LESSER PRAIRIE-CHICKEN CHICK SURVIVAL, ADULT SURVIVAL, AND HABITAT SELECTION AND MOVEMENTS OF MALES IN FRAGMENTED RANGELANDS OF SOUTHWESTERN KANSAS

by

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ABSTRACT

Lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations in Kansas declined from the mid-1970s to the mid-1990s in association with the loss of breeding habitat to center-pivot irrigated crop fields. The rate of habitat loss appeared to slow in the 1980s, but lesser prairie-chicken numbers continued to decline. The present research was initiated to gather specific demographic information on these populations.

Invertebrates were sampled in lesser prairie-chicken use and non-use areas, and in areas with varying sand sagebrush canopy cover. Invertebrate biomass was greater in use vs. paired non-use samples on 2 of 3 sampling occasions. Based on regression modeling, forb cover was a more important predictor of invertebrate biomass than sagebrush cover.

Daily survival rates ($D\hat{S}R$s) of lesser prairie-chicken chicks were estimated for pre- and post-fledge periods to 60 days post-hatch. Pre-fledge $D\hat{S}R$ was 0.941 (95% CI = 0.895 to 0.987) and post-fledge $D\hat{S}R$ was 0.983 (95% CI = 0.983 to 1.032). Daily survival rates of chicks in individually identifiable broods were compared to daily brood movements and invertebrate biomass collected in brood ranges, but no significant correlations were detected.

Potential depredators of lesser prairie-chicken nests were determined from evidence gathered at depredated nests and sightings of predators. All evidence suggested that mammalian predators were responsible for most nest depredation, and that coyotes (*Canis latrans*) were most likely the primary predator responsible for nest destruction.

Radio-marked male lesser prairie-chickens were located daily from spring through fall to document their movements and habitat selection. Two (2.63%) of 76 males performed emigration movements. Males exhibited strong selection for sand

sagebrush prairie during nearly all (24 of 25) months studied at 2 nested spatial scales of habitat availability.

Survival of adults and yearlings was monitored from spring through fall. The selected best survival model (of those models in the candidate set) suggested that survival varied across months, but did not differ appreciably between sexes or across years. The model-conditional survival estimate for spring through fall was 0.74 (95% CI = 0.65 to 0.81). Annual survival was estimated at 0.57 (95% CI = 0.35 to 0.76) from a composite data set of spring- and fall-trapped birds.

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INTRODUCTION

At least 4 subspecies of pinnated grouse once occupied vast areas of North America (Johnsgard 1983). The heath hen (*Tympanuchus cupido cupido*), which inhabited coastal New England, became extinct in the early 1930s. The Attwater's prairie-chicken (*T. c. attwateri*) was listed as endangered by the U. S. Fish and Wildlife Service (USFWS) in 1967. By 1994 the population of wild Attwater's prairie-chickens had dropped to less than 160 individuals (Morrow et al. 1996), and now is maintained only by a captive breeding program (Silvy et al. 1999). The range of the greater prairie-chicken (*T. c. pinnatus*) has been drastically reduced since the turn of the 20th Century. This subspecies now occurs only in isolated areas of the eastern Great Plains with highest densities in north-central Nebraska and eastern Kansas (Braun et al. 1994). Recent data show that some of these populations may be declining (Horton 1995, McCarthy et al. 1995). Two other extinct species of prairie grouse, *T. ceres* and *T. stirtoni*, are known only from fossil records (Giesen 1998).

Small populations of lesser prairie-chickens (*T. pallidicinctus*) inhabit semi-arid sand sagebrush (*Artemisia filifolia*) or shinnery oak (*Quercus havardii*) rangelands in southeastern Colorado, southwestern Kansas, southeastern New Mexico, and the panhandles of Oklahoma and Texas (Johnsgard 1983, Giesen 1998). These populations are historically unstable (Hoffman 1963, Jackson and DeArment 1963, Crawford and Bolen 1976) and some are still declining (Braun et al. 1994, Rodgers 1995, Jensen et al. In Press). The lesser prairie-chicken currently is a candidate species for listing as threatened under the Endangered Species Act of 1973 (U. S. Department of the Interior, USFWS 1998). Habitat loss to center-pivot irrigated crop fields has been cited as the

major cause of population declines in southwestern Kansas (Waddell and Hanzlick 1978, Taylor and Guthery 1980, Rodgers 1995). Less than 43% of the original sand sagebrush prairie area in Finney, Kearny, and Gray counties remained in 1980 (M. Sexson, Kansas Department of Wildlife and Parks [KDWP], unpublished data). The rate of conversion of sand sagebrush prairie to agricultural fields apparently declined in the early 1980s (Lloyd Stullken, U. S. Department of Agriculture, unpublished data; Rodgers 1995), but KDWP surveys indicated that lesser prairie-chickens continued to decline (Rodgers 1995, Jensen et al. In Press). Specific causes of the more recent declines were unknown.

Populations of prairie grouse, like populations of any organism, are determined by the complex interaction of 4 vital rates; birth, immigration, death, and emigration. Prairie grouse reach sexual maturity in 1 year and have large clutch sizes and subsequently high reproductive potential (Johnsgard 1973:62, Morrow et al. 1996). This, and population data for other North American grouse, led Bergerud (1988) to conclude that reproductive success is the primary determinant of prairie grouse populations. This conclusion was supported by a sensitivity analysis of greater prairie-chicken populations, which determined that nest success and survival of juvenile birds during their first year following hatch has the greatest influence on population fluctuations (Wisdom and Mills 1997).

Few published data are available on vital rates of lesser prairie-chickens anywhere in their range, and Schwilling (1955) is the only researcher who has studied the species in Kansas. Much of the research on lesser prairie-chickens was conducted before the widespread availability of reliable, light-weight radio-telemetry equipment. Nests of lesser prairie-chickens are difficult to locate without the aid of such a method for

following females (Scwhilling 1955, Copelin 1963, Bergerud 1988:578), and this, in conjunction with the short-term nature of most studies, has precluded estimation of the most important vital rates (nest success and brood survival) for the species (Giesen 1998).

Survival of lesser prairie-chicken chicks from individual identifiable broods never has been studied. Davison (1940) and Copelin (1963) captured and banded chicks from July through September, and Copelin (1963) noted that few chicks disappeared from broods after they reached that age. However, neither of those researchers attempted to estimate survival. Without the ability to identify individual broods, chick survival may be overestimated due to complete losses of broods shortly after hatch (Bergerud 1988:609). Factors affecting survival of lesser prairie-chicken broods are entirely unknown, but research on other gallinaceous birds suggests that brood survival may be highly dependent upon the quantity and availability of high-protein invertebrate foods (Hill 1985; Southwood and Cross 1969; Rands 1985; Erikstad 1978, 1985; Johnson and Boyce 1990; Griffon et al. 1997; Bergerud 1988:612; Silvy et al. 1999). Invertebrate characteristics of lesser prairie-chicken habitats seldom are studied (but see Doerr and Guthery 1983), and no research has been conducted in sand sagebrush habitats.

Immigration and emigration have obvious and important consequences with respect to population regulation. Copelin (1963), Campbell (1972), Giesen (1994), and Riley et al. (1994) studied movements of radio marked or banded birds, and reported that nearly all movements were less than 10 km. Schwilling (1955) provided general information on seasonal movements of lesser prairie-chickens in southwestern Kansas in what then was relatively continuous sand sagebrush habitat, but he was not able to follow individual birds to obtain estimates of immigration or emigration rates. The movements

of individual lesser prairie-chickens in fragmented sand sagebrush habitats have not been studied.

Habitat selection of lesser prairie-chickens also has not previously been studied. Although there is little disagreement as to the general habitat requirements of lesser prairie-chickens, few data are available that allow objective assessment of their habitat use. Davison (1940) and Copelin (1963) provided only general descriptions of habitat use. Observations of habitat use in southwestern Kansas were reported by Schwilling (1955), but he was not able to gather detailed information on the total areas used by individuals, and he did not present estimates of the proportions of different habitats that were available. Most other studies of habitat use have focused on the nest sites of hens (Merchant 1982, Haukos and Smith 1989, Giesen 1994). Although sand sagebrush is often recommended as a habitat component (Jackson and DeArment 1963; Giesen 1994, 1998; Mote et al. 1999), empirical evidence on the overall importance of sagebrush to lesser prairie-chickens is lacking. Recommendations appear to be based primarily on reports by Jackson and DeArment (1963), in which the authors commented that sagebrush treatment ruined the habitat. However, those authors did not establish a causal link or even strong correlation between sagebrush treatment and a decline in prairie-chicken reproductive success, survival, or population size. Prairie-chickens evolved in landscapes devoid of agricultural crops, but use them extensively when they are available. Clearly, an organism's use of a particular habitat does not indicate that it is necessary or beneficial for population viability (White and Garrott 1990).

Assessing a single habitat component's importance requires determination of how removing that habitat component affects vital rates. Determining how sagebrush density,

spatial distribution, and canopy cover manipulation affect nesting success and brood survival of lesser prairie-chickens is important but difficult, requiring either a logistically troublesome replicated experiment or a modeling approach in which nest success and brood survival are estimated for numerous areas of the lesser prairie-chicken's range in sand sagebrush habitats. Until more data are available, sagebrush treatment likely will be discouraged despite potential benefits of localized brush control (Donaldson 1969).

Despite their importance in population dynamics, estimates of lesser prairie-chicken survival are rare. Using mark-recapture data from 3 leks, Campbell (1972) estimated annual survival of male lesser prairie-chickens in New Mexico at 0.34. No other estimates of annual survival are available for lesser prairie-chickens. Estimates of annual survival for other species of prairie grouse range from 0.25 for sharp-tailed grouse (*T. phasianellus*) in South Dakota (Robel et al. 1972) to 0.46 for greater prairie-chickens in Wisconsin (Hamerstrom and Hamerstrom 1973). No available estimates of annual survival for prairie grouse exceed 0.50 (Johnsgard 1983, Bergerud 1988). The primary mortality factor for lesser prairie-chickens is predation by mammals and raptors (Giesen 1998).

The primary objective of the present research was to collect basic information on habitat use and vital rates that would help to determine the probable specific causes of the recent declines in numbers of lesser prairie-chickens. Data on vital rates were not available for the entire period during which populations declined, and it was necessary to assume that the rates observed during the present study and the factors affecting them were representative of those that would have been observed during that period. This assumption probably is valid because of the apparent absence of drastic changes in

landcover, land use, and weather during the recent population decline. However, the reader must be aware that this assumption is untested and wholly untestable without any specific data for the whole period. Furthermore, KDWP survey data collected since 1995 suggest that populations of lesser prairie-chickens may have stabilized somewhat over the last 5 years.

Field work for this study of lesser prairie-chickens in southwestern Kansas began in March 1997 and concluded in November 1999. Specific objectives of this research were 1) assess macro- and microhabitat selection relative to standing crops of invertebrates used as food by adult lesser prairie-chickens, 2) determine the relationship between vegetative composition and standing crops of those invertebrates, 3) estimate survival of chicks and determine if their survival was related to standing crops of invertebrates, 4) determine probable causes of nest failure and identify nest depredators, 5) document habitat selection of males, 6) gather movement data and emigration rates of radio-marked males, and 7) estimate survival of males and females in fragmented sand sagebrush rangelands of southwestern Kansas. These objectives formed the basis for the 5 separate chapters of this document. An abstract, introduction, methods, results, discussion, and implications for management are contained in each of these. Although this resulted in some minor redundancy (e.g., study area description), the intent was to provide the reader with separate and independent sections that would require little outside information to be clearly understood. Results of additional research on nest success, female movements and habitat selection, and internal parasites of lesser prairie-chickens are presented in Walker (2000).

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RELATIONSHIPS AMONG LESSER PRAIRIE-CHICKEN HABITAT USE, INVERTEBRATE BIOMASS, AND SAND SAGEBRUSH COVER IN SOUTHWESTERN KANSAS

Abstract: Invertebrates are important summer dietary components of lesser prairie-chickens (*Tympanuchus pallidicinctus*) in southwestern Kansas. Lesser prairie-chickens, therefore, were predicted to utilize summer habitats with greater invertebrate biomass. Invertebrates were sampled during summer in lesser prairie-chicken use and non-use areas with pitfall traps and sweepnets. Two sampling designs were employed in this study. Samples were collected in use and independent non-use areas and in use and paired non-use areas; these designs addressed macrohabitat and microhabitat use, respectively. Mean Acrididae biomass, total invertebrate biomass, and proportion of total invertebrate biomass comprised of Acrididae in use and independent non-use samples did not differ significantly ($P \geq 0.249$) but mean Acrididae and total invertebrate biomass were greater ($P \leq 0.061$) in use vs. paired non-use samples on 2 of 3 sampling occasions. Mean proportion of total invertebrate biomass comprised of Acrididae always was higher in use vs. paired non-use areas, but differences were statistically significant only on 1 of 3 sampling occasions. These results suggest that lesser prairie-chicken macrohabitat selection is not cued by invertebrate biomass, but that microhabitat selection may be dependent upon quantity of Acrididae and total invertebrate biomass, and also the relative abundance of Acrididae biomass.

Because most invertebrate taxa utilized as food by lesser prairie-chickens are phytophagous or predators of phytophagous invertebrates, biomass of these taxa was expected to differ among areas with varying vegetative structure. Invertebrates were sampled in habitats with different overall vegetation structure varying primarily in sand

sagebrush (*Artemisia filifolia*) canopy cover. Mean Acrididae and total invertebrate biomass were highest in areas with low sand sagebrush canopy cover, but significant differences in mean Acrididae and total invertebrate biomass were not detected among areas with low, moderate, or high sand sagebrush cover ($P \geq 0.324$). Based on regression modeling, forb cover was the most important predictor of Acrididae and total invertebrate biomass. Range management practices that reduce forb cover are expected to reduce Acrididae and total invertebrate biomass.

Key words: *Artemisia filifolia*, canopy cover, invertebrate biomass, lesser prairie-chicken, macrohabitat, microhabitat, sand sagebrush, *Tympanuchus pallidicinctus*, vegetation.

INTRODUCTION

Invertebrates are important food sources for many adult and juvenile Galliformes (Schwilling 1955, Dahlgren 1990) and their availability has been shown to directly affect chick survival of ring-necked pheasants (*Phasianus colchicus)* (Hill 1985), gray partridge (*Perdix perdix*) (Southwood and Cross 1969, Rands 1985), willow grouse (*Lagopus lagopus lagopus*) (Erikstad 1985), sage grouse (*Centrocercus urophasianus*) (Johnson and Boyce 1990), and Attwater's prairie-chickens (*Tympanuchus cupido attwateri*) (Griffon et al. 1997). Lesser prairie-chicken adults and chicks utilize invertebrates heavily during summer and early fall (Schwilling 1955; Jones 1963a, b; 1964).

Short-horned grasshoppers (Family Acrididae) are reported as the most abundant and utilized invertebrate food source of lesser prairie-chickens, but other families also appear to be important (Schwilling 1955, Jones 1963a, Crawford and Bolen 1976, Davis et al. 1980, Riley et al. 1993). Lesser prairie-chickens inhabit both sand sagebrush and

shinnery oak (*Quercus havardii*) rangelands. Invertebrates are expected to be more important as a summer food source in sagebrush than shinnery oak habitats because shinnery oak provides acorns, catkins, and galls that are unavailable in sagebrush habitats (Davis et al. 1980). If invertebrates are important components of habitat quality, lesser prairie-chicken adults and chicks are predicted to utilize habitats with greater invertebrate abundance.

Because the invertebrate taxa utilized as food by lesser prairie-chickens are phytophagous or predators of phytophagous arthropods (Borror et al. 1976), the cover of different vegetation types and bare ground is expected to directly affect invertebrate abundance (Southwood and Cross 1969; Sotherton 1982; Evans 1984, 1988; Baines et al. 1996).

Objectives of this study were to determine (1) if areas used by lesser prairie-chickens had higher Acrididae and total invertebrate biomass than other areas and, (2) if invertebrate abundance and diversity was related to sagebrush cover and vegetative structural composition.

STUDY AREA

The study area was a 5,760-ha fragment of sand sagebrush rangeland immediately south of the Arkansas River in Finney County of southwestern Kansas. The area was vegetated primarily by sand sagebrush, blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), paspalum (*Paspalum* sp.), bluestem grasses (*Andropogon* spp.), western ragweed (*Ambrosia psilostachya*), sunflowers (*Helianthus* spp.), and Russian-thistle (*Salsola iberica*). Prickly pear cactus (*Opuntia* sp.) and yucca (soapweed)

(*Yucca glauca*) were interspersed throughout. Buffalo-gourd (*Cucurbita foetidissima*) and purple poppy mallow (*Callirhoe involucrata*) were common in disturbed areas. Soils were in the Tivoli-Vona association and in the choppy sands range site category (U. S. Department of Agriculture 1965). Primary land uses were grazing by cattle (from May 1 through October 1) and petroleum production.

Over the past 30 years, the area received an average of 50 cm of annual precipitation with 74 % occurring between March and August. During this study (1997 through 1999) the area received an average of 55 cm of precipitation annually (U. S. Department of Commerce 1999).

METHODS

The study was conducted during the summers of 1997, 1998, and 1999. All invertebrate sampling was completed between the first week of June and the first week of August each year.

Defining Use and Non-Use Areas

Lesser prairie-chickens were captured on leks in spring or fall, radio-marked with 12-g necklace transmitters, and located daily until the transmitter stopped functioning, the bird left the study area, or the bird died. These daily location data were used to delineate areas frequented by lesser prairie-chickens (use areas); areas in which no locations of radio-marked birds were recorded were considered "non-use areas". Specifically, use areas were minimum convex polygon (Mohr 1947) ranges for ≥1 bird determined from locations for 5 to 7 days prior to sampling and areas outside these polygons were non-use

areas. These mutually exclusive designations will be used throughout this paper even though non-use areas may have been visited by lesser prairie-chickens.

Invertebrate Collection

Invertebrates were collected with grids of pitfall traps and with sweepnets. Pitfall trap bodies were 480-ml plastic beverage cups. These were fitted with funnels constructed from 270-ml Solo® cozy cups with the lower 5 mm removed to open the funnel. Catch jars placed inside trap bodies were graduated, 120-ml sample cups containing 75 ml of ethylene glycol as a killing agent. Traps were installed such that funnel tops were at ground level. Four 5 × 15 cm drift fences (cut from aluminum flashing) were erected at right angles perpendicular and adjacent to the trap funnel margin to increase trap efficacy (Morrill et al. 1990). Catch jars were collected from grids after traps had been operative for 5 days. Samples were labeled and stored below 0 C° until invertebrates could be processed. Pitfall grids were sampling units and individual pitfall traps were considered subsamples in data analyses. Subsamples were judged unusable if the pitfall trap's position was disturbed sufficiently to affect capture of crawling invertebrates (e.g., trampled by cattle, removed by rodents, filled with sufficient debris as to allow escape of trapped invertebrates, or destroyed in an unknown manner). Pitfall traps inundated with carrion beetles (Family Silphidae) also were excluded from analyses, because the maximum capacity of these traps had been reached prior to sample collection. Grid values were obtained by pooling samples from usable traps and calculating mean biomass for usable traps in the grid. Pitfall-trapped invertebrates were identified to family using standard keys (Borrer et al. 1976, Elzinga 1981) except for some larval forms and individuals in the orders Diptera, Lepidoptera, and Homoptera.

Individuals in these orders were diverse and scarce enough that sorting them to family level would not have yielded meaningful measures of biomass. After identification, individuals were placed by taxon in polystyrene Petri dishes, allowed to air-dry for approximately 1 day, and placed in a 60 C° oven until masses were constant (about 7 days). Masses of oven-dried samples (biomasses) were determined to 0.0001 g on an electronic balance.

Sweepnet samples were collected from the upper layer of vegetation with 100 sweeps in each sampling area using standard 30-cm insect nets between sunrise and 1000 hrs or between 1700 hrs and sunset. Sampling was avoided during rain or when winds exceeded 25 km/hr. All sweepnet samples were collected by the same individual to eliminate variability due to different observers (Southwood 1978). Collected invertebrates were restrained in the sweepnet and placed in killing containers containing ethyl acetate until dead. Dead invertebrates were removed from the sweepnet, placed in resealable plastic bags, labeled, and stored frozen.

Sweepnet-collected invertebrates were separated into 2 groups; short-horned grasshoppers (Family Acrididae) and other taxa (other). Sorted invertebrates were then oven-dried and their masses determined as were pitfall samples.

Sampling Design

Sampling design was modified among years to better address the 2 study objectives. Logistical constraints prohibited some designs and methods in some years therefore sampling design is described by year and method.

Invertebrates in Use and. Non-use Areas

First Summer - 1997.--One 25 × 25-m grid of 25 pitfall traps was established in each of 3 use and 3 spatially distinct and independent (not paired) non-use areas in July. Pitfall traps within these grids were arranged in 5 equally-spaced lines of 5 equally-spaced traps. Sweepnet samples were collected within pitfall grids by walking parallel and adjacent to lines of pitfall traps. Sweepnetting was conducted immediately after pitfall catch jars were collected and again 2 days later. These 2 sweepnet samples were treated as subsamples in data analyses.

Second Summer - 1998.--Sweepnet sampling was conducted in July in 11 use areas and 11 random non-use locations (1paired with each use area [Ratti and Garton 1996]). Sweepnet samples were collected along 2 parallel, 75-m, north-south transects spaced 10 m apart in each use and paired non-use area. Paired random non-use sampling locations were generated by selecting a random azimuth from the use area and a random distance from 200 to 800 m outside the use areas. Locations of sampling areas were plotted on topographic maps of the study area, and if random points fell within areas used by other lesser prairie-chickens or non-habitat areas (e.g., on roads) they were discarded and a new azimuth and distance was generated. Thus, non-use samples were collected in habitats that appeared similar to use areas. Random locations were reached by walking from the use area sampling location using a hand-held compass and roll-a-tape® measuring wheel. Each pair of use and non-use samples was collected consecutively on the same day to account for potential variability in invertebrate capture probability among days and time periods (Evans et al. 1983).

Third Summer - 1999.-- Sweepnetting was conducted as in 1998 but with the addition of a June sampling period. Ten use and paired non-use areas were sampled in June and 11 use and paired non-use areas were sampled in July. Because individual birds did not occupy exactly the same areas among years, the use and non-use areas also were in different locations each year.

Vegetation Structure and Invertebrate Biomass

First Summer - 1997.--Pitfall grids were established in areas that varied in sagebrush cover and vegetative structural composition. Three grids were placed in areas with low (0 to 10%), 2 in areas with moderate (11 to 30%), and 1 in an area with high (>30%) sand sagebrush cover.

Second Summer - 1998.--Invertebrate sampling intensity was increased in the second year of the study. Pitfall trapping grids in 1998 also were 25 × 25 m, but subsampling was reduced from 25 to 9 pitfall traps per grid. Low altitude aerial photographs were used to select 5 areas each of low, moderate, and high sand sagebrush canopy cover with varying vegetative structure spaced throughout the study area. One pitfall grid was placed in each of these 15 locations in June.

Third Summer - 1999.--Invertebrate sampling in areas with different sand sagebrush density was not conducted in 1999 because logistical constraints prohibited collection and sorting of samples.

Vegetation Sampling

Cover of vegetation types and bare ground was quantified within each pitfall grid using a modified line-point sampling strategy similar to that used by Heady et al. (1959) and Rotenberry and Wiens (1980). Cover was measured at 0.5-m intervals along 3

evenly-spaced, parallel, 25-m transects (153 sample points/grid). Each cover type present at each sample point was determined by placing a 2.5-cm diameter dowel alongside a taut measuring tape and recording the type of cover touching any part of the dowel as shrub, forb, grass, bare ground, or combinations of these. Per cent coverage of each vegetation type and bare ground then was determined from frequency of occurrence by dividing the total number of hits for each cover type by the total number of sample points per grid. Although this method is suitable for determining shrub canopy (Heady et al. 1959), it likely overestimated cover of grass and forbs due to the relatively large diameter of the dowel (Winkworth 1955). Therefore, values for grasses and forbs represented relative (rather than absolute) cover of these vegetative components across sampled areas.

Data Analysis

Data from each year and sampling period were analyzed separately because sampling design changed among years and because pooling could mask important year- or period-dependent variation in invertebrate biomass. Statistical tests were considered significant at $P = 0.10$.

Invertebrates in Use and Non-Use Areas

First Summer - 1997.--Means of invertebrate biomasses of sweepnet (g per 100 sweeps) and pitfall samples (mean biomass per trap) collected from lesser prairie-chicken use and independent non-use areas were compared using 2-sample t-tests (Zar 1984). Acrididae, total invertebrate biomass (all taxa combined), and proportion of total biomass comprised of Acrididae were compared separately.

Second and Third Summers - 1998 and 1999.--Sweepnet-collected Acrididae and total invertebrate biomasses from lesser prairie-chicken use and paired

non-use locations in 1998 were compared using 1-sample t-tests on the mean differences between use and non-use pairs. Mean differences in proportions of sweepnet-collected invertebrate biomass comprised of Acrididae in use and paired non-use areas also were compared with 1-sample t-tests (Zar 1984).

Vegetation Structure and Invertebrate Biomass

First Summer - 1997.--Mean invertebrate biomasses of pitfall and sweepnet samples could not be compared statistically among the 3 sagebrush density categories for 1997 because only 1 sampling grid was located in an area of high sagebrush canopy cover, thus no measure of variance was available for the high sagebrush category. Mean invertebrate biomass in pitfall and sweepnet samples from areas of low and from areas of moderate and high sand sagebrush cover combined were compared using a 2-tailed t-test (Zar 1984) because areas with "sparse" or no sagebrush differ drastically in appearance from areas of "moderate" or "dense" sagebrush. These qualitative visual differences appeared more extreme than visual differences between moderate and high sagebrush canopy areas. This was the sole criterion used when determining how pooling of data and statistical comparisons were to proceed. Acrididae and total invertebrate biomasses were compared separately.

Second Summer - 1998.--Mean Acrididae and total invertebrate biomass from pitfall samples were compared among sagebrush density categories using analysis of variance (ANOVA) (Zar 1984). Principal components analysis of vegetation coverage values for each grid was used to derive non-correlated variables that described the majority (>90%) of the variation in the plant community (Manly 1986). Factor loadings then were computed to determine which cover components were represented in these

variables (Jensen 1996). Principal components were calculated from the covariance matrix rather than the correlation matrix, but the correlation matrix was examined during interpretation of principle components and factor loadings. Invertebrate biomass for 11 families determined from the literature to be important lesser prairie-chicken foods and total invertebrate biomass were regressed on vegetation principal components in all-subsets linear regression models. Akaike's Information Criterion corrected for use with small sample sizes (AIC_c) was computed and used to select the least biased, most parsimonious regression model that described the structure in the data (Burnham and Anderson 1998). The regression models were ranked from best to worst for Acrididae and total invertebrate biomass based on differences in AIC_c values (Δ_is). AIC_c weight (W_i) can be considered as evidence in support of a model given a particular set of data and W_is were summed over all models in which a variable appeared to determine the relative importance of each principle component and their interaction in determining biomass of each of the 11 taxa and total invertebrate biomass (Burnham and Anderson 1998). Diversity of pitfall-collected invertebrate biomass was calculated using Shannon's index (H′) and was compared among habitats with different sagebrush canopy coverage with ANOVA (Krebs 1989, Brower et al. 1998).

RESULTS

Invertebrates in Use and Non-use Areas

During this 3-year study, invertebrates were sampled in 35 lesser prairie-chicken use areas and 35 non-use areas. No statistically significant differences were detected between invertebrate biomass collected in use and independent non-use areas but

Acrididae and total invertebrate biomass was significantly higher in use than paired non-use areas in 2 of 3 sampling periods. Details are reported by year.

First Summer - 1997.--Mean Acrididae biomass and proportion of total invertebrate biomass comprised of Acrididae in pitfall samples were higher in use than independent non-use areas, but significant differences were not detected (Table 1). Results for total invertebrate biomass were opposite, mean biomass was higher in independent non-use than use areas but, again, not significantly (Table 1). Sweepnet samples from independent non-use areas contained higher mean Acrididae biomass and total invertebrate biomass than use areas and a greater proportion of total invertebrate biomass was comprised of Acrididae, but these differences also were not statistically significant (Table 1).

Second Summer - 1998.--Sweepnet samples collected in lesser prairie-chicken use areas contained significantly higher Acrididae and total invertebrate biomass than paired non-use areas ($P \leq 0.061$). On average, Acrididae also comprised a greater proportion of the total biomass of use-area samples, but the difference was not statistically significant (Table 2).

Third Summer - 1999.--Sweepnet samples collected in lesser prairie-chicken use areas in June and July contained higher average Acrididae and total invertebrate biomass than paired non-use areas, but differences were statistically significant only for June samples (Table 2). Average proportion of total invertebrate biomass comprised of Acrididae also was higher in use than paired non-use areas, but significantly higher only in July (Table 2).

Vegetation Structure and Invertebrate Biomass

No consistent relationship was detected between invertebrate biomass and sand sagebrush canopy cover, but the results of regression modeling suggested that forb cover was the primary determinant of invertebrate biomass.

First Summer - 1997.--Pitfall samples from areas of low sagebrush canopy cover contained higher Acrididae and total invertebrate biomass than pooled samples from areas of moderate and high sagebrush canopy cover but no statistically significant differences were detected (Table 3). Results for sweepnet sample comparisons were similar (Table 3).

Second Summer - 1998.-Mean Acrididae and total invertebrate biomass were greatest in areas with low sagebrush density but no significant differences were detected among invertebrate biomass values for pitfall samples collected in areas with low, moderate, and high sagebrush canopy cover (Table 4).

