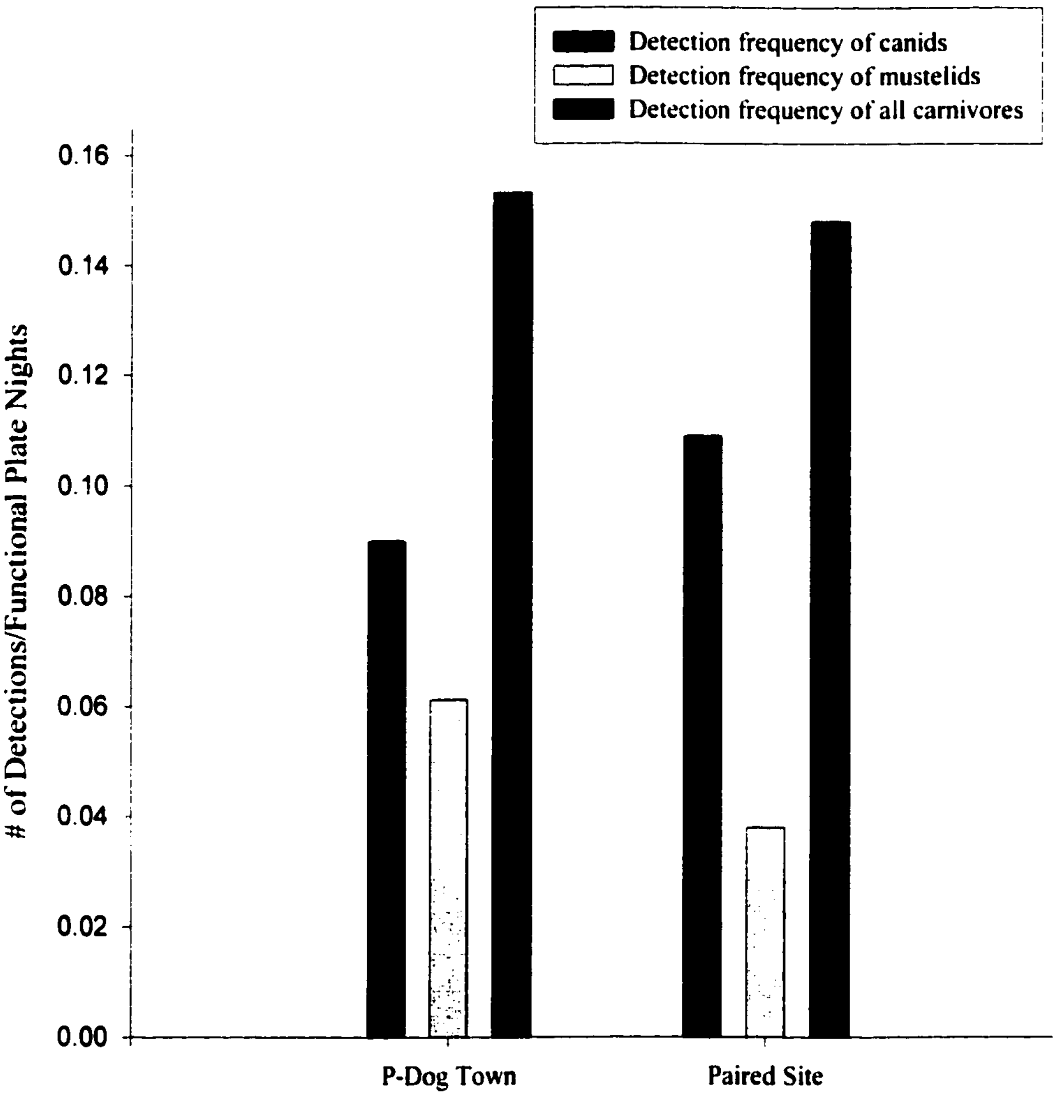


Figure 4-1. Comparison of canid, mustelid, and all carnivore detection frequencies at prairie dog towns and control sites in the Oklahoma panhandle, 1995 - 1997.

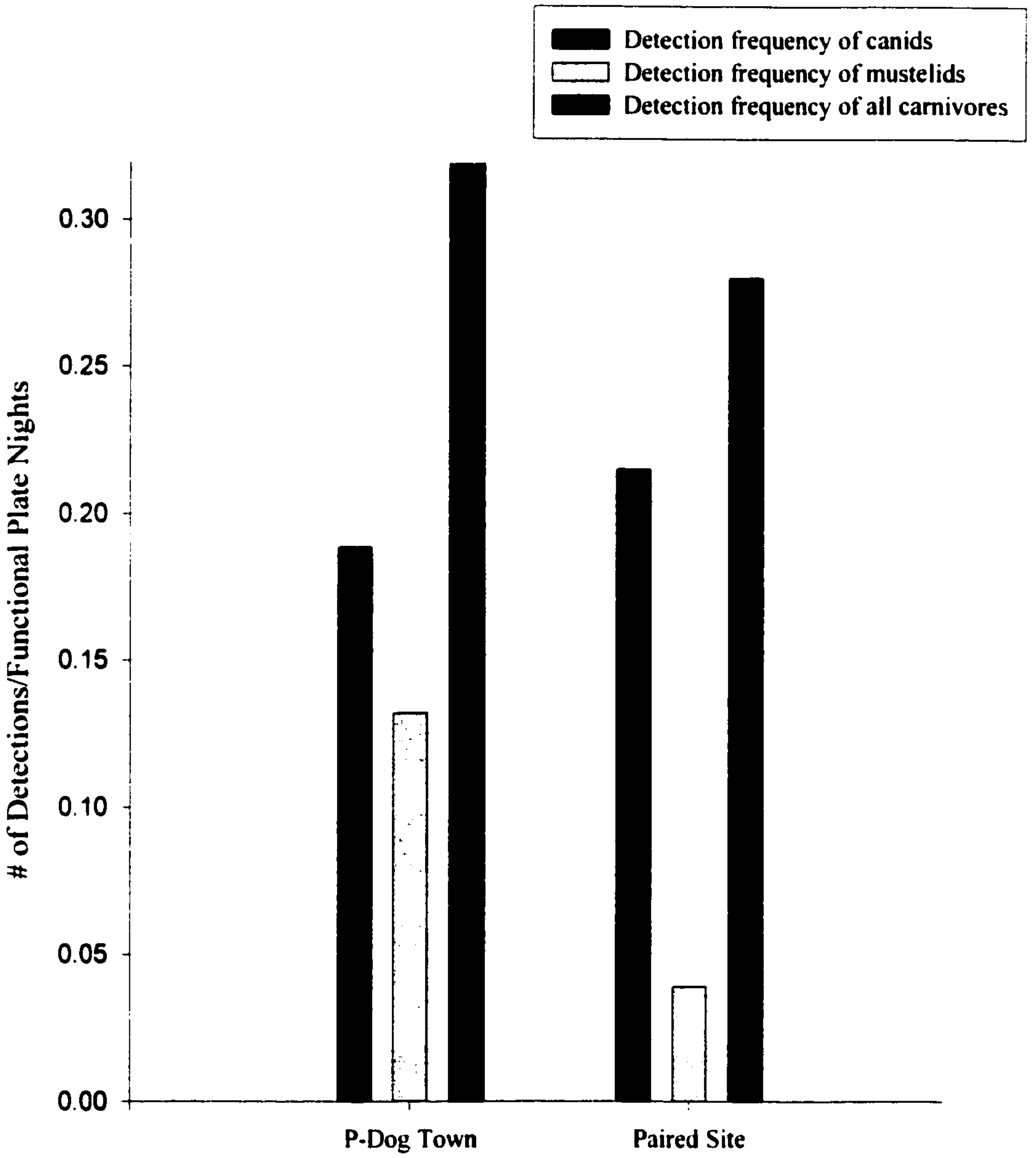


Figure 4-2. Comparison of canids, mustelids and all carnivores detection frequencies at prairie dog towns and control sites in Cimarron County, Oklahoma, 1995 - 1997.

