A Study of Factors Affecting Nesting Success And Mortality of Greater Prairie-Chickens in Northeastern Oklahoma 1997-2000

Final Report
(*Exclusive of vegetation analyses)

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EXECUTIVE SUMMARY

1. The Greater Prairie-Chicken (*Tympanuchus cupido*) has declined dramatically in numbers in Oklahoma and throughout its range in recent years. To begin to understand the causes of the decline, we carried out a study of Greater Prairie-Chicken ecology from 1997 – 2000 in northwestern Osage County, Oklahoma. The study area is almost entirely tallgrass prairie, and annually is extensively burned by ranchers.

2. We trapped 214 birds, 144 males and 70 females. Because cocks attend booming grounds (leks) daily for several months each year, the date of their capture largely reflects the time when trapping was taking place. The large majority of hens, however, was captured in April.

3. Approximately two-thirds of the study area was burned each year.

4. Lek surveys in 1998, 1999, and 2000 indicated that the number of prairie-chickens declined each year, from 173 to 168 to 146. Leks were not evenly distributed throughout the study area, but tended to cluster in two areas. Noticeable gaps correspond to areas that were burned in all three years.

5. Although the leks tended to be associated with unburned areas, the proportion of leks actually located on burned areas was about 78%. The birds may choose lek sites that provide visibility for displaying, but which are also close to cover (unburned areas) to which they can flee from predators.

6. In spring and early summer, prairie-chickens use unburned areas more regularly than burned areas, with about three-fourths of locations on unburned lands in May. Although the proportion of locations on unburned areas decreased as the season progressed and re-growth of grasses occurred, the birds' use of burned areas never reached the latter's proportion of the landscape. That is, even in September of both years, more than 50% of the locations were on unburned land, even though only about one-third of the land was unburned.

7. The prairie-chickens' concentration in May on unburned areas causes densities of the birds in the unburned areas to be approximately five times as high as in burned areas.

8. Mortality tended to be highest in the breeding season, when males are on leks every day and females are vulnerable because they are incubating and rearing broods.

9. Mortality tended to be higher on unburned areas, although the difference was not significant. This may be a consequence of the concentration of the birds in the unburned areas, where predators may be able to locate them more effectively. In addition, the predators themselves, especially mammalian predators, may be concentrated in the unburned areas to find their own cover.

10. We located 70 nests in the four springs of the project. The Mayfield nest success estimate for the four years was 24%, but it varied from a low of 11% in 1997 to a high of 31% in 1999.

11. The large majority of nests were placed on unburned lands, although later in the season some nests were found in areas burned earlier in the spring. Nest success, however, did not differ between burned and unburned areas.

12. Temperature data loggers in seven nests indicated that the hen appears to incubate without leaving during the final two or three days before the chicks leave the nest (in successful nests). Chicks tended to leave the nests in early morning. That was also

the time most nests were depredated. Neither incubating hens nor nest predators appear to be active in midday.

13. Within a day, both male and female prairie-chickens were most active in morning and evening, except in Summer, when their activity was generally lower, and more variable during the day.

14. Average daily movement distances were significantly greater in Fall and Winter (~840 m) than in Spring and Summer (~340m).

15. Home range size averaged about 7 km^2 and varied from 0.6 to 21.7 km^2. The home range size did not differ significantly between hens and cocks, although hens tended to have larger ranges. Hens were more likely to have split ranges (where the bird moves some distance between two, clearly-defined activity centers) than males; 50% of females had more than one activity center, but 3% of males did.

16. The maximum distance moved over seasons averaged about 5 km, ranging from 1 – 15 km. Females moved about twice as far as males.

17. Results of predator scent post surveys indicated that predator numbers in 1998 were generally as high or higher than during 1972 – 1981, using similar methods.

18. In early June, predator numbers did not differ between burned and unburned areas.

19. In conjunction with other researchers nationwide and including samples from both Greater (354 samples) and Lesser prairie-chicken (*Tympanuchus pallidicinctus*; 184 samples), we carried out a survey of blood samples for the presence of reticuloendotheliosis, a disease caused by REV. Of the 538 samples from both species, only two were positive for REV. Both positives were from Greater Prairie-Chickens from Osage County, Oklahoma, in 1998. These add to the few reports of REV in free-ranging galliforms. However, given only two positive birds in this study, REV is not considered to be a major threat to prairie-chicken populations.

20. The cause or causes of the decline in population of the Greater Prairie-Chicken in Oklahoma remains elusive. It is likely that there is no single cause, but rather a suite of factors acting in concert (see Conclusions, page 67). Further research is necessary before a management plan can be devised. Areas for study include the effects of extensive burning of the rangeland and chick survival. In addition, further monitoring of populations is important (see Recommendations, page 69).

INTRODUCTION

The Greater Prairie-Chicken (*Tympanuchus cupido*; Fig. 1) is a favorite game bird throughout its range, and is often viewed as an impressive icon of the tallgrass prairie. The spring courting displays on traditional booming grounds[1] by competing males, including stamping of the feet, inflation of neck sacs, various feather manipulations including the erection of long, pointed pinnae of the neck, and cooing and crowing, are dramatic and impressive.

Fig. 1. Greater Prairie-Chicken cock booming. Photo by Joel Sartore.

The species once occurred in New England, throughout the eastern Great Plains, and on the Gulf Coastal Plain. It is now in greatly reduced numbers, and gone from most of the eastern part of its range. It still occurs in 12 states (including the subspecies known as Attwater's Prairie-Chicken, *Tympanuchus cupido attwateri*, in Texas), although in some of the states (Illinois and Iowa) the populations are quite small, no more than 200 individuals (Svedarsky et al. 1999). Greater Prairie-Chickens have shown considerable declines in recent years in Oklahoma, as is documented by booming ground counts conducted by the Oklahoma Department of Wildlife Conservation (ODWC). The ODWC data show an 80% decline from the 1960s to the 1990s. Although the decline in numbers has been well documented, the factors contributing to the decline are not well understood.

Past efforts in saving declining forms of other prairie-chickens have met with little success. The best conservation strategies known during the latter half of the 19th century and early part of the 20th century were practiced with the Heath Hen (*Tympanuchus*

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[1] These may also be referred to as leks, the ornithological term for an area where males congregate and display to attract females to mate.

cupido cupido; described in Cokinos 2000), but in spite of these efforts, this eastern prairie-chicken became extinct in 1932. The same scenario is being played out in southern Texas today with the Attwater's Prairie-Chicken, where fewer than 50 birds remain in the wild.

Factors responsible for declines in the Greater Prairie-Chicken may vary between locations, but it is expected that at least some of those factors may be consistent across sites as well. Some of the factors seem obvious, such as weather and wide-scale conversion of prairies into cultivated fields. However, smaller agricultural areas (milo, beans, or winter wheat, for example) interspersed within native grasslands may provide food sources that could benefit the species. Subtle changes in plant composition in native prairies may be altering the availability of nesting or roosting habitat or food supplies.

This project was begun as an effort to obtain information on nest success, movements and home ranges, use of burned and unburned habitats, predation, survivorship, and possible diseases of Greater Prairie-Chickens in Oklahoma. The work was carried out in Osage County.

METHODS

Study Area Description

The study area was located in northeastern Oklahoma in Osage County (Fig. 2), about 100 km (60 mi) northwest of Tulsa. This area is the southern extension of the Flint Hills geological system, which extends southward through central Kansas from near Manhattan into Oklahoma. Much of the Flint Hills remains as unplowed tallgrass prairie.

The study area covered about 450 km^2 (about 174 mi^2). The habitat was fairly homogenous, with no cultivation. It was almost entirely unplowed tallgrass prairie, with few roads, and even the few county roads were graded dirt with no right-of-way. There were few fences. Wooded areas occupied only a small portion of the southeast corner of the study area, and a narrow gallery along the largest creeks, Bird and Sand creeks.

Fig. 2. Location of study area (green) within Osage County and the State of Oklahoma. Locations of Tulsa and Oklahoma City are given for reference.

However, there was some heterogeneity in the study area, both temporal and spatial. The use of prescribed fire is an important management technique for ranchers in the Flint Hills. Extensive areas are burned annually, from 60 to 80% of the study area (see "Burned Area," page 23), almost always in late winter or early spring, but by mid-summer the grasses have re-grown. Burning of the range is usually followed by grazing by cattle using the early intensive stocking system (Smith and Owensby 1978, Vermeire and Bidwell 1998), in which cattle, typically steers, are brought onto the ranches for about 100 days, from April through July, leaving the range to recover in fall and winter. A small portion of the area, about 10%, was occupied by cow-calf ranching operations, which graze at a lower stocking rate but throughout the year. The cow-calf operators tend not to burn extensive areas each year. Another small portion, about 5%, was grazed

year-round by bison (*Bos bison*) at a low stocking rate, on The Nature Conservancy's Tallgrass Prairie Preserve. The Tallgrass Prairie Preserve occupies about 25% of the study area (Fig. 3), including the bison range. The Preserve is burned in smaller patches and at more random intervals than the rest of the area. There were small areas of prairie haying, about 1% of the area. Therefore, while some heterogeneity exists in the study area, it can be thought of as grazing lands with only temporary (due to burning) and limited (due to different grazing regimes) heterogeneity, and little fragmentation due to cultivation, roads, or wooded areas.