Sand sagebrush canopy cover in pitfall grids ranged from 0.0 to 53.3%. Principal components analysis on vegetation cover proportions resulted in 2 independent variables that explained 93.6% of the variability in the vegetation community. Calculation of the correlation matrix showed that sand sagebrush and bare ground were positively correlated (0.64) and that both of these cover types were highly negatively correlated with grass cover (Table 5). Calculation of factor loadings indicated that sagebrush and bare ground both loaded highly (factor loadings 0.90 and 0.88 for sagebrush and bare ground, respectively) on the first principal component (PC1). The tradeoff between the sagebrush-bare ground correlation and grass cover, as represented by PC1, explained 79.2% of the variability in vegetation among pitfall sampling grids. This was not

surprising because the sampling areas were chosen based on sagebrush canopy. The second principal component (PC2) explained an additional 14.4% of the variability in vegetation and was loaded highly upon only by forb cover (factor loading 0.86).

Regression model selection produced different results for each taxa. The full model, incorporating PC1(the negative relationship between sagebrush-bare ground cover and grass cover), PC2 (forb cover), and the interaction term (INT), was selected as the best model (lowest AIC_c) for 4 of 11 individual invertebrate food taxa including Acrididae (Table 6). The model with only PC2 was selected as best twice, the model with only INT was selected twice, and the model with only PC1 never was selected as the AIC_c best model. Models for the 3 remaining individual taxa included varying combinations of 2 variables. The best model for total invertebrate biomass included only PC2 (Table 6).

In 7 of 12 cases the selected best model had a low W_i (≤ 0.31), and in these cases multiple models had Δ_is < 2. This suggests substantial model selection uncertainty and multiple competing models should be considered (Burnham and Anderson 1998). Variable importance, as determined by W_i sums, also differed among taxa. PC1was the most important predictor of invertebrate biomass in only 2 of 11 cases whereas PC2 and INT were the most important in 4 and 5 of 11 cases, respectively. PC2 was the most important predictor of Acrididae and total invertebrate biomass and was more than twice as important as PC1 in predicting total invertebrate biomass (Table 7). Parameter estimates of regression coefficients for PC2 always were positive when PC2 was the most important variable. Mean H′ values ranged from 0.79 to 0.94, but no statistically

significant differences were detected among habitats with different sagebrush canopy cover ($F = 1.17$, $P = 0.342$).

DISCUSSION

Results of comparisons between invertebrate biomass collected in use and non-use areas in 1997 may be uninformative because samples sizes were small. These data suggest only that lesser prairie-chickens may not select macrohabitats based on invertebrate abundance.

Results of comparisons between use and paired non-use samples in 1998 and 1999 suggest that prairie-chickens select areas (microhabitats) with higher Acrididae and total invertebrate biomass and in which a higher proportion of the invertebrates are acridid grasshoppers than surrounding areas (within macrohabitats). However, invertebrate biomasses collected in areas used by lesser prairie-chickens vary considerably. This suggests that lesser prairie-chickens can use areas with a wide range of invertebrate biomasses and that macrohabitat selection is influenced primarily by factors other than invertebrate biomass present. However, once macrohabitats are chosen, invertebrate biomass may play a role in selection of microhabitats.

It is possible that lesser prairie-chickens selected microhabitats based on cues other than invertebrate biomass. It has been suggested that lesser prairie-chickens seek shade during the hot summer months (Copelin 1963). Sand sagebrush seems the most likely source of shade in southwestern Kansas rangelands but invertebrate biomass appears to differ with forb rather than sagebrush cover (see below) so selection of microhabitat based on availability of shade would not result in higher invertebrate biomass in use areas. Lesser prairie-chickens also consume forbs (Jones 1964, Riley et

al. 1993) and microhabitat selection may actually have been based on the plant rather than the invertebrate community. However, during sampling periods, lesser prairie-chicken diets probably contained <30% broad-leaved plants and >70 % invertebrates (Schwilling 1955, Jones 1963b). Lesser prairie-chickens may not be food-limited, but use of areas with higher invertebrate biomass during some sampling periods suggests invertebrate foods in sand sagebrush habitats are an important component of habitat quality.

Results of the regression model selection and variable importance determination for 1998 data provide insight into how vegetation structure of sand sagebrush rangeland affects biomass of food taxa. Results of model selection agree with the results of t-tests between invertebrate biomass from low and moderate-high sagebrush categories for 1997 and the ANOVA for invertebrate biomass from low, moderate, and high sagebrush canopy areas for 1998. These results suggest that sand sagebrush canopy cover (or any of its correlates) alone is a poor predictor of invertebrate biomass and that changing sand sagebrush cover (e.g., brush removal) probably does not directly affect standing crops of important invertebrate foods in southwestern Kansas. That PC1 was the most important variable in predicting biomass of 2 important food taxa seems contradictory. However, biomass of both of these taxa (Family Tettigoniidae and Order Homoptera) comprised a small proportion of both pitfall and sweepnet samples. Their paucity suggests that, although they were considered important food in other previous studies (Jones 1963, Davis et al. 1980), they are probably not important foods for lesser prairie-chickens in southwestern Kansas. This supports the report by Schwilling (1955) who found that

short-horned grasshoppers (Acrididae) and beetles (Coleoptera) were the most frequent invertebrate foods in the crops and gizzards of lesser prairie-chickens in Kansas.

Determination of variable importance in the regression models supports conclusions of Jones (1963b), Southwood and Cross (1969), Hill (1985), Burger et al. (1993), and others that forbs are an important component of Galliforme brood foraging habitat because they provide substrate for invertebrates. Doerr and Guthery (1983) found that areas of shinnery oak habitat treated with 0.2 kg of tebuthiuron herbicide per ha exhibited increased forb diversity and increased numbers of grasshoppers (Orthoptera) but sampling was not adequate to detect significant differences. Tebuthiuron treatments of >0.4 kg/ha resulted in lower forb cover and lower grasshopper numbers. In contrast, Hull et al. (1996) did not detect positive relationships between invertebrate abundance and forbs in Conservation Reserve Program fields in northeastern Kansas and speculated that the range of forb cover values (0 to 23%) was not large enough to significantly affect invertebrate numbers.

Invertebrate populations are difficult to sample, and the typical high variations in invertebrate biomass measures in this and other studies makes determination of true patterns difficult. This high variability may be responsible for the relatively low W_is of the selected regression models. It is not suggested that model selection uncertainty is due entirely to sampling error but only that the degree of uncertainty may be decreased with increased sample sizes and sampling methods that yield less variable estimates of invertebrate biomass. Nonetheless, variable importance determination in this study supports the accumulating evidence that forb cover is the primary determinate of invertebrate biomass.

MANAGEMENT IMPLICATIONS

These findings may have important implications for management of lesser prairie-chicken habitats. Lesser prairie-chickens do not select macrohabitats based on invertebrate biomass, but do select microhabitats with higher invertebrate biomass. This invertebrate biomass is most affected by forb cover. Therefore, the spatial distribution of forb cover may be an important factor influencing the abundance and distribution of important invertebrate foods. Forbs distributed throughout the habitat may provide areas with abundant invertebrate foods that are available to more individual birds than forb cover that is clumped and widely scattered. This could be an integral part of the interspersion of different habitat types required by lesser prairie-chickens (Jones 1964, Donaldson 1969, Taylor and Guthery 1980). However, because no available evidence suggests that lesser prairie-chickens are food-limited, managers are cautioned against reducing the availability of favorable nesting cover solely to increase forbs.

Land management practices that reduce sand sagebrush cover in dense sagebrush stands will not likely have adverse impacts on biomass of invertebrates used as food by lesser prairie-chickens. However, practices aimed at reducing cover of forbs may negatively influence habitat quality by reducing abundance of important invertebrate and plant food taxa. Sagebrush may meet other life history requirements of lesser prairie-chickens, but this has not been clearly demonstrated.

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Table 1. Acrididae, total biomass, and proportion of total biomass comprised of Acrididae in 3 use and 3 independent non-use areas collected in southwestern Kansas in 1997. Pitfall values are g per trap and sweepnet values are g per 100 sweeps.

	Area			
	Use	Non-use		
	$\bar{x}$ (SE)	$\bar{x}$ (SE)	t	P[a]
Pitfall				
Acrididae	0.59 (0.27)	0.35 (0.22)	0.703	0.521
Total	1.62 (0.51)	2.02 (0.82)	0.413	0.701
P(Acrididae)[b]	0.31 (0.12)	0.14 (0.05)	1.349	0.249
Sweepnet				
Acrididae	4.62 (2.10)	6.92 (3.63)	0.532	0.623
Total	6.06 (1.71)	7.82 (3.53)	0.449	0.677
P(Acrididae)	0.67 (0.22)	0.83 (0.07)	0.699	0.523

[a] *P*-values are for 2-tailed test

[b] P(Acrididae) is proportion of total biomass comprised of Acrididae

Table 2. Acrididae, total biomass (g per 100 sweeps), and proportion of total biomass comprised of Acrididae in lesser prairie-chicken use and paired non-use areas collected during summer in southwestern Kansas, 1998-1999.

Year and Period	n	Variable	Use $\bar{x}$ (SE)	Non-use $\bar{x}$ (SE)	Difference $\bar{x}$ (SE)	t	P[b]
1998							
July	11	Acrididae	7.22 (0.88)	5.76 (0.86)	1.46 (0.86)	1.69	0.061
		Total	7.78 (0.97)	6.08 (0.87)	1.70 (0.96)	1.77	0.053
		P(Acrididae)[a]	0.94 (0.02)	0.90 (0.05)	0.04 (0.05)	0.74	0.238
1999							
June	10	Acrididae	2.66 (0.48)	1.15 (0.17)	1.50 (0.40)	3.76	0.002
		Total	3.29 (0.47)	1.59 (0.20)	1.70 (0.42)	4.04	0.001
		P(Acrididae)	0.75 (0.06)	0.70 (0.03)	0.05 (0.05)	1.02	0.167
July	11	Acrididae	5.44 (0.68)	4.96 (0.52)	0.48 (0.79)	0.61	0.278
		Total	6.08 (0.73)	5.93 (0.62)	0.15 (0.88)	0.17	0.433
		P(Acrididae)	0.89 (0.01)	0.85 (0.03)	0.05 (0.03)	1.75	0.055

[a] P(Acrididae) is proportion of total invertebrate biomass comprised of Acrididae

[b] P-value is for 1-tailed test

Table 3. Mean Acrididae and total invertebrate biomass collected in pitfall (g per trap) and sweepnet (g per 100 sweeps) samples in areas with low (0-10%), moderate (11-30%), and high (>30%) sand sagebrush canopy cover in southwestern Kansas, 1997.

	Sagebrush Density Category					
	Low $\bar{x}$ (SE) (n=3)	Moderate $\bar{x}$ (SE) (n=2)	High $\bar{x}$ (n=1)	Pooled[a] $\bar{x}$ (SE) (n=3)	t	P[b]
Pitfall						
Acrididae	0.55 (0.26)	0.16 (0.10)	0.87	0.40 (0.24)	0.416	0.699
Total	2.30 (0.79)	1.12 (0.45)	1.77	1.34 (0.34)	1.124	0.324
Sweepnet						
Acrididae	7.47 (3.43)	2.26 (1.52)	7.91	4.15 (2.08)	0.828	0.454
Total	8.35 (3.32)	3.80 (0.72)	9.00	5.53 (1.78)	0.748	0.496

[a] Pooled is value for grids in moderate and high sagebrush categories combined

[b] P-value is for 2-tailed test between low and pooled.

Table 4. Mean biomass (g) per pitfall trap of Acrididae and total invertebrate biomass collected in 5 areas each of low (0-10%), moderate (11-30%), and high (>30%) sand sagebrush canopy cover in southwestern Kansas during June 1998.

	Sagebrush canopy category				
	Low	Moderate	High		
	$\bar{x}$ (SE)	$\bar{x}$ (SE)	$\bar{x}$ (SE)	*F*	*P*
Acrididae	0.33 (0.11)	0.24 (0.12)	0.28 (0.04)	0.21	0.813
Total	3.37 (0.73)	2.79 (0.77)	2.38 (0.20)	0.64	0.544

Table 5. Correlation matrix for cover components in 15 invertebrate trapping grids in 1998 in sagebrush rangeland of southwestern Kansas.

	Grass	Forb	Bare ground
Shrub	-0.84	-0.07	0.64
Grass		-0.18	-0.82
Forb			0.47

Table 6. ΔAIC_c values for seven models expected to predict Acrididae and total biomass in sagebrush habitats of southwestern Kansas in 1998. Model with $\Delta_i = 0.00$ is selected best model. Models with $\Delta_i \leq 2$ are competing models. Numbers in parentheses are AIC_c weights.

Model	Acrididae	Total
PC1[a]	3.34 (0.06)	4.65 (0.03)
PC2	1.19 (0.16)	0.00 (0.30)
INT	4.13 (0.04)	4.86 (0.03)
PC1 and PC2	1.14 (0.17)	0.38 (0.24)
PC1 and INT	1.27 (0.16)	5.63 (0.02)
PC2 and INT	1.96 (0.11)	0.35 (0.25)
PC1, PC2, and INT	0.00 (0.30)	1.48 (0.14)

[a] PC1 (principal component 1) is interpreted as the negative correlation between shrubs and bare ground versus grass cover, PC2 (principle component 2) represents primarily forb cover, and INT is interaction.

Table 7. Relative importance of cover principal components (sum of Akaike weights) in determining pitfall-collected invertebrate biomass for 11 invertebrate taxa and total invertebrate biomass collected in sagebrush habitats of southwestern Kansas, 1998.

Taxon	PC1[a]	PC2	INT
Order Orthoptera			
Acrididae	0.68	0.75A[b]	0.61
Gryllidae	0.71	0.80	0.87A
Gryllacrididae	0.59	0.60	0.70A
Tettigoniidae	0.66A	0.58	0.53
Order Hemiptera			
Pentatomidae	0.54	0.42	0.62A
Order Homoptera	0.85A	0.51	0.59
Order Coleoptera			
Chrysomelidae	0.46	0.99A	0.54
Tenebrionidae	0.54	0.69	0.71A
Carabidae	0.70	0.91A	0.74
Order Hymenoptera			
Formicidae	0.45	0.69A	0.47
Order Lepidoptera	0.50	0.50	0.51A
Total	0.43	0.93A	0.65

[a] PC1 (principal component 1) is interpreted as the negative correlation between shrubs and bare ground versus grass cover, PC2 (principle component 2) represents primarily forb cover, and INT is interaction.

[b] Capital letter next to value denotes most important variable for that taxon or group

LESSER PRAIRIE-CHICKEN CHICK SURVIVAL AND DISPERSAL WITHIN A SAND SAGEBRUSH PRAIRIE FRAGMENT IN SOUTHWESTERN KANSAS

Abstract: Dispersal of lesser prairie-chicken chicks from hatch site and brood ranges to breeding sites (leks) is important to understanding grouse population dynamics and how dispersal affects spacing of grouse in a habitat. Lesser prairie-chicken chicks were marked shortly after hatching for identification upon recapture at leks. Two male lesser prairie-chickens marked as chicks were recaptured at the same lek 2234 and 2203 m from their respective hatch locations. None was recaptured at the lek nearest the hatch location or brood range. Survival of grouse chicks is an important component of breeding success. Chick survival was monitored using flush counts of individually identifiable broods and daily survival rates over all chicks ($D\hat{S}R$s) were estimated for pre- and post-fledge periods to 60 days post-hatch. Pre-fledge (hatch to 14 days) $D\hat{S}R$ was 0.941 (95% CI = 0.895 to 0.987) and was 0.983 (95% CI = 0.933 to 1.032) post-fledge. Nearly one half of the lesser prairie-chicken broods in this study suffered complete losses of chicks prior to fledge. Apparent chick survival was estimated by comparing the mean size of broods in summer to the mean clutch size. Using this method, chick survival was estimated at 0.31. Daily survival rates of chicks in individual broods ($D\hat{S}R_i$s) were expected to be positively correlated with the relative abundance of invertebrates in brood use areas and negatively correlated with brood movements pre- and post-fledge. Brood movements were expected to be negatively correlated with invertebrate abundance. Daily survival rates of chicks in individual broods were compared to total invertebrate biomass collected in sweepnet samples from brood use areas and brood movements pre- and post-fledge using simple linear correlation analyses.

No statistically significant correlations were detected between $D\hat{S}R_i$s and total invertebrate biomass ($P \geq 0.087$), $D\hat{S}R_i$s and brood movements ($P \geq 0.346$), or brood movements and invertebrate abundance ($P = 0.263$). However, all correlation coefficients were positive or negative as hypothesized. Results of this study suggest that effective dispersal of lesser prairie-chicken chicks within a habitat fragment is unrelated to the proximity of leks to nest sites or brood ranges. Estimating chick survival from mean size of unmarked broods in mid-summer may overestimate chick survival rates. If lesser prairie-chicken chick survival is related to abundance of invertebrates or brood movements within habitats, larger sample sizes may be needed to document these relationships.

Key words: broods, brood movements, chick survival, dispersal, invertebrates, lesser prairie-chicken, *Tympanuchus pallidicinctus*

INTRODUCTION

Distance from place of birth (hatch) to place of breeding (lek) (Johnston 1961) is important to understanding how populations are regulated and how spacing of grouse in a habitat is affected by dispersal of chicks (Bergerud and Gratson 1988). Little is known about the dispersal distances of lesser prairie-chickens.

Breeding success limits grouse populations (Amman 1957, Hamerstrom and Hamerstrom 1973, Wisdom and Mills 1997). Estimating survival of lesser prairie-chicken chicks is important because precocial young often experience high mortality. No estimates of chick survival from identifiable broods are available for lesser prairie-chickens. Chick survival has been estimated by comparing mean clutch size to mean

brood size in summer (Davison 1940, Schwilling 1955, Copelin 1963). Mortality of grouse during the first 7 to 21 days is higher than mortality during mid- to late-summer when broods are most visible (Schwilling 1955, Ammann 1957, Bergerud and Gratson 1988). Survival of chicks within a brood is not independent and, if early losses of entire broods are common, chick survival estimates from brood size in late summer may be unreliable (Bergerud and Gratson 1988:609). Breeding success is defined as the product of nest success, brood survival, and adult survival over summer, and has been estimated from juvenile to adult ratios in fall harvest and trapping samples (Campbell 1972). These estimates of breeding success will be biased if juveniles and adults differ in their susceptibility to trapping or harvest. Nest success, brood survival, and adult survival combined may provide more reliable estimates of breeding success than fall juvenile to adult ratios, but these population parameters must be estimated separately to determine their relative importance in determining breeding success.

It seems reasonable to estimate chick survival over 2 distinct periods; pre-fledge and post-fledge. Lesser prairie-chicken chicks are capable of short flights (fledge) by 14 days of age (Giesen 1998). Pre-fledge survival is expected to be lower than post-fledge survival because ability of chicks to escape predators probably increases as chick flight becomes more efficient. Furthermore, chicks are more vulnerable to inclement weather and starvation during the first few days posthatch because they have not developed the ability to thermoregulate (Aulie 1976). Survival of grouse chicks has been linked to the availability of invertebrate foods (Bergerud and Gratson 1988:614). Erikstad (1985) found survival of willow grouse (*Lagopus lagopus*) chicks was positively related to their

growth rates and negatively related to their home range sizes. Erikstad (1985) concluded that home range size was dependent upon the distance traveled in search of invertebrates.

It was hypothesized that pre- and post-fledge lesser prairie-chicken chick survival would be negatively correlated with brood movements and positively correlated with the amount of invertebrate biomass present in brood use areas. Movements were expected to be negatively correlated with invertebrate biomass in use areas.

Objectives of this study were (1) to mark chicks for identification upon recapture at leks, (2) estimate survival of lesser prairie-chicken chicks, and (3) determine if movements were related to invertebrate biomass and if survival was related to brood movements or abundance of invertebrates.

STUDY AREA

The primary study area was a 5,760-ha fragment of sand sagebrush rangeland immediately south of the Arkansas River in western Finney County of southwestern Kansas. The area was vegetated primarily by sand sagebrush, blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), paspalum (*Paspalum* sp.), bluestem grasses (*Andropogon* spp.), western ragweed (*Ambrosia psilostachya*), sunflowers (*Helianthus* spp.), and Russian-thistle (*Salsola iberica*). Prickly pear cactus (*Opuntia* sp.) and yucca (soapweed) (*Yucca glauca*) were interspersed throughout. Buffalo-gourd (*Cucurbita foetidissima*) and purple poppy mallow (*Callirhoe involucrata*) were common in disturbed areas. Soils were in the Tivoli-Vona association and in the choppy sands range site category (U. S. Department of Agriculture 1965). Primary land uses were grazing by cattle (from May 1 through October 1) and petroleum production. Research

also was conducted in sand sagebrush prairie fragments separated from the primary study area by cultivated fields. Vegetation and soils were similar in these other fragments but contained some sand plum (*Prunus angustifolia*) thickets in addition to sand sagebrush.

Over the past 30 years, the area received an average of 50 cm of annual precipitation with 74 % occurring between March and August. During this study (1997 through 1999) the area received an average of 55 cm of precipitation annually (U. S. Department of Commerce 1999).

METHODS

Lesser prairie-chicken hens were captured on the primary study area with walk-in traps on leks in spring. Hens were radio-marked with 12-g transmitters and released at the capture site. These hens were located daily until they nested, died, or the transmitter failed. Nesting hens were monitored daily via telemetry until their nests failed or hatched.

Capturing and Marking Chicks

Chicks were captured for marking 3 to 11 days after hatching. A radio-marked hen with chicks was located via telemetry approximately 1 hr before sunrise and its exact position determined by 2 researchers using close-range triangulation. Battery-powered, 500,000 candle-power spotlights then were used to illuminate the area and daze the hen by concentrating the spotlight beams on it. A third researcher then attempted to capture the hen and chicks by placing a long-handled dip net over them. If the hen flushed, the chicks were captured by hand.

Captured chicks were placed in 1 side of a bisected 25 × 15 × 45-cm plastic storage box lined with a cotton towel. On cool mornings, a disposable, oxidative reaction hand warmer was placed beneath the towel to prevent chicks from becoming chilled. If the hen was captured with the brood, she was held separately in a cotton laundry bag while chicks were individually marked with passive integrated transponder (PIT) tags. Appendix A (p. 173) provides a detailed description and an assessment of this marking procedure. Marked chicks were placed in the compartment of the plastic storage box opposite the chicks awaiting marking. Each chick's condition was assessed after implanting the tag and prior to release.

Releasing Marked Chicks

If hens were captured with the brood a soft release was attempted at the capture site. After chicks were marked, the hen was placed in 1 side of a 75 × 45 × 105-cm plastic opaque bisected release pen with a hinged release door that spanned the bisected halves on 1 end (Fig. 1). The marked chicks were transferred from the plastic storage box to the opposite side of the release pen so that a hen could not inadvertently injure its chicks. After allowing the hen and its brood to become calm, the release door was opened from a distance of approximately 25 m with a length of twine attached to the release door. The observer then exited the area to avoid disturbing the exiting hen and chicks. A few hours later, an observer returned to the release site to confirm that the hen and chicks had exited and to recover the release pen. Soft release attempts were considered successful when the hen and brood exited the holding pen without disturbance.

If the hen was not captured with the brood they were hard released near the hen. The hen's location was determined via telemetry. Marked chicks then were quickly taken to a site near it and 1 chick was allowed to emit a distress call to attract the hen's attention. Chicks then were placed on the ground, and the observers exited the area and monitored hen movements from a distance via telemetry.

Estimating Chick Survival

Data on the number of chicks in a brood were collected using flush counts (Hubbard et al. 1999). To estimate the number of chicks in a brood at a given time, an observer located the radio-marked hen with a brood, and approached it on foot until the hen flushed. After flushing the hen, the observer searched the flush area thoroughly until he felt that all chicks present had been located and flushed. If the observer could not find any chicks, the hen's reaction and approximate flush distance was noted and the information used to assess whether the brood may still have been present but hidden. Hens that allowed close approaches and flushed relatively short distances were assumed still to have chicks and flush counts were repeated at normal intervals. When chicks were detected in these later flush counts, the number of chicks flushed was used to update the previous count from 0. Similarly, when successive counts indicated an incomplete flush on a previous attempt, the number of chicks alive at the time of previous counts also were updated. Hens that flushed at long distances, flushed with other adult birds, or flew relatively long distances were categorized as having no chicks and later flush counts were used to confirm this. The number of chicks determined to be present at the time of flush counts was used to determine changes in brood size over time. For broods that were captured for marking during the first 14 days, flush counts began approximately 10 days

following marking and release of chicks. For broods that were not captured for marking, flush counts began approximately 14 days post-hatch. Flush counts were repeated at approximately 10-day intervals until the hen died, all chicks in a brood were assumed dead, or the brood was assumed to have broken up in fall.

Pre-fledge survival (period 1) and post-fledge survival (period 2) were defined as hatch to 14 days post-hatch and 14 to 60 days post-hatch, respectively. Although flush counts continued beyond the end of period 2, survival estimates were constrained to a shorter period because entire broods become increasingly difficult to flush as they gain some independence from the hen and begin to travel in a more widely spaced manner (Bowman and Robel 1977). Although lesser prairie-chicken broods probably do not break up until early September or at approximately 70 days of age, some hens abandon their broods prior to breakup (Bowman and Robel 1977, Taylor and Guthery 1980). The 60-day cutoff was chosen because chick survival was assumed to be independent from hen survival and hens may separate from the broods after this time.

Using data obtained during flush counts, daily survival rates of chicks in individual broods ($\hat{DSR}_i$s), and daily survival rates across all broods ($\hat{DSR}$) were estimated for each period using a Mayfield-type estimator (Mayfield 1975, Johnson 1979). Estimates of $\hat{DSR}$ are unaffected by dependence in survival among brood mates, but standard errors will be biased if dependence is ignored (Pollock et al. 1989, Flint et. al. 1995). Standard errors of overall chick survival therefore were adjusted for dependence among brood mates by weighting survival of chicks in individual broods by their total exposure days (Flint et al. 1995). Data were not sufficient to estimate $\hat{DSR}$ separately for each year so $\hat{DSR}_i$s were pooled across years. The number of chicks

assumed to have left the nest was used as the initial brood size for period 1. When initial brood size was unknown, $D\hat{S}R_i$ for period 1 could not be estimated and the brood was censored from the estimate of $D\hat{S}R$. However, $D\hat{S}R_i$ for period 2 was estimable for these broods (when ≥1 chick survived period 1) and they were included in the estimate of $D\hat{S}R$ for period 2. Thus, different sets of broods were used in the estimates of $D\hat{S}R$ for periods 1 and 2. Chicks that died due to capture or marking were censored from the brood and the exposure days adjusted accordingly. Survival for each period was estimated by raising $D\hat{S}R_i$ and $D\hat{S}R$ to the power of the period length in days (i.e., 14 and 46 for periods 1 and 2, respectively). Survival from hatch to 60 days was estimated as the product of period 1 and period 2 estimates. Approximate 95% confidence intervals for each period were calculated in the same manner using the lower and upper bounds of $D\hat{S}R$ (Flint et al. 1995). Confidence intervals for survival estimates from hatch to 60 days were calculated as the product of these bounds for periods 1 and 2. A Z-test was used to examine differences in $D\hat{S}R$s between periods (Johnson 1979).

For comparative purposes, chick survival also was estimated by comparing mean brood size in summer to mean clutch size of successful nests. A day in July was randomly selected and mean brood size was estimated from the actual number of chicks flushed during counts that occurred closest to the selected day.

Daily Movements and Survival

Distances between daily locations of hens with broods were used as brood movements. An index of brood movement was calculated as the mean distance between daily locations of the radio-marked hen with a brood. Separate indices were calculated

for survival periods 1 and 2. Relationships between movement indices and $D\hat{S}R_i$s for each period were examined using simple linear correlation analyses (Zar 1984).

Invertebrate Abundance and Survival

Invertebrates in brood habitats were sampled with sweepnets under a paired sampling design in 1998 and 1999 to estimate relative abundance of invertebrates in the habitats used by different broods (brood use areas). Invertebrates were sampled only during survival period 2 in 1998, and during survival periods 1 and 2 in 1999. A detailed description of invertebrate sampling methods is provided in Chapter 1. Acrididae and total invertebrate biomass collected in sweepnet samples were compared using simple linear correlation (Zar 1984) to determine if these 2 groups of invertebrates should be used separately in further analyses or if 1 group was sufficient. Invertebrate biomass in brood use areas was compared to $D\hat{S}R_i$s for each survival period using simple linear correlation. Invertebrate biomass collected in 1 brood use area July 1998 (brood 3198) was included in correlation analyses even though the sample was collected 69 days post-hatch (i.e., 9 days past the end of period 2). Spearman's rank correlation coefficients were calculated when data did not appear to be from a normal distribution (Zar 1984). All correlations were considered statistically significant when $P \leq 0.05$.

Dispersal of Marked Chicks

Distances between leks where PIT-tagged birds were recaptured and their hatch locations were used to estimate the effective distance of dispersal within the study area (Johnston 1961). Distances between leks where PIT-tagged birds were recaptured and their locations at 60 days post-hatch were used as estimates of minimum dispersal from summer brood range to place of breeding. These estimates were compared to distances

between recaptured birds' hatch locations and other known leks and their location at 60 days post-hatch and other known leks.

RESULTS

Eighty-five hens were captured and radio-marked during the 3 years of this study. Seventy-four nests of these hens were located and 19 were determined to have hatched. Clutch size of these hens ranged from 7 to 15 ($\bar{x}$ = 11.9) eggs. Nine of these 19 broods of radio-marked hens suffered complete losses of chicks during the first 14 days post-hatch and ≥1 chick was known to have survived past 60 days in only 6 broods. Means are presented ± 1 SE unless otherwise noted.