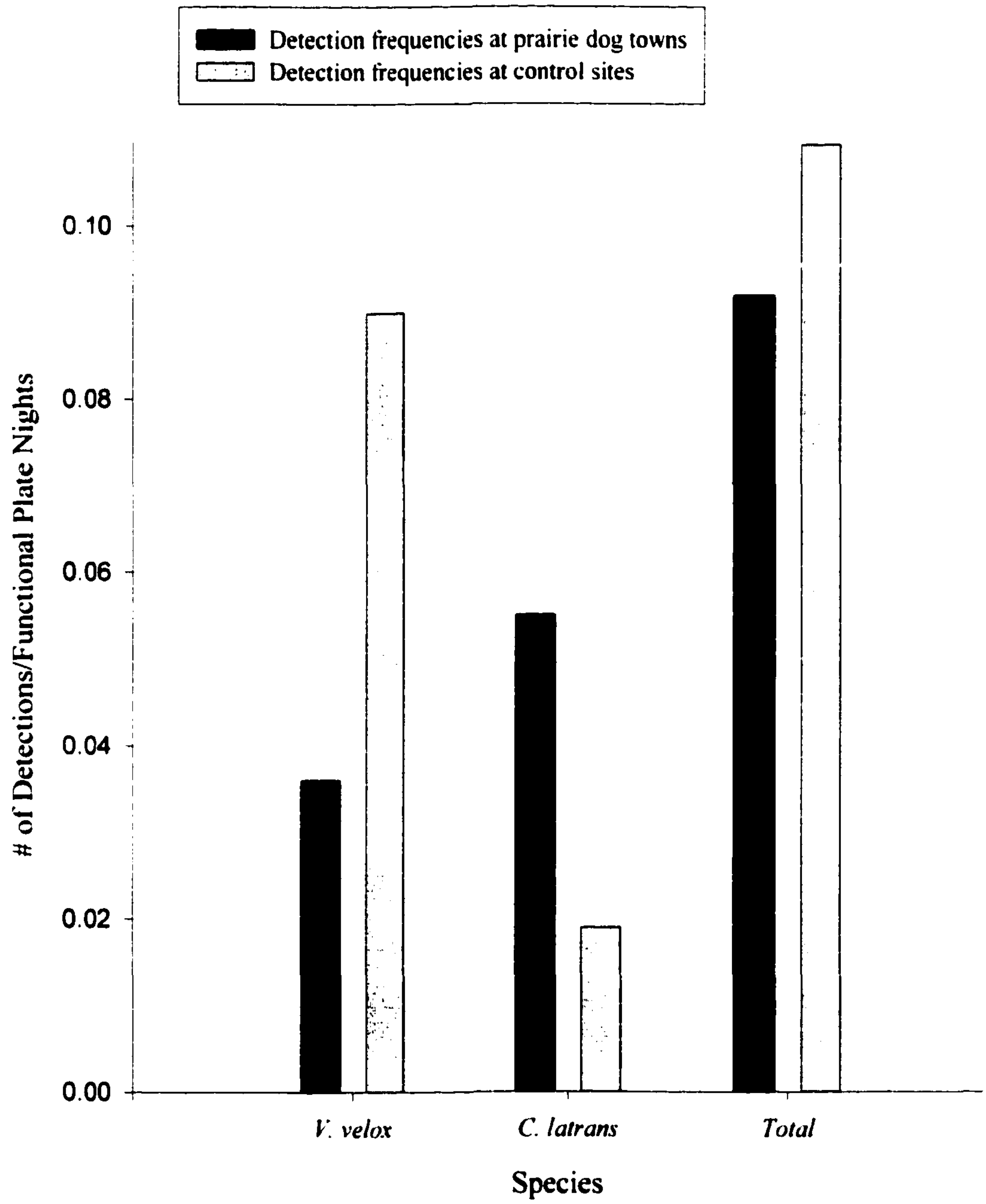


Figure 4-3. Comparison of *Vulpes velox* and *Canis latrans* detection frequencies at prairie dog towns and control sites in the Oklahoma panhandle, 1995 - 1997.

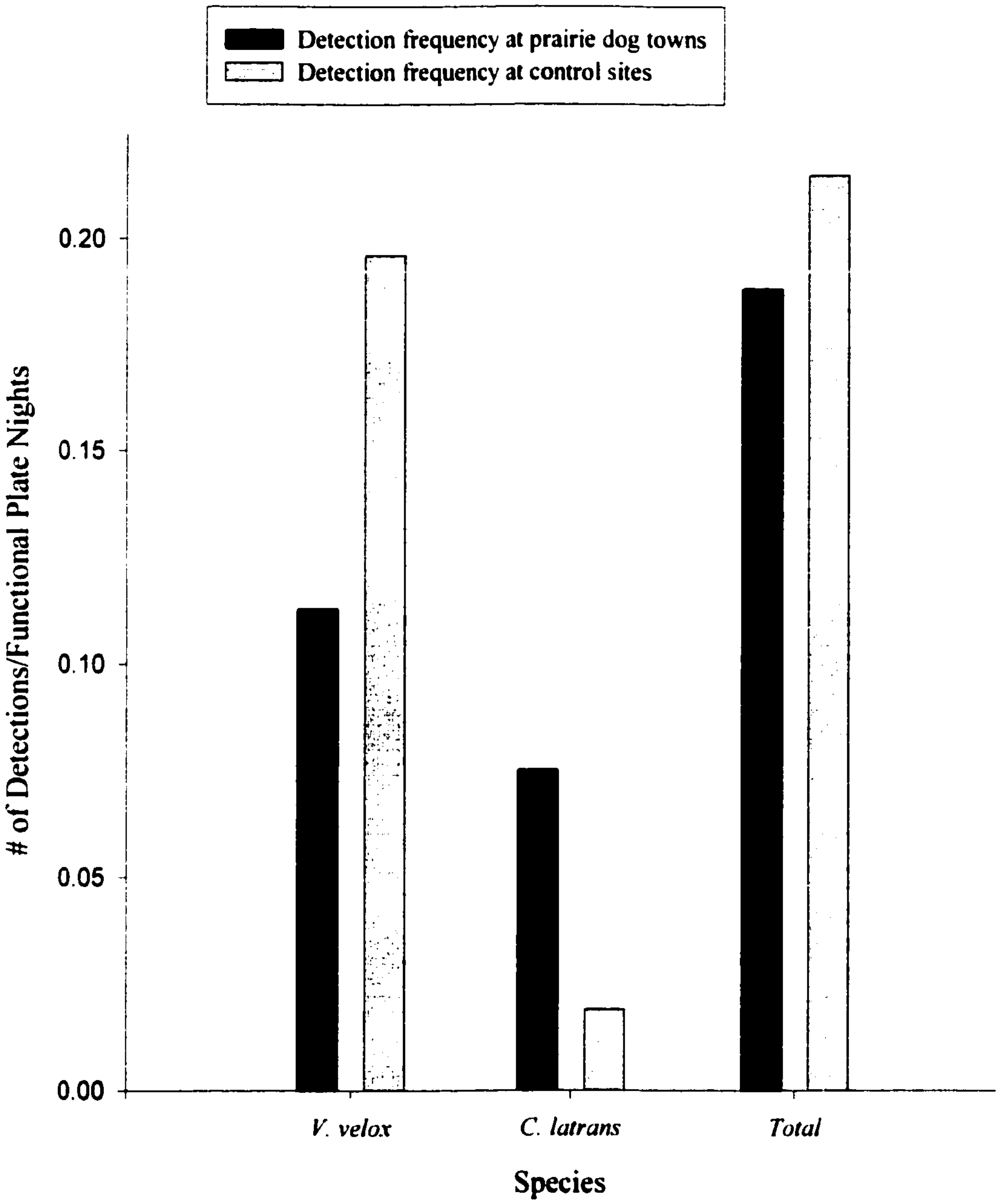


Figure 4-4. Comparisons of *V. velox* and *C. latrans* detection frequencies at prairie dog towns and control sites in Cimarron County, Oklahoma, 1995 - 1997.