Fig. 3. Study area (green outline), showing roads (both paved and graded dirt county roads; brown lines), and The Nature Conservancy's Tallgrass Prairie Preserve (blue).

8 km (5 mi)
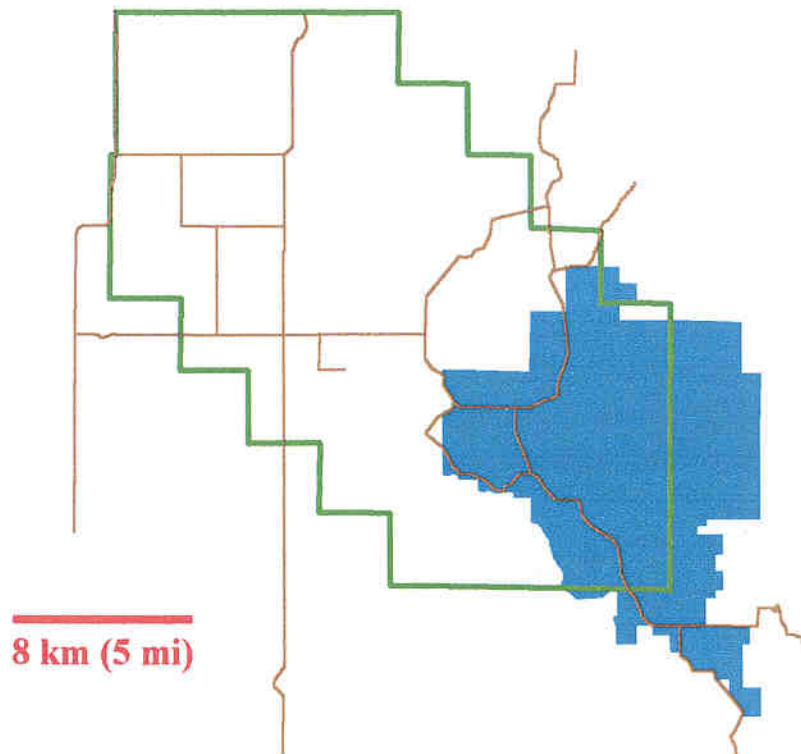
Time Period

Data on locations and vegetation were collected year-round beginning in April 1997 and ending in July 2000.

Seasons

For several analyses, results are most interpretable and significant when compared among and between seasons. Prairie-chicken seasons do not conform exactly to calendar seasons. The seasons we used were Spring, corresponding to the active booming season

(15 February to 14 May); Summer, corresponding to the nesting and brood-rearing period for hens and a lull in lek activity for males (15 May to 14 August); Fall, a period of some lek activity for males (15 August to 14 November); and Winter (15 November to 14 February). Hereinafter, all use of the capitalized words "Spring," "Summer," "Fall," and "Winter" will refer to these time periods; lower case use of the words will refer to a more general season. Greater Prairie-Chickens are known to lek in all months of the year (pers. obs.; N. Silvy, pers. comm.), so some booming may occur in any of these "seasons."

Age Classes

For some analyses the birds were divided into age two classes "adult" or "AHY" and "juvenile" or "HY" using feather replacement to identify the age classes (Ammann 1944; Wright and Hiatt 1943). The Age Class a bird was placed in refers to the age at time of first capture; for birds tracked over a long period of time, of course the age class changed. Juveniles were birds less than one year old (the cut-off date used is 1 July each year), sometimes called "hatch year" (HY) birds. Adults were birds at least one year old, but some individuals may have been up to three or four years old. These individuals are sometimes classified as "after hatch year" (AHY) birds. No attempt was made to distinguish among the ages of birds beyond one year; after that time all were considered "adult."

Trapping

We trapped birds on their booming grounds in spring and fall 1997, spring and fall 1998, spring 1999, and spring 2000. Trapping in spring 1997 did not begin until the first week of April, so was not complete for the season. In 2000, the amount of trapping was scaled back significantly, so a relatively small number of birds were trapped.

Trapping was accomplished using walk-in funnel traps, starting with methodology developed by other researchers (J. Toepfer, pers. comm.), but further perfecting the methods. We trapped using a series of walk-in funnel traps connected by 8 m (25 foot) lengths of plastic drift fence in a large "W" array. Anywhere from seven to 20 traps were used on each booming ground, depending on the booming ground size and trap availability.

Two different trap sizes were used for this project, two-funnel and four-funnel. Besides having different numbers of funnel entrances, the two-funnel traps were smaller in diameter. The construction of the traps was generally the same except for the difference in size. Four-funnel traps were constructed from 2x4 inch (5x10 cm), 12.5-gauge welded wire, were 122 cm (48 inches) in diameter and 71 cm (28 inches) tall, and had four funnel-shaped openings. Nylon netting was stretched tight across the trap at a height of 41 cm (16 inches). The traps also had a welded wire top, and the 30 cm between the top and the net kept the birds from injuring themselves on the top of the trap, as well as offering protection from above in the unlikely case of a raptor attempting to catch a bird inside a trap. All cut wire ends were filed smooth to prevent birds cutting themselves, and traps were inspected daily for broken welds, loose wires, etc. Traps were never left unattended when they were set for catching birds. When trapping ceased each

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day, at least two access doors on the traps were wired open to allow for an exit if a bird entered a trap when we were not present.

After one bird was inside a trap, a second or third bird was likely to get caught in the same trap. So, to facilitate further trapping we would leave birds in traps for up to an hour. We would continue to observe the bird, and were ready to intervene immediately if the bird seemed stressed, hurt, or was fighting with a second bird. Birds were removed by opening one or two of the access doors, and reaching in and grabbing the bird by hand. The handler would immediately place an infant-sized sock over the bird's head to keep it calm, and place it in a large cotton bird bag. If three or more birds were caught in a trapping session, they were placed in wooden holding boxes to keep them calm and cool until they could be processed.

Processing consisted of weighing the bird to the nearest 10 g while still in the bag (the empty bag was weighed after the bird was removed, and that weight subtracted from the first to get the bird's weight). We then measured the wing chord length and tail length. We also measured the diameters of the shafts of primaries 8 and 9, which were used to calculate the bird's age (other aging methods were used as well, including the shape of the primaries and relative wear on the primary tips). All birds were fitted with a 7/16 inch (11 mm) diameter, serially-numbered aluminum band to allow for positive identification when recaptured or recovered, and a similar, blue plastic band, bearing the same number, for more easy identification in the field.

Birds were then fitted with a 18 g bib-mounted radio transmitter with a tuned-loop antenna (Fig. 4). These transmitters weighed ≤2% of the bird's weight (~800 – 1000 g). The transmitters were custom-made to our specifications by Telemetry Solutions, Inc. and Wildlife Materials, Inc, and have a battery life of about 1½ years. Battery life of this length greatly reduces the need to recapture birds for battery replacement, as very few individuals should outlive the battery life of the transmitters. Campbell (1972) estimated an annual survivorship of 35%; assuming this is true, on the average, less than 20% of the birds are expected to live longer than 20 months. However, to assure that the battery life did outlast the bird, we replaced the transmitters on some birds each summer (see below).

Fig. 4. Radio-tagged Greater Prairie-Chicken cock showing transmitter on bib around neck as well as plastic and aluminum leg bands.

The loop antenna is believed to be safer for the bird than the more commonly used whip antennas, which are suspected to cause higher mortality due to flight feather abrasion. The bib mount is also thought to be safer than the more common ligature devices used on most necklace-mounted transmitters, as there is no possibility of attaching it too tightly. The bib material is made of brown-colored 19 oz. vinyl-coated nylon, and the transmitter itself is attached to the bib with cyanoacrylate cement and monofilament. The transmitters were attached to the birds by cutting a small hole (about 1 cm diameter) in the bib in the middle of the antenna loop, and cutting eight slits radiating from the center. The transmitters would then be test-fitted to the birds, and if necessary the opening enlarged to go snugly over the bird's head. If the transmitter slipped over too easily (i.e. the hole was too large), a different transmitter was used. Once over the bird's head, the transmitter was worked down the neck toward the breast, and breast feathers were pulled through the opening. This assured that the transmitter was totally or mostly hidden, as well as unlikely to come off since the feathers helped hold it in place. Transmitter frequencies ranged from 148.010 MHz to 149.990 MHz, and each was separated from other transmitters by at least 10 kHz, thus a maximum of 198 unique frequencies could be deployed.