Capturing and Marking Chicks

Hens with broods were captured for chick marking an average of 7.2 ± 0.7 days after hatch confirmation. One hen that hatched a brood was killed by a predator before capture could be attempted. Fourteen attempts were made to capture hens with broods. Eight captures included both the hen and brood, 2 included the brood only, and 2 attempts failed completely (Table 1). Two hens hatched chicks but had no brood at time of capture; 1 was captured on its roost and the other flushed with another adult bird and no sign of a brood was found at the flush location. Average brood size (excluding incomplete counts and hens that no longer had chicks) at time of capture attempts was 7.09 ± 0.86 chicks (Table 1).

In the 10 successful capture attempts, 71 chicks were captured and 67 were marked and released. Five chicks died during capture and marking, or as a result of these procedures. Two chicks were accidentally killed during capture; 1 when a researcher knelt on the unseen chick and 1 when it became entangled in the capture net and was

struck by the hen's wing. Two died during the implant procedure, and 1 chick that was marked and released was found dead at the release site. This chick was assumed to have died as a result of the implantation based on its poor condition at release. The remaining 66 chicks showed no adverse effects from marking at the time of release (i.e., chicks were active and behaved as they had prior to implantation). Overall mortality of chicks caused by capture and marking was 7.0% (5 of 71).

Releasing Marked Chicks

All hens were eventually reunited with their marked chicks. Of the 8 broods captured with hens, 5 were successfully soft-released from the holding pen. On the first attempt of a soft-release, the observer returned to the release pen (without telemetry equipment) before the hen and brood had exited. This hen flushed a short distance and the observer exited the area to avoid further disturbance. One hen flushed from the holding pen when the observer opened the release door. In this instance the chicks were released from the holding pen and the pen was removed from the area. On another occasion, the twine used to open the release pen was forgotten and the chicks and hen were hard-released near the capture point; chicks were released first and the hen was allowed to make visual contact with them prior to its release. This hen flew approximately 100 to 150 m. Post-release monitoring of hens during unsuccessful soft-release attempts indicated that the hen had returned to the chicks at the release site within 30 minutes in all cases.

When broods were captured without the hen, the hen was either heard or seen near the location where chicks were hard-released. These hens returned to their broods within 30 minutes after the chicks were released.

Chick Survival Estimates

Overall daily chick survival was 0.941 (95% CI = 0.895 to 0.987) and 0.983 (95% CI = 0.933 to 1.032) for periods 1 and 2, respectively (Tables 2 and 3). No significant difference was detected between $D\hat{S}R$s for periods 1 and 2 ($z = 0.876$, $P = 0.191$), but the null hypothesis of equal survival rates during these 2 periods was not accepted. Overall chick survival for period 1 was 0.425 (95% CI = 0.212 to 0.832) and was 0.448 (95% CI = 0.380 to 1.559) for period 2. Chick survival from hatch to 60 days (survival for period 1 × survival for period 2) was 0.190 (95% CI = 0.079 to 1.301). Mean brood size estimated from actual flush counts of 6 broods alive near 20 July was 3.67 ± 1.02. This represents an apparent chick survival rate of 0.31.

Daily Movements and Survival

Indices of daily brood movements ranged from 195 to 434 m ($\bar{x}$ = 248 ± 17, n = 14) and from 186 to 658 m ($\bar{x}$ = 320 ± 57, n = 8) for periods 1 and 2, respectively. Although r_s was negative as predicted, no statistically significant correlations were detected between $D\hat{S}R_i$s and movement indices for period 1 or period 2 (Table 4).

Invertebrate Abundance and Survival

Total invertebrate biomass was highly dependent upon Acrididae biomass in both period 1(June samples, 1999, $r = 0.969$, $P \leq 0.001$, $n = 7$) and period 2 (July samples, 1998 and 1999, $r = 0.990$, $P \leq 0.001$, $n = 7$) so only total invertebrate biomass from brood use areas was used as an index of the amount of invertebrate biomass present in brood use areas. Total invertebrate biomass collected in sweepnet samples in brood use areas during period 1 ranged from 1.25 to 5.66 g ($\bar{x}$ = 3.63 ± 0.58, n =7) and from 3.78 to

13.57 g ($\bar{x}$ = 8.09 ± 1.37, n = 7) for period 2. Correlation coefficients (r_s) were positive as predicted but no statistically significant correlation was detected between $D\hat{S}R_i$s and total invertebrate biomass for period 1 or period 2 (Table 4). The correlation (r) between movement indices and total invertebrate biomass in brood use areas was negative but also not statistically significant (Table 4).

Dispersal of Marked Chicks

Of the 66 lesser prairie-chickens PIT tagged as chicks, 15 chicks from 5 broods were assumed to have survived to 60 days post-hatch based on flush count data. Nine of these chicks from 4 broods were on the primary study area. Two PIT-tagged males from separate broods were recaptured at leks. One, bird 551E from brood 3198, was captured the spring following marking at a lek 2334 m from the nest location and 1078 m from its brood range (Fig. 2). The other, bird 2B30 from brood 3163, was captured the fall after marking at the same lek as bird 551E. This lek was 2203 m from 2B30's hatching location and 2882 m from its brood range (Fig. 2). No other PIT-tagged lesser prairie-chicken was recaptured. At least 4 known leks were closer to both bird 551E and 2B30's hatch locations than the lek where they were recaptured. One known lek was closer to 551E's location at 60 days post-hatch and 5 were closer to 2B30's location at 60 days post-hatch than the lek where they were recaptured (Fig. 2). However, trapping effort was not equal among all known leks. Trapping was conducted on the 4 leks closest to 551E's hatching location and the 1 lek closest to its summer brood range during the period when he was recaptured. None of the 4 leks nearest 2B30's hatching location and only 1 of 5 leks closest to its summer brood range was trapped during the period when he was recaptured.

DISCUSSION

Few published reports are available for survival rates of lesser prairie-chicken chicks. Schwilling (1955) reported an average brood size of 3.27 chicks for 11 broods observed in July and August in southwestern Kansas. Average brood sizes of lesser prairie-chickens in Oklahoma in summer and early fall ranged from 5.2 to 7.5 over 4 years (Davison 1940). Later studies in Oklahoma documented summer brood sizes of 5.7 to 7.8 chicks (Copelin 1963, Merchant 1982). However, Copelin (1963) documented substantial brood mixing during his study and suggested that the brood sizes he observed actually represented 1 to 3 rather than individual broods. Assuming an average clutch size of 12 eggs, these values represent chick survival estimates of 0.27, 0.43 to 0.63, and 0.48 to 0.65, respectively.

These estimates of lesser prairie-chicken chick survival are higher than the estimated survival rate of 0.19 in this study. These differences are most likely due to the inability of previous studies to account for complete losses of broods and simultaneous inclusion of mixed broods in estimates of chick survival from brood size. Many broods in the present study suffered complete losses and failure to account for these losses would have resulted in overestimation of survival rates of lesser prairie-chicken chicks. Estimates of chick survival from brood size in late summer probably are useful for assessing variation in chick survival across years, but they may overestimate actual survival rates when early and complete losses are common. The apparent survival estimate from mean brood size in July in this study was 12 percentage points higher (0.31 vs. 0.19) than that obtained using the Mayfield-type estimator.

Brood mixing apparently is common when hens with broods gather under shinnery oak (*Quercus havardii*) motts during hot, dry weather (Copelin 1963). Hens with broods are probably spaced more widely in sand sagebrush habitats than shinnery oak habitats because sagebrush is more widely scattered throughout the habitat than are shinnery oak motts. Assuming that the resource provided by the oak motts was shade, as Copelin (1963) suggested, the spatial distribution of that resource in sand sagebrush habitats would not encourage brood mixing. Brood mixing was documented on only 1 occasion in the present study and, although the Mayfield survival estimator used here can account for brood mixing, this brood was censored from the estimates for other reasons.

Chicks are difficult to locate and flush in sagebrush habitats (Schwilling 1955). Consequently, increases in brood size during successive counts in this study were assumed to represent incomplete flushes on previous counts rather than actual increases in brood size due to adoption of chicks or mixing of broods. For purposes of chick survival estimation in this study, brood mixing and adoption was assumed not to occur because flush counts exceeded initial brood size on only 1 occasion. If undetected brood mixing occurred to any great degree, the estimates of chick survival would be biased low because early flush counts were updated based on later ones. This would increase the estimated number of exposure days thereby lowering the survival estimate. Additionally, if brood adoption occurred, adopted chicks were assumed dead when they actually had survived. This again would result in negative bias in the survival estimates. However, based on field observations, it is highly unlikely that brood mixing occurred to such an extent that it would have significant impact on the present survival estimates. Brood sizes obtained from flush counts are probably biased low (Godfrey 1975) therefore

leading to underestimates of daily survival. Updating early flush counts may have minimized this negative bias in this study.

Many researchers have linked survival of gallinaceous chicks to the abundance and availability of high protein invertebrate biomass (Southwood and Cross 1969, Erikstad 1985, Hill 1985, Rands 1985, Johnson and Boyce 1990, Griffon et al. 1997). Lesser prairie-chicken chicks utilize invertebrates heavily during summer and early fall (Schwilling 1955; Jones 1963*a*, *b*, 1964). Survival of lesser prairie-chicken chicks in southwestern Kansas also may be related to invertebrate abundance, but if present, this relationship was not detected in the present study. Important variation in the relationships between brood survival and invertebrate abundance may occur across years, but sample sizes in this study were small even after pooling the data from the 2 years in which invertebrates were sampled in brood use areas. Data simply were not sufficient to perform separate analyses for each year.

Erikstad (1985) documented a negative relationship between survival of willow grouse chicks and distance traveled. Although results of the correlation between movements and survival in this study failed to reveal such a pattern, it would be unwise to conclude that such a pattern does not exist based upon such limited data. However, if such a pattern exists for prairie grouse, it has not yet been documented. Prairie-chicken populations appear to be negatively affected by drought (Scwhilling 1955, Horak 1985), and Copelin (1963) noted increased brood movements during hot, dry weather. If movements negatively affect brood survival this could be 1 mechanism by which drought affects populations.

As summarized by Bergerud and Gratson (1988:612), Barrett (1970) and Erikstad (1978) found that movements of grouse broods were negatively correlated with the abundance of available invertebrates. Results of this study failed to reveal any clear association between movements and invertebrate biomass but, again, concluding that these 2 variables are unrelated would be fatuous.

Hamerstrom and Hamerstrom (1973) marked 162 greater prairie-chicken chicks with wing tags over a 10-year period and subsequently recovered (recaptured or documented hunter kills of) 17 of these. None of these chicks, that later proved to be males, was recovered more than 7400 m from the nest where they had hatched. These movements of male greater prairie-chickens are greater than those documented for recaptured lesser prairie-chicken males in the present study. However, the distances reported for greater prairie-chickens are not distances to leks but are distances to feeding areas in cultivated fields where the birds were trapped or harvested. The leks where those males eventually established territories may actually have been closer to the hatch location than those feeding areas. However, when the winter-trapped birds were resighted on leks in spring, their movements from winter trapping location to leks in spring were combined with other winter-trapped birds. Thus, it is not possible to determine the effective distance of dispersal for those males marked as chicks from their report. Copelin (1963) relocated 14 lesser prairie-chickens that he had marked as 4 to 14-week-old chicks. They had moved from 800 to 4640 m from their capture locations as chicks. Neither the sexes nor the hatch locations of these birds were contained in his report. If we assume that the hatch location was relatively close to the location where

those chicks were marked, the estimates of dispersal distance documented in the present study are similar.

Estimates of dispersal distance are most meaningful when compared to distances from the hatch site and brood range to other leks. Copelin (1963) noted that none of the 14 birds marked as chicks in his study was relocated at the lek nearest their capture location. Results of this study are similar and suggest that males do not simply compete for territories at the lek closest to where they were hatched or reared. It is interesting to note that the lek where both of the PIT-tagged males were recaptured was 1 of the largest known leks (attended by the most males) on the study area. This may suggest that juvenile males choose leks based on lek size. However, this is speculation rather than a conclusion, because only 2 chicks were recaptured and trapping effort was not equal at all known leks.

MANAGEMENT IMPLICATIONS

Chick survival is low and complete losses of chicks may occur in nearly 50% of lesser prairie-chicken broods prior to fledge. Estimates of chick survival from sizes of unidentifiable broods during summer or early fall probably are biased high. Future research should strive to obtain data that are sufficient to examine annual variation in chick survival, and to determine cause-specific mortality of chicks. These efforts should consider conducting counts at night rather than daylight flush counts to minimize count bias (Bowman and Robel 1977), and to document the extent of brood mixing in sand sagebrush habitats.

Dispersal of male lesser prairie-chickens from hatch locations and brood ranges to leks appears relatively short and independent of the proximity to leks within a habitat fragment. If large leks are more likely to attract dispersing juveniles, this positive feedback may contribute to greater persistence of large versus small leks. Processes determining lek selection by juvenile males are not understood.

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Table 1. Attempts to capture lesser prairie-chicken hens with broods in southwestern Kansas, 1997 through 1999.

Year and brood ID #	Capture attempted	Hen captured	Chicks captured	Chicks detected	Chicks marked and released
1997					
3159	No				
3277	Yes	No	0	6	
1998					
3038	Yes	No	0	≥1	
3737	Yes	Yes	0	0	
3198	Yes	Yes	7	7	7
3232	Yes	No	6	6	6
3299	No				
3398	Yes	No	1	1	1
3870	No				
1999					
3163	Yes	Yes	9	9	8
3941	Yes	Yes	9	9	8
4111	Yes	Yes	4	5	4
3881	No				
3951	Yes	Yes	8	8	6
3430	Yes	Yes	12	12	12
3114	No				
3600	Yes	Yes	6	6	6
3859	Yes	Yes	9	9	9
3280	No				
Total	14	9[a]	71	78[b]	67

[a] Includes 1 hen that hatched chicks and was captured, but no longer had a brood

[b] Minimum total number of chicks; assumes that brood 3038 contained only 1 chick

Table 2. Mayfield estimates of daily chick survival, timing of event dates, and number of actual counts (flush counts and counts during capture attempts) to 14 days post-hatch for 13 lesser prairie-chicken broods in southwestern Kansas, 1997 - 1999.

Year & brood ID #	Initial brood size[a]	Event days (DPH)[b]	Actual counts	ΔBS_i[c]	EXP_i[d]	$D\hat{S}R_i$[e]	$D\hat{S}R_i^{14}$
1997							
3159	6		1	0	84.0	1.000	1.000
1998							
3038	3	5	1	3	15.0	0.800	0.044
3737	5	3	1	5	15.0	0.667	0.003
3198	7	9	1	3	72.0	0.958	0.551
3232	7	3, 11	1	5	72.0	0.931	0.365
3299	7	1	0[f]	7	7.0	0.000	0.000
3398	8	3	1	8	33.5	0.761	0.022
3870	8	5.5	1	8	44.0	0.818	0.060
1999							
3941	9	12.5	1	2	120.0	0.983	0.790
4111	6	4.5	1	1	69.5	0.986	0.816
3881	8		1	0	112.0	1.000	1.000
3430	12		1	0	168.0	1.000	1.000
3600	11	3, 11	2	11	81.0	0.864	0.130
			Total	53	893.0	0.941	0.425

[a] Initial brood size is number of chicks assumed to have left the nest

[b] Time (days post-hatch) of event dates

[c] Change in number of chicks from initial brood size during first 14 days post hatch

[d] Total chicks exposure days assuming event days occurred at mid-point between actual counts

[e] $D\hat{S}R_i = 1 - \frac{\Delta BS_i}{EXP_i}$.

[f] Hen movements indicated brood had not survived

Table 3. Mayfield estimates of daily chick survival, timing of event dates, and number of actual counts (flush counts) from 14 to 60 days post-hatch for 9 lesser prairie-chicken broods in southwestern Kansas, 1997 - 1999.

Year & Brood ID #	Initial brood size[a]	Event days (DPH)[b]	Actual counts	ΔBS_i[c]	EXP_i[d]	$D\hat{S}R_i$[e]	$D\hat{S}R_i^{46}$
1997							
3159	6	18, 46	4	6	164.0	0.963	0.180
1998							
3198	3		4	0	138.0	1.000	1.000
3232	1		4	0	46.0	1.000	1.000
1999							
3951	1	32.5	3	1	18.5	0.946	0.078
3941	6		5	0	276.0	1.000	1.000
4111	4		5	0	184.0	1.000	1.000
3881	8	58	3	1	366.0	0.997	0.882
3430	9	25	3	9	99.0	0.909	0.012
3163	8	15.5, 55	5	7	96.0	0.927	0.031
			Total	24	1387.5	0.983	0.448

[a] Initial brood size is number of chicks assumed to have survived first 14 days post-hatch

[b] Time (days post-hatch) of event dates

[c] Change in number of chicks from initial brood size during 14 to 60 days post-hatch

[d] Total chicks exposure days assuming event days occurred at mid-point between actual counts

[e] $D\hat{S}R_i = 1 - \frac{\Delta BS_i}{EXP_i}$.

Table 4. Correlations between daily brood movements (M) and invertebrate biomass collected in brood use areas (IB), M and daily survival rates of chicks in individual broods ($D\hat{S}R_i$s), and IB and $D\hat{S}R_i$s for 2 survival periods, hatch to 14 days old (Period 1) and 14 to 60 days old (Period 2), for lesser prairie-chickens in southwestern Kansas, 1997-1999.

Variables and Period	n	r_s	P[a]
M vs. IB			
Period 1	7	-0.292	0.263[b]
Period 2	2	-1.000	
M vs. $D\hat{S}R_i$s			
Period 1	7	-0.185	0.346
Period 2	8	-0.146	0.365
IB vs. $D\hat{S}R_i$s			
Period 1	3	0.500	0.334
Period 2	6	0.638	0.087

[a] P-value is for 1-tailed test

[b] Pearson correlation coefficient and associated P-value

Figure 1. Dimensions and design of a plastic opaque, bisected pen for soft-release of lesser prairie-chicken broods and hens. (A) is all-thread bent into an inverted "L" shape with an eyelet attached to the end. Twine (passed through the eyelet and attached to the lower part of the release door [D]) permitted opening the door from a distance. (B) is the opening used to introduce marked chicks to the release pen and (C) represents the 1-cm mesh nylon netting separating the 2 halves of the pen. Netting allowed a hen on the opposite side to make visual and auditory contact with the brood, but prevented the hen from inadvertently injuring the chicks.

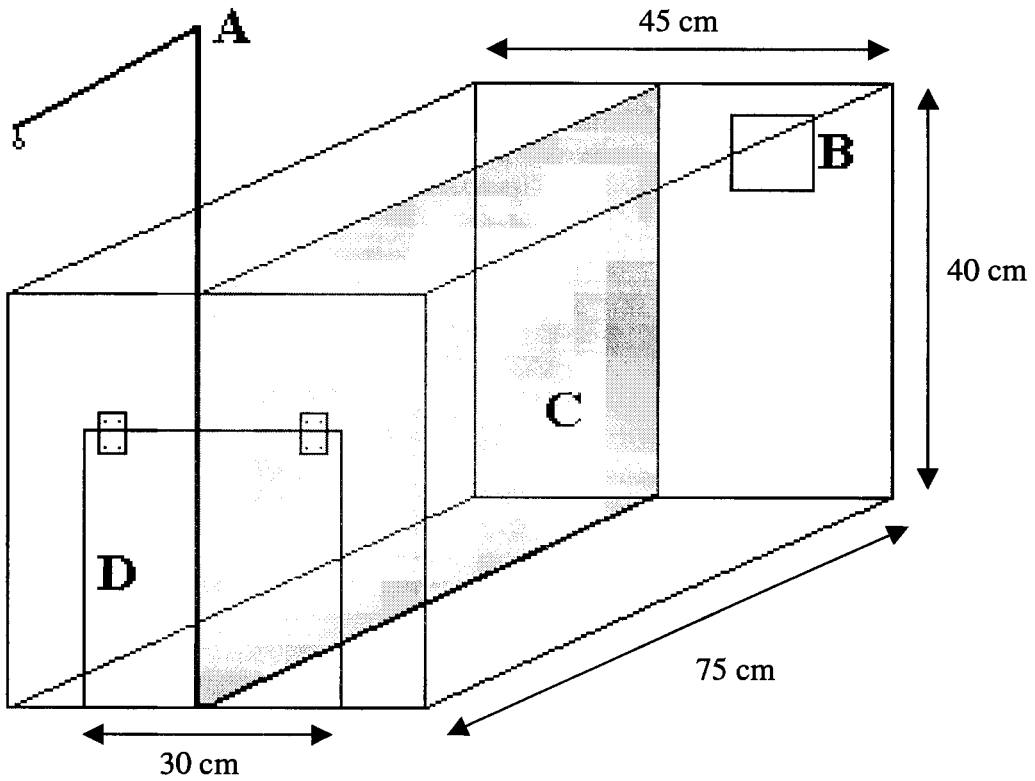
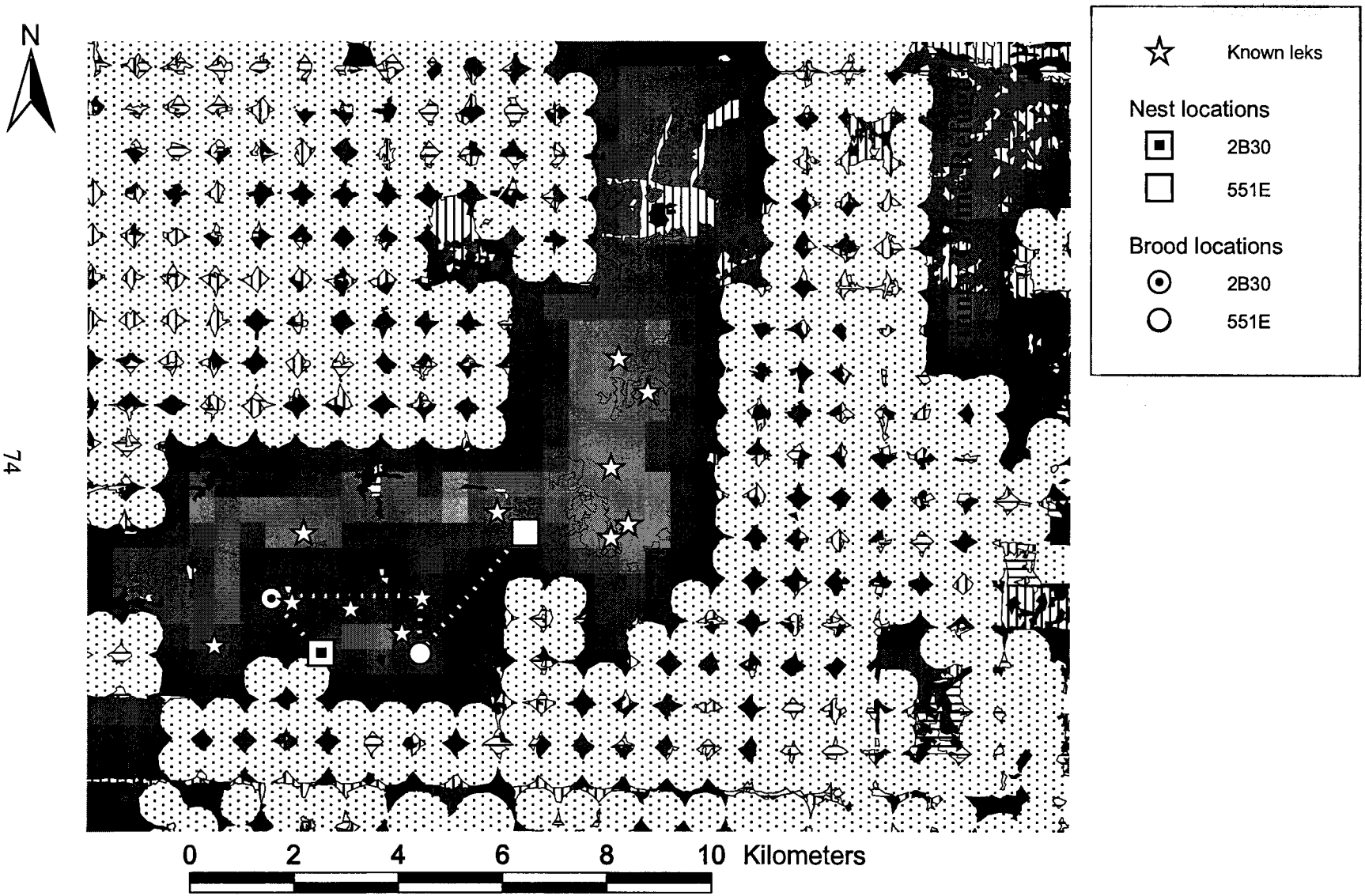

A
45 cm
B
40 cm
C
D
75 cm
30 cm

Figure 2. Nest locations (hatch locations) and locations of chicks 60 days post-hatch (brood locations) for 2 lesser prairie-chickens marked as chicks and recaptured at leks in southwestern Kansas, 1997 to 1999. Chick 551E was from brood 3198 and chick 22B30 was from brood 3160.


N
Known leks
Nest locations
2B30
551E
Brood locations
2B30
551E
0
2
4
6
8
10 Kilometers

POTENTIAL DEPREDATORS OF LESSER PRAIRIE-CHICKEN NESTS IN SOUTHWESTERN KANSAS

Abstract: Depredation is the primary cause of nest failure in prairie grouse. Predator species that depredate nests must be identified to guide management, because different predator species may be affected differently by the same management practice. Potential and likely predators responsible for depredation of lesser prairie-chicken nests were identified from their relative abundance, an artificial egg study, and the condition of egg remains and other information collected at depredated nests. Mammalian predators were more abundant than potential avian or reptilian predators and were the cause of most nest failures. Coyotes (*Canis latrans*) appear to be the primary depredator of lesser prairie-chicken nests in southwestern Kansas. Habitat management practices that reduce mammal densities, especially coyotes, or decrease their ability to locate nests are expected to decrease nest depredation rates.

Key words: coyotes, *Canis latrans*, depredation, Kansas, lesser prairie-chicken, nests, predators, *Tympanuchus pallidicinctus*

INTRODUCTION

It is well accepted that depredation is the primary cause of nest failure in birds (Ricklefs 1969) and nest losses of grassland birds often exceed 50% (Best et al. 1997). Grouse populations are limited by breeding success (Bergerud and Gratson 1988, Peterson and Silvy 1996) and prairie grouse often suffer high rates of nest depredation (Ammann 1957, Schroeder and Robb 1993, Riley et al. 1992).

Species responsible for nest depredation must be documented to understand how management practices affect nest depredation rates. Management practices targeted at reducing depredation pressure when primary predators have been misidentified could be both financially and ecologically costly. The objective of this study was to identify the potential and likely depredators of lesser prairie-chicken nests in southwestern Kansas.

STUDY AREA

The primary study area was a 5,760-ha fragment of sand sagebrush rangeland immediately south of the Arkansas River in western Finney County of southwestern Kansas. The area was vegetated primarily by sand sagebrush, blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), paspalum (*Paspalum* sp.), bluestem grasses (*Andropogon* spp.), western ragweed (*Ambrosia psilostachya*), sunflowers (*Helianthus* spp.), and Russian-thistle (*Salsola iberica*). Prickly pear cactus (*Opuntia* sp.) and yucca (soapweed) (*Yucca glauca*) were interspersed throughout. Buffalo-gourd (*Cucurbita foetidissima*) and purple poppy mallow (*Callirhoe* sp.) were common in disturbed areas. Soils were in the Tivoli-Vona association and in the choppy sands range site category (U. S. Department of Agriculture 1965). Primary land uses were grazing by cattle (from May 1 through October 1) and petroleum production. Research also was conducted in sand sagebrush prairie fragments separated from the primary study area by cultivated fields. Vegetation and soils were similar in these other fragments but contained some sand plum (*Prunus angustifolia*) thickets in addition to sand sagebrush.

Over the past 30 years, the area received an average of 50 cm of annual precipitation with 74 % occurring between March and August. During this study (1997

through 1999) the area received an average of 55 cm of precipitation annually (U. S. Department of Commerce 1999).

METHODS

Lesser prairie-chicken hens were captured on leks in spring from 1997 to 1999 using walk-in traps (Haukos et al. 1990). Hens were radio-marked with 12-g necklace transmitters and monitored daily until they nested. Nest sites were marked with wire flags, flagging tape, or radio transmitter beacons on the initial visit. Nesting hens were monitored daily via telemetry until the nest hatched or failed. Infrequent visits were made to nests in 1997 to record their status (e.g., number of eggs) or to place artificial eggs in them (see below). Nest visits in 1998 and 1999 were reduced to a minimum. Nests were revisited to replace malfunctioning radio transmitter markers, determine final clutch sizes of nests initially visited during laying, or to determine the status of nests from which the hen was absent. A final visit was made (usually within 1 day) after nests had succeeded or failed to document the condition of nest remains.

Identifying Potential Nest Predators

The potential for different animals to depredate lesser prairie-chicken nests was evaluated based on their relative abundance on the study area, their perceived ability to consume eggs, an artificial egg study, and the condition of nest remains following depredation events. In this paper, predator refers to a particular species and depredator to those that potentially destroyed nests.

Relative abundance.--Sightings of avian, mammalian, and reptilian predators that could depredate lesser prairie-chicken nests was noted while conducting routine field

work. Field work was done primarily during the day but also during several night-trapping sessions as part of a side project in 1997 and 1998. Any animal sighted on the study area or adjacent cultivated land and large enough to break the shells of lesser prairie-chicken eggs was considered a potential nest depredator. To describe the apparent spatial distribution of the more common predators, they were categorized as "localized" or "scattered." These designations are necessarily qualitative and are used only to distinguish between species that were seen in few places, but regularly, and those that were regularly seen on all parts of the study area, respectively. The capability of these animals to depredate nests was categorized as low, moderate, or high based on reports in the literature. When no published information was available, the author's perception of their capability destroy eggs was used as the basis for this categorization. These assessments relied primarily on the size of individuals encountered in the field.