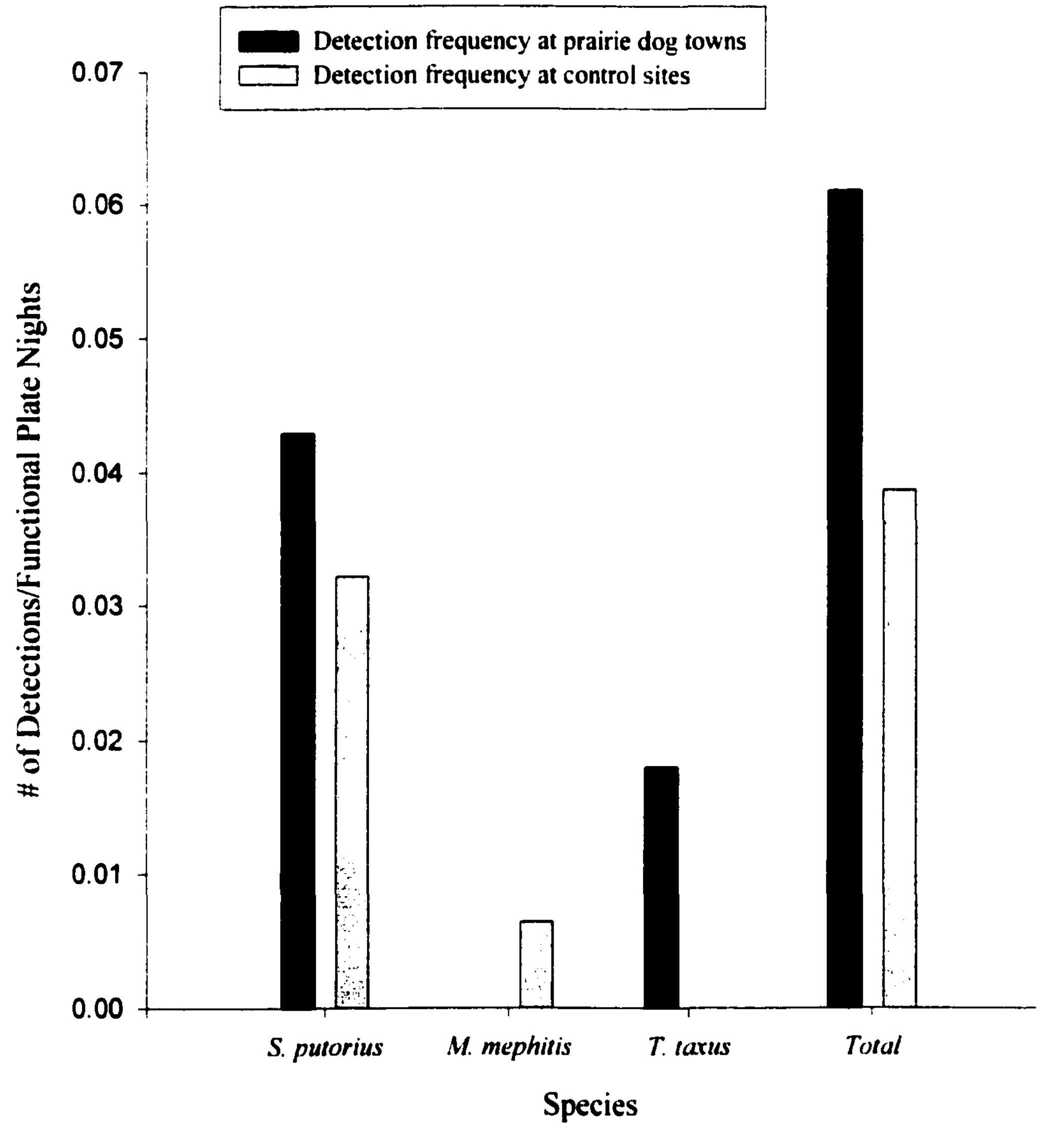


Figure 4-5. Comparison of mustelid detection frequencies at prairie dog towns and control sites in the Oklahoma panhandle, 1995 - 1997.

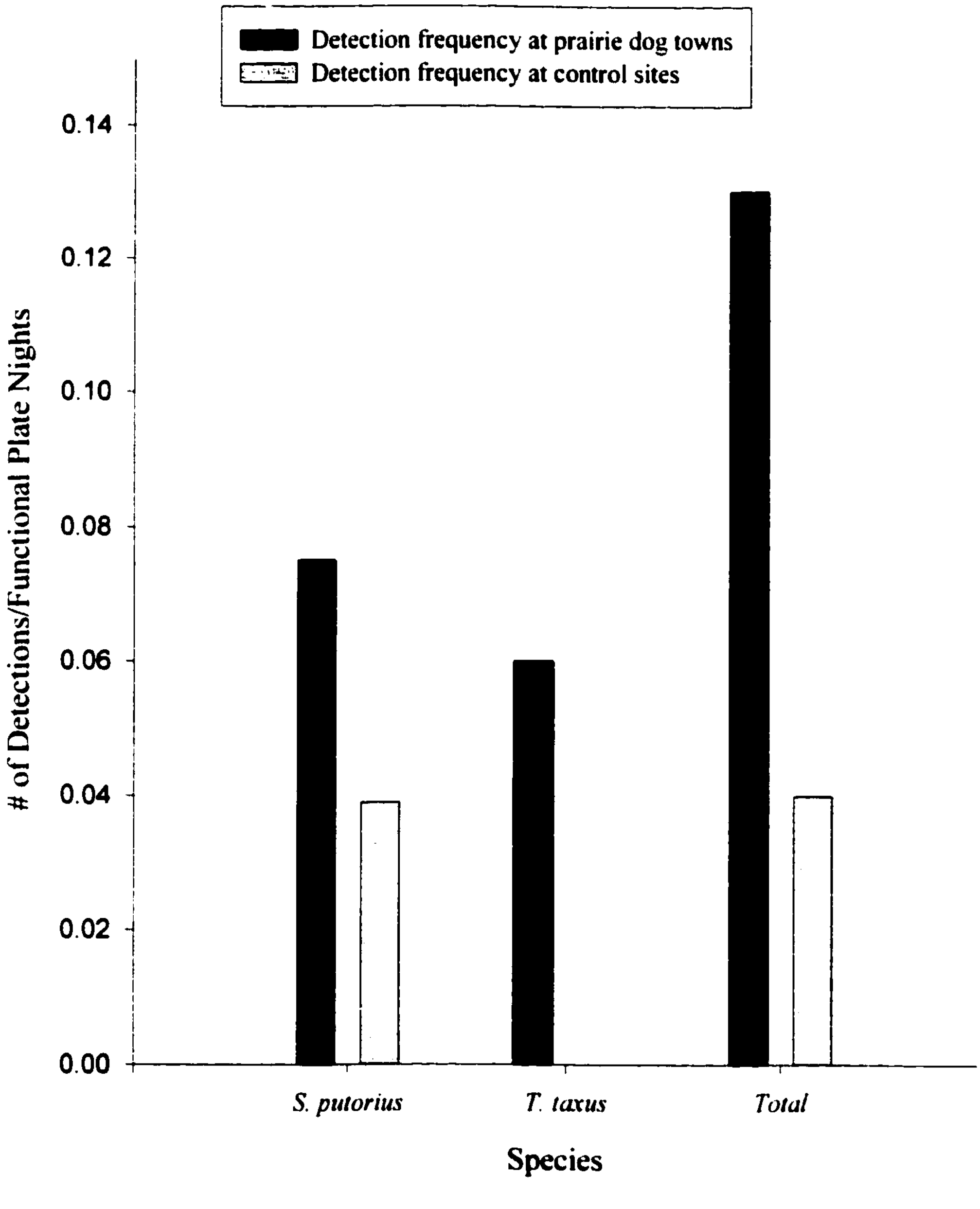


Figure 4-6. Comparison of mustelid detection frequencies at prairie dog towns and control sites in Cimarron County, Oklahoma, 1995 - 1997.

CHAPTER 5

A LOGISTIC REGRESSION MODEL RELATING CARNIVORE OCCURRENCE AND VEGETATION IN THE OKLAHOMA PANHANDLE

BACKGROUND

A major, recent emphasis in ecology has been the impact of large scale landscape features on the distributions of organisms (Brown, 1995; Edwards et al., 1994; Miller et al., 1994; Stone and Roberts, 1990). Increasingly, research in ecology has focused on patterns and processes that transcend local community dynamics (Marquet, 1994; Gaisler et al., 1991). Associated with this new ecological approach has been the technological advancement of remote sensing techniques and the ability to differentiate accurately between vegetation types and conditions (Everitt et al., 1996; Price et al., 1992; Musick and Grover, 1991). Remote sensing techniques permit real time, large scale, vegetational sampling which permit classification of major landforms and vegetation types based upon the dominant vegetation, vegetation health, seasonality, and/or larger time series (Everitt et al., 1996; Loveland et al., 1995; Price et al., 1992; Musick and Grover, 1991).