Starting in 1998, once the transmitter was attached and all data were collected on a bird, about 1 cc of blood was taken with a syringe from the ulnar vein to be used for genetic analyses and for survey of possible retroviruses, and the bird was examined for the presence of ectoparasites (lice and ticks).

Once the processing had been completed, the bird was held upright for several minutes to allow it to equilibrate and regain its balance. If the bird showed any sign of

scrapes or cuts from the traps, alum (clotting agent) and / or Neosporin® (antibiotic ointment) was applied to the wound. Cyanoacrylate cement (super glue) was kept on-hand in case a larger cut needed to be closed, but it was never necessary. The birds were then set gently on the ground at a location free of obstructions (fences, trees, bushes, etc.), so that they could escape by flying or walking.

Transmitters were replaced on some of the birds in July and August each year, to ensure that the battery would survive at least until the next trapping season. At that time of year, the birds are molting flight feathers and typically, over the course of 8-10 weeks, molt primaries at the rate of one or two per week. Since it takes about two weeks for the new primaries to reach full size, most birds will be missing two or three primaries at any given time. Although the birds are never flightless, this molt period alters their behavior somewhat, causing them to attempt to elude predators by either sitting extremely still or by running on the ground. (They likely expend much more energy when flying in this condition). We tried to use this time period to our advantage, with the idea that a fresh battery deployed then would last at least until that time the following year. This involves two field personnel equipped with receivers and Yagi antennas tracking the target bird at night, and trying to get good directional signals from 90° apart, relative to the bird's position. Once the radio trackers had the bird pin-pointed, two to four other field personnel would converge on the spot with long-handled, 24-inch diameter fish-landing nets, and look for the bird on the ground. Once spotted, the closest person would stealthily approach the bird to within the length of the net and attempt to catch the bird on the ground. Prior to initiating this procedure in 1997, a considerable number of nights were spent tracking birds, to determine how many times they are disturbed from predators while roosting. Most birds were being "bumped" one or more times each night, so we feel like our efforts (especially since it was usually only one night on each bird) contributed only a minor amount of additional disturbance in an already restless night.

Radio Tracking

Radio tracking of birds began the same day they were first captured and radioed. Birds were then tracked as often as time allowed (on average about once every three days), and at varying times of day and night. Tracking of birds was begun in April 1997 and ended in July 2000, and was carried out year round.

Radio tracking equipment consisted of five-element, handheld Yagi antennas and ATS Inc. model R-2000 or R-4000 receivers. These receivers have built-in memory banks and scanners to aid in detecting birds. Once a bird was detected, our personnel would walk toward the bird until signal strength noticeably increased, at which time they would start walking around the bird, keeping it on one side of them until they had proceeded at least 90 degrees around it and within 50 meters of it. Great care was practiced in tracking to avoid accidentally flushing the birds. Occasionally, however, birds were intentionally flushed, for example, when a bird was found to be at the same location for two or more consecutive days (mortality switches might not be working or scavengers might be moving the transmitter around), or if there was some concern over the bird's health. Once an individual's location was confirmed, a handheld Global Positioning System (GPS) unit was used to determine the latitude and longitude (to the nearest 0.01 minute). The latitude, longitude, date, time, and any pertinent notes were

recorded in a pocket notebook, and transcribed onto standardized data forms later in the day.

Depending on the number of birds being tracked and the number of field personnel, each technician was assigned a group of up to 35 birds to track. Each person was scheduled to begin the first day of the five-day work week at 1400, and work until 2300. Each subsequent day began and ended two hours earlier; by the last day of the workweek, the technician was working 0600-1500. This schedule facilitated tracking birds at various times of the day and night, and maximized the number of hours per day that someone was in the field (e.g., with four field personnel, someone was starting at 0600 four days each week, three days someone was starting at 0800, and four days someone was out until 2300). During the trapping season, this schedule was modified so that we could maximize the available personnel for early morning trapping.

As movements by radio-tagged birds of more than about 2 km (1.2 mi) would occasionally cause technicians to lose track of the birds, searching from the air allowed us to relocate lost birds.

If a bird was found dead (our transmitters have a mortality feature incorporated into them that causes the pulse rate to double if the transmitter does not move for 12 hours), the carcass or remains were photographed, all remains were collected, and the area was searched for tracks, feces, etc. Other information collected at the mortality site included the distance to the nearest fence, the distance to the nearest power lines, the type of habitat, the distance to the nearest cultivated field, etc. The carcasses were examined for clues (stripped tendons, bite marks on bones or transmitters, plucked feathers, chewed feathers, etc.) that could aid in determining mortality causes (Dumke and Pils 1973).

Often when scanning, more than one bird would be detected. Personnel would usually track the individual that had gone the longest since last being tracked. Also, during nesting season, hens were tracked more frequently than cocks, sometimes even to the exclusion of tracking cocks. When trapping on booming grounds, a scan was made every 30 minutes to determine which birds were present; sometimes birds were detected at these intervals, but appeared merely to be in the area and not on the booming ground. In all of these cases, birds detected but not tracked were still recorded as detected, as their presence can be used to calculate daily survivorship rates.

Triangulation on signals to determine a bird's location was rarely necessary. Triangulation was used only when situations (land access, etc.) made obtaining a location by any other means impractical, or when more than one bird was being tracked simultaneously.

Lek Surveys

Surveys of booming ground locations and number of birds were carried out in 1998, 1999, and 2000. The objective of these surveys was to locate all leks in the study area. However, the study area is too large to survey completely in a short amount of time, so surveys were carried out on one-fourth of the sections, laid out as the southeast section of each two-by-two section square (Fig. 5). With this design, there were 44 sections to be sampled.

All sampling was carried out between ½ hour before dawn and 2½ hours after dawn, during the six weeks from 27 March to 7 May. It was only carried out on mornings with good weather, that is, low winds and no precipitation.

One hour was spent by the surveyor on each of the sections in the sampling design. All prairie-chickens seen on the section were recorded and identified to sex if possible. All leks that were located were flush-counted[2] to ensure that all birds at the booming ground had been seen.

If a booming ground were heard on any adjacent sections (not in the sampling design) they too were located and counted. Some leks found otherwise in the course of our work or previously known were also located and counted. Because the sounds from booming grounds can be heard at times over distances greater than 2 km (~1 mi), this ensured that nearly all leks in the study area were recorded.

Although this survey method is somewhat haphazard, it provides a systematic search of the entire study area to locate all leks and provide an estimate of the numbers and distribution of prairie-chickens within the study area.

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[2] Throughout the project we made extensive efforts to avoid harassing the prairie-chickens by flushing them unless necessary. However, in the case of the lek surveys, most of the leks were visited by us only once; therefore, a single flush of the birds probably did not affect their behavior or success. Prairie-chickens are often flushed at least once a day by natural predators.

RESULTS AND DISCUSSION

Number of Birds Trapped

A total of 214 birds were trapped and radio-tagged during the study. An additional two chicks were captured with hens in summer 1999, but these birds were not radio-tagged. As mentioned above, trapping in spring 1997 did not begin until the first week of April, so was not complete for the season. In 2000, the amount of trapping was scaled back significantly, so a relatively small number of birds were trapped.

The year 1998 produced the greatest number of newly-captured birds (Table 1), followed by 1999 and 1997. This corresponds largely to trapping effort. Trapping was carried out full-season in spring and fall in 1998; therefore that year had the greatest number of captures. In 1997 trapping was carried out in spring and fall, but was started late in spring. In 1999 trapping was only carried out in spring. In 2000, the lowest year, trapping was only carried out in spring, and with fewer personnel and trap days.

Table 1. Number of first captures (i.e., not including recaptures) by year, sex, and age class. Age Class refers to the age at time of first capture; for birds tracked over a long period of time, of course the age class changed.

Sex	Age Class	1997	1998	1999*	2000	Total	TOTAL
Males	AHY	14	22	19	6	61	
	HY	19	15	14	9	57	144
	UNK	9	8	8	1	26	
Females	AHY	7	14	8	1	30	
	HY	4	12	4	2	22	70
	UNK	6	9	3	0	18	
TOTAL		59	80	56	19		214

* In 1999, an additional two chicks of unknown sex were captured in the summer.

The ratio of males to females was approximately 2:1 throughout the study. This ratio probably does not reflect the actual sex ratio of the population, but is an artifact of the method of capture. All trapping was carried out on the booming grounds. Males attend the leks every morning for several months per year, and the likelihood for a male to be caught is therefore very high. In fact, it is fairly common for us to have captured and radio-tagged every male on a lek. Females, in contrast, only visit the lek during part of the year (see below) and therefore have a much lower likelihood of being captured. To assess the population sex ratio would probably require efforts to survey the prairie-chicken population away from the lek.