Clay eggs.--In an effort to record beak or tooth imprints of predators when they depredated nests, 1 artificial egg was placed in each of a sample of active lesser prairie-chicken nests during 1997 (Møller 1989, Major 1991). Different colors of Plastilina® non-hardening modeling clay were mixed and formed to approximate the color and size of lesser prairie-chicken eggs. The clay egg then was coated with pulverized vegetation or corn starch to reduce the tackiness of its surface and minimize surface-area contact with real eggs in the nest. Corn starch was mixed with the clay of some eggs to make the clay eggs more firm and potentially more resistant to high temperatures. Latex gloves were worn during clay mixing, artificial egg creation, and egg placement in nests to minimize contamination with human scent (Small and Hunter 1988). Clay eggs were placed in active nests during the laying or incubation period.

Nest remains.--Areas within a 5- to 10-m radius of depredated nests were searched for egg shells and additional signs (e.g., mammal tracks, fur, feces, etc.) that would indicate predator type. Remains of eggs at depredated nests were examined to gather evidence for determining potential predators. Condition of egg shells and their locations relative to the nest often were noted. A sample of egg shells collected at depredated nests was sent to the U. S. Geological Survey's Northern Prairie Wildlife Research Center (Northern Prairie) in North Dakota for evaluation. Because many predators show similar patterns of nest depredation (Sargeant et al. 1998, Larivière 1999), the evidence found at nests was used in conjunction with the relative abundance of predator sightings to determine potential and likely nest predators. Additional information, such as whether the hen was killed on the nest and whether partial depredation of clutches occurred, also was used to deduce potential predators.

RESULTS

Over the 3 years of this study, 74 nests of radio-marked lesser prairie-chickens were located. Fifty-five of these failed and 47 (85%) of the failed nests were known to be depredated. Of those nests that eventually were depredated, 1 to 3 (*mode* = 2) visits were made to them while they were active in 1997and 1 to 2 (*mode* = 1) were made in 1998 and 1999. Final visits following nest failures were made up to 2 days after depredation events but most (43 of 47) were within 1 day.

Relative Abundance of Predators

Few species of avian and reptilian predators that could prey upon nests were observed on the study area, but mammalian predators were common. Black-billed

magpies (*Pica pica*) sometimes constructed their nests in old center-pivot irrigation equipment at the edges of crop fields, in natural gas well structures, or trees and often were seen at these locations. Three such nests were present on the primary study area and 2 of these in areas frequented by lesser prairie-chickens. Western meadowlarks (*Sturnella neglecta*) were abundant throughout the study area and common grackles (*Quiscalus quiscula*) sometimes nested in natural gas well structures and subsequently were seen near these. Neither American crows (*Corvus brachyrhynchos*) nor Chihuahuan ravens (*C. cryptoleucus*) ever were seen on or near the study area during the nesting period.

Bullsnakes (*Pituophis catenifer sayi*) often were seen as they crossed roads within the study area. Other species of snakes sighted were hognose snakes (*Heterodon nasicus*), coachwhips (*Masticophis flagellum*), milk snakes (*Lampropeltis triangulum*), and western prairie rattlesnakes (*Crotalus viridis*).

Coyotes, American badgers (*Taxidea taxus*), striped skunks (*Mephitis mephitis*), and ground squirrels (*Spermophilus* spp.) were the most abundant mammalian predators. Coyotes seemingly were ubiquitous on the study area and were heard howling nearly every morning and evening. They often were seen on the study area and also were seen hunting in freshly cut alfalfa fields adjacent to the primary study area. American badgers were sighted less frequently; about 6 times throughout the course of 3 summers. Striped skunks apparently were less abundant than American badgers; only 3 were sighted during the study. Two weasels (*Mustela frenata*) were seen crossing roads; 1 on the primary study area and 1 in adjacent cultivated fields. Spotted ground squirrels (*Spermophilus*

spilosoma) and thirteen-lined ground squirrels (S. *tridecemlineatus*) commonly were seen along roads and within black-tailed prairie-dog (*Cynomys ludovicianus*) towns (Table 1).

Clay Eggs

One artificial egg was placed in each of 16 lesser prairie-chicken nests in 1997, and 12 of these nests were depredated. Few data were obtained from artificial eggs. Two clay eggs recorded evidence of mammalian predators; 1 was found with tooth imprints and a small piece of clay was all that remained of the second. The tooth imprints were not sufficiently distinct to allow positive identification of the predator, but it is speculated that they were those of a coyote based on the size of molar marks. Clay eggs were noted missing from 3 nests prior to the event date (the date the nest hatched or failed) and 5 were missing on the event date (Table 2). One clay egg was found flattened and depressed to the bottom of the nest bowl.

Nest Remains

A specific pattern of nest depredation developed over the course of this study. Egg shells broken open on 1 side were found within 10 m of 28 (60%) of the depredated nests. The size and shape of the holes varied but most were approximately 2.0 to 2.5 cm in diameter (Fig. 1). Egg contents always were completely removed. Personnel at Northern Prairie determined that likely predators were striped skunks or coyotes. Eggs were depredated in this manner on 3 of the 5 occasions when a mammalian predator had killed the incubating hen.

The condition of egg shells at 11 nests was recorded as "crushed" or "chewed" and 6 nests were empty. No data on the condition of shells were recorded for the remaining 2 depredated nests. The nest lining was disturbed at 1 depredated nest. Partial

losses of clutches prior to hatch or failure were noted for 3 nests, but the limited number of nest visits precluded documentation of potential partial losses from most nests. Most depredated clutches appeared to have been destroyed during a single depredation event because recovered egg shells appeared to be of the same age, and hens probably removed damaged eggs from nests following partial clutch destruction (Lariviére 1999). Tracks of coyotes were noted at 4 nests. Post-depredation contents of these nests varied; 1 contained crushed shells, 1 contained shells broken open on the side as described above, and 2 were empty. No other mammal tracks were noted at depredated nests, but tracks of small species (e.g., ground squirrels) could easily have been overlooked and vegetation at nests sites often could have prevented even large animals from leaving tracks.

DISCUSSION

Riley et al. (1992) found that 17 of 26 (65%) lesser prairie-chicken nests studied in New Mexico were destroyed by predators. The proportion of unsuccessful nests destroyed by predators in this study was 20% higher. No additional published studies have attempted to determine specific causes of nest failure in lesser prairie-chickens. Giesen (1998) listed Chihuahuan raven, coyote, American badger, striped skunk, spotted ground squirrel, and bullsnake as nest depredators but no published references were provided .

Artificial egg experiments were not as effective as anticipated. Initially, when clay eggs were noted missing following a depredation event, it was thought that a predator had consumed the egg. However, because clay eggs were displaced from nests during incubation it is suggested that lesser prairie-chicken hens may recognize these

artificial eggs as foreign objects and subsequently remove them. Some birds recognize artificial eggs or eggs of other species (e.g., brood parasites) and have developed simple or elaborate ways to contend with these perceived threats (Rothstein 1971). This may be the first report of grouse rejecting artificial eggs. During this study, ring-necked pheasant (*Phasianus colchicus*) eggs were found in 3 lesser prairie-chicken nests, but hens did not remove them. Hens apparently were able to distinguish between clay eggs and their own but not pheasant eggs and their own. The non-hardening clay used to construct artificial eggs in this study is soft at room temperature and becomes softer as its temperature increases. If the clay eggs softened as a result of high ambient temperatures or under the heat of an incubating hen, this may have facilitated the hens' ability to recognize them. Most researchers that have used artificial eggs have placed them in artificial nests (Major and Kendall 1996, Major 1991, Major et al. 1994, Picman 1987) and thus did not face potential egg rejection.

Sightings of predators in this study likely were biased toward those species that are diurnal and most visible (Seber 1973). Red foxes (*Vulpes vulpes*), swift foxes (*Vulpes velox*), bobcats (*Felis rufus*) never were sighted on study areas, and it is doubtful that these species were present in sufficient numbers to depredate a significant proportion of lesser prairie-chicken nests. Furthermore, coyotes may directly limit the abundance of swift and red foxes (Sovada et al. 1998, Thacker and Flinders 1999). Objective methods of determining relative abundance of predators obviously are desirable, but even structured predator surveys may yield questionable results (Havens and Sharp 1998). For purposes of this study, the categorization of predators by perceived relative abundance appears sufficient.

Coyotes commonly depredate waterfowl nests and are the suspected depredators of many grouse nests (Bowen et al. 1976, Riley et al. 1992, Sargeant et al. 1998). The pattern of depredation exhibited by coyotes is highly variable (Sargeant et al. 1998). The variability in the pattern of nest depredation observed in this study is explainable even if coyotes are assumed to be the only depredator. Although the pattern of depredation certainly does not exclude other predator species, the relative abundance of coyotes, mammalian predation of nesting hens, complete destruction of clutches, tracks found at depredated nests, and the suggestions of Northern Prairie personnel indicate that coyotes probably were the most common nest depredators in this study.

Ground squirrels have been documented depredating passerine, waterfowl, and grouse eggs (Patterson 1952, Sargeant et al. 1987, With 1994, Pietz and Granfors 2000). Schwilling (1955:62) stated that spotted ground squirrels were "probably the most serious predator due to [their] relative abundance", and that they prey on "nests and young." However, Schwilling (1955) provided no data to support this claim. Richardson's ground squirrels (*Spermophilus richardsonii*), thirteen-lined ground squirrels, and American badgers were thought to be the primary predator of sage grouse (*Centrocercus urophasianus*) nests at 2 study sites in Wyoming but little direct evidence was provided (Patterson 1952). Patterson (1952) described a pattern of depredation similar to that noted in this study but reported sighting coyotes only twice, implicating ground squirrels for the damage. Observations made by a game warden in Wyoming who watched what apparently was an Uinta ground squirrel (*S. armatus*) depredating a sage grouse nest were cited as support for Patterson's (1952) conclusion, but the ability to consume eggs or depredate nests varies among species of ground squirrels (Larivière 1999). Richardson's

ground squirrels are larger than thirteen-lined ground squirrels and thus may be more capable predators of grouse eggs. However, when Sargeant et al. (1987) placed 2 mallard (*Anas platyrhynchos*) or blue-winged teal (*A. discors*) eggs in simulated nests near Richardson's and thirteen-lined ground squirrels 104 and 54 times, respectively, these species never depredated these duck eggs whereas the larger Franklin's ground squirrel (*S. franklinii*) preyed upon them nearly 97% of the time. Blue-winged teal eggs are only slightly larger than eggs of lesser prairie-chickens (47 × 34 mm vs. 42 × 31 mm) (Bellrose 1976, Giesen 1998). Ground squirrel behavior and egg destruction capability may vary geographically, but the species of ground squirrels observed during this study do not appear able to depredate eggs larger than those of passerines.

Striped skunks commonly are thought to be important predators of nests of ground-nesting birds (Bowen et al. 1976, Sargeant et al. 1998) and the pattern of depredation in this study easily could suggest skunks as the predator (Larivière and Messier 1997), however, the infrequency of skunk sightings does not indicate that they were the primary depredator in the present study. Although weasels were sighted nearly as often as skunks, they are considered extremely rare due to their preference for more mesic environments (Schwartz and Schwartz 1981:295).

Corvids often are implicated in the destruction of passerine (Picman 1987) and grouse nests (Andrén et al. 1985, Bowen et al. 1976). The relative abundance and distribution of black-billed magpies on study areas, and the pattern of nest depredation, suggests that they were not major predators. Western meadowlarks and common grackles are known to destroy eggs of passerines (Creighton and Porter 1974, Peer and Bollinger 1997), but it is not clear whether they are able to (or if they even would attempt

to) break the thicker shells of lesser prairie-chicken eggs. Additionally, they probably are not capable of total clutch destruction, and nesting hens likely would be able to defend their nests from such small birds if they attempted to depredate nests while the hen was in attendance.

Snakes are important predators of grassland passerine nests and young (Zimmerman 1984, Cavitt 1998), but snakes probably did not play a major role in destruction of lesser prairie-chicken nests. Snakes consume entire eggs; the eggs are swallowed whole and then crushed by contraction of neck muscles (Stebbens 1954:336). This foraging pattern is not consistent with the majority of depredation events in this study, but bullsnakes may be responsible for partial clutch losses and the depredation events where no egg remains were found at nest sites. The relative abundance and predatory capability of other snake species suggests they did not depredate a significant proportion of lesser prairie-chicken nests in this study.

Coyotes, striped skunks, and bullsnakes probably were responsible for nearly all lesser prairie-chicken nest depredation, but a lack of substantial evidence in favor of other predator species suggests coyotes are the primary nest depredators in southwestern Kansas. Without objective methods of obtaining data on depredation events, other species cannot be excluded from consideration.

MANAGEMENT IMPLICATIONS

Most nest failure of lesser prairie-chickens in southwestern Kansas is due to depredation, and mammalian predators were responsible for a majority of depredation events. Habitat manipulations that reduce mammal populations or impede discovery of

nests by them probably would decrease nest depredation rates (Riley et al. 1992, Giesen 1994).

Experimental tests of the predatory ability of thirteen-lined and spotted ground squirrels should be conducted in the laboratory and in situ to confirm the conclusion that they are not capable of destroying lesser prairie-chicken eggs. Researchers attempting to identify specific predators should consider the problems encountered in this study when artificial eggs were placed in active lesser prairie-chicken nests. Artificial eggs that are resistant to heat and that mimic lesser prairie-chicken eggs more closely may be more effective. Other, more objective methods are recommended to confirm that coyotes are the primary mammalian predator and to determine if other species contribute to depredation losses. Time-lapse video taping (Pietz and Granfors 2000) currently is cost-prohibitive and presence of camera equipment in the sparse vegetation in southwestern Kansas may influence results by attracting or repelling predators (Hernandez et al. 1997). Lethal methods of determining nest predators (e.g., toxicant-laced eggs) should not be ruled out if specific predator species are to be identified.

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Table 1. Relative abundance, spatial distribution, and perceived predatory capability of avian, reptilian, and mammalian predators observed in southwestern Kansas, 1997 to 1999. Relative abundance is rated as rare (R), uncommon (U), common (C), or abundant (A). Distribution is categorized as localized or scattered based on the locations of sightings. Ability to depredate lesser prairie-chicken nests is rated as low (L), moderate (M), or high (H) based on reports in the literature and body sizes of individuals encountered in the field.

		Relative Abundance				Distribution		Predatory capability		
Class	Species	R	U	C	A	Localized	Scattered	L	M	H
Birds	Black-billed magpie (*Pica pica*)		X			X				X
	Western meadowlark (*Sturnella neglecta*)				X		X	X		
	Common grackle (*Quiscalus quiscula*)			X		X		X		
Reptiles	Bullsnake (*Pituophis catenifer sayi*)			X			X		X	
	Western hognose snake (*Heterodon nasicus*)	X						X		
	Coachwhip (*Masticophis flagellum*)	X						X		
	Milksnake (*Lampropeltis triangulum*)	X						X		
Mammals	Coyote (*Canis latrans*)			X			X			X
	American badger (*Taxidea taxus*)		X							X
	Spotted ground squirrel (*Spermophilus spilosoma*)				X		X	X		

Table 1. Continued.

Class	Species	Relative Abundance				Distribution		Predatory capability		
		R	U	C	A	Localized	Scattered	L	M	H
Mammals	Thirteen-lined ground squirrel (*S. tridecemlineatus*)			X			X	X		
	Long-tailed weasel (*Mustela frenata*)	X							X	
	Striped skunk (*Mephitus mephitus*)	X								X

Table 2. Nests to which artificial (clay) eggs were added, date added, fate of nest, result obtained, date result was obtained, date the nest hatched or failed (event date), and number of eggs lost from initial clutch size during incubation for 16 lesser prairie-chicken nests in southwestern Kansas, 1997.

Nest ID #	Date added	Nest fate	Result	Date of result	Event date	Eggs lost[a]
173.040	1 June	Depredated	Missing	5 July	5 July[b]	
173.621	17 May	Failed	CNL[c]			
173.277	9 May	Hatched	CNL			
173.923a	4 May	Depredated	Missing	8 May	8 May	
173.201a	6 May	Depredated	Intact	14 May	14 May	
173.829	9 May	Depredated	Pieces[d]	14 May	14 May	
173.560	9 May	Failed	CNL		21 May	
97-TRH	4 May	Failed	Missing	11 May	23 May	
173.239	4 May	Depredated	Flattened	26 May	26 May	
173.923b	31 May	Depredated	Missing	2 June	2 June	
173.201b	1 June	Depredated	Missing	6 June	6 June	

Table 2. Continued.

Nest ID #	Date added	Nest fate	Result	Date of result	Event date	Eggs lost[a]
173.779	1 June	Depredated	Missing	5 June	6 June	
173.061	1 June	Depredated	Tooth imprint	10 June	10 June	2
173.400	31 May	Depredated	Missing	14 June	14 June	
173.422	1 June	Depredated	Intact	19 June	19 June	
173.958	1 June	Depredated	Missing	28 June	13 July	1

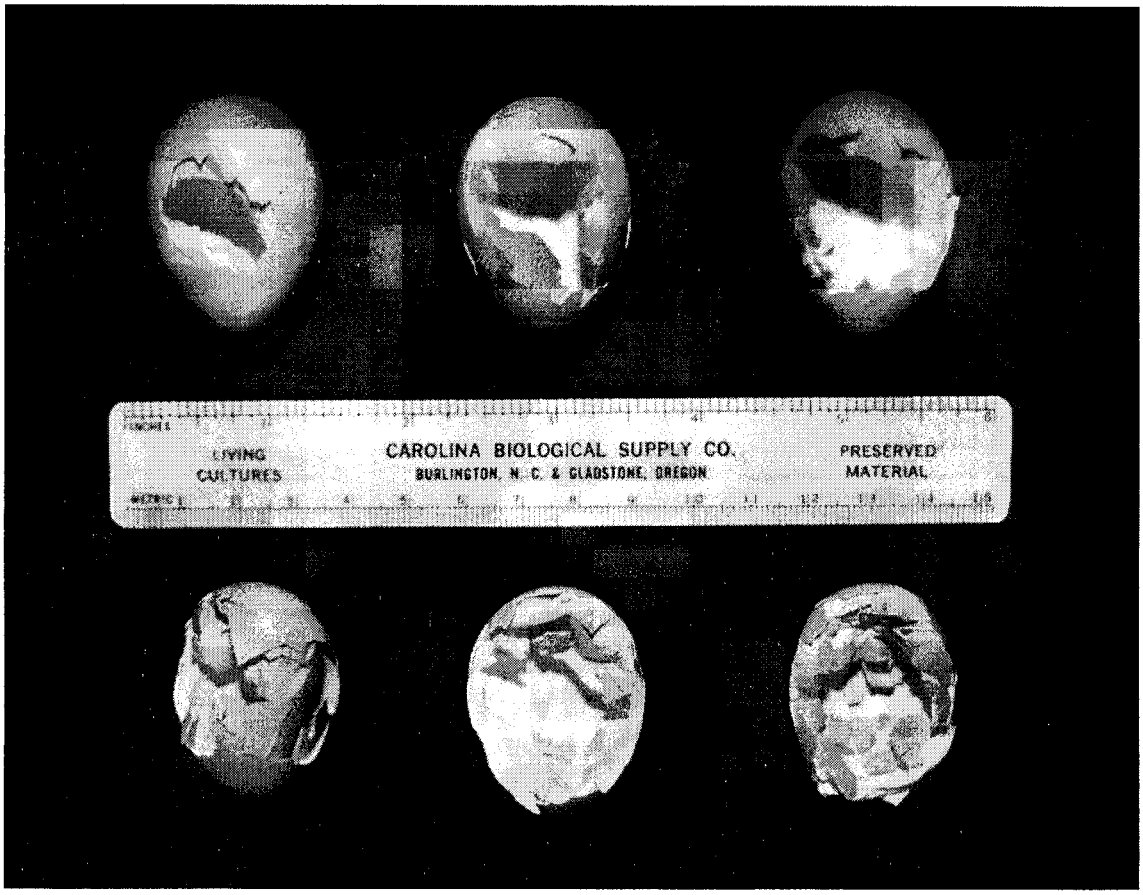
[a] Number of eggs known to have disappeared during incubation

[b] Hen incubated non-viable eggs >40 days

[c] Nest could not be relocated

[d] Small pieces of clay egg recovered near nest; considered evidence of mammalian predator

Figure 1. Remains of eggs collected from depredated lesser prairie-chicken nests in southwestern Kansas, 1997 to 1999, demonstrating some of the variability in the observed pattern of depredation.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MOVEMENTS, RANGES, AND HABITAT SELECTION OF MALE LESSER PRAIRIE-CHICKENS IN FRAGMENTED RANGELANDS OF SOUTHWESTERN KANSAS

Abstract: Little published information is available on basic natural history of lesser prairie-chickens in sagebrush habitats. Mark-recapture and radio-telemetry were used to examine movements (emigration, daily movements, and interlek movements) and habitat selection of male lesser prairie-chickens in fragmented sand sagebrush (*Artemisia filifolia*) habitats in southwestern Kansas. During the 3-year study, only 2 of 76 radio-marked males were known to have emigrated from the primary study area. Interlek movements were recorded for 10 males (20.8% of those recaptured) and occurred more often than previously has been documented for lesser prairie-chickens. Male lesser prairie-chickens exhibited strong selection for sand sagebrush habitats during nearly all (24 of 25) months studied at 2 nested scales of habitat availability. These results suggest that yearling and adult male lesser prairie-chickens do not frequently disperse, and that remaining occupied sand sagebrush habitat fragments should be protected. Future research should examine the effects of male movements on population indices derived from lek survey data.

Key words: emigration, habitat selection, interlek movements, lesser prairie-chicken, *Tympanuchus pallidicinctus*

INTRODUCTION

Populations of lesser prairie-chickens in Kansas declined sharply between 1975 and 1995 (KDWP unpublished data) and followed trends in habitat loss to center-pivot irrigated cropland (Taylor and Guthery 1980). Conversion of sand sagebrush prairie to

cropland appeared to slow in the early 1980s, but populations of lesser prairie-chickens continued to decline. Specific causes of further declines, however, were not known.

Emigration and immigration affect numbers of birds directly at the local level and at large spatial scales through metapopulation or source-sink dynamics (Pulliam 1988, Newton 1998). Movements and home ranges within a given habitat provide correlative information about species-specific resource and habitat requirements during different seasons (Samuel and Fuller 1996). Because prairie-chicken population indices are derived from spring lek surveys (Applegate 2000), knowledge of male movements among different leks is critical to the evaluation and appropriate use of those indices.

Few published data are available on movements and habitat use by lesser prairie-chickens and most researchers have studied them in shinnery oak (*Quercus havardii*) grasslands in more southern portions of the species' geographic range. Some researchers have suggested that movements and habitat use patterns may differ between shinnery oak and sand sagebrush habitats (Taylor and Guthery 1980, Mote et al. 1999). Schwilling (1955) studied lesser prairie-chickens in sand sagebrush habitats of Kansas but did not have the advantage of telemetry to study individual birds. As a result, most conclusions were drawn from observations of unmarked birds. With this type of study, estimates of individual movements obviously are unavailable and validity of habitat use estimates are dependent upon constant detection rates over the period of interest and across habitat types. Although important assumptions are implicit in radio-telemetry studies, the technique allows more quantitative, and somewhat more objective, measures of individual movements and habitat use (White and Garrott 1990).

This study was initiated in 1997 to obtain quantitative estimates of movements and habitat selection of male lesser prairie-chickens in sand sagebrush rangelands fragmented by agricultural activities.

STUDY AREA

The primary study area was a 5,760-ha fragment of sand sagebrush rangeland immediately south of the Arkansas River in western Finney County of southwestern Kansas. The area was vegetated primarily by sand sagebrush (*Artemisia filifolia*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), paspalum (*Paspalum* sp.), bluestem (*Andropogon* spp.), western ragweed (*Ambrosia psilostachya*), sunflowers (*Helianthus* spp.), and Russian-thistle (*Salsola iberica*). Prickly pear cactus (*Opuntia* sp.) and yucca (soapweed) (*Yucca glauca*) were interspersed throughout. Buffalo-gourd (*Cucurbita foetidissima*) and purple poppy mallow (*Callirhoe involucrata*) were common in disturbed areas. Soils were in the Tivoli-Vona association and in the choppy sands range site category (U. S. Department of Agriculture 1965). Primary land uses were grazing by cattle (from May 1 through October 1) and petroleum production. Research also was conducted in sand sagebrush prairie fragments separated from the primary study area by cultivated fields. Vegetation and soils were similar in these other fragments but some contained scattered sand plum (*Prunus angustifolia*) thickets in addition to sand sagebrush.

Over the past 30 years, the area received an average of 50 cm of annual precipitation with 74 % occurring between March and August. During this study (1997

through 1999) the area received an average of 55 cm of precipitation annually (U. S. Department of Commerce 1999).

METHODS

Lesser prairie-chicken males were captured on leks on the primary study area during spring (1997 to 1999) or fall (1998 only) using walk-in traps (Haukos et al. 1990). All captured birds were marked with individually numbered aluminum leg bands, and a subset of birds was fitted with 12-g necklace transmitters with a projected battery life of 180 days (6 months). Transmitters also were equipped with 4- or 8-hour inactivity (mortality) switches. Ages of captured birds were recorded as yearling (hatched the previous spring) or adult (hatched > 1 year prior to capture) in 1998 and 1999. Ages were not determined for birds captured in 1997. Radio-marked birds were located once daily with mobile ground telemetry units (truck-mounted single-Yagi antenna in 1997 and truck-mounted null-peak antennae in 1998 and 1999) until they left the primary study area, died, or radio contact was lost. Daylight hours were divided into equal thirds and the third of daylight in which location data were collected was varied systematically from one day to the next. Daily locations were determined by triangulation of ≥2 bearings that were plotted by hand (1997) on 1:24,000 scale topographic maps using drafting equipment or by computer (1998 and 1999) using Locate II (Nams 1990). For 1998 and 1999 location data, error areas around locations were estimated at 95% via maximum likelihood estimation (Lenth 1981) using Locate II with the default bearing standard deviation of 2.5°. All location data were recorded in Universal Transverse Mercator (UTM) coordinates, NAD27. Error areas were not estimated in 1997 because bearings

were plotted by hand and locations were determined using a mylar overlay of the UTM grid. Telemetry equipment mounted on a fixed-wing aircraft was used to search for prairie-chickens that were suspected of leaving the primary study area. Male prairie-chickens that emigrated from the primary study area were located at approximately 1-week intervals until radio contact was lost.

Movements

Distances between radio locations collected on consecutive days were used to estimate daily movements. Distances between radio locations separated by >1 day were excluded from analysis. Daily movement data were pooled across individuals and means and medians were estimated for each month. Movements of birds from the primary study area to other sand sagebrush prairie fragments (emigration distances) are reported for each individual that performed this movement. Movements of male lesser prairie-chickens between leks among years (interlek movements) were determined from recaptures of banded birds.

Although not a primary objective of this study, field notes on the stability and sizes of leks (lek dynamics) were used to supplement recapture data on interlek movements. Because no data were available on the number of consecutive years each lek was attended by males, stability was defined subjectively in terms of the relative numbers of males attending among years. Those leks at which the numbers of males did not fluctuate greatly were considered "stable" and those leks where the numbers of attending males varied considerably were defined as "unstable". Unstable leks appeared in the same location among years. These definitions were used only because other information that has previously been used to categorize lek stability (e.g., lek age; Haukos and Smith

1999) were not available. The use of these definitions in the future is not encouraged and their use here is not intended to contradict or modify definitions used by other researchers (Hamerstrom and Hamerstrom 1973, Robel et al. 1970).

Monthly Ranges

Kernel methods produce non-parametric estimates of the utilization distribution from a sample of the organism's locations (Worton 1989). Monthly ranges of individual birds were estimated at 95% from fixed kernel density estimates with smoothing parameters chosen by least-squares cross-validation (LSCV; Silverman 1986, Worton 1989, Seaman and Powell 1996) using the Animal Movements extension (Hooge et al. 1999) for ArcView GIS version 3.1 (Environmental Systems Research Institute 1992). These ranges were estimated only for those birds for which ≥25 locations were available in a given month.

Habitat Selection

A geographic information system (GIS) was developed using ArcView to obtain estimates of habitat use and habitat availability. A draft landcover map of the study areas was obtained from the Kansas GAP Analysis Program (GAP) at Kansas State University for use as a base habitat map. Seventeen landcover classes were present in the draft landcover. Landcover categories that contained obvious classification errors or that were considered non-habitat were deleted. Remaining landcover classes were combined into 4 habitat types for analysis based on knowledge of dominant vegetation across study areas and descriptions of the landcover classes provided by GAP personnel. Areas of each habitat inside individual monthly ranges were used as estimates of individual habitat use and were obtained by overlaying the kernel estimates of monthly ranges on the habitat

map using the UNION feature in ArcView's Spatial Analyst. The resulting data set then was queried for habitat polygons inside those monthly ranges. The results of the query were exported to a spreadsheet, converted to text files, and summarized using SAS (Appendix B). Because habitat selection probably occurs in a hierarchical manner (Johnson 1980, Manly et al. 1993), available habitat was defined at 2 nested spatial scales; a large area (level 1) and a smaller area within (level 2). Both scales were defined using data on bird movements. Level 1 was a circular area with its center at the approximate middle of the primary study area and with the radius equal to the distance of longest movement recorded for a radio-marked bird. Level 2 was delineated as the area encompassed by any of 1) a minimum convex polygon (MCP) of all locations of radio-marked males, 2) a fixed kernel 95% "population range" estimate derived from those locations, or 3) any individual monthly range. A map of available habitat at level 2 was obtained by overlaying the MCP, population range, and all monthly range estimates on the level 1 map and clipping the level 1 map to the perimeter of the overlayed themes.

Each month was treated as a separate experiment, and habitat selection ratios (W_is) with Bonferroni-corrected 95% confidence intervals were estimated for each habitat type each month at both spatial scales of habitat availability (Manly et al. 1993). All movement and monthly range data were analyzed and all habitat selection ratios were estimated using SAS release 6.12 (SAS Institute 1996). No statistical tests were conducted because the confidence intervals around W_is clearly show which selection ratios differ (Cherry 1998).