While these techniques have been valuable in delineating communities, assessing ecosystem health, and documenting patterns of vegetational succession and change (Nagendra and Gadgil, 1999; Reed et al., 1994; Price et al., 1992; Walker et al., 1992), few studies have attempted to use these techniques to relate vegetational patterns with animal distributions (Debinski et al., 1999; Strong and Trost, 1993; Jorgensen and Nohr, 1996). Until only recently, many approaches directed at associating remotely sensed vegetation data and patterns of animal distributions were focused upon the responses of single species to vegetational conditions and neglected treatments of organisms at higher orders of classification (Hodgson et al., 1988; DeWulf et al., 1988; Ormsby and Lunetta, 1987). Research of this kind examining habitat and spatial relationships of faunal environmental elements has met with success. Remotely sensed vegetational data have been used as a reliable predictor for some bird and mammal distributions (Blan and West, 1997; Mladenoff et al., 1995; Herr and Queen, 1993; Pereira and Itami, 1991). However, the usefulness of remotely sensed data as a faunal distribution predictor and as a management tool in conservation biology has not yet reached its full potential.

The carnivore community of the Oklahoma panhandle and the occurrence data of this present study offered a unique opportunity to examine and compare the spectral reflectance data of the panhandle with the observed carnivore distributions. I attempted to model carnivore occurrence in the panhandle using remotely sensed data from the National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) sensor located on sun synchronous polar orbiting satellites. Specifically, I tested whether vegetational spectral data from the AVHRR sensor could be used as a reliable predictor of carnivore occurrence in the Oklahoma panhandle. I attempted to model the six individual carnivore species detected during this study, as well as all canids, all mustelids, and all carnivores as groups. The ability to develop models of these types would be of great predictive value in similar environments and would have significant conservation and ecosystem management implications.

MATERIALS AND METHODS

Field methods used to determine carnivore presence in the Oklahoma panhandle and carnivore detection data were consistent throughout this study. Remotely sensed vegetational data were collected using AVHRR imagery. The AVHRR sensors record data in a swath 2700 km wide at approximately one square kilometer spatial resolution (Jensen, 1996). The satellites that the sensors are mounted on orbit the earth approximately once every 102 minutes and the sensors acquire complete global coverage every 24 hours (Jensen, 1996). AVHRR data were collected for 78 bi-weekly periods in the Oklahoma panhandle from January 1995 to December 1997. The raw AVHRR data collected were transformed into normalized difference vegetation indices (NDVI) for the purposes of statistical analyses. NDVI is computed by subtracting the near infra-red band values from the visible band values and dividing that by the sum of the near infra-red and visible band values (Jensen, 1996):

NDVI = (visible band - near infra-red band)/(visible band + near infra-red band)

This transformation standardizes differences in brightness between the visible and infra-red spectrums. NDVI provides a method of broad comparison for remotely sensed data. The brighter a pixel is in an NDVI standardized output, the greater the amount of photosynthesizing vegetation is present in that pixel (Jensen, 1996). In this way, NDVI provides a method for comparing relative growth and health of vegetation over large scales.

Statistical Methods

NDVI data for the ninety pre-established tracking stations in the panhandle were collected bi-weekly for three years between 1995 and 1997. All samples were of sufficient quality except for one (bi-weekly composite 26). Cloud cover during this period affected the readings during these measurements. In order to adjust for this error, the readings between periods 25 and 27 were averaged and those values were used as the NDVI values for period 26.

In order to reduce the size of the data set, all data were analyzed using principal components analysis (PCA). This is a standard data reduction/transformation procedure used in remote sensing applications to reduce data, isolate sources of variation within the data and aid in interpretation of the NDVI values (Eastman and Fulk, 1993). Only those components with eigenvalues greater than one were retained for the next step of the analysis (Dunteman, 1989).

Discriminant analysis and logistic regression were both appropriate procedures for modeling carnivore occurrence. Because of the dichotomous nature of the detection data and the assumption in discriminant analysis that all groups are drawn from populations with multivariate normal distributions, logistic regression was chosen to model carnivore occurrence (Menard, 1995; Hosmer and Lemeshow 1989; Klecka, 1980). Carnivore detection data for each permanent tracking plate station were compiled according to whether any carnivore visited the station, then according to the family affiliation of the carnivore, and then by individual species. Carnivores were recorded as either present (1) at a station or absent (0). Multiple visits at stations, either over time or during the same session, had no bearing on the data table and therefore the effects of detection pseudoreplication during these analyses were reduced.

The compiled detection data was then entered into a multiple logistic regression analysis with the factor values of the retained NDVI principal components according to which treatment was being modeled (all carnivores, families, or individual species). The models were evaluated for significance and biological usefulness.

RESULTS

Principal components were extracted from a raw data set consisting of 7020 phenometric vegetation measurements (90 tracking stations X 78 satellite passes over the study area during the three year study). The principal components analysis identified ten components with eigenvalues greater than one, which accounted for 88% of the observed variation in the 78 bi-weekly NDVI composites. Each component generated a factor value for every tracking station in the panhandle which represented a measurement of component loading at that site. This resulted in a reduced data set of 900 measurements (90 tracking stations X 10 component values/station). This data set was used in the regression models along with the carnivore detection data.

The first four components were interpreted (Figure 5-1) (Eastman and Fulk, 1993). The first component was identified as variation in brightness. This component accounted for 45.1% of the observed variation in the NDVI composites. The second component was interpreted as variation associated with the green-up of seasonal crops. This component accounted for 15.9% of the variation in the NDVI composites. The third component was not as clearly interpreted. This component possessed a spring minimum and a fall maximum over the three year observation period (Figure 5-1). This component may have been associated with range land and/or a brief period of fall green-up associated with late season rains. This component accounted for 7.2% of the observed variation in the NDVI composites. Finally, the interpretation of the fourth component was even more ambiguous. Component four showed weak summer maxima and winter minima (especially for the last two years of sampling)(Figure 5-1). Component four accounted for

5.4% of the observed variation. The sum of the variation accounted for by these components was 73.6%.

The logistic regression model attempting to predict the presence of any carnivore based upon NDVI measurements was marginally significant ($p = 0.0632$). The model predicted carnivore presence accurately in 86.79% of cases (46 of 53 cases) but was not as accurate at predicting carnivore absence (54.05%; 20 of 37 cases). However, when logistic regression was re-run as a stepwise backwards regression, the model was significant after the removal of principal component five ($p = 0.0410$). In both models, principal component two was identified as having a significant role in defining carnivore absence based upon NDVI measurements (Table 5-1a) (Menard, 1995; Hosmer and Lemeshow 1989).

The logistic regression modeling canid occurrence was also marginally significant ($p = 0.0946$). The model accurately predicted canid occurrence in only 44.12% of cases (15 of 34 cases). Canid absence was more accurately predicted by the model (87.50%; 49 of 56 cases). When the model was rerun as a stepwise backward regression, a significant model was developed after the removal of principal components seven and one ($p = 0.0411$). In each model, principal component two was again identified as the component having the most significant role in predicting canid absence (Table 5-1b).

The regression model of swift fox occurrence was significant ($p = 0.0422$). The model accurately predicted swift fox occurrence in habitats based upon NDVI components only 22.73% of the time (5 of 22 cases). However, the model predicted swift fox absence in 95.59% of cases (65 of 68 cases). Principal components one and four had the most significant effect in determining swift fox absence from habitats (Table 5-1c).

The model of coyote occurrence was also significant (p = 0.0111). Coyote presence was accurately predicted in 7 of 17 cases (41.18%). Coyote absence in habitats was accurately predicted in 71 of 73 cases (97.26%). Principal component two was significantly associated with determining coyote absence, while principal component one was valuable for predicting coyote presence (Table 5-1d).

Mustelids, as a group, were modeled as well. The regression model for mustelids was not significant (p = 0.67). While the model accurately predicted mustelid absence in habitats 93.65% of the time (59 of 63 cases), the model only accurately predicted presence 18.52% of the time (5 of 27 cases). No component was observed to contribute significantly to the predictive value of the model. Stepwise regression of the mustelid group also never resulted in a significant model.

The first individual mustelid species to be modeled was the spotted skunk. The regression model for spotted skunks was not significant (p = 0.4621). The model accurately predicted spotted skunk absence from habitats 100% of the time (73 of 73 cases). However, presence was only predicted 11.76% of the time (2 of 17 cases). Principal component two was useful for predicting absence, but no component contributed significantly to the predictive value of the model. Backward stepwise regression also never resulted in a significant model.