The sex ratio of the birds captured varied significantly from year to year (Table 2; $\chi^2 = 8.2$, df = 3, P = 0.042). Most years had a ratio slightly higher than 2, especially 2000. The ratio in 1998, however, was nearer to 1:1 than other years, and because so many birds were captured in 1998, it brings the overall ratio closer to 2. Although the

the nest (the same person who found the nest would monitor it in order to avoid accidental disturbance by someone unfamiliar with the nest location) would come to within about 100 meters and dial up the hen's frequency and the marker radio's frequency, and take a compass bearing on each to confirm the location of the hen relative to the location of the marker radio. After it was confirmed that a hen was no longer incubating on the nest (if she were not present for two consecutive visits during midday), the marker radio was used to relocate the nest.

After a nest either failed or hatched, the entire nest and contents were photographed, and the egg remains were collected (nest success could be evaluated from the egg remains). Technicians would then return within 24 hours to complete vegetation sampling at and around the nest. For many nests, an "artificial" clutch consisting of three or four Ring-necked Pheasant (*Phasianus colchicus*) eggs and one clay egg (pliable, non-hardening modeling clay) were placed in the nest, and a hair-catcher (dowel rod wrapped with double-sided tape) was suspended ten to 20 cm above the nest. We continued monitoring the artificial nest until this clutch was destroyed or until the artificial clutch had been in place for four weeks. From these artificial clutches, we could identify predators potentially responsible for destroying actual prairie-chicken clutches (positive identification was possible from tooth impression in the clay egg and hairs stuck to the hair-catcher). Also, the patterns of egg destruction or consumption could then be compared to actual depredated prairie-chicken eggs, thereby allowing a reasonable level of confidence in determining the predator species. These artificial clutches were also collected and cataloged after they were destroyed.

We additionally monitored some nests using temperature data loggers. By recording the temperature, these loggers allowed us to determine the times when the hen was on the nest and when she was not. This can allow us to determine the exact time when the nest was abandoned, the chicks hatched and left the nest, or when the nest was depredated, because each of these produces a sharp change in temperature in the nest, either colder or warmer.

The data loggers used were Hobo® Temp data loggers (Onset Computer Corporation). The loggers detect and record the temperature to about the nearest 1°C every 5 minutes for nearly 28 days. Once the 28 days have passed, the logger begins overwriting the earliest data. Each logger is 58 X 45 X 18 mm. Because they are not waterproof, before deployment each was wrapped in multiple layers of plastic wrap and an outer layer of duct tape. Each was also equipped with a short monofilament line approximately 5 cm long attached to a large nail.

For deployment, the logger was placed into an active prairie-chicken nest. Loggers were only placed in nests when the hen was already not present; we did not flush a hen to place the logger. The logger was placed into the nest and the nail was driven through the bottom of the nest to anchor it. The short monofilament tether allowed the prairie-chicken hen to move the logger as she normally rotated the eggs, but did not allow her to eject it entirely from the nest.

Once the data logger was deployed, the nest was marked as described above, and not checked by approaching the nest until it was certain that the nest had either hatched or failed. After it had been removed from the nest, the logger was returned to the office and the data downloaded from it. The data logger was then reset and prepared for its next deployment.

Predator Survey

Scent-post surveys were carried out in 1998 and 2000, with slightly different objectives. All preparation and reading of scent posts were carried out by personnel of USDA Wildlife Services, trained in the use of scent posts.

In 1998 a general survey was run to estimate predator[3] levels in the study area. Three transects of 3 – 5 km (2 – 3 mi) length each with a total of 22 scent posts at least 0.8 km (0.5 mi) apart were established along county road sides (Fig. 6). Two of the transects were established within the study area; a third was established southwest of the study area to provide comparison with earlier surveys. The scent post surveys were read on three consecutive mornings in each of three seasons (1-3 April, 10-12 June, and 29 September-1 October 1998). We also obtained data from similar scent post surveys conducted by Wildlife Services in September each year during the years 1972 – 1981 near Bluestem Lake, approximately 6 km east of the transect outside the study area and 6 km south of the southern edge of the study area.

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[3] Throughout this report, the word "predator" will be used to refer to mammalian predators such as coyote (*Canis latrans*), striped skunk (*Mephitis mephitis*), opossum (*Didelphis virginiana*), and raccoon (*Procyon lotor*), unless otherwise specified. These predators may primarily destroy nests, but some (especially coyotes) may take adult prairie-chickens.

Fig. 6. Locations of three scent post predator survey routes that surveyed three times in 1998. Each route is 3 –5 km long.
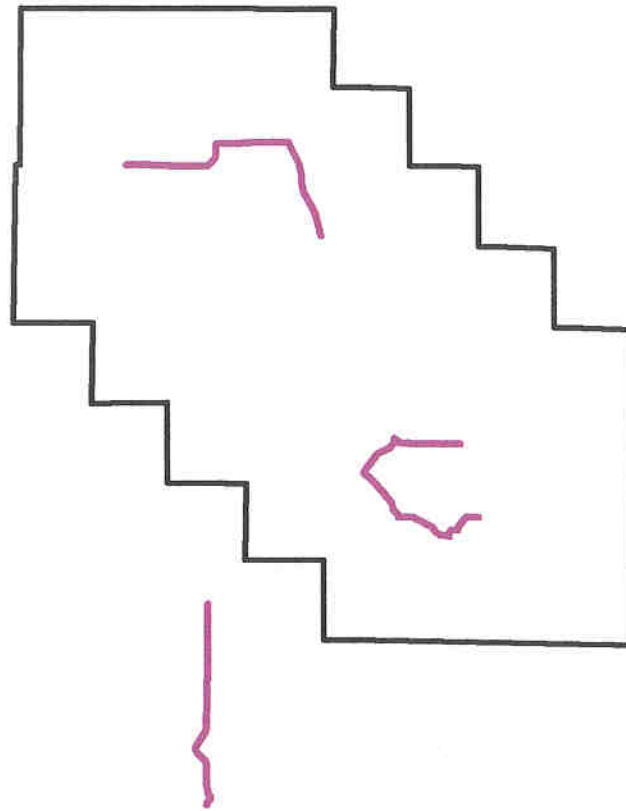
In 2000, scent posts were made to compare predator numbers in unburned vs. burned areas. Seven transects were established with scent posts about 0.5 km apart (~0.3 mi). The transects were laid out to run away from an edge toward the interior of a burn or an unburned area (Fig. 7). Most transects were laid out to cross a burned / unburned edge. There were 33 scent posts among the seven transects. The scent posts were read five mornings from 31 May – 8 June 2000.

Fig. 7. Locations of scent post transects used in comparison of predator numbers during May and June 2000. Green is unburned area. This map is a detail of the study area, and is a portion of the northern part of the Tallgrass Prairie Preserve and the adjacent ranch.
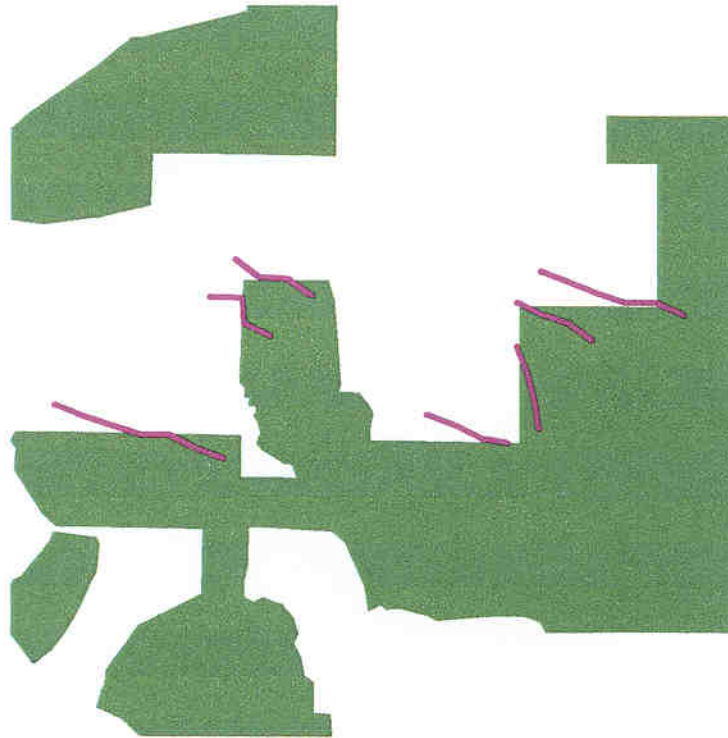
Burn Mapping

Burn mapping was carried out in 1998, 1999, and 2000. An area was considered to be "burned" if it had been burned since the previous growing season. Therefore, an area burned in the previous spring but not the current spring was considered to be "unburned," whereas an area burned in the previous October was considered "burned."