RESULTS

Two hundred eight individual males were captured and 76 of these were equipped with transmitters. Transmitters emitted signals for up to 8 months, and daily tracking yielded 13,663 radio locations from these males. Estimates of error areas around individual locations ranged from 0.00 to 375.09 ha ($\bar{x}$ = 14.27 ha, SE = 0.219, n = 7,562). Radio contact rarely was permanently lost (n = 5 suspected transmitter failures) and 12,718 movements were obtained on consecutive days. Three transmitter failures were obvious (e.g., preceded by sporadic or weak signals or known due to inability to obtain signals immediately after release of marked birds), but the 2 remaining failures can not be explained. An additional 316 movements were recorded at intervals separated by >1 day. It is assumed that no losses of radio contact were due to undetected emigration from the primary study area. However, transmitter battery depletion and subsequent loss of radio contact coincided with increasing distances of daily movements during fall. It is not possible to separate losses of radio contact due to depleted transmitter batteries from loss of radio contact due to fall emigration because few aerial searches were made during fall and winter.

Movements

Inspection of stem-and-leaf plots of the data indicated that daily movements were not normally distributed so medians are presented in conjunction with means and standard errors. The overall monthly changes in median daily movements was rather consistent across years. Median daily movements were longest in March each year and ranged between 435 and 786 m/day. Movements were shortest during May through September and ranged from 140 to 365 m/day (Fig. 1). Across years, median daily

movements were most variable in April and ranged from 219 m/day in 1997 to 622 m/day in 1999.

Only 2 radio-marked males were known to have permanently emigrated from the primary study area and both departed the primary study area between the last week of March and the first week of April, 1999. One, a yearling, first was captured and radio-marked during that period. The other initially was captured and banded during spring 1998, but was not radio-marked until he was recaptured in fall 1998 and thus was an adult at the time he emigrated. The yearling was relocated approximately 44 km west of the primary study area, and the adult was relocated approximately 13.5 km east of the primary study area (Fig. 2). The adult was found near a lek in the prairie fragment to which he immigrated and was relocated in this habitat fragment 3 times during April and May before radio contact was permanently lost in early June. Again, whether loss of radio contact was attributable to additional movements or transmitter failure is not known. The specific location of the yearling relative to other birds or leks in the area was not determined because the request for property access was denied.

During 3 recapture occasions (spring and fall 1998 and spring 1999), 48 males were recaptured 54 times (6 individuals were recaptured twice). Ten (21%) of these birds were recaptured at leks other than where they initially were banded. Ages were determined for 7 of these birds upon their initial capture. Four first were captured as yearlings and 3 as adult birds. Seven males (15% of the recaptures) were captured and recaptured during spring trapping, and the remaining 3 were first captured or were recaptured during fall trapping in 1998. For the 10 birds performing interlek movements, distances between lek of initial capture and lek of recapture ranged from 0.42 to 4.41km

($\bar{x}$ = 1.62 km, SE = 0.40). Examination of the recapture data in conjunction with field notes revealed that 3 of the males (2 adults and one that could not be aged) that exhibited interlek movements first were captured during spring at an unstable lek. This lek was located late in the male display period of 1997, and was attended by approximately 8 males. This lek was not trapped upon during that year. During spring 1998, 17 different males were captured at that lek and a maximum count of 25 birds (males and females) was noted. During spring 1999, the number birds on the lek had declined to 7 males and only 1 was captured during trapping efforts in that period.

Movements of males at another lek suggest that males may shift to form new leks. Three males radio-marked in 1999 were found displaying on a new (or previously undiscovered) lek approximately 1.1 km east of the lek at which they were captured. This lek was found when 2 of those males were relocated in the same area several consecutive days during the spring display period. The discovery of this new lek coincided with a decline in numbers of males attending the lek at which the 3 radio-marked birds were captured. Field notes indicate that several other males (e.g., 10 individuals in 1999 alone) captured and radio-marked at various leks were relocated at 1 to 2 different leks between 20 March and 20 June during the year in which they were radio-marked.

Monthly Ranges

Monthly ranges (Fig. 3) were determined for ≥2 birds for 25 months yielding 380 bird-months of data (Table 1). Similar to daily movement data, monthly range sizes did not appear normally distributed and medians are reported as well as means and standard errors. Monthly range sizes showed annual patterns similar to those of daily movements.

Across years, median monthly range size ranged from 12 to 140 ha between April and May when males regularly attended leks. Ranges remained small throughout the summer, ranging from 77 to 144 ha from June through September, and then increased abruptly to peak median range sizes of 229 to 409 ha in October as birds began feeding in newly harvested grain (primarily corn) fields. Across years, median monthly range sizes varied most in October (Fig. 4).

Habitat Selection

The area available to male lesser prairie-chickens at level 1 had a radius of approximately 44 km and a total area of 618,120 ha. Eight landcover classes were deleted from the coverage prior to analysis. Two of these were deleted because they contained obvious classification errors ("Cottonwood floodplain woodland" and "Salt cedar or tamarisk shrub"), and 6 because they were considered non-habitat. Remaining landcover classes were categorized as sand sagebrush prairie, crop, tallgrasses and Conservation Reserve Program (CRP) fields, or other grassland (Table 2). The level 1 habitat map contained 588,452 ha of habitat after deletion of the 8 landcovers (Fig. 5). The area available at level 2 was 10,463 ha before deletion of the 8 landcovers and contained 10,275 ha of habitat after (Fig. 6). Polygons of those habitats that were deleted from the available habitat also were deleted from the file containing the results of the habitat use estimates (i.e., the UNION results).

From a hypothesis testing viewpoint, the null hypothesis for all selection ratios (W_is) is no selection for or against a given habitat type (i.e., the confidence interval around W_i includes 1). All results reported here for selection ratios reference the 95%

confidence intervals rather than the point estimates of the selection ratios. Radio-marked male lesser prairie-chickens showed selection for sand sagebrush prairie habitat ($W_i s > 1$) in all months at availability level 1. At this level of availability, male lesser prairie-chickens showed selection against all other habitats ($W_i s < 1$) in all months (Fig. 7). Sand sagebrush prairie comprised 9.5% of the available habitat at level 1.

Patterns of selection at availability level 2 were similar to those at level 1. Radio-marked males exhibited selection for sand sagebrush prairie in all months except November 1997. In November 1997, they showed selection for other grassland habitat, and no selection for or against ($W_i s \approx 1$) crop habitat (Fig. 8). Sand sagebrush prairie comprised 56.5% of the available habitat at level 2.

DISCUSSION

In the context of metapopulation regulation and population monitoring via lek surveys, the most important movements exhibited by males during this study are those between habitat fragments and among leks. Results suggest that most males present on leks in spring can be considered resident birds and are likely to remain within a given fragment of sand sagebrush prairie. However, those males that did emigrate moved relatively long distances and passed several kilometers over what appeared to be suitable habitat. Important movements by males (emigration) may occur during their first 6 to 10 months of life, but essentially no data are available on those movements. Results of concurrent studies of males marked as chicks (Chapter 2) and results obtained by Copelin (1963) indicate that at least some juvenile males remain in the general vicinity of their brood range. Dispersal rates of juveniles have not been documented in fragmented sand

sagebrush habitats, possibly because juveniles are more difficult to capture than yearlings or adults. Factors limiting dispersal rates in fragmented habitats are of paramount importance in population regulation and persistence (Wiens 1996). Although only a small proportion of radio-marked males moved to other sand sagebrush prairie fragments, those movements suggest that lesser prairie-chickens are physically capable of long-distance dispersal. The specific movement paths of those males that emigrated is not known, however, and the yearling that demonstrated the furthest emigration may have used smaller fragments of sand sagebrush prairie southwest of the primary study area during emigration.

Further evidence of long-distance dispersal capability was demonstrated during a transplant effort conducted by the Colorado Division of Wildlife. A female lesser prairie-chicken translocated to southeastern Colorado from the primary study area of the present study was recovered by hunter in Kansas <40 km from the capture location and >320 km from the release site (K. Giesen, Colorado Division of Wildlife, personal communication). Based on these movements, the factors that limit male lesser prairie-chicken dispersal appear to be behavioral (i.e., site fidelity) rather than habitat-oriented. The crop habitat between sand sagebrush prairie fragments is used as a feeding area from fall through late spring. Field observations also indicate that some birds will roost overnight in these crop fields. Based on the movement data, fall through late spring is the time at which dispersing birds are likely to be affected by habitat suitability. Because crop fields provide food resources from fall through early spring, they probably do not pose a barrier to dispersal. Loss of sand sagebrush prairie habitat appears to be more detrimental than subsequent fragmentation effects. Fragmentation may have important

effects on other life history processes (e.g., nest success and brood survival) of lesser prairie-chickens if predation rates are positively correlated with perimeter to area ratios (Wiens 1996).

Telemetry data for males that remained on the primary study area support the findings of Scwhilling (1955) and Copelin (1963) that movements of lesser prairie-chickens are shortest during summer months and longest during fall and winter months. These data also agree with conclusions of Robel et al. (1970) for movements of greater prairie-chickens (*Tympanuchus cupido*) in northeastern Kansas. Distances between consecutive daily locations of lesser prairie-chickens probably do not represent their actual daily movements (Laundré et al. 1987), and cluster sampling designs under which radio locations are recorded at high frequencies over short (i.e. 24-hour) time periods (Samuel and Fuller 1996) may be more useful to determine the actual distances moved. Data collected in this study, however, appear to sufficiently reflect relative daily movements across months.

The proportions of birds recaptured at leks other than where they initially were captured was greater during the present study than previously has been documented. Campbell (1972) reported that only 4 of 114 recaptures (involving 3 individual males) were at leks other than where birds initially were captured, and none of the 6 males recaptured by Haukos in 1988 was recaptured at a different lek than where they were marked the year previous (Haukos and Smith 1999).

Recaptures of birds initially banded at an unstable lek suggest that male movements also may be responsible for lek dynamics of lesser prairie-chickens (Haukos and Smith 1999) rather than solely recruitment of immigrants or locally produced

juveniles as Copelin (1963:29) implied. Haukos and Smith (1999) felt that males generally remained on the leks where they established territories and that unstable or satellite leks were formed by males unable to establish territories at ones that were stable (i.e., usually yearling males). Robel et al. (1970) reported that yearling male greater prairie-chickens often were unable to establish lek territories and that they moved among leks (within a year) while apparently attempting to do so. If this is true, the results of the present study suggest that some males in this population may not be able establish territories on leks until they are ≥2 years old or more. Robel (1970) felt that most male greater prairie-chickens that owned lek territories were >2 years old and felt that many males (~ 45% of those in the population) were unable to establish territories. However, only 3 leks were studied and on an area of only about 2400 ha. Those males that were unable to establish territories on those 3 leks could have established territories on existing leks, or established "new" satellite leks, outside the bounds of Robel's (1970) study area.

It is not known what proportion of lesser prairie-chicken males do not establish territories in a given year but all of the males radio-marked in the current study were present at leks throughout the display period (March through mid-June). However, some excess males that are not territory holders may be present in the population (Robel 1970). If these excess males become territory holders as previous territory holders leave the population through death or emigration (Robel 1972), it is probable that counts of individual birds at leks do not reflect annual changes in the population. This may be particularly important if the proportion of non territory-holding excess males present in the population varies with population density. However, no data are available on this phenomenon.

Robel (1972) and Hamerstrom and Hamerstrom (1973) also felt that aggressive behavior was a more important determinant of whether a male was able to establish a territory than its age. Movements of adult males from the unstable lek in this study appear to support their hypothesis.

Changes in numbers of males at a given lek may be affected more by male movements and less by the actual changes in numbers of birds in a habitat than has been suggested. Lek age (years of continuous activity) may be an important predictor of bird numbers at individual leks (Haukos and Smith 1999), but data are not available on the ages of leks examined in the present study. Notes obtained from Colorado Division of Wildlife personnel indicate that the unstable lek referenced in this study was active in 1993 and 1994 when those personnel conducted trapping on the present primary study area, but no information is available for that lek for 1995 or 1996.

Davison (1940) warned against the use of coarse or inappropriate population estimates and referred to them as a "menace to the conservation" of lesser prairie-chickens. Hamerstrom and Hamerstrom (1973:14) felt that there was "too little consistency to permit use of either size or number [of booming grounds] as a short-cut to an annual population estimate." Annual changes in rangewide population indices derived from lek survey indices remain valid only if the surveys monitor a representative sample of lesser prairie-chicken leks. A representative sample would mean that increases and decreases in numbers of birds as a result of movements are equally observable and equally likely to occur across survey routes. Habitat attributes affecting, or even correlated with, interlek movements by males are not understood. It is clear, however, that numbers of males at some leks fluctuate more than others and that some fluctuation

is due to movements rather than actual changes in numbers. Determining how much these movements affect the population indices derived from counts of individual birds at leks seems worthy of further study in light of results of the current research.

Habitat selection analyses at level 1 and level 2 could be considered first- and second-order selection, respectively, as defined by Johnson (1980). The geographic association of lesser prairie-chicken populations with shrub-grassland habitats in the southern High Plains has long been recognized (Davison 1940) and generally accompanies the species account of the lesser prairie-chicken (Giesen 1998). Because most radio-marked males remained on the primary study area, results of level 1 habitat selection do little more than quantify this association. High selection ratios were expected with such a large area of available habitat and so little of that area comprised of suitable habitat. Defining available habitat always is arbitrary (Johnson 1980, White and Garrott 1990), and much of the level 1 habitat map may have been unavailable to most radio-marked birds. Habitat selection ratios at level 1 may be somewhat biased because monthly range estimates (and thus habitat use estimates) were not available for those birds that did emigrate. However, because only 2 birds were known to have emigrated and loss of radio contact was rare, this bias probably is not severe. Furthermore, those birds that left the primary study area traveled to other fragments of sand sagebrush prairie habitat where their post-emigration movements and ranges likely were similar to those of birds that remained on the primary study area.

Area bias of kernel home range estimators increases as sample size (i.e., the number of locations from which they are derived) decreases (Seaman et al. 1999). Seaman et al. (1999) demonstrated that kernel home range estimators performed best

(had lowest area bias and highest precision) with ≥50 locations and recommended minimum sample sizes of 30 locations. Because monthly ranges were estimated, the maximum possible sample size for these estimates was 31. The minimum sample size used to estimate monthly ranges (25 locations) was arbitrarily chosen because it was near the recommended minimum of 30 but large enough that few bird-months of data would have to be sacrificed. Lowering the minimum cutoff further would have increased the area bias (Seaman et al. 1999). Although the monthly range estimates in this study probably were biased slightly high, it is argued that the resulting estimates still are more accurate and meaningful than estimates obtained from other methods (e.g., minimum convex polygon, harmonic mean) because other estimators have serious inherent flaws (Anderson 1982, Seaman and Powell 1996, Boulanger and White 1990). Furthermore, the inner contours of kernel density estimates (i.e., estimates at 50 or 75%) exhibit the most serious area bias (Seaman et al. 1999) and use of those contours was purposely avoided in the present study.

White and Garrot (1990:201) advised against the use of home ranges as estimates of habitat use and called the extra effort required to obtain them unnecessary considering the lack of a "perfect" home range estimator. However, the same authors pointed out that location error can result in somewhat arbitrary assignment of locations to habitat type if the error area overlaps ≥2 habitat types. Kernel home range estimates were used as individual estimates of habitat utilization because it avoided these arbitrary decisions and the somewhat difficult task of plotting error areas and assigning individual locations to 1 of the 2 (or more) habitat types. Kernel home ranges are not "perfect" but seem more

objective estimates of habitat use than the raw location data from which they were estimated.

Habitat selection ratios for level 2 may be more meaningful than those for level 1. Although sand sagebrush prairie made up about 56% of the available area at level 2, male lesser prairie-chickens still exhibited rather strong selection for this habitat during most months. The exceptional values for selection ratios in November 1997 likely are due to small sample sizes and will not be discussed further. However, the wide confidence intervals around the selection ratios for some habitats likely can be explained. High variance estimates and subsequently large confidence intervals can occur when few individuals use a particular habitat and do so in drastically different ways (Manly et al. 1993). Monthly ranges were estimated from fewer locations than is optimal, and therefore their areas are biased high. Because monthly ranges were used as estimates of habitat use, more area and potentially more habitat types were included in the use estimates than would probably have been obtained by using individual locations as estimates of use. Additionally, some habitat types occur in small patches widely scattered throughout the level 2 map. Area bias of the kernel estimates coupled with the spatial distribution of small patches of habitat probably resulted in a large proportion of these available habitats being included in the habitat use estimates of only a few birds. Thus, it is easy to understand how habitat use estimates could differ drastically among a few birds "using" these habitats. Considering this situation, it is somewhat surprising that wide confidence intervals were not more common at level 2, and the consistently small confidence intervals add support to the selection ratio estimates.

The habitat selection analyses have other important limitations. First, only a spatial extent was used to define available habitat in this study. Some researchers likely would not have considered a crop field with growing corn plants to be available summer habitat for lesser prairie-chickens. Constraining the estimate of available habitat to include only permanent grassland or analyzing habitat selection within individual monthly ranges (third-order selection; Johnson 1980) would not have resulted in more useful selection ratios because a detailed habitat map was not available. Attempts to quantify within-grassland habitat differences (e.g., sagebrush density) using remotely sensed data were unproductive. Initial clustering had little correspondence to known vegetation differences within the primary study area suggesting that habitats that differed a great deal visually were spectrally similar at the 30-m resolution of Landsat-TM data. Aside from differences in sagebrush density, vegetation across the primary study area was relatively homogeneous. Traditional cover-mapping was not completed because of logistical constraints and the difficulty associated with choosing an appropriate plot size with which to sample vegetation. Mapping relatively homogeneous vegetation over large areas with useful resolution would be an intimidating task. Although the estimates of radio location error probably are extremely conservative overestimates, they suggest fine scale analysis of habitat selection using those location data may not be valid even if a detailed map were at hand. Furthermore, use of individual kernel home ranges as habitat use estimates appears to contradict and therefore preclude their simultaneous use as estimates of "available" habitat.

Second, the present selection analyses are not spatially explicit (Wilson et al. 1998). That is, they do not incorporate patch size or spatial distribution of the available

habitats. Therefore, potentially important interactions between patch size and habitat type are undetectable. Although not specifically analyzed, patches of tallgrasses and CRP habitat and other grassland habitat types generally were small (<10 ha). Area sensitive species such as lesser prairie-chickens may avoid small patches irrespective of habitat type. Sand sagebrush prairie habitat (for which lesser prairie-chickens showed selection in most months) often occurs in small remnant patches in the "corners" of center-pivot irrigated crop fields but few birds ever used these patches during winter and none did so from June through September. Also, lesser prairie-chickens recently have been found inhabiting landscapes dominated by crops, shortgrasses, and CRP (habitats that prairie-chickens generally selected against in this study) in the northern portion of their historical range in Kansas (KDWP unpublished data). However, it is not known whether vital rates (survival and reproduction) of lesser prairie-chickens in these habitats are sufficient to maintain these populations. It is suggested here that the interaction between patch size and habitat type may be a more important determinant of habitat selection by lesser prairie-chickens than habitat type alone. Range-wide modeling of lesser prairie-chicken occurrence and population persistence (Oyler-McCance 1999), or vital rates such as reproduction, as a function of patch size and habitat type, will be required to determine the relative importance of these factors. Selection ratios for sand sagebrush prairie habitat and crop habitat types may be subject to higher rates of type I error than suggested by the 95% confidence intervals because those habitats generally occurred in continuous blocks that were large relative to monthly range sizes of lesser prairie-chickens (Wilson et al. 1998).

Finally, habitat use-availability studies require that habitat use among individuals is independent (Manly et al. 1993). This assumption probably is violated during spring and fall months when male lesser prairie-chickens form loose "lek flocks" and winter flocks, respectively. Individuals from the same lek often were seen flying to and from crop fields during spring and association among birds during fall and winter is common. However, it is not felt that this violation of independence assumption is serious enough to severely affect the selection ratio estimates and conclusions drawn from them, because birds from several different leks were radio-marked and male lesser prairie-chickens are not directly dependent upon one another for survival (Millspaugh et al. 1998). Despite the limitations of the selection analyses, the results are not considered invalid. However, inference must be limited to the present population of birds and the landscape in which they were studied.

MANAGEMENT IMPLICATIONS

Most grouse are poor dispersers (Braun et al. 1994) and male lesser prairie-chickens are no exception. The rate at which males emigrated in this study suggests that they contribute little to population persistence in disjunct habitat fragments. Based on their movements and habitat selection, remaining large fragments of sand sagebrush prairie should be protected. Populations of lesser prairie-chickens in fragmented habitats probably are maintained by dispersing females and local reproduction, but dispersing juvenile (<1 year-old) males also may contribute (Robel et al. 1970). Because most male lesser prairie-chickens can be considered residents and the males that did emigrate moved considerable distances, habitat management probably should be aimed at protection and

expansion of remaining habitats rather than efforts to increase their connectivity by adding smaller isolated patches between large sand sagebrush prairie fragments.

Up to 20% of males exhibit interlek movements among years and some leks may reflect losses of over three-fourths of the attending males to interlek movements. Because some males move among leks, lesser prairie-chicken population indices estimated from the mean number of birds per lek may not be valid to detect annual, route-specific changes in numbers. Such application of the indices may be an inappropriate use of those data (Applegate 2000). Future research should compare total area counts of males within habitat fragments to survey data, and determine what proportion of leks surveyed annually are unstable or <2 years old (Haukos and Smith 1999). The recommendations of Cannon and Knopf (1981) that lek surveys should use the number of active leks over large (> 4,200 ha) areas as an index to population change may be even more important than was suggested by Haukos and Smith (1999).

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Table 1. Numbers of individual male lesser prairie-chickens in southwestern Kansas for which 95% fixed kernel monthly ranges were estimated and from which subsequent habitat selection ratios were derived, 1997 to 1999.

	Year		
Month[a]	1997	1998	1999
January	[b]		10
February			10
April	14	19	23
May	18	21	25
June	17	19	22
July	17	19	19
August	16	17	13
September	14	14	11
October	5	12	6
November	2	17	

[a] No monthly ranges were estimated for March or December due to inadequate numbers of locations for birds radio-tracked in those months

[b] Blank spaces indicate that location sample sizes were not large enough to estimate ranges in that month

Table 2. Gap analysis program (GAP) vegetation alliances, habitats to which they were assigned for selection analyses, and proportion of the original map which they comprised. Blank spaces under habitat type indicate that the alliance was deleted prior to selection analyses.

		Proportion of map	
GAP alliance	Habitat type	Level 1	Level 2
Cultivated land	Crop	0.752	0.393
Sandsage shrubland	Sand sagebrush prairie	0.077	0.513
CRP	Tallgrasses and CRP	0.059	0.016
Cottonwood floodplain woodland		0.018	0.014
Sand prairie	Sand sagebrush prairie	0.018	0.052
Shortgrass prairie	Other grassland	0.016	< 0.001
Western wheatgrass prairie	Other grassland	0.015	< 0.001
Salt cedar or tamarisk shrub		0.010	0.003
Mixed prairie	Other grassland	0.007	
Non-native grassland	Other grassland	0.007	0.006
Salt marsh/prairie		0.005	0.001
Alkaline marsh		0.005	
Urban		0.005	
Water		0.003	
Cattail marsh		0.002	< 0.001
Alkali sacaton prairie	Other grassland	0.001	
Playa lake		< 0.001	

Figure 1. Distances (m) between radio locations of male lesser prairie-chickens recorded on consecutive days in southwestern Kansas, 1997 through 1999. Error bars around means represent 1 SE. Sample sizes are in Appendix B.

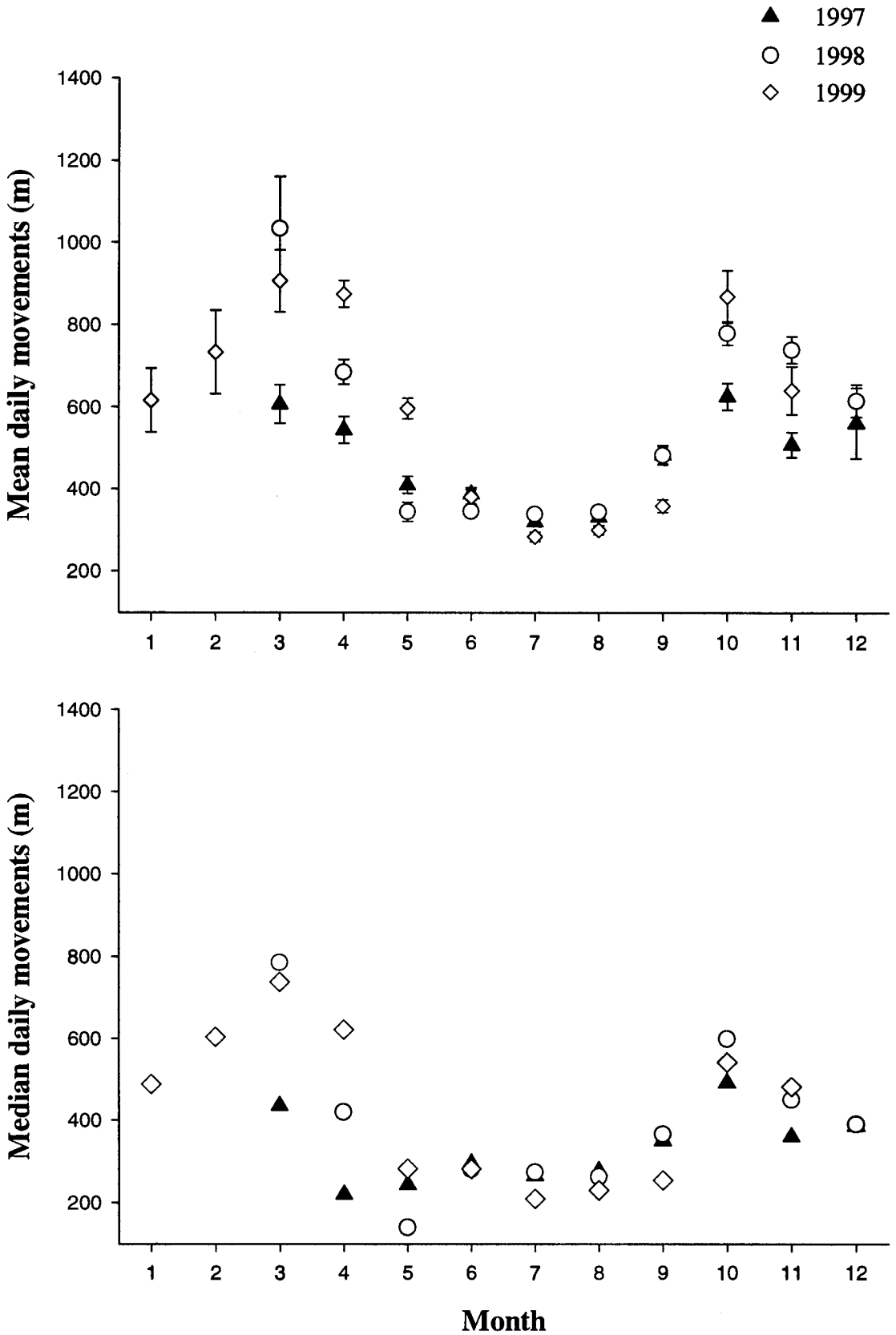

1997
1998
1999
Mean daily movements (m)
1400
1200
1000
800
600
400
200
1
2
3
4
5
6
7
8
9
10
11
12
Median daily movements (m)
1400
1200
1000
800
600
400
200
1
2
3
4
5
6
7
8
9
10
11
12
Month

Figure 2. Emigration distances of the 2 radio-marked male lesser prairie-chickens that departed from the primary study area in southwestern Kansas, spring 1999. Squares represent areas to which birds moved.