Striped skunks were modeled next. The model for striped skunks was also not significant (p = 0.6532). Although striped skunk absence from habitats was accurately predicted 100% of the time (83 of 83 cases), presence was never accurately predicted (0 of 7 cases). Additionally, no principal component was observed to contribute significantly to the model. Again, backward stepwise regression did not result in a significant model.

Badgers were the final mustelid species modeled. Again, the logistic regression model was not significant (p = 0.5302). Badger absence was accurately predicted 98.77% of the time (80 of 81 cases), but presence was accurately predicted only 11.11% of cases (1 of 9 cases). No principal component contributed significantly as a predictor to the model and stepwise regression was not significant.

The final carnivore modeled was the bobcat. The logistic regression for bobcats was not significant (p = 0.4775). Bobcat absence was accurately predicted in 100% of cases (81 of 81), but bobcat presence was never accurately predicted (0 of 9 cases). Again, no component contributed significantly to the predictive value of the model and stepwise regression did not result in any significant models.

DISCUSSION

The principal components were interpreted first. The first component in the analysis was determined to be generalized variation associated with brightness and accounted for most of the variation in the NDVI data set. This determination was made because all of the factor loadings for this component were positive throughout the course of the study (Figure 5-1). In addition, in analyses utilizing principal components to reduce and categorize variation, brightness is often the source of the greatest variation (Eastman and Fulk, 1993). Component mapping helped to more precisely describe what each component represented (Figure 5-2). When mapped on the panhandle, principal component one corresponded well with agricultural areas of the panhandle (Figure 5-2a). The bright areas on the map represent those areas where component one showed heavy loading. These areas were concentrated around Guymon, Oklahoma in the central part of the panhandle, south of the Rita Blanca National grasslands (in Texas) in the southwestern corner of the image and eastern Beaver County. These areas were known to have large agricultural land use elements.

The second principal component was analyzed as variation due to seasonal crops because the factor loadings were positive in the summer and negative in the winter for all three years (Figure 5-1). This pattern is consistent with the green-up of summer agricultural crops and their subsequent die-off during the winter. Analysis using the principal component map (Figure 5-2b) confirmed this conclusion. Higher component two loadings were prevalent around Guymon, Oklahoma and in Texas County in general. The areas covered by components one and two, however, did not correspond exactly. In order to determine why these two components both representing agriculture differed, a higher spatial resolution Landsat Thematic Mapper (TM) image of the same area was analyzed. The Landsat TM image possesses a spatial resolution of 30 meters while the AVHRR imagery used in the analyses records spatial resolutions down to only 1 kilometer (Jensen, 1996). The Thematic Mapper could reveal land features not present in the AVHRR imagery. The Thematic Mapper image showed that the major difference between components one and two were the presence of irrigation circles in the areas covered by component two. Irrigation circles indicate the presence of crop watering systems and different types of crops grown in these areas. It was therefore determined that while both components represented agriculture, component one represented dry land/non-irrigated agriculture and component two represented irrigated agriculture. These first two components accounted for 61% of the variation in the data set.

The third and fourth components were more difficult to interpret cleanly because as orthogonal variation is assigned to the first two components, any remaining variation must be interpreted without including the sources of variation ascribed to the first two components. The third component exhibited fall maxima and spring minima, with positive values reaching their highest in late summer/early fall and remaining high through the winter while negative values reached their lowest in late spring/early summer (Figure 5-1). This pattern might be associated with the planting of fall crops such as winter wheat or a late fall green-up due to increased seasonal moisture that typically occurs in the panhandle at this time. In either case, the peaks are not as large as for components one and two, which could suggest sparser or lower growing cover/vegetation (Eastman and Fulk, 1993). Mapping component three clarified the interpretation of this component (Figure 5-2c). Component three loaded heavily in central Beaver County and secondarily in the mesa region, the Rita Blanca National Grassland region and along the major riparian corridors of the panhandle (Figure 5-2c). These areas are all grassland, range (cattle grazed), and/or natural vegetation areas. Component three, therefore, likely represents areas of natural and generally low growing vegetation. This conclusion is supported by the loading pattern of Figure 5-1.

Finally, component four is the most difficult to interpret. Component four exhibited no consistent trend over all three sampling periods. Over the last two years of sampling though, component four does show a mid-summer peak and a winter minimum followed by a gradual spring increase in factor loadings (Figure 5-1). It is difficult to confidently assign a source to this variation, however speculatively, the variation could be accounted for by water storage in vegetation. This would coincide with the general moisture pattern in the panhandle and would fit the fall/winter die-off as well. This explanation does, however, stretch the limits of interpretation and should not be considered explanatory with relation to the logistic regression models. Component four was mapped and a weak loading pattern can be seen around major riparian areas of the panhandle (Figure 5-2d).

The standard ten component model attempting to predict occurrence or absence of all carnivores based upon vegetational NDVI variation was marginally insignificant. However, stepwise, backwards regression removed component five and the model became significant. Component five contributed very little to the overall validity of the carnivore model (Table 5-1a). In addition, the coefficient assigned to component five in the regression model was very small (Table 5-1a). The significant stepwise, backwards regression was good at predicting both carnivore presence and absence.

The component which exerted the most influence on the model was component two (Table 5-1a). Component two's R value was highest of all components and negative, indicating that component two was most valuable in predicting carnivore absence. Since component two was interpreted as representing seasonal crop variation, and more specifically, irrigated cropland in the panhandle, it seems apparent that carnivores respond strongly in their distributional patterns to the presence or absence of irrigated agricultural land. This is not surprising since irrigated croplands tend to be areas of high human and machine activity. This analysis was also supported by the geographic distribution of component two (Figure 5-2b). Component two's geographic distribution corresponded well with areas of the panhandle that did not record regular carnivore occurrences as described in Chapter 3. In addition, components six and four were also valuable towards predicting carnivore absence in habitats, while component ten was intrinsic towards predicting carnivore occurrence. Since direct interpretation of these components was not possible, it is hard to qualify the nature of the relationship between these components and carnivores, in general.

Agriculture, in general, may support higher prey densities and may be a preferred habitat for carnivores during part of the year. It may also be a less optimal habitat at other times due to its seasonality and lack of cover. The regression model demonstrates the response of carnivores to different types of agriculture. Carnivores, in general, seem to respond to agriculture by avoiding those agricultural areas that possess the highest human and machine presences. In contrast, the univariate analysis of Chapter 3 indicated that carnivores preferred agricultural areas. However, these results did not specify whether the preference was for irrigated or dryland agriculture, since no effort was made to distinguish between these areas for that analysis. The ability of the regression model to differentiate between these areas and more precisely define carnivore preferences makes the model particularly valuable.

Another consideration that may account for the disparity between the univariate and the modeling analyses is the lack of carnivore data for the spring sampling session in

1996. This session was heavily impacted by precipitation events and as a result, many of the plates were washed clean and no tracks were recovered. The modeling analyses are most likely to be impacted by that event because these analyses are the most time/season sensitive. The interpretations of the other univariate techniques were not as sensitive to time or season. The impact of this period is difficult to assess however, since it has to be assumed that all areas of the panhandle were impacted equally, even though this might not be the case.

A final factor that may account for the disparity between the modeling results and the univariate analysis is the consideration of scale. The univariate analysis examined occurrence at landscape and local scales and no efforts were made to differentiate between irrigated and dryland agriculture. At these scales, carnivores did not appear to show an aversion to agricultural areas and some species even preferred these areas (Chapter 3). The regression model considers distributions at a broader, regional scale and was able to differentiate the two types of agriculture. While carnivores may be locally attracted to agricultural areas by some limited or landscape factor, regionally and as a group, they are able to assess qualitatively these areas and avoid the irrigated areas (Figure 5-2b).

A map of the panhandle showing a color composite of the first three principal components demonstrates the full potential of this model (Figure 5-3). Agriculture does play a large predictive role in the distributions of carnivores in the panhandle. In general, carnivores can be expected to avoid the green and yellow areas of the map which represent irrigated agricultural areas. Carnivores can be expected to occur with less frequency in these areas and in similar areas of the prairie environment. Naturally, the further the area in question is from the study area used to construct the model, the more the predictability of the model will decrease.