Mapping was carried out on the ground from the first of the year throughout the spring. As burns occurred, their location and extent was marked on maps, and these later transferred to the project's Geographic Information System (GIS). Additional maps were obtained for the Tallgrass Prairie Preserve portion of the study area from The Nature Conservancy. These maps were produced in ArcView by Peter Earle (Oklahoma State University).

Data Analysis

All mapping was carried out using ArcView 3.2. Base maps were obtained from the Digital Atlas of Oklahoma (Rea and Becker 1997). All statistical tests (linear regression, χ^2 analysis of contingency tables, Mann-Whitney U tests, and t-tests) were made using SYSTAT 7.0 (SPSS Inc. 1997) and Microsoft Excel 2000®. All t-tests were made using

separate (not pooled) variances. For statistical tests, home range sizes were log-transformed. For three-day movement data, however, a square-root transformation was found to be more satisfactory; for statistical tests using those data, the values were therefore square-root transformed. LOWESS smooths were calculated according to the methods of Cleveland and Devlin (1988).

RESULTS AND DISCUSSION

Number of Birds Trapped

A total of 214 birds were trapped and radio-tagged during the study. An additional two chicks were captured with hens in summer 1999, but these birds were not radio-tagged. As mentioned above, trapping in spring 1997 did not begin until the first week of April, so was not complete for the season. In 2000, the amount of trapping was scaled back significantly, so a relatively small number of birds were trapped.

The year 1998 produced the greatest number of newly-captured birds (Table 1), followed by 1999 and 1997. This corresponds largely to trapping effort. Trapping was carried out full-season in spring and fall in 1998; therefore that year had the greatest number of captures. In 1997 trapping was carried out in spring and fall, but was started late in spring. In 1999 trapping was only carried out in spring. In 2000, the lowest year, trapping was only carried out in spring, and with fewer personnel and trap days.

Table 1. Number of first captures (i.e., not including recaptures) by year, sex, and age class. Age Class refers to the age at time of first capture; for birds tracked over a long period of time, of course the age class changed.

Sex	Age Class	1997	1998	1999*	2000	Total	TOTAL
	AHY	14	22	19	6	61	
Males	HY	19	15	14	9	57	144
	UNK	9	8	8	1	26	
	AHY	7	14	8	1	30	
Females	HY	4	12	4	2	22	70
	UNK	6	9	3	0	18	
TOTAL		59	80	56	19		214

* In 1999, an additional two chicks of unknown sex were captured in the summer.

The ratio of males to females was approximately 2:1 throughout the study. This ratio probably does not reflect the actual sex ratio of the population, but is an artifact of the method of capture. All trapping was carried out on the booming grounds. Males attend the leks every morning for several months per year, and the likelihood for a male to be caught is therefore very high. In fact, it is fairly common for us to have captured and radio-tagged every male on a lek. Females, in contrast, only visit the lek during part of the year (see below) and therefore have a much lower likelihood of being captured. To assess the population sex ratio would probably require efforts to survey the prairie-chicken population away from the lek.

The sex ratio of the birds captured varied significantly from year to year (Table 2; $\chi^2 = 8.2$, df = 3, P = 0.042). Most years had a ratio slightly higher than 2, especially 2000. The ratio in 1998, however, was nearer to 1:1 than other years, and because so many birds were captured in 1998, it brings the overall ratio closer to 2. Although the

sex ratio varied significantly among the years, it is not clear whether this has biological significance or was simply a result of trap effort.

Table 2. Ratio of males : females by year.

|	1997	1998	1999	2000	Overall
Males / Female	2.47	1.29	2.73	5.33	2.06

Because the cocks attend the booming grounds daily for several months each year, the date of capture of the cocks largely reflects the time when trapping was taking place. That is, whenever we began trapping we would catch males. Therefore, the date of capture of the males has little biological significance. Hens, however, do not attend leks regularly over an extended season, although they may visit the leks irregularly any time of year. Because the hens only visit during a short period, the date of their capture does reveal the season of their visits to the lek.

The time period during which hens were captured was quite short. Over four years of spring trapping (1997-2000), 64% of hens (45 individuals) were captured in the month of April, and 31% (22 individuals) were actually caught in one week of that month, the week from 5-12 April (Fig. 8). A total of 87% (61 hens of 70) were captured in the 10 weeks from 8 March to 21 May. Only 13% (nine hens of 70) were captured outside that time period.

These results clearly indicate that the hens tended to visit the lek, where they could be trapped, at a very specific time of the season. This period peaked in the second and third week of April each year, and corresponds to the time when hens are likely initiating nests. The hens must mate before egg-laying (so that the eggs are fertilized). Therefore, it is likely that egg-laying generally does not begin before about mid-April. Nest building (without eggs) may begin a day or two before the first egg is laid, and nest site selection may begin even earlier. The fact that nest site selection may occur as early as early April may be important, in that prescribed burning of the rangeland by ranchers in the study area generally occurs in March to early April (see page 36 for additional information on nest sites in relation to burns).

An additional implication of these results is that anyone wishing to trap Greater Prairie-Chicken hens in northern Oklahoma should probably focus his efforts on trapping in the first three weeks of April.

22

Fig. 8. Combined data from four years of spring trapping, showing number of hens captured by week for the period 1 March to 29 May.
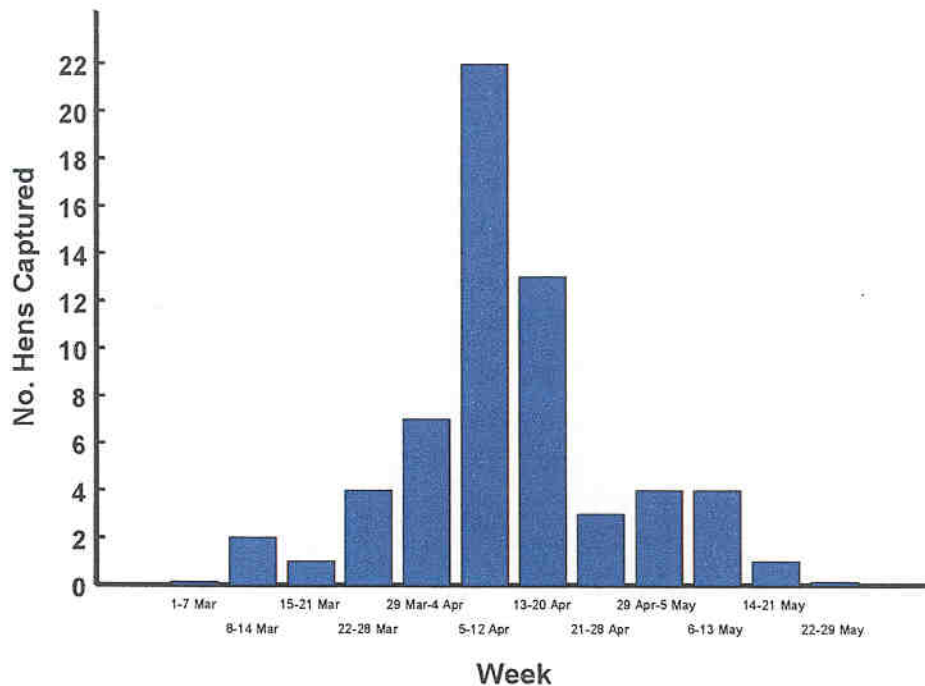
Burned Area

Approximately two-thirds of the study area was burned each year, 1998 – 2000, averaging 67.7% (that is, 32.3% was unburned). The proportion burned varied from about 60% to 80% (Fig. 9). The patchiness of the burns can be seen in the maps in Fig. 10. Approximately half of the area was burned all three years (Fig. 10), and a portion of the area not burned all three years was burned in two of the three years. Little of the study area was not burned at all during the three years, and the majority of that was on the Tallgrass Prairie Preserve and an area of about four sections north of Foraker and east of Grainola.

Because of the extensive amount of burning in the study area, locations of booming grounds and placement of nests will be interpreted with regard to the areas burned.