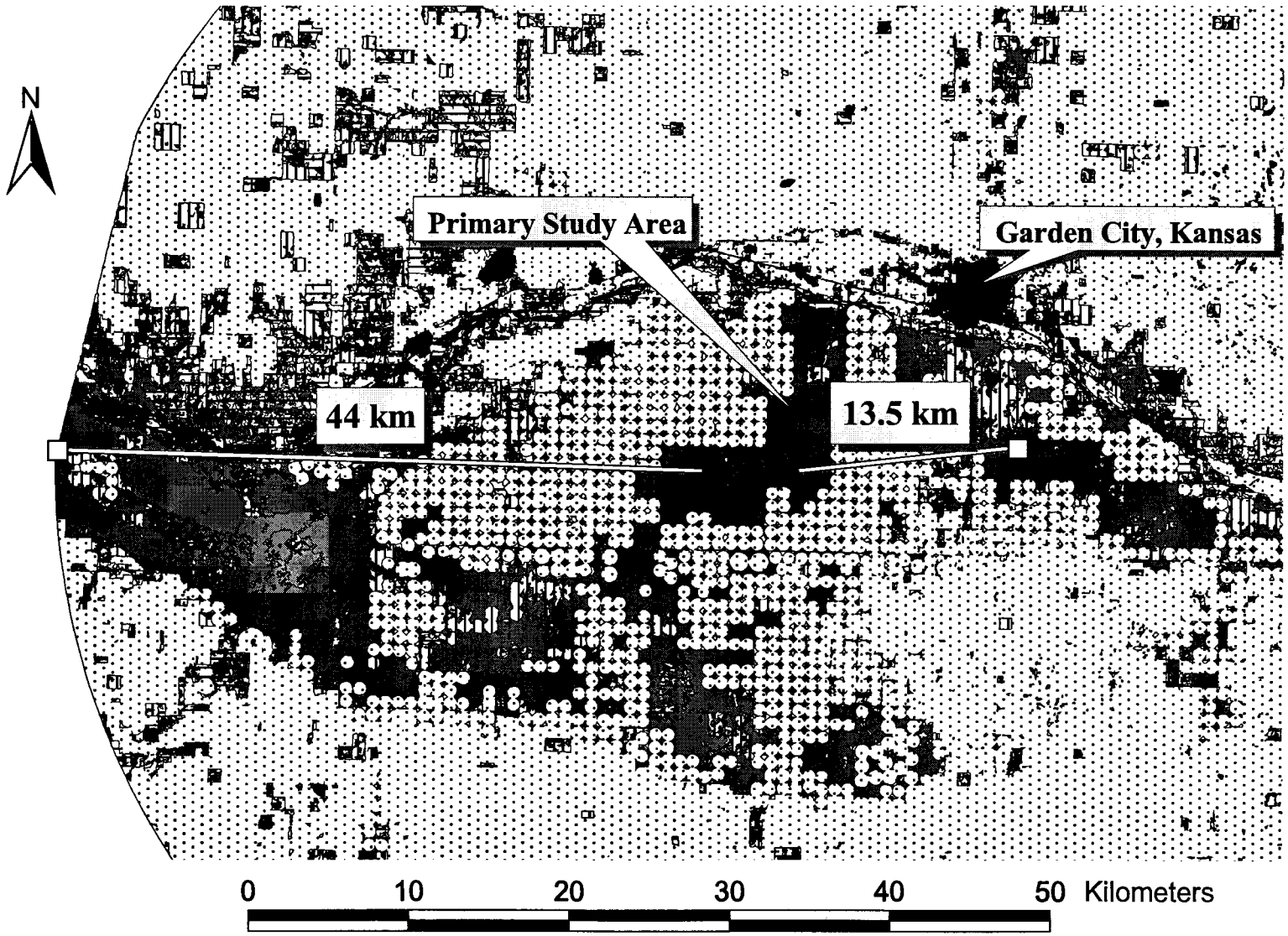

N
Primary Study Area
Garden City, Kansas
44 km
13.5 km
0
10
20
30
40
50 Kilometers

Figure 3. Examples of monthly range estimates for male lesser prairie-chickens radio-marked in southwestern Kansas, 1997 through 1999.

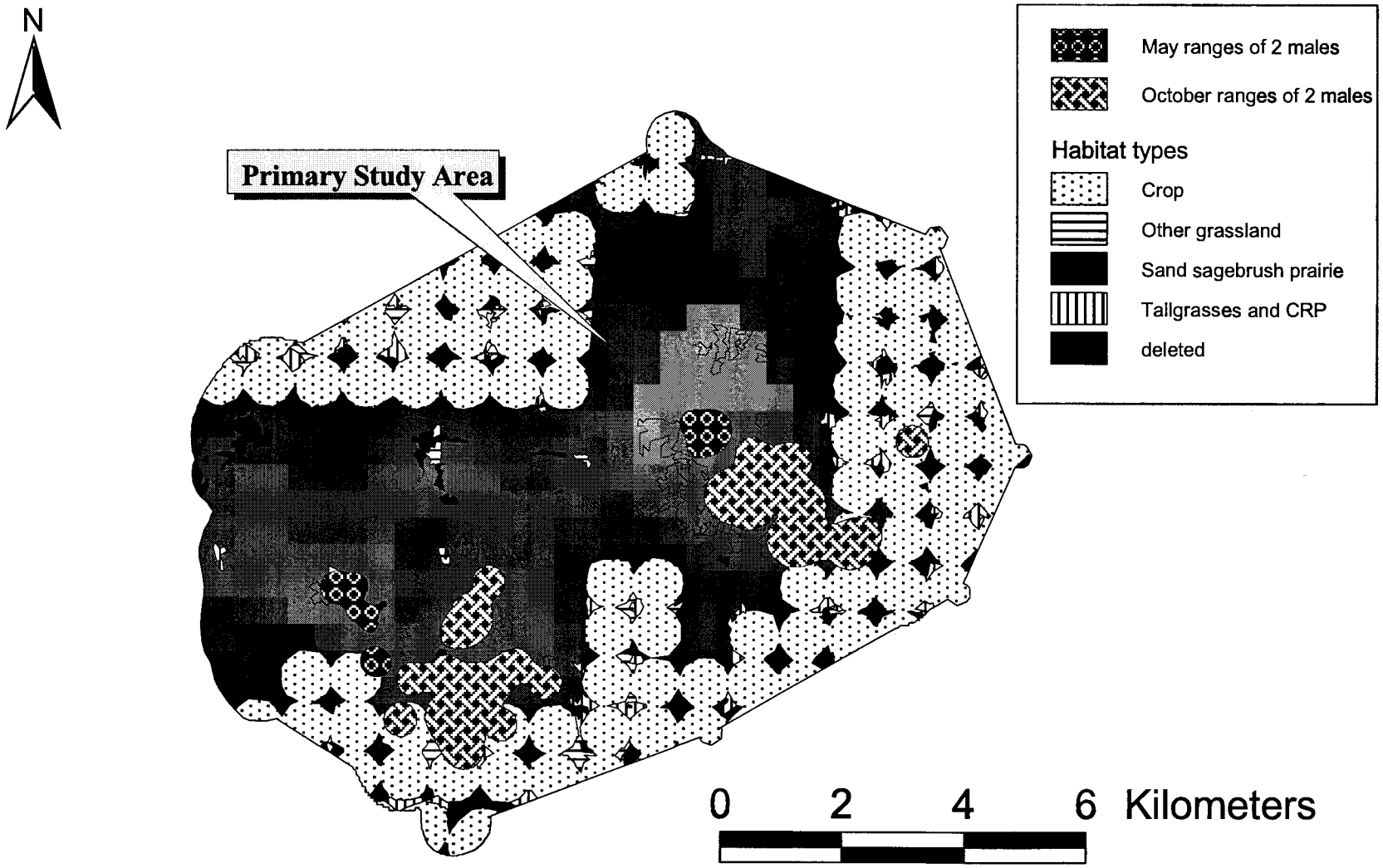

N
Primary Study Area
May ranges of 2 males
October ranges of 2 males
Habitat types
Crop
Other grassland
Sand sagebrush prairie
Tallgrasses and CRP
deleted
0 2 4 6 Kilometers

Figure 4. Monthly estimates of 95% kernel home range size for radio-marked male lesser prairie-chickens in southwestern Kansas, 1997 through 1999. Error bars around means represent 1 SE. Sample sizes are in Table 1.

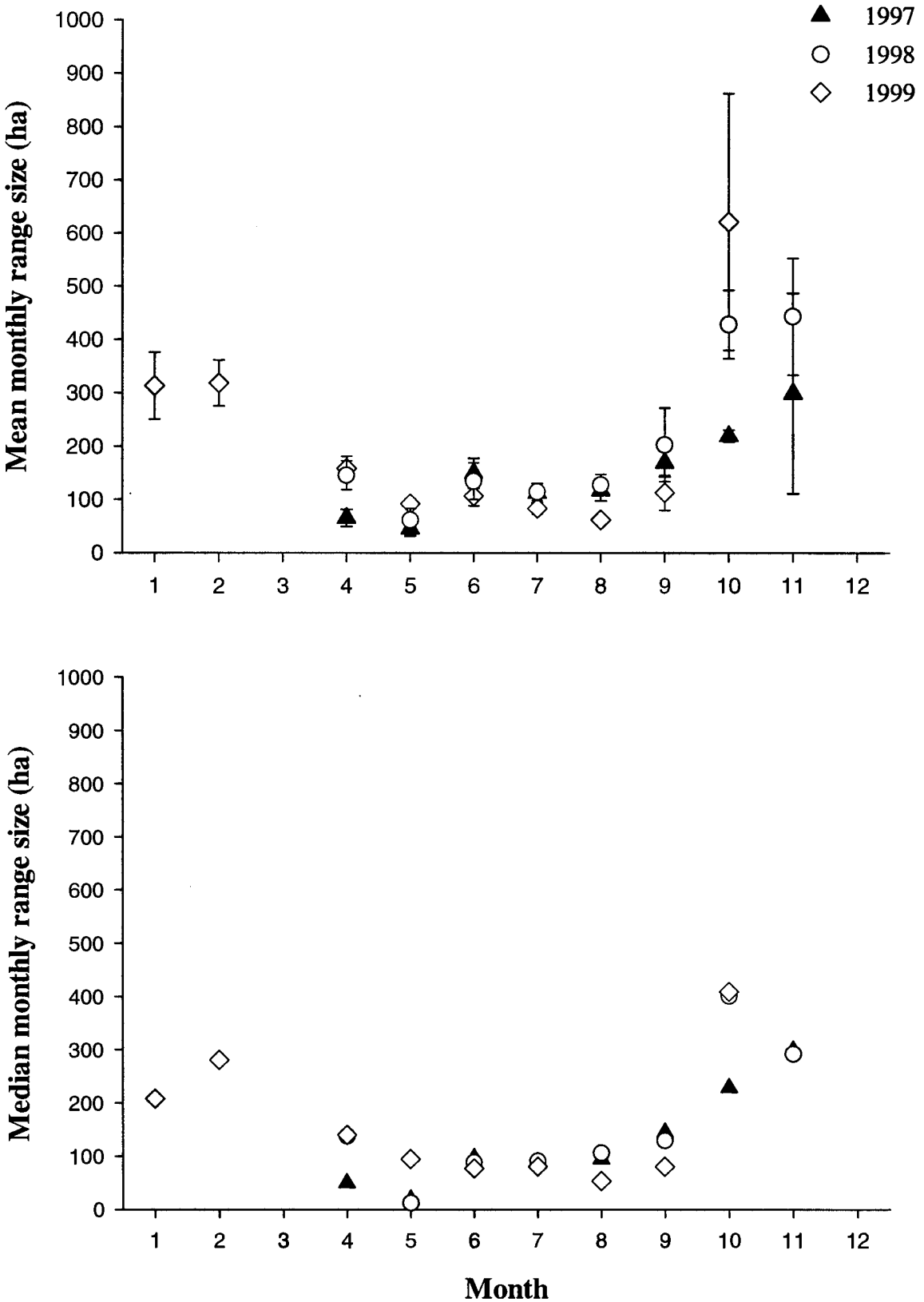

1997
1998
1999
Mean monthly range size (ha)
Median monthly range size (ha)
Month
0
100
200
300
400
500
600
700
800
900
1000
1
2
3
4
5
6
7
8
9
10
11
12

Figure 5. Map used to estimate habitat available to male lesser prairie-chickens for habitat selection analysis at level 1.

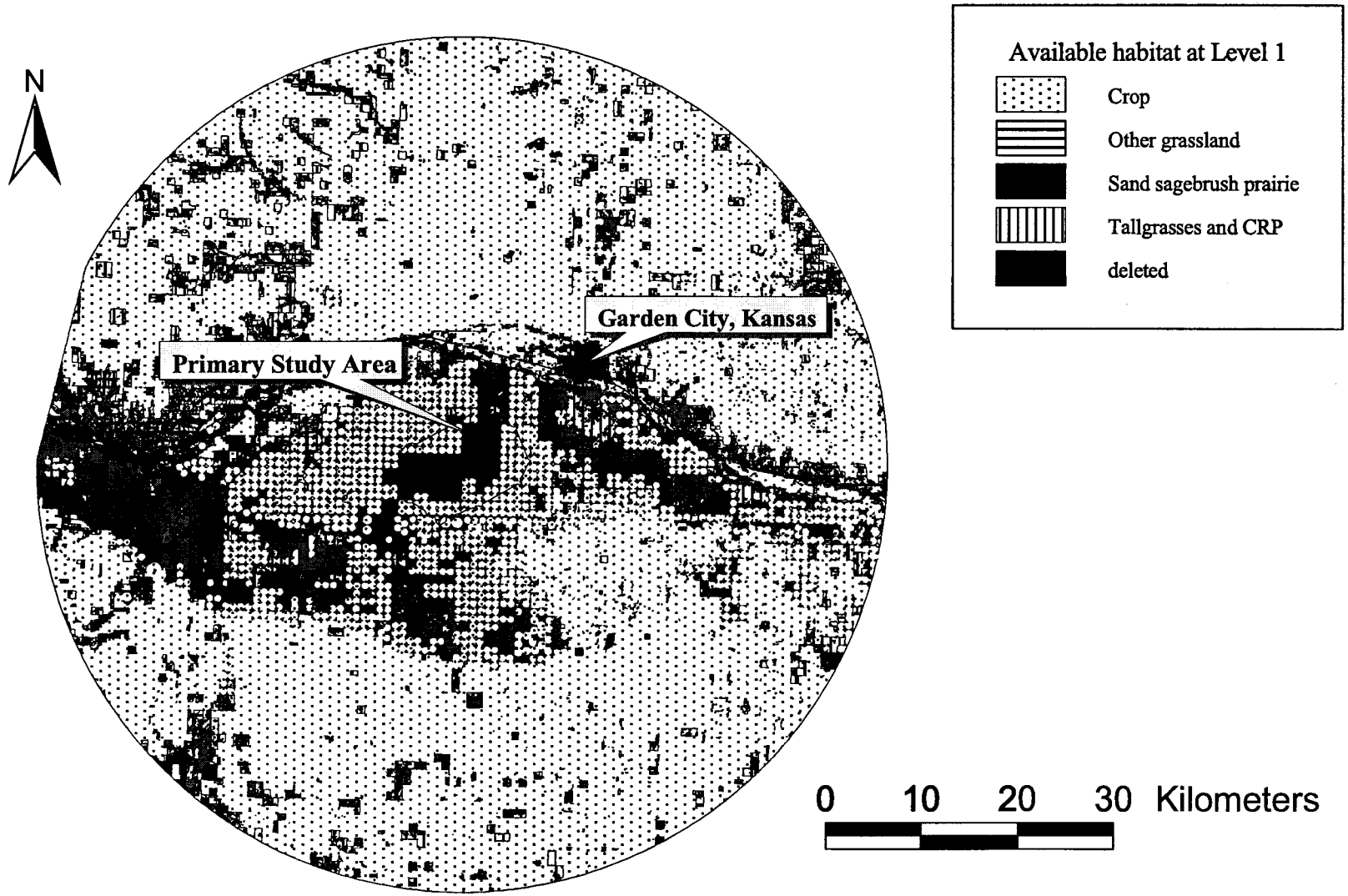

N
Garden City, Kansas
Primary Study Area
Available habitat at Level 1
Crop
Other grassland
Sand sagebrush prairie
Tallgrasses and CRP
deleted
0 10 20 30 Kilometers

Figure 6. Map used to estimate habitat available to male lesser prairie-chickens for habitat selection analysis at level 2.

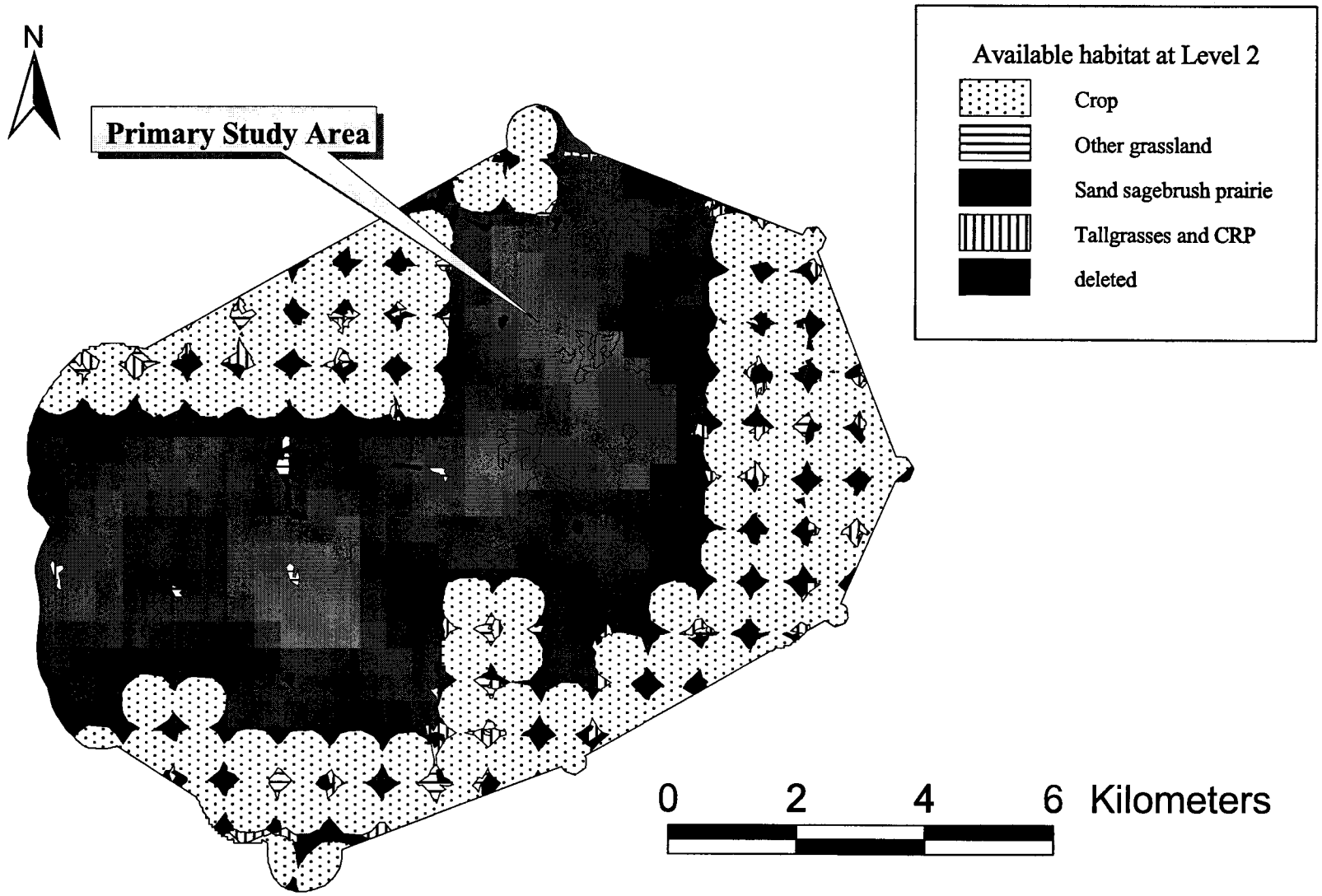

N
Primary Study Area
Available habitat at Level 2
Crop
Other grassland
Sand sagebrush prairie
Tallgrasses and CRP
deleted
0
2
4
6
Kilometers

Figure 7. Habitat selection ratios (W_is) and 95% confidence intervals (error bars) for habitats available to male lesser prairie-chickens at level 1in southwestern Kansas, 1997 through 1999. Month 1 is January, 2 is February, etc.

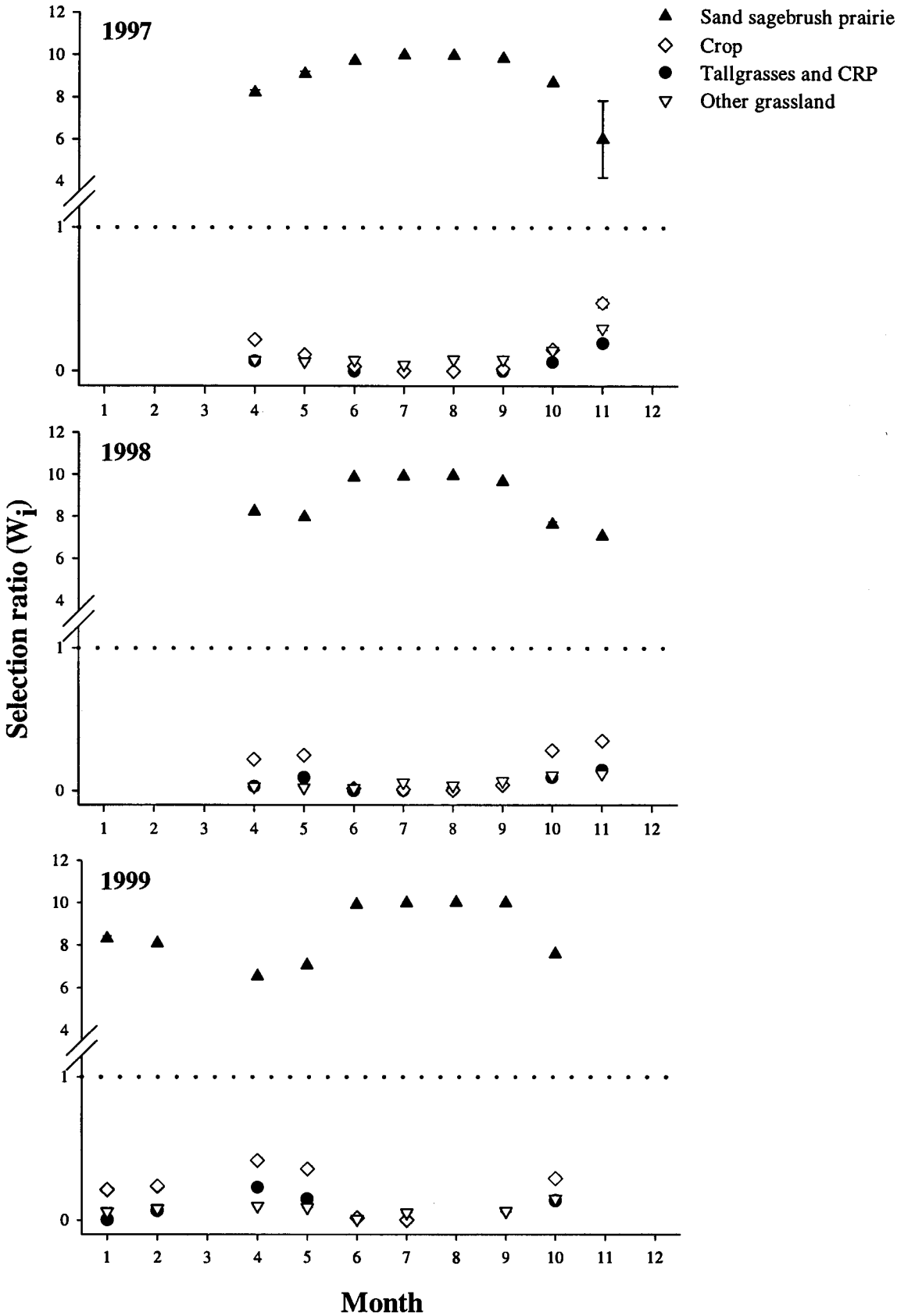
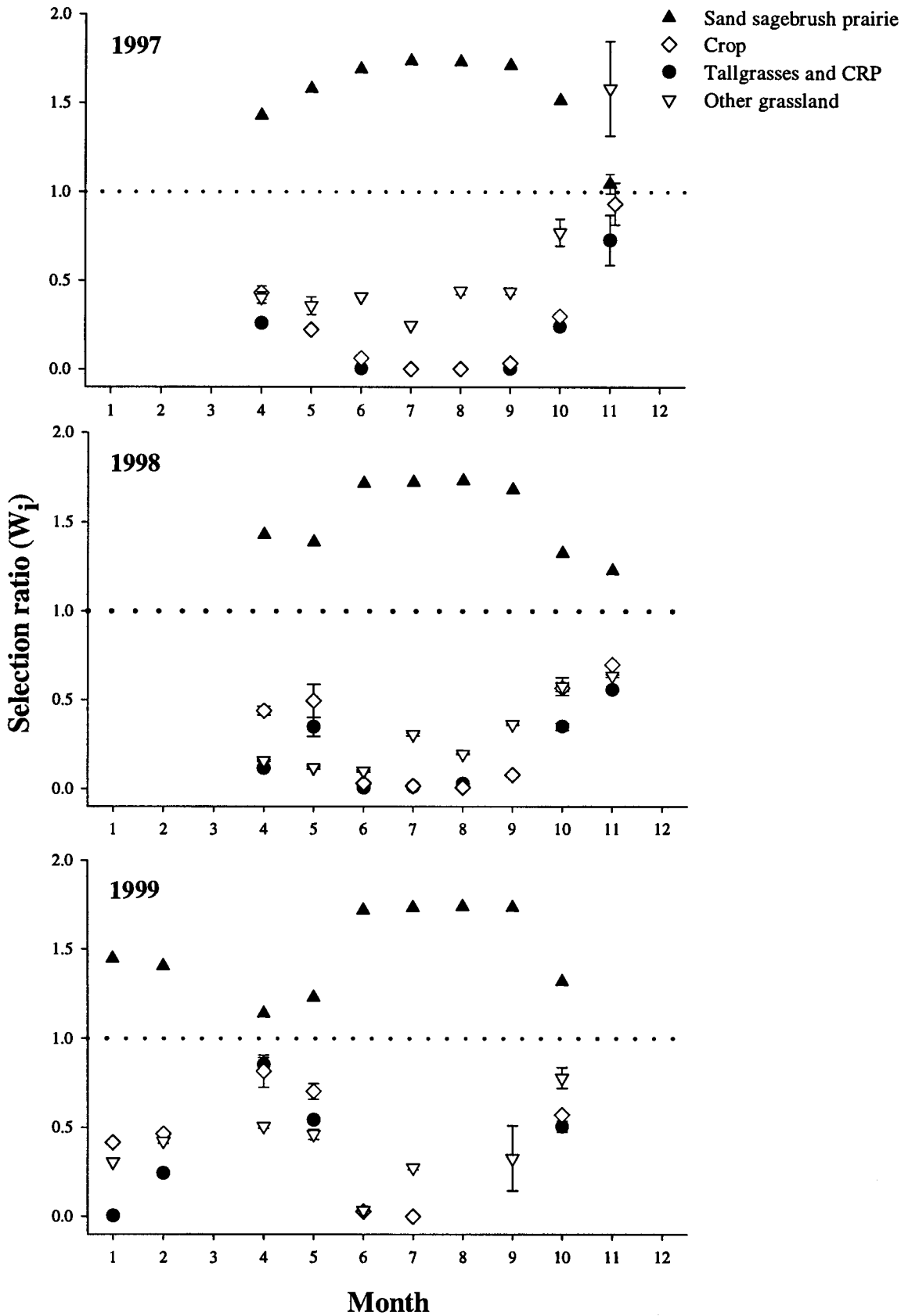

1997
1998
1999
Sand sagebrush prairie
Crop
Tallgrasses and CRP
Other grassland
Selection ratio (W_i)
Month
12
10
8
6
4
1
0
1 2 3 4 5 6 7 8 9 10 11 12

Figure 8. Habitat selection ratios (W_is) and 95% confidence intervals (error bars) for habitats available to male lesser prairie-chickens at level 2 in southwestern Kansas, 1997 through 1999. Month 1 is January, 2 is February, etc.


Sand sagebrush prairie
Crop
Tallgrasses and CRP
Other grassland
1997
1998
1999
Selection ratio (W_i)
Month
2.0
1.5
1.0
0.5
0.0
1 2 3 4 5 6 7 8 9 10 11 12

SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF LESSER PRAIRIE-CHICKENS IN SOUTHWESTERN KANSAS

Abstract: Lesser prairie-chicken populations in southwestern Kansas declined for nearly 20 years in association with loss and fragmentation of breeding habitat to center-pivot irrigated agriculture. The number of birds continued to decline despite an apparent drop in the rate of habitat loss during the 1980s. Survival is of obvious importance in population dynamics and also serves as an indicator of fitness for individuals in a particular habitat. Two hundred eighty-one (196 male and 85 female) individual lesser prairie-chickens were captured on leks, banded, and released from 1997 through 1999. One hundred sixty radio transmitters were placed on lesser prairie-chickens (76 on males and 84 on females) during spring, and survival of these birds was monitored daily from spring through fall (1 April through 30 September) over 3 consecutive years. Eleven different models were fit to the spring through fall data using Program MARK. Their usefulness then was ranked using a variant of Akaike's Information Criterion (AIC_c), and the subset of competing models was used to obtain survival estimates. Only 1 model was considered a competing model, and this selected model of survival estimated 6 survival parameters (1 for each month). The model-conditional estimate of survival for the spring through fall interval was 0.74 (95% CI = 0.65 to 0.81). Most (>70% of the total) mortality from April through November was due to predation, primarily by mammals, during May and June. Twelve additional transmitters were deployed on males in fall 1998, and annual survival was estimated from a composite data set of these birds and male lesser prairie-chickens radio-marked in spring 1998. The selected best model from the spring through fall data was fit to the composite data to obtain an estimate of annual

survival. Few mortalities were recorded for fall-trapped birds from fall 1998 through spring 1999, and annual survival was estimated at 0.57 (95% CI = 0.35 to 0.76). An attempt was made to obtain an additional estimate of annual survival from a joint live recapture and band recovery model for males. Because of the small number of releases and the short time frame over which recaptures and recoveries were recorded, the joint model had little utility for estimating annual survival. Survival model selection results for the spring through fall data suggested that survival varied across months, but probably did not differ appreciably between males and females or across years during this study. Estimates of spring through fall and annual survival rates in this study were similar to or higher than those of lesser prairie-chickens and other prairie grouse studied elsewhere. These results suggest that low reproduction rather than low adult survival limits lesser prairie-chicken populations in southwestern Kansas. Future research should focus on finding ways to increase reproductive success.

Key words: lesser prairie-chicken, model selection, mortality, survival, *Tympanuchus pallidicinctus*

INTRODUCTION

Lesser prairie-chickens have experienced dramatic rangewide declines since the early 1900s (Taylor and Guthery 1980). These declines prompted the Colorado Biodiversity Legal Foundation to petition the U. S. Fish and Wildlife Service (USFWS) to list the lesser prairie-chicken as a threatened species under the provisions of the Endangered Species Act in 1995. The USFWS issued a finding that stated listing the

lesser prairie-chicken as threatened was "warranted but precluded" (U. S. Department of the Interior, Fish and Wildlife Service 1998).