The model of canid distributions was also, initially, insignificant. However, with the removal of components one and seven, the model became a significant predictor of canid distributions (Table 5-1b). While the removal of component seven offers little insight into the model, the removal of component one is noteworthy. Component one accounted for the most variation in the NDVI data set and was identified as variation associated with brightness and was specifically associated with dryland agriculture. That the significance of the model is contingent upon the removal of the variable that describes the most variation is significant in itself. The removal of this variable might suggest that brightness has no effect on canid occurrence to any degree and that dryland agriculture in general, has little influence on carnivores. This conclusion is not accurate though. The analysis of brightness and dryland agriculture on individual canid species shows that swift foxes and coyotes both respond strongly to variation in vegetational brightness and dryland agriculture, but in opposite ways. Swift foxes respond to brightness and dryland agriculture in a strongly negative way, while coyotes respond to brightness and dryland agriculture in a strongly positive way (Table 5-1c, 5-1d). These interpretations are supported by the analyses in Chapter 3. The result of these two inputs to the model is effectively to negate each other's influence on the model.

The factor that both canids seem to have in common is irrigated agriculture (component two). Irrigated agriculture appears to be, once again, a good predictor of absence. The disparity between this analysis and the univariate analyses is again, probably one of scale as well as the ability of the model to distinguish different agricultural types. Additionally, component nine was also a good predictor of canid absence (Table 5-1b). The distribution of these components corresponds well to areas of canid absence in the panhandle (Figure 5-3). Canids would be expected to occur with less frequency in the green and yellow regions of the color composite map (Figure 5-3).

The model predicting swift fox distribution was significant with the inclusion of all ten components and stepwise regression was not required to produce a significant model (Table 5-1c). Two components were valuable in predicting swift fox absence in the panhandle. Principal components one and four were highly significant in the outcome of the model (Table 5-1c). Swift fox distributions responded in a strongly negative way to both components. Principal component one was defined as vegetational brightness and dryland agriculture. Swift foxes avoided areas that loaded heavily on principal component one (Figure 5-2a). Vegetational brightness may also be an indicator of vegetational health, growth and height. Small carnivores, such as the swift fox, are very sensitive to predation from a variety of sources (Chapter 3). As previously discussed (Chapter 3), swift foxes may selectively avoid areas with dense or tall vegetation because it interferes with their ability to detect predators (Allardyce, pers. comm.). Additionally, coyotes demonstrated a preference for dryland agricultural areas. Given the negative interaction between swift foxes and coyotes (Chapter 3), it is not surprising that swift foxes respond negatively to a component that may be indicating these areas (Figure 5-2a). Areas with lower brightness values may also represent low vegetation height and/or productivity and be more attractive to swift foxes.

Component four was also an indicator of swift fox absence. If component four is a measure of vegetational moisture as previously suggested, then the model fits this analysis as well. Vegetational moisture may also serve as an indicator of plant health and height. Those areas with higher moisture values may contain vegetation in greater heights and densities, which swift foxes would avoid because of their inability to detect predation in those areas. Component four's distribution does correspond with some of the major riparian areas of the panhandle, which fit this vegetational profile and were conspicuously absent of swift foxes at all scales (Figure 5-2d).

The color composite map (Figure 5-3) indicates that swift foxes would be predicted to be absent from the red and green areas of the panhandle and similar regions. These areas correspond well to areas that recorded few swift fox detections (Figure 2-4).

The final significant predictive model was for coyotes. Again, all ten components produced a significant model and stepwise regression was not necessary. The components that had the greatest predictive value for coyote distributions were one, two, six and nine. Components two, six and nine were all identified as being significant predictors of coyote absence (Table 5-1d). The disparity between the regression model and the univariate analysis with regard to the agricultural component was probably due to analytical differences in scale and the ability of the regression model to differentiate between agricultural areas, as previously discussed. Irrigated agriculture was still the primary predictor of coyote absence. This is probably due to the seasonal nature of agriculture and the human presence that tends to dominate these agricultural areas. Figure 5-2b shows the geographical distribution of this component.

Component one was a significant predictor of coyote presence (Table 5-1d). In all four significant models, this was one of only two components that were significant predictors of presence. The value for this component was almost identically opposite of the value of the same component for swift foxes (Table 5-1c). Swift foxes and coyotes respond to variation in brightness and dryland agriculture in opposite and nearly equal ways. This corresponds well with the previously documented antagonistic interactions between swift foxes and coyotes (Chapter 3). It is not surprising, therefore, that the two canids should separate themselves regionally as well as locally. Coyotes seem to prefer areas with higher brightness values that predominate with dryland agriculture, suggesting that taller and denser regional vegetation does not deter the larger canid (Figure 5-2a). Thicker, taller vegetation may represent greater availability of plant and seed resources. This often results in higher rodent and other small mammal densities, which serve as a primary resource for carnivores. Taller, thicker vegetation is not a hazard to coyotes, so coyotes may tend to prefer these areas for their increased prey availability.

The color composite map predicts that coyotes can be expected to be detected more frequently in the red regions of the map, while the green regions would be expected to be more coyote depauparate. These patterns once again correspond well to patterns of coyote occurrence presented in Chapter 3.

No model of any kind was significant for mustelids, either as a group or as individual species. Mustelids are much smaller than the canids of the panhandle and as a result, tend to have smaller home ranges (Caire et al., 1989). It is not unlikely that mustelids are more sensitive to local variation rather than landscape or regional variation.

Mustelid home ranges may be small enough that individuals are not effected by regional processes in the same way that larger carnivores are. This would explain their sensitivity as a group to local features such as prairie dog towns (Chapter 4) and their overall insensitivity to broader scale analyses such as logistic regression modeling.

Bobcats were not successfully modeled either. It is likely that too few bobcats were detected over the course of the study to permit the construction of an accurate or significant model. The bobcat models did predict bobcat absence from areas perfectly, but they also failed to predict presence in any cases. In general, all carnivore models predicted absence very well. The primary factor that separated significant from non-significant models was their ability to predict presence, while no model predicted presence as well as absence, only a slight increase in the ability to predict presence was required to improve a model to the point where it became statistically significant. This increase could probably have been achieved in the bobcat model with more sampling.

Habitat/species models of this type offer a novel method for analyzing carnivore distributions. The application of remotely sensed data in traditionally biological models introduces a predictive component to the model that has been previously unavailable (Debinski et al., 1999; Bian and West, 1997; Jorgensen and Nohr, 1996; Pereira and Itami, 1991). In the past, biological investigation has been environmentally intrusive and required on-site sampling and manipulation of the species in question. The development of regional distribution models based upon vegetation characteristics allows investigators to make inferences regarding organismal distributions over broad scales without impacting the habitat being investigated. Tools such as these can have tremendous value in conservation and reintroduction efforts as well as in environmental impact assessments. Agriculture, for instance, is apparently having a significant impact on carnivore distributions. However, through this type of modeling, not only the presence of agriculture is evaluated, but the quality and type of agriculture can be evaluated for its effect on carnivore distributions. Application of a model such as this should be confined to those regions that are most like the study region, in this case, the Oklahoma panhandle.

SUMMARY

The results of these models suggest that certain generalizations can be made about carnivore and canid distributions in the Oklahoma panhandle. Generally, carnivores and canids avoid seasonal agriculture in the panhandle. Where this agriculture occurs (Figure 5-2), carnivore and canid distributions can be expected to be sparser. Swift foxes and coyotes also respond to variability in brightness. Swift fox distributions can be expected to be more sparse where brightness values are higher presumably because this represents higher or thicker vegetation which impairs the smaller carnivores ability to detect predators. In contrast, coyote distributions can be expected to be more dense in areas with higher brightness values. Thicker, more dense vegetation offers more plant resources and possibly greater prey resources in terms of small mammal populations. Since coyotes experience no increased predation cost in these areas, it is not surprising that their regional distributions favor these areas.

Finally, this model offers a novel approach to analyzing carnivore distributions. With this model, relative distributions of comparable carnivore groups and species can be predicted in regions similar to the panhandle. Ultimately, accurate vegetation/species models may be used to influence conservation and land use decisions without seriously impacting the systems in question.