Fig. 9. Proportion of the study area burned each year. Percent is given above each
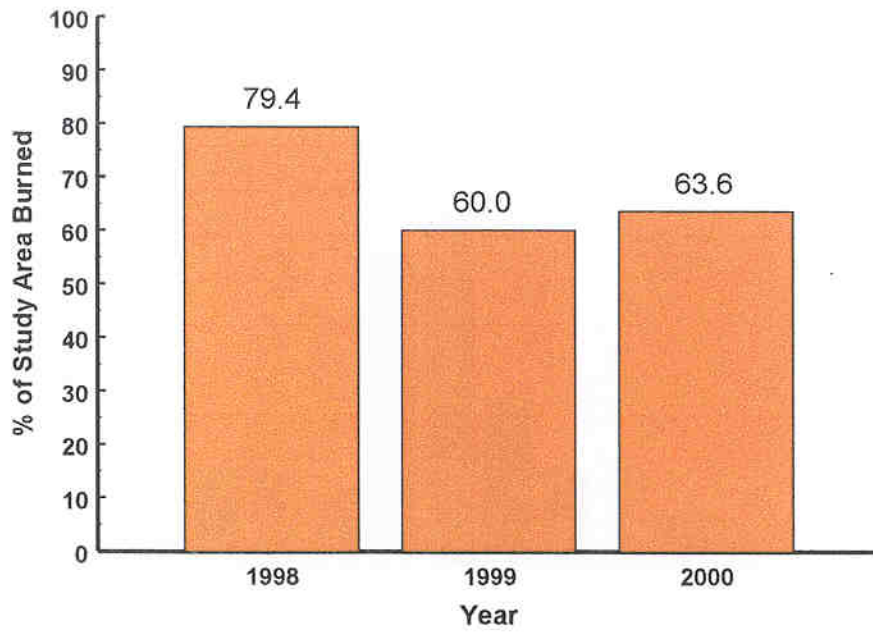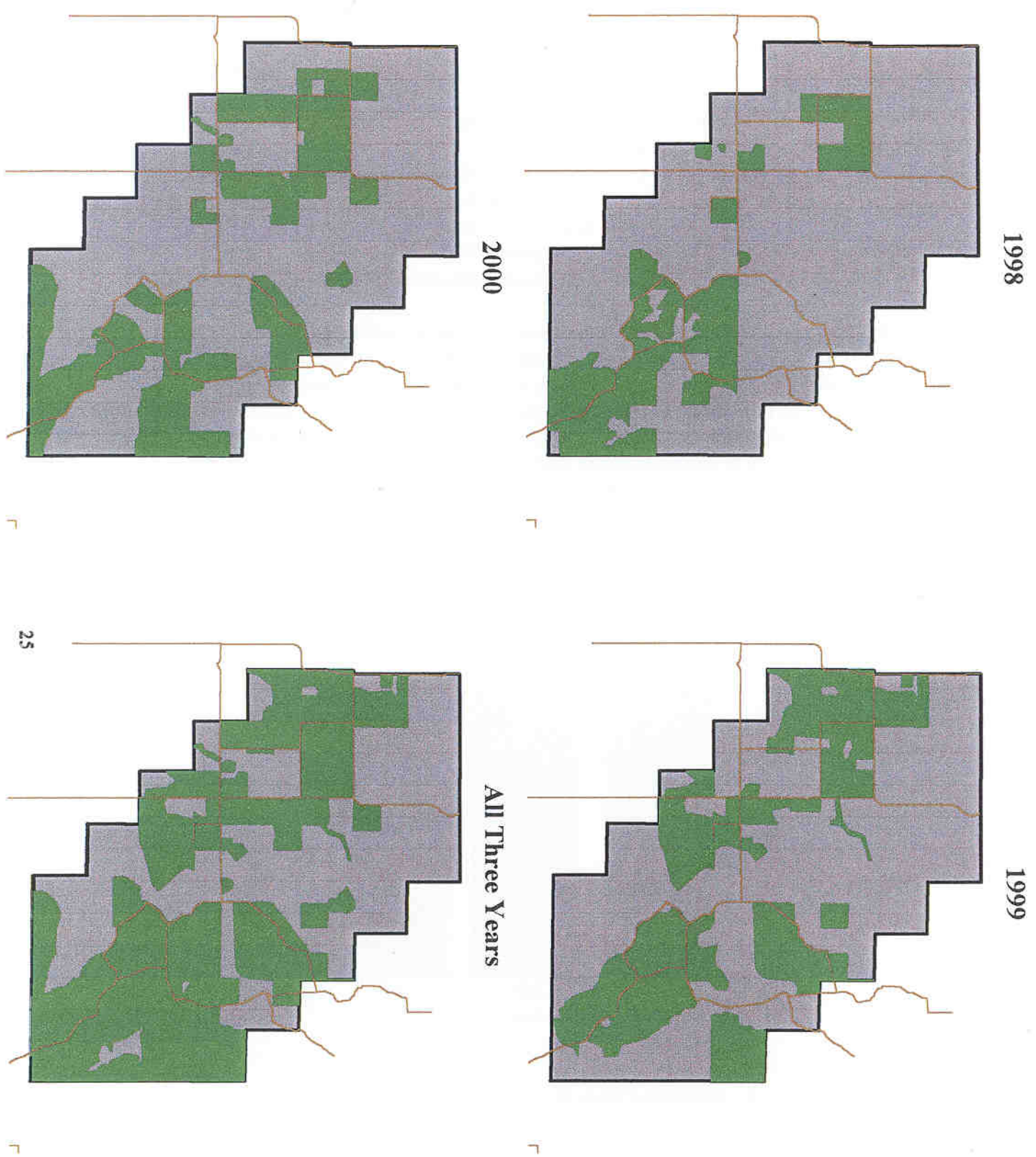column.

Fig. 10. Areas burned, 1998 – 2000. Gray is burned rangeland within the study area; green is unburned area. On map labeled "All Three Years" the gray areas were burned all three years; green areas were not burned at least one of the three years.

1998

2000

1999

All Three Years

Lek Surveys

The lek surveys underestimate the number of prairie-chickens in the study area, because the large majority of birds recorded are males. Females, because they spend much less time on the lek, are less likely to be counted. Therefore, assuming a 1:1 sex ratio, the actual number of prairie-chickens in the study area is probably nearly twice the number of birds recorded during the surveys.

The lek surveys carried out in 1998, 1999, and 2000 and show a decline in numbers each of the three years (Fig. 11), from 173 to 168 to 146. It is also important to note that in 2000, no lek had more than 11 birds, whereas the largest leks in 1998 and 1999 had 21 and 26 birds, respectively. This decline in number of birds recorded suggests that the decline of the Greater Prairie-Chicken in Oklahoma was continuing during the period of the study.

The lek surveys also show the distribution of the prairie-chickens in the study area in a way that locations of radio-tagged birds do not. The distribution of locations of radio-tagged birds is biased because birds (especially males; see section on home ranges and movements) tend to remain in the area where they were trapped. The locations of radio-tagged birds therefore represent the locations where we trapped birds rather than the actual distribution of all of the birds in the study area. The lek surveys include all prairie-chickens in the study area, not just radio-tagged birds, and therefore more closely reflect the distribution of the prairie-chickens within the study area.

Fig. 11. Total number of Greater Prairie-Chickens recorded on lek surveys, by year.
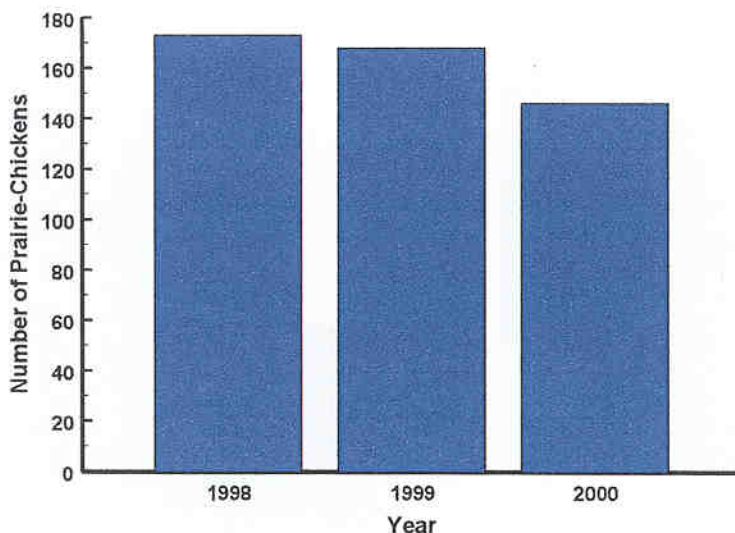
Leks were not evenly distributed throughout the study area, but tended to cluster in two areas. One of these is within the Bison Loop on the Tallgrass Prairie Preserve; the second is north of Foraker and east of Grainola (Fig. 12, map labeled "All Three Years"). Noticeable gaps, where no leks or only small leks were recorded during the three years include the area northeast of Grainola, an area in the central-northern part of the study area, and an area southeast of Foraker. Note that these areas correspond to lands that

were burned in all three years (compare maps labeled "All Three Years" on Figs. 10 and 12).