In Kansas, lesser prairie-chicken populations declined from 1965 (when lek surveys began) to the mid-1990s (Jensen et al. In Press). The development of center-pivot irrigation systems in the late 1960s permitted the conversion of large tracts of previously untillable sand sagebrush prairie (preferred lesser prairie-chicken habitat in southwestern Kansas) to cropland. Each of these center-pivot systems irrigates approximately 64.8 ha. After peaking in the mid-1970s, populations of lesser prairie-chickens declined in concert with conversion of sand sagebrush (*Artemisia filifolia*) prairie habitat to center-pivot irrigated crop fields (Fig. 1). Although the rate of habitat loss appeared to slow in the early 1980s, populations continued to decline.

Survival rates are of obvious importance in population dynamics of all organisms, because survival is 1 of several vital rates that directly affect population size (Pollock et al. 1990). When populations decline, death and emigration have exceeded reproduction and immigration. Few studies of lesser prairie-chickens have estimated survival and none have done so for lesser prairie-chickens inhabiting sand sagebrush rangeland. The objective of this study was to obtain estimates of lesser prairie-chicken survival and gather cause-specific mortality data in sand sagebrush rangelands fragmented by rowcrop agriculture.

STUDY AREA

The primary study area was a 5,760-ha fragment of sand sagebrush rangeland immediately south of the Arkansas River in western Finney County of southwestern

Kansas. The area was vegetated primarily by sand sagebrush, blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), paspalum (*Paspalum* sp.), bluestem grasses (*Andropogon* spp.), western ragweed (*Ambrosia psilostachya*), sunflowers (*Helianthus* spp.), and Russian-thistle (*Salsola iberica*). Prickly pear cactus (*Opuntia* sp.) and yucca (soapweed) (*Yucca glauca*) were interspersed throughout. Buffalo-gourd (*Cucurbita foetidissima*) and purple poppy mallow (*Callirhoe involucrata*) were common in disturbed areas. Soils were in the Tivoli-Vona association and in the choppy sands range site category (U. S. Department of Agriculture 1965). Primary land uses were grazing by cattle (from May 1 through October 1) and petroleum production. Research also was conducted in sand sagebrush prairie fragments separated from the primary study area by cultivated fields. Vegetation and soils were similar in these other fragments but some contained scattered sand plum (*Prunus angustifolia*) thickets in addition to sand sagebrush.

Over the past 30 years, the area received an average of 50 cm of annual precipitation with 74 % occurring between March and August. During this study (1997 through 1999) the area received an average of 55 cm of precipitation annually (U. S. Department of Commerce 1999).

METHODS

Capture, Marking, and Radio Telemetry

Male and female lesser prairie-chickens were captured on 11 leks during spring (1997, 1998, and 1999) or fall (1998 only) using walk-in traps, marked with serially numbered aluminum leg bands, and released at the capture site. A sample of these birds

was fitted with 12-g necklace transmitters equipped with 8-hour inactivity (mortality) switches and a projected battery life of 180 days (6 months). Spring trapping began the last week of March each year and usually ended by mid-April. Fall trapping was begun in late September and ended in mid-October. Radio-marked birds were monitored daily with truck-mounted telemetry equipment until they died, left the primary study area, or transmitter batteries were depleted. Telemetry equipment mounted on a fixed-wing aircraft was used to search for radio-marked prairie-chickens that were suspected of emigrating from the primary study area. Birds located from the aircraft off the primary study area were monitored at approximately 1-week intervals.

Survival Modeling

Encounters of radio-marked birds were considered to be known-fate data (White and Burnham 1999). Lesser prairie-chickens that were suspected of emigrating from the primary study area (primarily females) were censored only if they were not located during aerial searches. Those that were not located from the air were censored at the time of last radio contact on the primary study area. Lesser prairie-chickens that were located off the primary study area were considered at risk until tracking effort for those birds was terminated following nesting or brood-rearing. Implicit is the assumption that relocation probability for a radio-marked bird was independent of survival (i.e., predators did not destroy transmitters and mortality signals were as likely to be detected as normal signals).

Spring Through Fall Estimates.--Survival and mortality data of radio-marked lesser prairie-chickens were summarized by sex and year prior to analysis for 26 weekly time intervals beginning approximately 1 April and ending 30 September each year. Generally, these birds were captured and radio-marked in the spring of the year, but

males trapped in fall 1998 that had survived over winter were allowed to enter the 1999 data set as they were recaptured during that spring. Fall-trapped males that survived over winter but were not recaptured were included in the analysis as if they had been recaptured at the beginning of trapping in 1999. For modeling purposes, survival of radio-marked birds was considered independent of capture history.

Because appropriate estimates of survival are model-dependent, the question of what model to use is at least as important as obtaining estimates from a given model (Burnham and Anderson 1998). Eleven survival models for these data were considered *a priori*, including a model with only 1 parameter representing a constant survival rate over time for both sexes. These models incorporated various combinations of 4 variables, as follows. Habitat selection ratios for sand sagebrush prairie (W_is; Manly et al. 1993, Chapter 4) were used as a variable. These ratios were calculated separately for each sex, month, and year, and therefore the variable "W_i" represented the manner in which males and females utilized the available habitat across months for 3 different years. Models with the variable "sex" estimated separate survival parameters for males and females, and the 2 remaining variables were generic time effects ("month" and "year").

A smaller group of competing models was selected from the 11 original models based on a variant of Akaike's Information Criterion (AIC_c). The model with the lowest AIC_c was selected as the "best" model in the set of candidate models. Because of inherent uncertainty in the results of model selection, the remaining models were ranked from best to worst based on the difference in values of AIC_c (ΔAIC_cs) between each remaining model and the selected best model. Models with ΔAIC_cs < 2.00 were considered competing models (Burnham and Anderson 1998). Model-conditional

survival estimates and confidence intervals then were obtained from each of the competing models. Spring through fall survival and ΔAIC_c values were estimated in Program MARK (White and Burnham 1999).

Annual Estimates.--A composite data set of males radio-marked in spring and fall 1998 was used to obtain 1 estimate of annual survival. Fall trapping in 1998 coincided with the depletion of batteries in some of the spring-deployed transmitters. Fall-trapped males were allowed to enter the data set as they were captured and marked and spring-trapped birds were censored as their transmitters failed. These data also were summarized at weekly intervals, but data began in March 1998 when the first male was captured that spring and ended when trapping began again in spring 1999.

Rather than following model selection procedures employed for the spring through fall data, only those models that were considered competing models for the spring through fall data were used for the annual composite data. Therefore, rather than focusing on determining the most appropriate model for these limited data, it was assumed that models selected for a larger data set were appropriate.

A second estimate of annual survival was obtained from a joint live-recapture and band recovery model (Burnham et al. 1993). Because trapping efforts primarily targeted leks at which it was felt captures of hens would be maximized (i.e., the most active leks with the most males), a different group of leks was trapped upon during each encounter occasion. Because most (but certainly not all) males probably are faithful to a single lek throughout their lives (Chapter 4), focusing trapping efforts at different leks among encounter occasions alters recapture probabilities. Also, females are re-encountered only rarely because they spend less time at leks than do males (Campbell 1972). Therefore,

only data on male recaptures at the 4 leks that were trapped upon during all encounter occasions (continuously trapped leks) were analyzed.

Band recoveries from dead birds were obtained in 2 ways. Concurrent research on the internal parasites of lesser prairie-chickens led to the organization of hunting trips to collect birds during the regular Kansas hunting season (1 December through 31 January), and all birds harvested during these outings were examined for bands. Males also were collected from leks during late May 1998 after trapping efforts had concluded. Banded birds collected in May 1998 were categorized as losses on capture if they had been captured (or recaptured) during spring 1998. They were categorized as dying during the spring to fall interval of 1998 if they had been marked in spring 1997, but were not recaptured during spring 1998. Again, only those collected males that were marked at the 4 continuously trapped leks were included in the data analyzed.

Live encounter occasions were not equally spaced through time. The first interval length (in years) was 1.00, and the second and third intervals both were 0.50. Because data for the joint model ended at the last live encounter occasion (spring 1999 trapping), the final time interval was set to a length near 0.00, the last reporting probability was set to 0.00, and survival for the last interval was set to 1.00 to force more appropriate estimation of the remaining parameters.

Mortality Causes

Cause-specific mortality data were obtained from male and female lesser prairie-chickens radio-marked during spring and fall. Mortality signals were investigated immediately after detection to determine proximate causes of mortality. Causes of death were recorded as mammalian predation, raptor predation, accidental, or unknown. The

presence of crushed and broken bones and feathers, or body feathers and no carcass, at the transmitter recovery site was considered evidence of mammalian predation. Presence of a partial carcass from which feathers had been plucked and flesh had been peeled away was considered evidence of raptor predation. Other evidence at the transmitter recovery site (e.g., whether the carcass had been buried, disturbance to the vegetation, mammal tracks, raptor feces, etc.) also was used to elucidate predator type. Lesser prairie-chickens that apparently were killed when they struck powerlines in flight or killed by farming activities were categorized as accidental mortalities. In cases where predator type or cause of death was questionable based on evidence at the recovery site, proximate causes of death were listed as unknown.

RESULTS

Three hundred fifty captures of lesser prairie-chickens were recorded, and 281 individual lesser prairie-chickens (196 males and 85 females) were banded and released, during 4 encounter occasions over 3 years (Table 1). Twelve losses on capture (all males) and 57 recaptures (54 of males and 3 of females) were recorded. One hundred sixty transmitters were placed on spring-trapped birds (76 on males and 84 on females), and 12 additional transmitters were deployed on males in fall 1998 (Table 2). Six individuals (3 males and 3 females) were radio-marked twice.

Spring Through Fall Survival

The selected best model of survival ($\Delta AIC_c = 0.00$) for the 1 April through 30 September data estimated 6 separate survival parameters, 1 for each "month". The estimate of survival for the spring through fall period obtained using this model was 0.74

(95% CI = 0.65 to 0.81). None of the remaining models had ΔAIC_cs < 2.00, and therefore none were considered competing models (Table 3).

Annual Survival

Survival of radio-marked males from March 1998 to March 1999 was estimated using the selected best model for the spring through fall data. The estimate of annual survival from that 12-parameter model was 0.57 (95% CI = 0.35 to 0.76).

Approximately one-half of the males that were banded and released were captured at the 4 continuously trapped leks (Table 4). The estimates of survival from the joint live-recapture and band recovery model were 0.47 (95% CI = 0.26 to 0.69) , 0.29 (95% CI = 0.10 to 0.61), and 0.80 (95% CI = 0.00 to 1.00) for the first, second, and third time intervals, respectively. The first value is an estimate of annual survival from spring 1997 to spring 1998, but the second and third estimates are for 0.5-year periods (spring 1998 to fall 1998 and fall 1998 to spring 1999, respectively). Therefore, the product of the second and third estimates (0.23) is a second estimate of annual survival.

Cause-Specific Mortality

Mortalities were recorded for 44 radio-marked lesser prairie-chickens during this study (25 males and 19 females). Thirty-seven of these birds (18 males and 19 females) died between 1 April and 30 November, the period for which the most data were available. The 7 remaining males died before 1 April (1 in March 1997 and 3 in March 1999) or after 30 November (1 each in December 1998, January 1999, and February 1999).

Of the 37 mortalities recorded between 1 April and 30 November, 25 (67.6%) were attributed to mammalian predation, and 15 of these mortalities were recorded during

May and June (Table 5). An additional 5 mortalities (13.5%) were attributed to raptor predation, and 4 of these also occurred during May and June. Of the 19 females that died from April through November, 6 were killed on their nests and 4 were killed while raising broods. One of the females that was killed on its nest apparently was struck by a hay-mowing machine (the only female to nest in an agricultural field), but the other 5 deaths were attributed to mammalian predators.

Only 2 mortalities (1 male and 1 female) from 1 April to 30 November were attributed to accidents. The female death is described above and the male struck a utility line in October 1998 while flying between sand sagebrush prairie and a crop field in which he regularly fed.

The causes of 5 deaths were recorded as unknown. One partial carcass was recovered near a utility line and could easily have been an accidental death that was scavenged. Another partial carcass was recovered in the prairie interior. Two transmitters were recovered on mortality mode, but no carcass and only a few feathers were found at the recovery sites. The remaining bird was found as a whole carcass; no external wounds were visible, and the carcass was found in a crouching position when it was recovered from under a sagebrush plant. This carcass was frozen and delivered to the College of Veterinary Medicine at Kansas State University for necropsy, but results of the necropsy were inconclusive.

The 7 deaths of males that occurred outside of the April through November period were due to a variety of causes. Five were attributed to by mammalian predation, 1 to raptor predation, and 1 apparently struck a utility line. Four of these mortalities were recorded in late March.

Only 3 transmitter recoveries were made outside of sand sagebrush prairie. Two males were recovered at the edge of center-pivot irrigated crop fields adjacent to sand sagebrush prairie and the female killed by the hay mower was recovered at its nest site.

DISCUSSION

The results of the model selection process for the spring through fall data suggested that survival rates from April through September varied across months, but did not differ appreciably between males and females or among years during this study. Those data also did not support the hypothesis that survival would vary with the habitat selection ratios for sand sagebrush prairie. Essentially, the inference with respect to the models incorporating the habitat selection ratios is that survival probably is independent of habitat use. It may also be reasonable to interpret the habitat selection ratios as a biological time effect. Because the W_i for sand sagebrush prairie changes through time, it probably reflects time-of-year or season, as perceived by lesser prairie-chickens, more objectively than a non-biological time effect such as "month" or "year". However, despite having only 2 parameters, the model with only W_i (and an intercept term) had a rather high ΔAIC_c value (5.58), and was not as useful as the models with more parameters that incorporated generic time effects. Habitat use may affect an individual's probability of surviving. Such effects cannot be detected using the approach taken here, because the selection ratios represent habitat use of the population, and thus are not specific for individuals. In the present situation, individual habitat use could not be used as a covariate, because individual covariates must remain constant throughout the period of interest and must be independent of survival. Because habitat use obviously changes

through time, individuals that died early would exhibit different average estimates of habitat use than those individuals that survived for longer periods of time. Thus, individual habitat use is confounded with time effects and the biological cause and effect of survival are inseparable. A compositional approach (Aebischer et al. 1993) may be useful for determining if survival and habitat use are related.

It is important to note that the spring through fall data did not support different estimates of survival for males and females despite the fact that the period encompassed the nesting and brood-rearing periods of 3 separate years. Higher mortality of nesting hens often is cited as an explanation for the apparently male-biased sex ratios of prairie grouse (Ammann 1957:94-95, Bergerud 1988:627, Campbell 1972). During the present study, males appeared just as likely as hens to experience mortality during the spring through fall interval. If survival rates of male and females differed, it seems that the April through September data would have reflected this and supported a model with sex as a variable. The results of the present study support Ammann's (1957:95) speculation that mortality of displaying males may offset selective mortality of nesting hens.

The estimate of annual survival from the composite data set of spring- and fall-trapped males probably is more useful than the estimates obtained from the joint model. It is speculated that lower rates of lek attendance for males in fall than in spring introduced serious bias into the estimate of survival for the second time interval (spring 1998 to fall 1998). Estimates of known fate survival for this same period (spring through fall) were much higher than that estimated by the joint model. The small numbers of released birds and the small number of encounter occasions likely further reduced precision and resulted in the absurd confidence interval for the third time interval.

Bergerud (1988:586-590) reviewed over 30 studies of North American grouse and determined that clutch sizes of grouse and annual mortality rates were positively correlated ($r = 0.76$). Based on this relationship, lesser prairie-chickens (with a clutch size of about 12 eggs) might be expected to exhibit annual survival rates of about 35 to 45%. No available estimates of survival for any species of prairie grouse exceed 50%, suggesting that annual survival of lesser prairie-chickens in the present study could be considered very high.

Merchant (1982) monitored the survival of 41 radio-marked female lesser prairie-chickens from spring through summer during a 2-year study in New Mexico. Due to emigration or radio failure, the fated of only 29 of these were known. Twelve were killed by predators and 17 survived. Roughly, this translates to a spring-summer survival rate of 59% for those females, considerably lower than the 74% spring through fall survival estimate obtained in the present study. Merchant (1982) speculated that radio-marking may have increased mortality slightly.

Campbell (1972:694) estimated annual survival of male lesser prairie-chickens from recaptures at 3 continuously trapped leks at approximately 35%, but noted that not accounting for recapture probability may have resulted in underestimating survival "possibly by 5 to 10 percent." If Campbell's estimate is increased by 10%, it still is lower than that the annual estimate obtained from the composite data set of radio-marked males in this study. However, the wide confidence intervals around the present estimate include his adjusted value.

Robel et al. (1972) banded 5,680 sharp-tailed grouse (*Tympanuchus phasianellus*) in South Dakota on over 5 winters and estimated annual survival of both sexes at 29 and

25% from recaptures and hunter band returns, respectively. Amman (1957) estimated annual survival of sharp-tailed grouse in Michigan at 40%. Both of these estimates are lower than that obtained in the present study.

During their 22-year study in Wisconsin, Hamerstrom and Hamerstrom (1973) estimated an average annual survival rate of greater prairie-chickens (*Tympanuchus cupido*) at 47% for males and 44% for females using mark-resighting techniques. They estimated survival for both sexes combined at 46%.

Cause-specific mortality data collected in the present study was similar to that reported by Merchant (1982) and Giesen (1994) for female lesser prairie-chickens in New Mexico and Colorado, respectively. Eleven of the 12 mortalities recorded by Merchant (1982) were due to mammalian predation with the remaining mortality attributed to avian predation. Giesen (1994) reported that 20 of 76 radio-marked hens in southeastern Colorado were killed by mammalian and avian predators, but did not specify what proportions were attributed to each.

Male display begins as early as late February and continues through late May. Hens begin nesting April and May, and are incubating and raising broods in May and June (Copelin 1963). Although May and June are the same period during which the most radio-marked birds were followed, both sexes probably were most susceptible to mammalian predation during this time (Ammann 1957, Bergerud 1988).

Avian predation occurred far less frequently than mammalian predation in this study. This most likely is attributable to lower raptor populations during summer than winter, and the absence of what Bergerud (1988:621-622) termed "effective" grouse predators, such as large falcons and accipiters, in lesser prairie-chicken range.

MANAGEMENT IMPLICATIONS

Survival of lesser prairie-chickens was similar to or higher than that observed in stable prairie grouse populations. It seems unlikely that the recent decline of lesser prairie-chickens in southwestern Kansas was a result of low adult survival. These results, and the results of other research (Bergerud 1988, Morrow et al. 1996, Wisdom and Mills 1997), suggest that low reproductive success limits prairie grouse populations. If managers wish to increase fall populations of lesser prairie-chickens in remaining sand sagebrush areas of southwestern Kansas, increasing nest success and brood survival should be the primary goal.

Because most of the remaining lesser prairie-chicken habitat in southwestern Kansas is privately owned rangeland, there appears to be little opportunity to directly manage the remaining populations. The KDWP probably can only directly affect adult survival through manipulation of hunting regulations. Daily bag limits and season lengths already have been reduced, and limiting the consumptive use of lesser prairie-chickens further probably would do little to increase populations. Future research should focus on finding creative and feasible means of increasing nest success that would not reduce the financial income of private landowners. Offering payments to landowners for implementing range management practices that increase nesting cover may be one way of enhancing populations. Obviously, there is an upper limit to lesser prairie-chicken densities in remaining habitats, and habitat restoration should be pursued when feasible.

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Table 1. Numbers of male and female lesser prairie-chickens banded and released at 11leks in southwestern Kansas, 1997 through 1999.

Sex	1997 spring	1998 spring	1998 fall	1999 spring	Total
Males	75	73	9	39	196
Females	23	30	1	31	85
Total	98	103	10	70	281

Table 2. Number of transmitters deployed on lesser prairie-chickens captured at 11 leks in southwestern Kansas, 1997 through 1999.

Sex	1997 spring	1998 spring	1998 fall	1999 spring	Total
Males	25	24	12	27	88
Females	23	27	0	34	84
Total	48	51	12	61	172

Table 3. Model names, ΔAIC_c values, model weights (AIC_c weight), and the number of parameters estimated for 11 models that were fit to known-fate survival data summarized at 7-day intervals from 1 April through 30 September for male and female lesser prairie-chickens in southwestern Kansas, 1997 through 1999. Model names show which variables were included in that model. Model S (.) estimated a constant survival rate over time for both sexes combined.

Model name	ΔAIC_c	AIC_c weight	Number of parameters
S (month)	0.00	0.519	6
S (year)	2.04	0.187	3
S (sex)	3.34	0.098	2
S (.)	3.95	0.072	1
S (sex*year)	5.12	0.040	6
S (W_i)	5.58	0.032	2
S (sex*month)	5.99	0.026	12
S (W_i*year)	6.04	0.025	5
S (month*year)	11.48	0.002	18
S (sex*month*year)	25.24	0.000	36
S (W_i*sex*month*year)	29.35	0.000	38

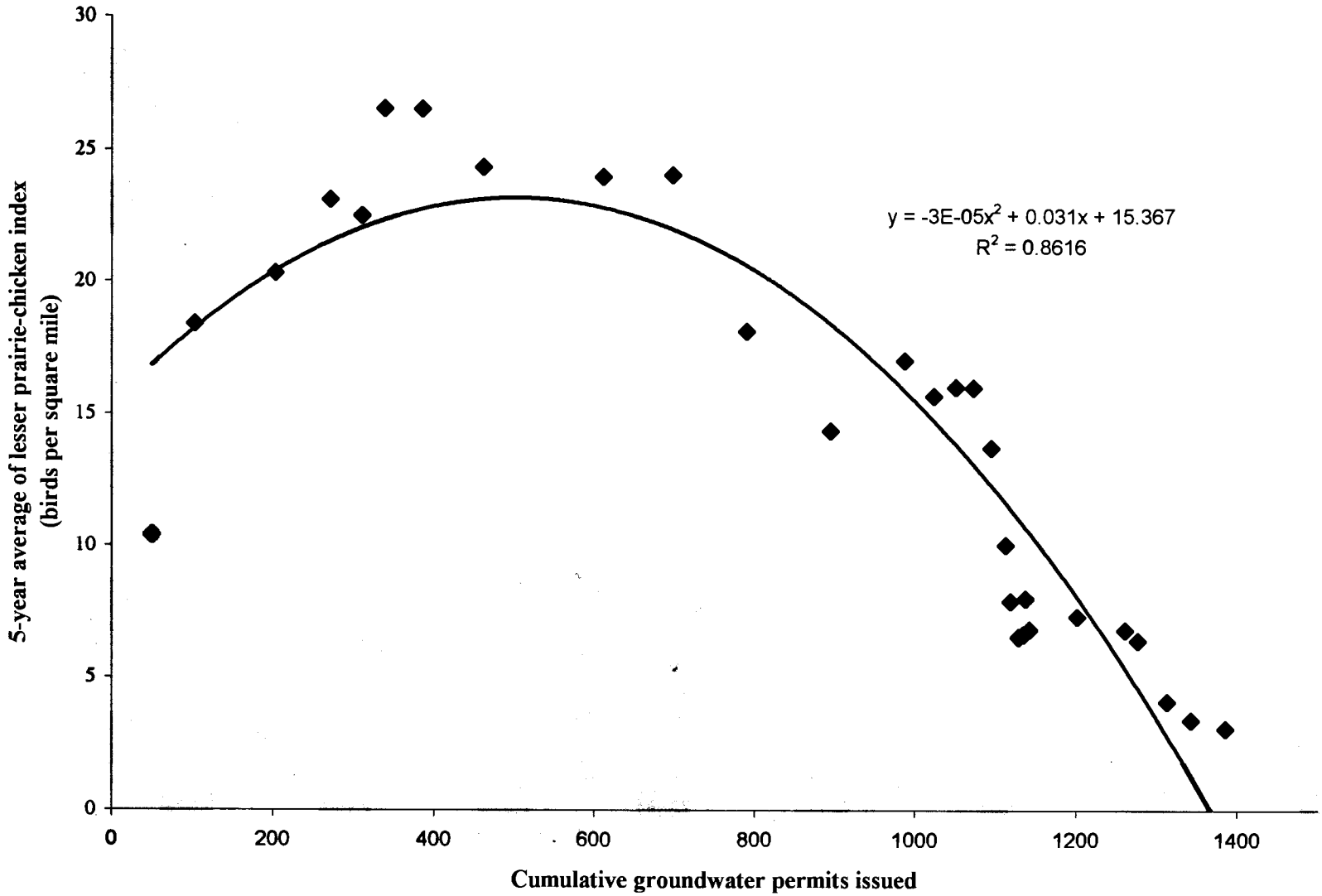
Table 4. Capture-recapture data (m array) for male lesser prairie-chickens banded, released, and re-encountered at 4 leks trapped upon during all 4 encounter occasions in southwestern Kansas, 1997 through 1999.

Banding occasion	Number released	Encounter occasion			Never recaptured
		1998 spring	1998 fall	1999 spring	
1997 spring	45	9	4	4	33
1998 spring	33		2	14	22
1998 fall	9			3	6

Table 5. Number of radio-marked male (M) and female (F) lesser prairie-chicken mortalities attributed to mammalian predation (mammal), raptor predation (raptor), accidents (accident), and unknown causes (unknown) during each month from 1 April through 30 November in southwestern Kansas, 1997 through 1999.

	Proximate cause of mortality									
	Mammal		Raptor		Accident		Unknown		Total	
Month	M	F	M	F	M	F	M	F	M	F
April	2	1	1	0	0	0	1	0	4	1
May	2	5	2	0	0	0	0	1	4	6
June	1	7	1	0	0	1	1	0	3	8
July	1	1	0	0	0	0	0	0	1	1
August	1	1	0	1	0	0	1	1	2	3
September	0	0	0	0	0	0	0	0	0	0
October	2	0	0	0	1	0	0	0	3	0
November	1	0	0	0	0	0	0	0	1	0
Total	10	15	4	1	1	1	3	2	18	19

Figure 1. Relationship between an index of habitat loss to center-pivot irrigation (number of groundwater use permits issued) and an index of lesser prairie-chicken abundance obtained from lek survey data (birds per square mile) for Finney County, Kansas 1965-1995.


y = -3E-05x2 + 0.031x + 15.367
R2 = 0.8616
5-year average of lesser prairie-chicken index
(birds per square mile)
Cumulative groundwater permits issued
0
5
10
15
20
25
30
0
200
400
600
800
1000
1200
1400

SUMMARY

1) Mean Acrididae biomass, total invertebrate biomass, and the proportion of total invertebrate biomass comprised of Acrididae did not differ significantly between use and independent non-use areas but mean Acrididae and total invertebrate biomass were greater in use vs. paired non-use areas. These results suggest that macrohabitat selection of lesser prairie-chickens during summer probably occurs independently of invertebrate food resources, but microhabitat selection within home ranges may be dependent upon the quantity and family composition of invertebrates in those habitats. Mean Acrididae and total invertebrate biomass were highest in areas with low sand sagebrush cover, but no significant differences in mean Acrididae and total invertebrate biomass were detected among areas with low, moderate, or high sand sagebrush cover. Regression model selection suggested that forb cover was the most important predictor of Acrididae and total invertebrate biomass.
2) Dispersal distances of 2 males marked as chicks and recaptured at leks were less than 2.5 km, and neither of these males was captured at the lek nearest their brood range. Lesser prairie-chicken chick survival to 60 d post-hatch was estimated at 0.19. Chick survival was overestimated by comparing mean brood size in July to mean clutch size. Daily survival rates of chicks in individual broods were not statistically correlated with estimated daily movements or estimates of standing crops of invertebrate biomass in brood ranges. If survival of lesser prairie-chicken chicks is related to movements or invertebrate biomass, larger sample sizes may be needed to detect these relationships.

3) Mammalian predators were responsible for at least 60% of the nest failures over 3 years. Coyotes, striped skunks, and bullsnakes probably were responsible for nearly all depredation events, but coyotes were most likely the primary depredators of lesser prairie-chicken nests. Reduction of mammal populations or increasing nest cover likely would decrease depredation rates.

4) Only 2 of 76 radio-marked male lesser prairie-chickens permanently emigrated from the primary study area. Both of these males left the primary study area during late March or early April. Interlek movements were recorded for 10 males (20.8% of those recaptured). Male lesser prairie-chickens exhibited strong selection for sand sagebrush prairie habitats during 24 of 25 months in which selection was evaluated. Most male lesser prairie-chickens appeared to be permanent residents of the habitat fragment in which they were captured, and remaining areas of sand sagebrush habitat should be protected.

5) Survival of male and female lesser prairie-chickens from spring through fall was estimated at 0.74. Annual survival was estimated at 0.57 and 0.47 from known-fate telemetry data and live-recapture dead-recovery data, respectively. Survival model selection suggested that survival varies across months, but did not support different survival rates for males and females or variation in survival across years. Most (>70% of the total) mortality of adult lesser prairie-chickens recorded between 1 April and 30 November over 3 years was attributed to mammalian and avian predation. This is the first estimate of annual survival for any species of prairie grouse to exceed 0.50. Low adult survival likely was not responsible for the recent declines in numbers of lesser prairie-chickens in southwestern Kansas.

APPENDIX A

Manuscript submitted 9 November 1999 to *Poultry Science* and accepted 9 March 2000 (format has been altered to conform to thesis guidelines, but style is largely that required by *Poultry Science*).

PASSIVE INTEGRATED TRANSPONDERS AS MARKERS FOR CHICKS

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Abstract: Passive integrated transponder (PIT) tags have been used to mark a variety of organisms and have potential for marking poultry chicks. We examined the effects of PIT tags subcutaneously implanted in 3- and 7-d-old leghorn chicks and found no significant differences over 40 d in survival or rate of daily body mass gain among tagged chicks and controls. The PIT-tagged birds were not more susceptible to pecking by other chicks than controls. No birds died, but 1 of 20 chicks lost its tag during the study. We believe that PIT tags provide a viable technique for marking individual juvenile birds, if tag loss can be reduced. Costs may be prohibitive in studies involving large numbers of birds.