Table 5-1. Logistic regression statistics from all carnivore (a), canids (b), swift fox (c) and coyote (d) regression models. Regression based upon relationship between detection data and Normalized Difference Vegetation Index (NDVI) Principal Components. 'B' indicates the coefficient of the component in the regression equation; 'R' indicates the relative contribution of the component to the predictive value of the model; * indicates components dropped by the stepwise, backwards regression.

a) All Carnivores

Variable	B	S.E.	Wald	df	Sig	R	Exp(B)
NDVI PC 1	.1506	.2345	.4124	1	.5208	.0000	1.1625
NDVI PC 2	-.6512	.2662	5.9866	1	.0144	-.1808	.5214
NDVI PC 3	.2973	.2423	1.5045	1	.2200	.0000	1.3462
NDVI PC 4	-.3848	.2669	2.0789	1	.1493	-.0254	.6806
NDVI PC 5*	.0267	.2356	.0128	1	.9099	.0000	1.0270
NDVI PC 6	-.3767	.2533	2.2124	1	.1369	-.0417	.6861
NDVI PC 7	-.2141	.2514	.7255	1	.3943	.0000	.8072
NDVI PC 8	-.2946	.2520	1.3665	1	.2424	.0000	.7448
NDVI PC 9	.1113	.2417	.2119	1	.6453	.0000	1.1177
NDVI PC 10	.3845	.2441	2.4807	1	.1152	.0628	1.4689
Constant	.4452	.2428	3.3638	1	.0666		

b) Canids

Variable	B	S.E.	Wald	df	Sig	R	Exp(B)
NDVI PC 1*	-.0604	.2293	.0693	1	.7923	.0000	.9414
NDVI PC 2	-.6640	.2719	5.9642	1	.0146	-.1823	.5148
NDVI PC 3	.3462	.2584	1.7948	1	.1803	.0000	1.4137
NDVI PC 4	-.1678	.2391	.4922	1	.4829	.0000	.8456
NDVI PC 5	-.1740	.2398	5266	1	.4680	.0000	.8403
NDVI PC 6	-.3421	.2468	1.9216	1	.1657	.0000	.7102
NDVI PC 7*	.0320	.2359	.0184	1	.8921	.0000	1.0325
NDVI PC 8	-.3036	.2334	1.6915	1	.1934	.0000	.7382
NDVI PC 9	-.3532	.2426	2.1190	1	.1455	-.0316	.7024
NDVI PC 10	.3237	.2433	1.7699	1	.1834	.0000	1.3822
Constant	-.6026	.2462	5.9909	1	.0144		

c) Swift fox

Variable	B	S.E.	Wald	df	Sig	R	Exp(B)
NDVI PC 1	-.9357	.4040	5.3627	1	.0206	-.1833	.3923
NDVI PC 2	-.2214	.3474	.4060	1	.5240	.0000	.8014
NDVI PC 3	-.3628	.3809	.9073	1	.3408	.0000	.6957
NDVI PC 4	-1.1269	.4570	6.0793	1	.0137	-.2019	.3240
NDVI PC 5	-.2330	.2662	.7658	1	.3815	.0000	.7922
NDVI PC 6	-.2809	.2654	1.1207	1	.2898	.0000	.7551
NDVI PC 7	.2667	.3115	.7330	1	.3919	.0000	1.3056
NDVI PC 8	-.0726	.2709	.0719	1	.7886	.0000	.9300
NDVI PC 9	-.3999	.3109	1.6550	1	.1983	.0000	.6704
NDVI PC 10	.2880	.3216	.8022	1	.3704	.0000	1.3338
Constant	-1.6694	.4014	17.2957	1	.0000		

d) Coyote

Variable	B	S.E.	Wald	df	Sig	R	Exp(B)
NDVI PC 1	.6137	.3163	3.7646	1	.0523	.1422	1.8472
NDVI PC 2	-.7230	.3653	3.9165	1	.0478	-.1482	.4853
NDVI PC 3	.5189	.3521	2.1721	1	.1405	.0444	1.6802
NDVI PC 4	.1639	.2881	.3237	1	.5694	.0000	1.1781
NDVI PC 5	-.3068	.3031	1.0249	1	.3114	.0000	.7358
NDVI PC 6	-.5034	.3266	2.3756	1	.1232	-.0656	.6045
NDVI PC 7	-.2612	.3004	.7562	1	.3845	.0000	.7701
NDVI PC 8	-.3071	.3094	.9848	1	.3210	.0000	.7356
NDVI PC 9	-.5653	.3047	3.4429	1	.0635	-.1286	.5682
NDVI PC 10	.4036	.3140	1.6522	1	.1987	.0000	1.4972
Constant	-2.0011	.4003	24.9887	1	.0000		

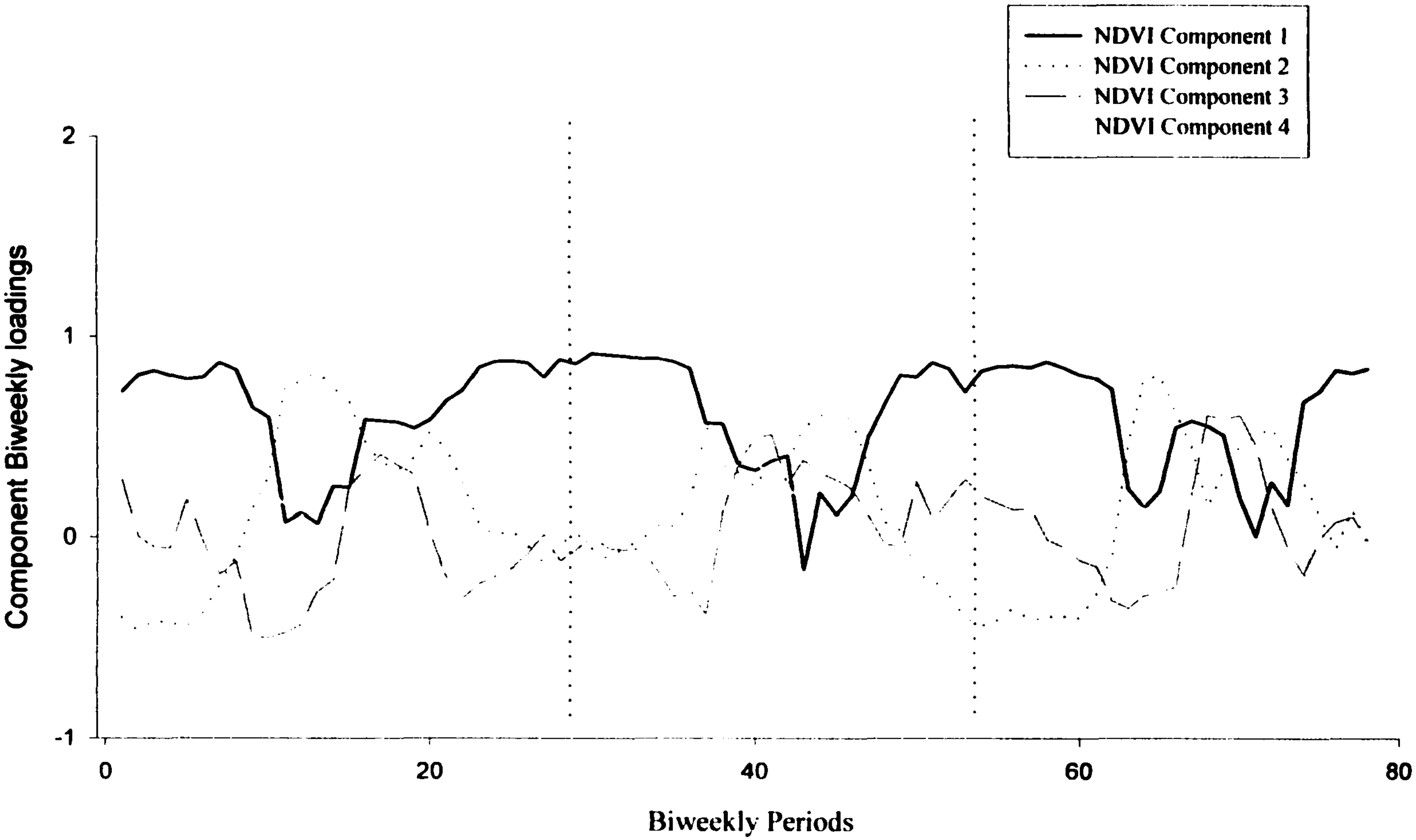
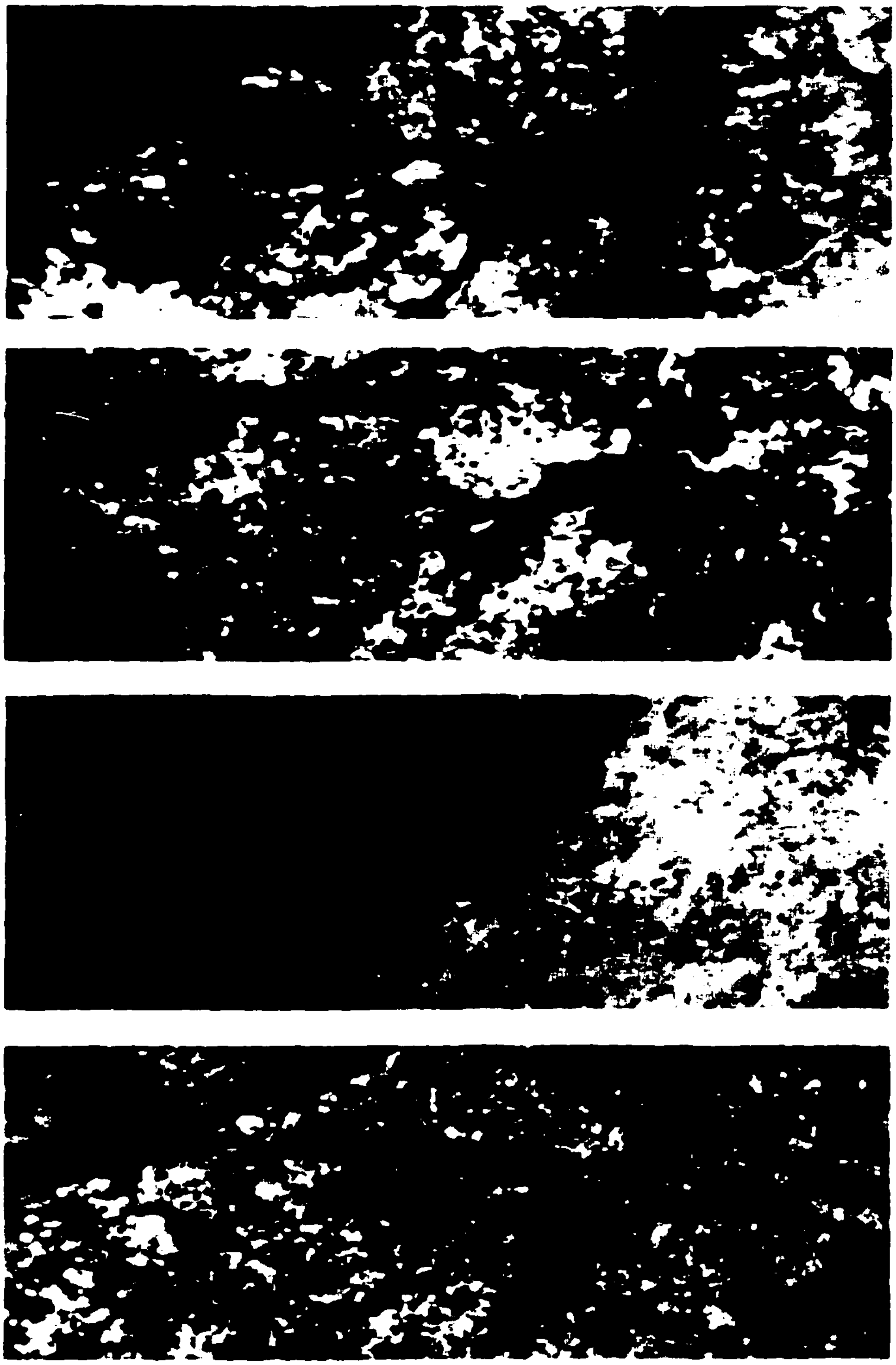