Fig. 12. Locations of leks in relation to burned and unburned areas, 1998 – 2000. Gray is burned rangeland within the study area; green is unburned area. Blue dots are locations of leks. The size of the dot corresponds to the number of birds recorded at the lek: small dot = 1 – 5 birds; medium-sized dot = 6 – 13 birds; largest dot = 14- 26 birds. Map labeled "All Three Years" shows all leks for 1998 – 2000, and the dot size corresponds to the greatest number of individuals recorded at that lek during those three years. Note that some leks were located outside the study area. Area in black square on 1998 map is enlarged in Fig. 14.
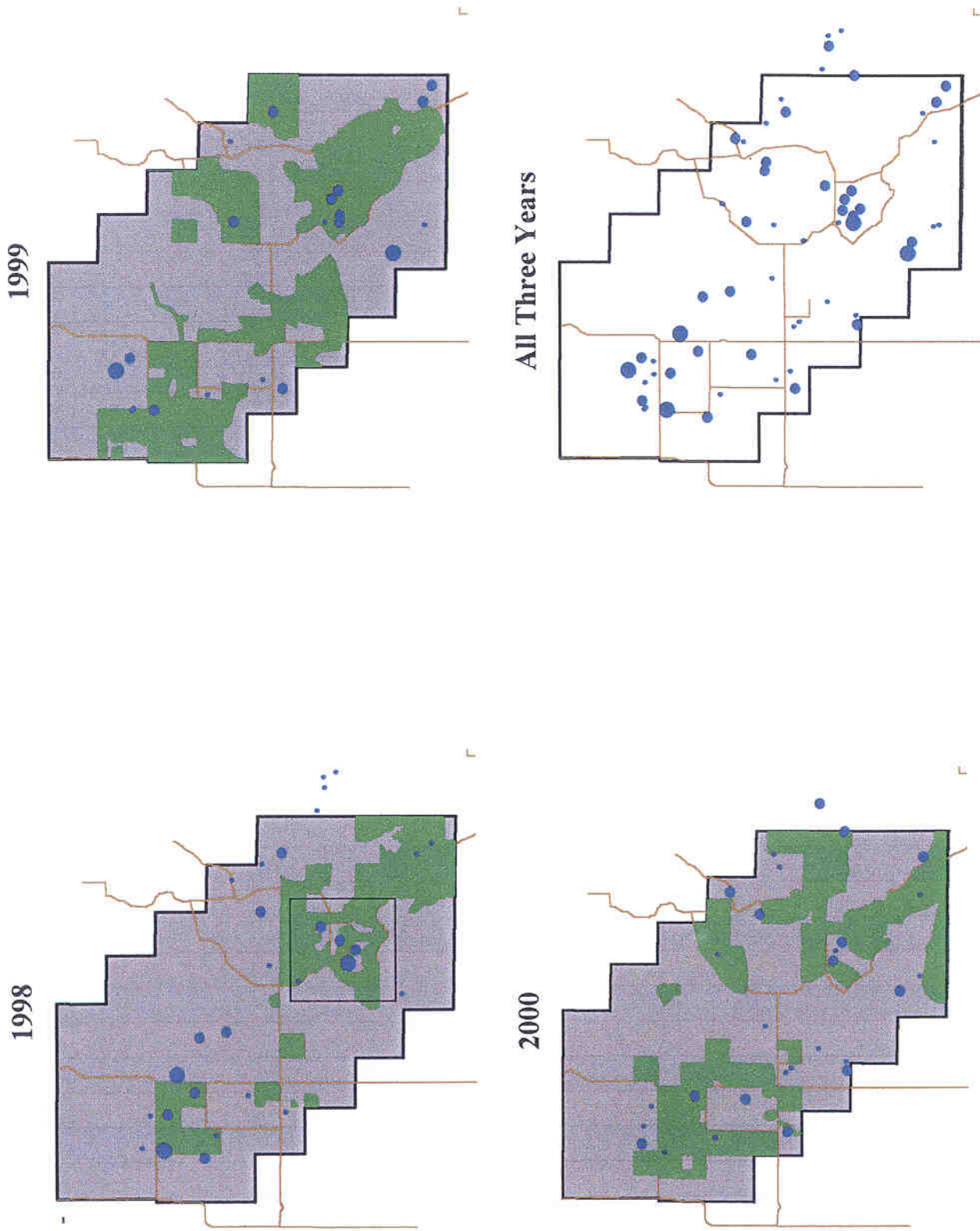

1999

All Three Years

1998

2000

Although the leks tended to be associated with unburned areas, the proportion of leks actually located on burned areas (areas burned in the spring of the year the survey was made and which were often on still-blackened ground) was high, averaging about 78% (Fig. 13).

Fig. 13. Proportion of leks located on burned ground. The average is about 78% for the three years covered.
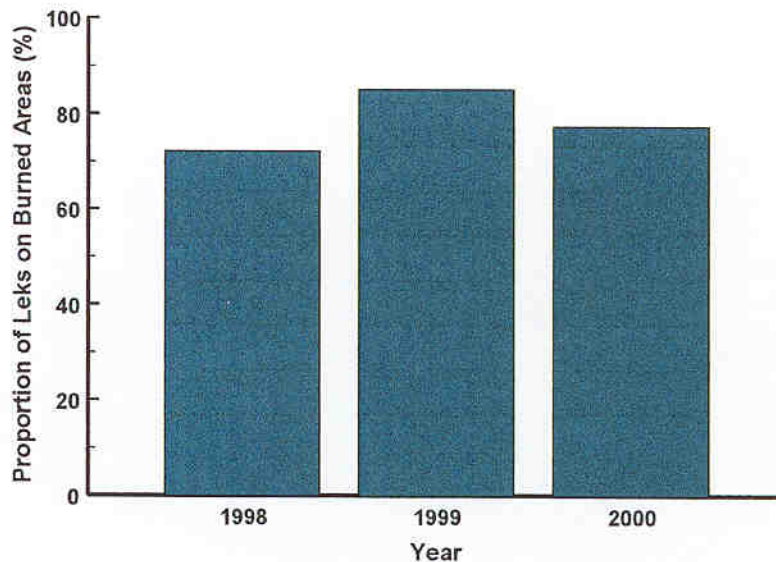
However, although the leks themselves (that is, the actual area where the males were displaying) were on burned ground, they tended to be associated with nearby unburned areas. For example, in Fig. 14, although all leks but one were located on burned ground, all were located very near to a burn edge. The one lek located on unburned land was also the lek with the fewest birds.