Key words: passive integrated transponders, tag retention, survival, body mass gain, leghorns

INTRODUCTION

Many techniques are available to individually mark birds, including numbered leg bands, patagial tags, nasal tags, and branding or tattooing. Serially numbered leg bands and patagial tags are employed most commonly; however, these can cause tissue malformation as juvenile birds outgrow the band or tag and may contribute to increased

pecking of marked birds by other birds in an enclosure (Hannon et al.,1990; Jackson and Bünger, 1993).

Passive integrated transponder (PIT) tags consist of an electromagnetic coil, tuning capacitor, and microchip sealed in a biologically inert glass capsule. When the transponder is activated by a low-frequency radio signal emitted by the PIT tag reader, the tag transmits a unique, 10-digit, alphanumeric code to the reading system. These tags were developed initially to mark fishes (D. Oliver, Biomark, Inc., Boise, ID 83709, personal communication) and since have been used to mark various wild and captive animals including reptiles, amphibians, mammals, and birds (Elbin and Burger 1994). Use of PIT tags in birds has been limited (Jackson and Bünger, 1993; Becker and Wendeln, 1997; Carver et al., 1999), and we are not aware of any published reports of PIT tag use in chickens.

We initiated this study to determine if PIT tags were suitable for marking poultry chicks. We evaluated the effects of subcutaneously implanted PIT tags on survival, body mass gain, and pecking behavior, and determined the retention of tags over a 40-d period.

METHODS

We obtained 50, 1-d-old, male, leghorn chicks (Hy-Line W-36) from a commercial hatchery. We randomly assigned 10 chicks to each of three experimental groups; a 3-d implant group (3-d group), a 7-d implant group (7-d group), and an unimplanted group (control group). Numbered, size 4, plastic, leg bands were placed on all chicks so we could identify individuals in the control group. We replaced these leg

bands with larger sizes as chicks outgrew them. Birds were housed by treatment group in standard Petersime brooder batteries and provided food and water ad libitum.

We used 11 × 2.5-mm PIT tags and implanted them with modified 10-cc syringes equipped with 12-ga hypodermic needles.[1] Needles and tags were disinfected with a 10% solution of Roecal® sterilant for 60 s and rinsed in sterile saline before each implant. Implant procedures were similar to procedures for standard vaccinations of 1-d-old chicks.

Two individuals performed the implantations. One held the chick and extended its neck, while the other lifted a flap of skin on the nape, inserted the needle anterior to posterior under the flap, and injected the tag by depressing the plunger of the syringe. The implant site was treated with Betadine® antiseptic to reduce risk of infection. The senior author performed all injections and had no prior experience in implanting tags.

The 3-d and 7-d groups were implanted with PIT tags at 3 and 7 d of age, respectively. Except for receiving an implant, the control group was handled like the other groups including extending the neck and application of Betadine® to the nape.

Body masses of individual birds in each treatment group were determined with an electronic balance to 0.10 g each day for 40 d. Initially, we observed birds daily for 1, 10-min interval to monitor instances of pecking at the implant sites. Pecking was minimal, so observations were terminated after 10 d. Tagged birds were scanned each day with a Destron-Fearing MPR HS-5900L portable PIT tag reader[3] to determine retention of implanted tags. Control group birds also were scanned to maintain consistent handling among treatment groups.

Mean initial and final body masses were compared among treatments using ANOVA. Rates of body mass gain were analyzed by fitting quadratic regression models with unstructured covariance matrices to account for increasing variation and repeated measures in mass changes over time (Wolfinger, 1996; Littel et al., 1996). Because the implants were made at two different times (3 and 7 d of age), three model fits and tests were done according to when tags were implanted. For example, to compare 3- and 7-d implant groups, body masses at day seven were subtracted from body masses at every subsequent day in both treatments, and these mass differences were used as 'data' in the analyses. Model fits and tests were done using Proc Mixed (SAS Institute, 1997). Numbers of pecking events associated with the implant site were not compared statistically, because we observed few pecking events and they occurred only on the day of tagging. Survival and tag retention rates were not compared statistically, because no chicks died and only one chick lost its tag during the study.

This study was conducted in accordance with the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (Federation of Animal Science Societies, 1999). Injections are accepted as standard animal husbandry practices. Experimental birds were euthanized with CO_2 at the end of the study.

RESULTS

The PIT-tagging did not affect rates of body mass gain of leghorns over a 40-d period. Mean beginning body masses (3-d-old birds; n = 10/group) were 55.7 (SE = 1.2), 53.8 (SE = 2.2), and 53.2 g (SE = 1.5) for the control, 3-d, and 7-d groups, respectively,

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[1, 3] Biomark, Inc., Boise, ID 83709.

and did not differ statistically ($P = 0.56$). Mean final body masses (43-d-old birds; n = 10/group) were 539.1 (SE = 17.4), 541.2 (SE = 25.4), and 563.6 g (SE = 20.2) for the control, 3-d, and 7-d groups, respectively, and did not differ statistically ($P = 0.67$). We found no differences in rates of daily body mass gain in pair-wise comparisons between the 3-d and 7-d groups ($P = 0.69$), the 3-d and control groups ($P = 0.59$), or the 7-d and control groups ($P = 0.85$).

The PIT tags did not contribute to aberrant pecking behavior. Pecking events associated with implant sites occurred on the day of tagging and in both the 3-d (three pecking events) and 7-d (one pecking event) groups. No other instances of pecking at the implant sites occurred during observation periods on any other day. No instances of nape pecking occurred in the control group.

No chicks died, but one of 10 birds in the 3-d group lost its PIT tag on day 8 of the 40-d study. No birds in the 7-d group lost tags. This represents an overall tag-loss rate of 5.0%. We assume that the lost tag exited through the insertion hole created by the needle during implant. We located the functional, lost tag in the dropping pan below the cage.

DISCUSSION

Our results support those of Carver et al. (1999), who tested PIT tags versus patagial tags in 0.5- to 0.6-h-old northern bobwhite (*Colinus virginianus*) chicks (n = 50/tag type) and found no differences in weekly body mass gains, survival, or tag retention rates over 84 d. Passive integrated transponder tagging did not appear to affect behavior (e.g., pecking) in bobwhites after the first day of marking. Our results also

support those of Jackson and Bünger (1993), who tested PIT tags in turkey poults and reported no apparent differences in behavior (pecking) and no differences in average masses of PIT-tagged poults and controls at 84 d.

We observed a rate of PIT tag loss similar to loss rates reported for patagial tags in bobwhites (4.6%) by Carver et al. (1999) and in willow ptarmigan (*Lagopus lagopus*) (2.1 to 6.5%) reported by Hannon et al. (1990). We speculate that the tag loss in our study was due to implanting the tag too close to the entrance wound created by the needle probably because of the chick's small size (51.5 g; third smallest in 3-d group) and inexperience of the individual performing the implants. During this and other studies, we found implanting tags to be more difficult in small chicks before we gained PIT-tagging experience.

Becker and Wendeln (1997) were able to reduce tag losses in adult common terns (*Sterna hirundo*) by sealing the insertion hole with surgical glue. Surgical glue applied to the implant site also may reduce or eliminate tag losses in poultry chicks (Becker and Wendeln, 1997; Carver et al. 1999). Passive integrated transponder tags are now available with a polypropylene antimigration cap designed to reduce s.c. tag migration in large animals. These also might prevent tag migration toward the insertion hole and subsequent tag loss in poultry chicks (D. Park, Biomark, Inc., Boise, ID, 83709, personal communication). In some cases, extra chicks could be tagged in anticipation of tag losses, and chicks that lose tags then could be culled to improve uniformity of experimental groups. Tag losses also might be reduced by providing researchers the opportunity to practice the implanting procedure prior to placing implants in study birds. Carver et al. (1999) practiced the implant procedure on 50 chicks prior to their

experiment but still observed a PIT tag loss of 5.1 %. However, those bobwhite chicks had an average body mass of <10.0 g at time of implanting. Because implanting tags in small birds may be more difficult, the opportunity to practice may have averted even greater potential tag losses.

During observation periods, we noted that the four instances of implant-site pecking were targeted at the reddish-brown stain left by the Betadine® antiseptic rather than any visible alteration to appearance caused by the PIT tag. However, no instances of pecking occurred at these application sites on control chicks. Nonetheless, eliminating use of antiseptic or using a transparent or neutral-colored antiseptic might reduce or eliminate implant-site pecking in leghorns.

Passive integrated transponder tags generally cost about $5.50/tag versus $0.16/tag and $0.07/tag for leg bands and patagial tags, respectively (1999; U. S. currency), and antimigration caps add $0.10/tag to the cost. The PIT tag readers range in price from $375.00 to $575.00 for portable, hand-held models and from $2,500.00 to $10,000.00 for fully automated remote systems. These high-cost remote systems can automatically reference tag numbers in a PC database, thus, allowing researchers to add new data without the need to manually look up band numbers (D. Park, Biomark, Inc., Boise, ID 83709, personal communication).

Passive integrated transponder tags can be read quickly and easily with fewer chances for errors caused by misreading leg bands or patagial tags that can become worn, obscured by skin, or encrusted with feces. The tags are reusable and remain readable for approximately 50 yr (D. Park, Biomark, Inc., Boise, ID 83709, personal communication), allowing costs to be amortized over a long period of time. In our study, tags were located

easily and removed from euthanized chicks using a scalpel and forceps. In a similar study with captive, ring-necked pheasant chicks (*Phasianus colchicus*), PIT tags were removed from live birds with no apparent negative effects (R. Applegate, Kansas Department of Wildlife and Parks, Emporia, KS 66801; unpublished data).

We believe that PIT tags provide a viable method for marking poultry chicks. Although PIT tagging is more expensive than traditional marking methods, the additional costs may be justified in some research applications. Although PIT tag losses can be reduced by gaining experience in implant procedures, using PIT tags with antimigration caps, or sealing the insertion hole with surgical glue, we caution researchers about the potential for tag losses.

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APPENDIX B

Tables 3 through 10. Tabular results from Chapter 4. Sample sizes, means, standard errors, and medians for daily movement and monthly range data, and selection ratios (W_is) and 95% confidence intervals at level 1 and level 2 habitat availability for radio-marked male lesser prairie-chickens in southwestern Kansas, 1997 through 1999. Daily movements are pooled across birds.

SAS code used to summarize monthly range data, habitat use data, and calculate selection ratios follows Table 10.

Table 3. Daily movements (m) of radio-marked male lesser prairie-chickens in southwestern Kansas, 1997 through 1999.

	Year											
	1997				1998				1999			
Month	*n*	$\bar{x}$	SE	Median	*n*	$\bar{x}$	SE	Median	*n*	$\bar{x}$	SE	Median
January									54	616	78	488
February									39	733	101	604
March	140	607	47	435	52	1034	127	786	136	906	76	738
April	577	544	32	219	593	685	30	420	752	874	32	622
May	599	409	21	243	639	344	23	140	775	596	25	282
June	547	387	16	294	592	345	13	280	683	380	17	281
July	527	319	9	265	580	338	10	273	599	283	12	209
August	502	331	11	276	547	344	13	262	473	299	11	229
September	381	483	21	349	393	483	24	365	352	358	15	253
October	297	626	32	490	571	780	29	599	222	869	63	542
November	239	509	31	358	522	740	33	449	79	641	58	481
December	29	562	86	385	227	616	40	389	[a]			

[a] Data collection ended 30 November 1999

Table 4. Monthly ranges (ha) of *n* radio-marked male lesser prairie-chickens in southwestern Kansas, 1997 through 1999.

	Year											
	1997				1998				1999			
Month	*n*	$\bar{x}$	SE	Median	*n*	$\bar{x}$	SE	Median	*n*	$\bar{x}$	SE	Median
January	[a]								10	313	63	208
February									10	317	43	281
March												
April	14	65	16	50	19	145	27	137	23	158	23	140
May	18	45	14	19	21	61	22	12	25	92	9	95
June	17	149	28	97	19	134	35	88	22	106	19	77
July	17	112	18	89	19	114	16	90	19	83	11	80
August	16	117	19	94	17	127	20	106	13	62	9	53
September	14	169	26	144	14	202	69	129	11	112	33	80
October	5	220	11	228	12	428	64	401	6	621	241	409
November	2	299	188	299	17	443	110	292				
December												

[a] Blank spaces indicate inadequate numbers of radio locations for home range estimation

Table 5. Sample sizes (n = number of birds), selection ratios (W_is), and 95% confidence intervals (CI) for 4 habitat types available to radio-marked male lesser prairie-chickens at level 1 in southwestern Kansas, 1997. Habitat types are defined in Table 2 and displayed in Figure 5.

		Habitat type							
		Sand sagebrush prairie		Crop		Tallgrasses and CRP		Other grassland	
Month	n	W_i	CI	W_i	CI	W_i	CI	W_i	CI
April	14	8.215	8.070 - 8.360	0.218	0.208 - 0.227	0.069	0.068 - 0.069	0.076	0.074 - 0.077
May	18	9.089	8.969 - 9.209	0.113	0.112 - 0.114	[a]		0.067	0.065 - 0.069
June	17	9.723	9.714 – 9.731	0.032	0.032 - 0.032	0.001	0.001 - 0.001	0.077	0.076 - 0.077
July	14	9.991	9.991 – 9.991	0.000	0.000 - 0.000			0.047	0.046 - 0.047
August	16	9.969	9.968 – 9.969	0.001	0.001 - 0.001			0.083	0.082 - 0.084
September	14	9.843	9.836 – 9.850	0.017	0.017 - 0.017	0.001	0.001 - 0.001	0.082	0.082 - 0.083
October	5	8.711	8.707 – 8.716	0.151	0.151 - 0.151	0.064	0.063 - 0.065	0.145	0.142 - 0.148
November	2	6.018	4.182 -7.854	0.472	0.442 - 0.502	0.193	0.183 - 0.203	0.297	0.288 - 0.307

[a] Blank spaces indicate that the selection ratio is undefined because the habitat was not used by any individuals during the month

Table 6. Sample sizes (n = number of birds), selection ratios (W_is), and 95% confidence intervals (CI) for 4 habitat types available to radio-marked male lesser prairie-chickens at level 1 in southwestern Kansas, 1998. Habitat types are defined in Table 2 and displayed in Figure 5.

		Habitat type							
		Sand sagebrush prairie		Crop		Tallgrasses and CRP		Other grassland	
Month	n	W_i	CI	W_i	CI	W_i	CI	W_i	CI
April	19	8.224	8.202 - 8.245	0.222	0.216 - 0.228	0.031	0.031 - 0.031	0.030	0.030 - 0.030
May	21	7.968	7.868 - 8.069	0.250	0.227 - 0.274	0.092	0.089 - 0.096	0.022	0.022 - 0.023
June	19	9.879	9.881 - 9.876	0.016	0.016 - 0.016	0.002	0.002 - 0.002	0.019	0.019 - 0.019
July	19	9.919	9.917 - 9.921	0.008	0.008 - 0.008	0.003	0.003 - 0.003	0.058	0.057 - 0.058
August	17	9.960	9.959 - 9.960	0.004	0.004 - 0.004	0.008	0.008 - 0.008	0.037	0.037 - 0.037
September	14	9.669	9.661 - 9.676	0.040	0.040 - 0.040	[a]		0.068	0.068 - 0.068
October	12	7.632	7.514 - 7.750	0.287	0.283 - 0.292	0.093	0.092 - 0.094	0.108	0.107 - 0.110
November	17	7.070	7.033 - 7.108	0.353	0.353 - 0.354	0.148	0.147 - 0.148	0.120	0.120 - 0.120

[a] Blank spaces indicate that the selection ratio is undefined because the habitat was not used by any individuals during the month

Table 7. Sample sizes (n = number of birds), selection ratios (W_is), and 95% confidence intervals (CI) for 4 habitat types available to radio-marked male lesser prairie-chickens at level 1 in southwestern Kansas, 1999. Habitat types are defined in Table 2 and displayed in Figure 5.

		Habitat type							
		Sand sagebrush prairie		Crop		Tallgrasses and CRP		Other grassland	
Month	n	W_i	CI	W_i	CI	W_i	CI	W_i	CI
January	10	8.320	8.247 - 8.393	0.211	0.209 - 0.213	0.001	0.001 – 0.001	0.058	0.058 - 0.058
February	10	8.079	8.049 - 8.110	0.235	0.234 - 0.236	0.065	0.064 - 0.065	0.079	0.079 - 0.080
April	23	6.557	6.472 - 6.641	0.414	0.391 - 0.437	0.226	0.223 - 0.229	0.095	0.095 - 0.096
May	25	7.069	7.031 - 7.106	0.356	0.345 - 0.367	0.144	0.143 - 0.144	0.087	0.086 - 0.088
June	22	9.899	9.896 - 9.901	0.014	0.014 - 0.015	[a]		0.007	0.007 - 0.007
July	19	9.989	9.989 - 9.989	0.000	0.000 - 0.000			0.052	0.051 - 0.052
August	13	10.016	10.016 - 10.016						
September	11	9.986	9.985 - 9.986					0.062	0.055 - 0.068
October	6	7.577	7.403 - 7.750	0.289	0.287 - 0.291	0.134	0.132 - 0.136	0.147	0.145 - 0.149

[a] Blank spaces indicate that the selection ratio is undefined because the habitat was not used by any individuals during the month

Table 8. Sample sizes (n = number of birds), selection ratios (W_is), and 95% confidence intervals (CI) for 4 habitat types available to radio-marked male lesser prairie-chickens at level 2 in southwestern Kansas, 1997. Habitat types are defined in Table 2 and displayed in Figure 6.

		Habitat type							
		Sand sagebrush prairie		Crop		Tallgrasses and CRP		Other grassland	
Month	n	W_i	CI	W_i	CI	W_i	CI	W_i	CI
April	14	1.427	1.423 - 1.432	0.430	0.392 - 0.468	0.259	0.251 - 0.268	0.402	0.369 - 0.435
May	18	1.579	1.576 - 1.583	0.223	0.219 - 0.228	[a]		0.356	0.306 - 0.406
June	17	1.689	1.689 - 1.690	0.064	0.063 - 0.064	0.004	0.004 - 0.004	0.407	0.397 - 0.407
July	17	1.736	1.736 - 1.736	0.000	0.000 - 0.000			0.248	0.244 - 0.252
August	16	1.732	1.732 - 1.732	0.002	0.002 - 0.002			0.441	0.420 - 0.461
September	14	1.710	1.710 - 1.710	0.033	0.033 - 0.033	0.003	0.003 - 0.003	0.437	0.422 - 0.453
October	5	1.514	1.513 - 1.514	0.298	0.297 - 0.299	0.240	0.225 - 0.254	0.771	0.697 - 0.846
November	2	1.046	0.990 - 1.101	0.932	0.815 - 1.049	0.728	0.585 - 0.870	1.581	1.316 - 1.847

[a] Blank spaces indicate that the selection ratio is undefined because the habitat was not used by any individuals during the month

Table 9. Sample sizes (n = number of birds), selection ratios (W_is), and 95% confidence intervals (CI) for 4 habitat types available to radio-marked male lesser prairie-chickens at level 2 in southwestern Kansas, 1998. Habitat types are defined in Table 2 and displayed in Figure 6.

		Habitat type							
		Sand sagebrush prairie		Crop		Tallgrasses and CRP		Other grassland	
Month	n	W_i	CI	W_i	CI	W_i	CI	W_i	CI
April	19	1.429	1.428 - 1.429	0.439	0.415 - 0.463	0.116	0.115 - 0.117	0.159	0.154 - 0.164
May	21	1.384	1.381 - 1.387	0.494	0.402 - 0.586	0.348	0.296 - 0.400	0.119	0.112 - 0.127
June	19	1.716	1.716 - 1.716	0.032	0.032 - 0.032	0.006	0.006 - 0.006	0.101	0.096 - 0.107
July	19	1.723	1.723 - 1.723	0.017	0.017 - 0.017	0.012	0.012 - 0.012	0.307	0.298 - 0.315
August	17	1.730	1.730 - 1.730	0.008	0.008 - 0.008	0.029	0.028 - 0.029	0.197	0.193 - 0.201
September	14	1.680	1.680 - 1.680	0.078	0.078 - 0.078	[a]		0.362	0.357 - 0.368
October	12	1.326	1.323 - 1.330	0.568	0.551 - 0.585	0.350	0.331 - 0.370	0.576	0.526 - 0.626
November	17	1.228	1.227 - 1.230	0.698	0.697 - 0.699	0.557	0.554 - 0.560	0.637	0.630 - 0.644

[a] Blank spaces indicate that the selection ratio is undefined because the habitat was not used by any individuals during the month

Table 10. Sample sizes (n = number of birds), selection ratios (W_is), and 95% confidence intervals (CI) for 4 habitat types available to radio-marked male lesser prairie-chickens at level 2 in southwestern Kansas, 1999. Habitat types are defined in Table 2 and displayed in Figure 6.

		Habitat type							
		Sand sagebrush prairie		Crop		Tallgrasses and CRP		Other grassland	
Month	n	W_i	CI	W_i	CI	W_i	CI	W_i	CI
January	10	1.446	1.443 - 1.448	0.416	0.409 - 0.423	0.004	0.004 - 0.004	0.307	0.302 - 0.313
February	10	1.404	1.403 - 1.405	0.464	0.459 - 0.469	0.243	0.237 - 0.250	0.422	0.411 - 0.434
April	23	1.139	1.137 - 1.142	0.817	0.727 - 0.907	0.853	0.812 - 0.895	0.507	0.496 - 0.518
May	25	1.228	1.227 - 1.229	0.703	0.659 - 0.748	0.542	0.533 - 0.552	0.462	0.433 - 0.491
June	22	1.720	1.720 - 1.720	0.028	0.028 - 0.029	[a]		0.035	0.034 - 0.035
July	19	1.736	1.736 - 1.736	0.000	0.000 - 0.000			0.275	0.260 - 0.290
August	13	1.740	1.740 - 1.740						
September	11	1.735	1.735 - 1.735					0.328	0.145 - 0.510
October	6	1.316	1.311 - 1.322	0.571	0.562 - 0.579	0.506	0.475 - 0.537	0.780	0.721 - 0.838

[a] Blank spaces indicate that the selection ratio is undefined because the habitat was not used by any individuals during the month

```
/*SAS code used to summarize monthly range data and calculate selection ratio estimates*/
Title 'MANLY ET AL.(1993)HABITAT SELECTION ANALYSIS-LESSER PRAIRIE-CHICKEN DATA- W-47-R';
/*2 external files are required;*/
/*1 with habitat use data and 1 with availability data*/
/*user is required to specify alpha level for confidence intervals - near end of code*/
/*user is required to input total area of available habitat -- this is calculated
herein*/

dm 'output;clear;log;clear;';

options ls=80 ps=56;

/*"NON-HABITAT" and landcovers with obvious classification errors have been DELETED*/
/*deleted alliance codes are 11,27,29,32,33,42,81,82*/
/*note: grdcode is alliance code from GAP landcover map*/
/*note: newcode is alliance codes "pooled" into 4 habitat types*/
/*habitat types are sand sagebrush prairie (100), tallgrass and CRP (101), cropland
(102),*/
/*and other grassland (103)*/
/*Table 2 in text specifies which vegetation alliances are contained in each habitat*/

/*BEGIN SELECTION RATIO COMPUTATION*/

/*Get results of GIS query from text file*/
/*in this case home ranges overlayed on GAP landcover using UNION feature*/
/*in ArcView and queried for all polygons inside those
/*ranges-i.e., with probability =95*/

data habuse;
        infile 'C:\WINDOWS\Desktop\sasinput\newcodes97.prn';
        input grdcode newcode perim useha id month;
        drop perim;

proc sort data = habuse;
        by month id;

/*DETERMINE HOME RANGE SIZE OF EACH BIRD EACH MONTH (uplusj) */

     /*BY NEWCODE */

        proc univariate data=habuse noprint;
                var useha;
                by month id;
                output out=hrsize sum=uplusj;

        proc print data=hrsize;

/*print mean home range size (ha) by month*/
      proc univariate plot normal data=hrsize noprint;
                var uplusj;
                by month;
                output out=hrstats mean=mean stdmean=se n=n median=median;

        proc print data=hrstats;

/*Determine number of birds in data set for each month (N) */
```

```
        proc sort data=hrsize;
                by month;

        proc univariate data=hrsize noprint;
                var id;
                by month;
                output out=samplsiz n=N;

        proc print data=samplsiz;

/*Determine area of individual ranges in each HABITAT type (uij) */

        proc sort data = habuse;
                by newcode month id;

        proc univariate data=habuse noprint;
                var useha;
                by newcode month id;
                output out=induse sum=uij;

        proc print data=induse;

/*Determine total area of all individuals' ranges comprised of each HABITAT code
(uiplus)*/
        data uijs;
                set induse;

        proc sort data=uijs;
                by month newcode id;

        proc univariate data=uijs noprint;
                var uij;
                by month newcode;
                output out=alluse sum=uiplus;

        proc print data=alluse;

        /*Determine total area of all individuals' ranges (uplsplus)*/
        proc sort data=hrsize;
                by month;

        proc univariate data=hrsize noprint;
                var uplusj;
                by month;
                output out=allhr sum=uplsplus;

        proc print data=allhr;

/*PROPORTION OF EACH HABITAT TYPE AVAILABLE WITHIN 44km RADIUS*/

     /*BY NEWCODE */

        /*Get habitat polygon attributes from GAP landcover stored in text file*/
        /*in this case attributes of *.shp file of available habitat -- EDITED*/
```

```
        /*NON-HABITAT POLYS AND LANDCOVERS WITH OBVIOUS CLASSIFICATION ERRORS DELETED FROM
        TXT FILE*/
        data avlblty;
                infile 'c:\windows\desktop\sasinput\available_newcodes.prn';
                input perim ha grdcode newcode cover $;

        proc sort data=avlblty;
                by newcode ha;

        /*proc print data=avlblty;*/

        proc univariate data=avlblty noprint;
                var ha;
                by newcode;
                output out=habtatha sum=codeha;

        /*proc print data=habtatha;*/

/*Determine proportion of total area comprised of each HABITAT code (pisubi)*/
        /*Display total area of all available habitat types*/

        proc univariate data= habtatha noprint;
                var codeha;
                output out=total sum=totalha;

        proc print data=total;

        /*Divide area of each habitat by total area*/
        data pisubs;
                set habtatha;

/*USER INPUT REQUIRED--ENTER TOTAL AREA FROM PREVIOUS PRINT STATEMENT*/
                totalha =588451.51;
                pisubi=codeha/totalha;

        proc print data=pisubs;

/*COMBINE ABOVE OUTPUT FOR SELECTION RATIO COMPUTATION*/

data select;
        merge alluse allhr;
        by month;

/*proc print data=select;*/

proc sort data=select;
        by newcode;

data select2;
        merge select pisubs;
        by newcode;
        drop codeha;

proc sort data=select2;
        by month;
```

```
proc print data=select2;

/*CALCULATE SELECTION RATIO (W) FOR EACH HABITAT TYPE (i) BY MONTH (Wi) */
     /*BY HABITAT CODE*/

     data select3;
                set select2;
                wi= uiplus/(pisubi*uplsplus);

        proc sort data=select3;
                by month;

        proc print data=select3;

/*CALCULATE VARIANCE ESTIMATES*/

  /*First set*/
        data var1;
                merge induse pisubs;
                by newcode;

        proc sort data=var1;
                by id;

        /*proc print data=var1*/

        proc sort data=hrsize;
                by id;

        data var2;
                merge var1 hrsize;
                by id;
                drop codeha;

        proc print data=var2;

        proc sort data=var2;
                by newcode month id;

        proc sort data=select3;
                by newcode month;

        data var3;
                merge var2 select3;
                by newcode month;
                drop uiplus uplsplus;

        proc print data=var3;

        data var4;
                set var3;
                div = (uij/pisubi-wi*uplusj)**2;

       proc print data=var4;

        proc sort data=var4;
```

```
            by month newcode;

    proc univariate data=var4 noprint;
            var div;
            by month newcode;
            output out=part1 sum=joneto_n;

   proc print data=part1;

    data nless1;
            set samplsiz;
            nminus1=n-1;

    proc sort data=nless1;
            by month;

    proc print data=nless1;

    proc sort data=nless1;
            by month;

    proc sort data=part1;
            by month;

    data var5;
            merge part1 nless1;
            by month;
            drop n;
            half1=joneto_n/nminus1;

/*Second set*/

    proc sort data=select3;
            by month;

    proc sort data=samplsiz;
            by month;

    data var6;
            merge select3 samplsiz;
            by month;
            drop pisubi wi uiplus;
            uplssqr=uplsplus**2;
            half2=n/uplssqr;

    /*proc print data=var6;*/

/*First set * Second set = variance est (VARWI) */
    data var7;
            merge var5 var6;
            drop joneto_n nminus1 uplsplus;
            varwi=half1*half2;

    proc print data=var7;

    data variance;
```

```
            merge select3 var7;
            drop uiplus uplsplus pisubi half1 uplssqr half2;

        proc print data=variance;

        proc sort data=variance;
            by month;

        proc univariate data=variance noprint;
            var newcode;
            by month;
            output out=numhabs n=capi;

        data stderror;
            merge variance numhabs;
            by month;
            sewi=varwi/(n**0.5);

        proc sort data=stderror;
            by month;

        proc print data= stderror;

/*COMPUTE 1-ALPHA LEVEL SIMULTANEOUS CONFIDENCE INTERVALS FOR Wi (upper) and (lower)*/

        data interval;
            set stderror;
            drop totalha;
        /*SPECIFY ALPHA LEVEL FOR CIs (e.g., for 90% CI specify alpha=0.10) */
            alpha=0.05;
            upper = wi + probit (1-alpha/(2*capi)) * sewi;
            lower = wi - probit (1-alpha/(2*capi)) * sewi;

        proc print data=interval;

run;
```