Figure 5-1. Patterns of Principal Components 1-4 loadings during the 78 biweekly AVHRR passes, 1995 - 1997.



a)
b)
c)
d)

Figure 5-2. Oklahoma Panhandle NDVI Principal Components Maps.
(a) Principal Component 1 image;
(b) Principal Component 2 image;
(c) Principal Component 3 image;
(d) Principal Component 4 image.

Figure 5-3. Color Composite Map of Principal Components 1-3
(PCA 1 = red; PCA 2 = green; PCA 3 = blue).

GENERAL CONCLUSIONS

By far, the best method for detecting carnivores in the panhandle was the baited, chalk-coated tracking plate. This was at least in part due to the lack of available field help. Spotlighting was effective only when sufficient numbers of observers were present and infrared triggered cameras were useful but cost prohibitive. Other methods of carnivore detection, monitoring and identification such as live trapping, den surveys and radiotelemetry were not used or evaluated due to expense or lack of field help as well. Direct comparison of the tracking methods used in this study and the other methods not specifically examined would be difficult. Differences in habitat, time, season, carnivore assemblages and investigator experience between this study and the other non-tested methods in the published literature introduce too much variation to make comparison meaningful. However, while the tracking in this study did produce sound results, one drawback to this method was apparent. No measure of carnivore population size and no measure of movement was possible with this method as individuals could not be identified. Depending upon the goals of future work, live-trapping/tagging, den surveys, and/or radiotelemetry might be more applicable methods if numbers of individuals and their movements are important to the outcome of the project.

In general, canids were more responsive to analyses than mustelids at all scales except local. This may be due to the larger overall size of the two canid species in the study area relative to the three mustelid species. Larger sized carnivores would likely have larger home ranges and travel more than smaller carnivores. Carnivores that move more would therefore be more likely to be sensitive to landscape and regional changes while more sedentary carnivores or those with smaller home ranges would be influenced most prominently by local features and be insensitive to variation at larger scales. This appears to be the case between the canids and mustelids in the Oklahoma panhandle.

Between local features (prairie dog towns and paired sites), canids did not exhibit any occurrence differences, although there was a trend in swift foxes to avoid prairie dog towns. Mustelids as a group were significantly associated with prairie dog towns indicating that the smaller carnivores are more sensitive to local features than the larger ones. Swift foxes probably also avoided prairie dog towns in response to coyote presence there. In general, prairie dogs were determined to be valuable, but not keystone members of the plains ecosystem, with regard to the carnivores existing today in the Oklahoma panhandle.

Landscape level habitat analysis indicated that carnivores also exhibited habitat preferences. Canids were more responsive to this scale than mustelids. Swift foxes and coyotes both displayed preferences for specific and different habitats. Mustelids did not exhibit such clear habitat preferences, which again may be due to their smaller size and possible decreased sensitivity to larger scale habitat features. The one mustelid that did display a habitat preference was the striped skunk. This species is one of the larger mustelid species recorded for the panhandle.

Regional analyses indicated large scale distributional differences among carnivores. Both canid species were unevenly distributed across counties and physiographic regions. Mustelids were, again, less responsive to the large scale analyses.

Bobcats were not detected often during the course of the study and as a result, power for statistical tests involving bobcats were low and results were not significant. It is unlikely that bobcats are habitat generalists in the panhandle. Only a weak habitat preference could be supported for the felid. Felids, in general, tend to be shy, secretive and nocturnal. It is therefore not surprising that bobcats were not detected often and it is likely that their numbers were underestimated. Due to their cautious nature and their general avoidance of new environmental features, tracking plates may not have been the best method for detecting bobcats in the panhandle. In the future, research on panhandle carnivores should be designed to include detection techniques aimed specifically at bobcats.

The logistic regression models in the panhandle demonstrated that carnivore occurrence, and in particular, canid occurrences were associated with phenological metrics of panhandle vegetation. In addition, satellite remotely sensed imagery offered the capability of investigating carnivore distributions over large areas while simultaneously being able to distinguish between very similar habitat types (dryland versus irrigated agriculture). The value of this modeling approach extends beyond standard scientific inquiry though. Models such as these that permit predictions from remotely sensed data can become valuable tools in conservation and endangered species biology.

The overriding factor that exerts the most influence on carnivore occurrences in the panhandle is the interaction between swift foxes and coyotes. Swift foxes avoid interactions with coyotes at all scales. This interaction exerts the greatest influence on canid distributions in the panhandle and may also have secondary effects on mustelid distributions. This interaction is not surprising and has been well documented among other similar sized canid species. Due to the universal presence of this agonistic dynamic, the separation of swift foxes and coyotes at all scales and the subsequent structure of the resulting carnivore assemblages have to be considered to at least be partly the result of this antagonistic interaction between the canid species.

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