Fig. 14. Enlarged view of area in black square on Fig. 12. Gray is burned rangeland within the study area; green is unburned area. Blue dots are locations of leks. The size of the dot corresponds to the number of birds recorded at the lek.
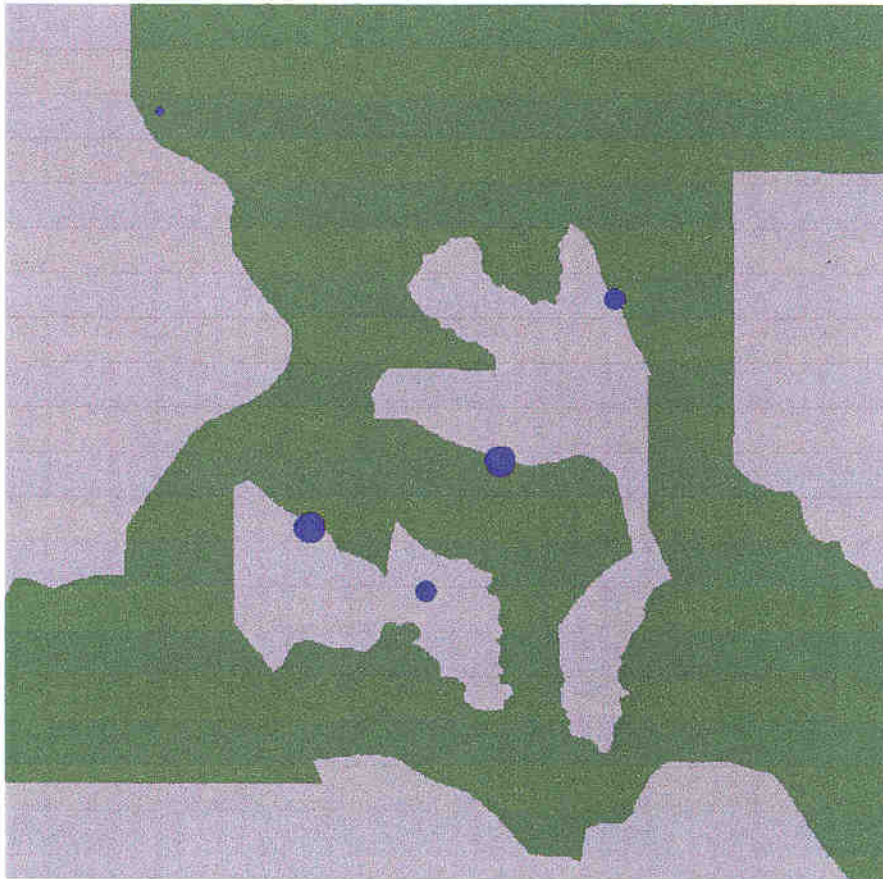
Combining the facts that leks tended to be located on burned ground but near unburned areas suggests that Greater Prairie-Chickens are probably using both areas. The prairie-chickens generally display in a very open area, where their booming and displaying can be seen well by any approaching hens—and predators. Burned areas, with their relatively low vegetation provide suitable booming ground sites. However, in open areas, the birds become more visible to predators. The birds may therefore choose lek sites that provide the visibility required for displaying, but which are close to taller vegetation cover (unburned areas) to which they can flee when escaping from (especially aerial) predators. This explains both the gaps in distribution of leks where the range was burned each year (seen in Fig. 12) and the contrasting fact of the high proportion of leks located on burns.
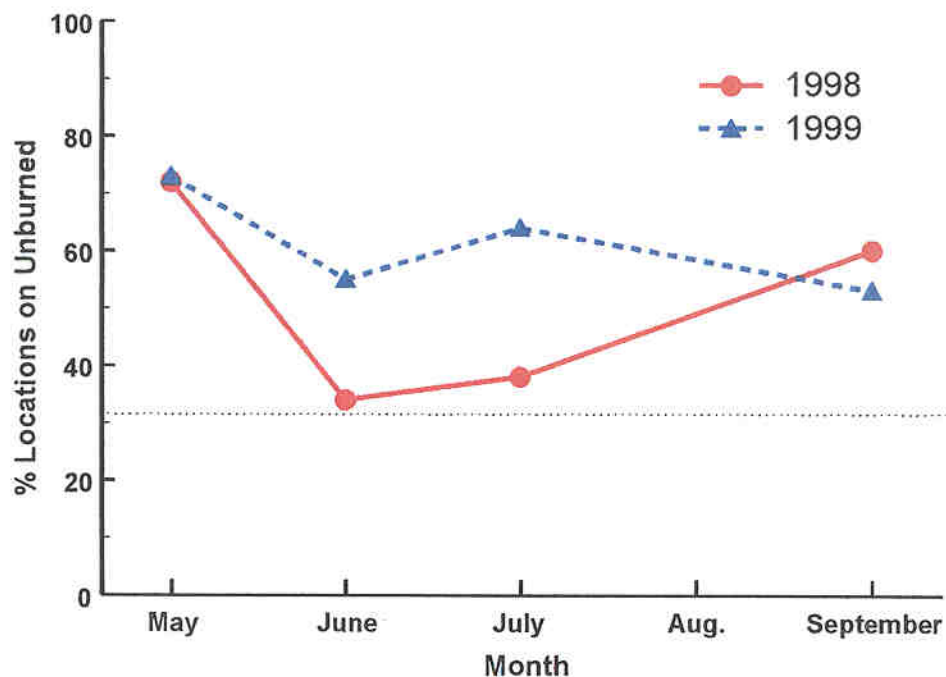

Use of Burned and Unburned Areas
Use by the Greater Prairie-Chickens of burned and unburned areas for general habitat use (that is, not for booming grounds or nests) was assessed using about 1750 non-lek,

non-nest locations from May – September 1998 and 1999. The locations were classified as to whether they were on burned or unburned land.

About 56% of the locations taken on the radio-tagged birds were on unburned land. However, only about 32% of the land was unburned; therefore, the prairie-chickens were located more frequently on unburned areas than would be expected. In May, soon after the burning had taken place (usually March – early April) and before much re-growth of the grass had occurred, about three-fourths of the locations were on unburned lands in both 1998 and 1999 (Fig. 15). Although the proportion of locations on unburned areas decreased from this high number as the season progressed and re-growth occurred (making the difference between burned and unburned areas less dramatic), the prairie-chickens' use of burned areas never reached their proportion of the landscape. That is, even in September of both years, more than 50% of the locations were on unburned land, even though only about one-third of the land was unburned.

Fig. 15. Proportion of non-lek non-nest locations on unburned land in May – September 1998 and 1999. The dotted horizontal black line indicates the proportion of land that was unburned, 32.3% (see above).


The prairie-chickens' selection of unburned areas in a larger matrix of burned areas causes the birds to be concentrated. Densities of prairie-chickens in the unburned areas in May would be approximately five times as high as in burned areas (75% of birds on 33% of land vs. 25% of birds on 67% of land). This increased density may have two effects detrimental to the birds: a) both mammalian and avian predators may learn to search unburned areas, knowing that the likelihood of finding prey (in this case, prairie-

chickens) is much greater there; and b) the predators themselves, seeking their own cover, may be concentrated in the unburned areas. These two possibilities are not mutually exclusive, and both likely are affecting the prairie-chickens. For additional information on differences in mortality in burned and unburned areas, see page 34.

The changes in seasonal use of burned and unburned rangelands by the prairie-chickens can also be seen in Fig. 16. In May, all locations were fairly tightly clustered, and most were in the unburned areas. Even those locations in the burned areas tended to be clustered in lines along the edges of burns. No birds were located in the center of the large burns. In September, in contrast, after more than four months of re-growth of the grasses in the burned areas, prairie-chickens were located far into the centers of the largest burns. The distribution of points is similar, however, in that most locations were on unburned lands, and even those on burned ground still tended to cluster along the edges of the burns.

Fig. 16. Non-lek non-nest locations of radio-tagged Greater Prairie-Chickens in May and September 1998. Gray areas are burned. Red points are those on burned lands; yellow dots are on unburned lands.

May   **September**
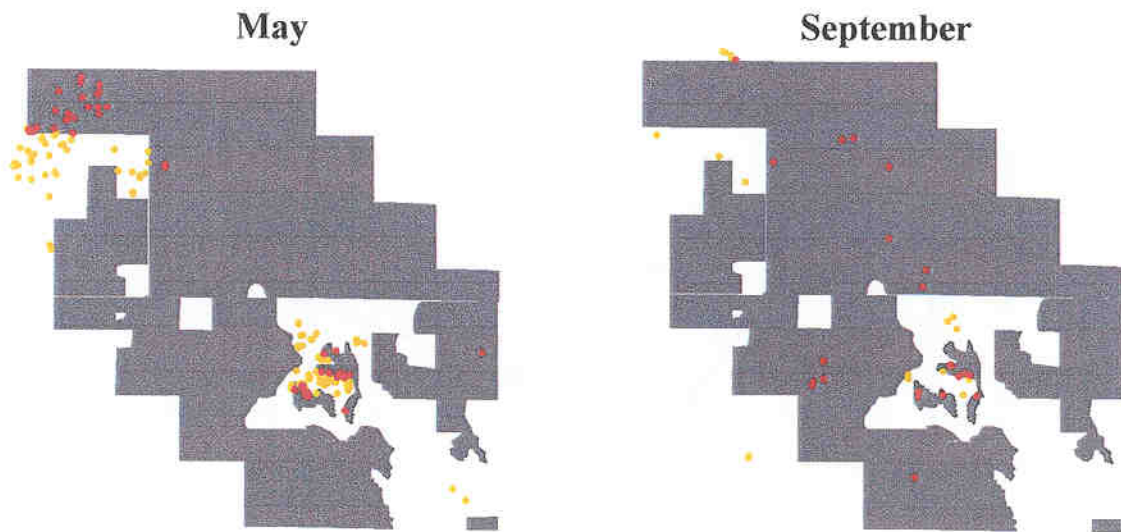
Survivorship

The life expectancy of Greater Prairie-Chickens, as with most other galliforms birds, is short. Annual survivorship[4] is expected to be low, as with Campbell's (1972) estimate of 35% annual survivorship for Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). Therefore, few prairie-chickens live to be more than two years old.

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[4] Mortality and survivorship are opposite sides of the same coin: Survivorship = 1 − mortality, or, when expressed as percentages, % Survivorship = 100% − % mortality.

Seasonal Survivorship

We analyzed mortality data from 1997 – 1999 by quarter year (January – March, April – June, July – September, and October – December) for radio-tagged birds. The fate of all of the birds was not known. Although many birds are found dead, some individuals disappear and are never found again, alive or dead. It is not possible to determine whether those individuals that disappeared were still alive and had just left the study area, or were actually dead and their transmitter damaged or lost (chewed by a coyote or dragged deep into a badger hole, for example) so that they could not be located. Therefore, the estimates of crude mortality were made two ways, one using only birds known to be dead and assuming that all missing birds were actually still alive, and the other using all birds known dead and assuming that all missing birds were actually dead. This produces estimates that are upper and lower bounds of the crude mortality estimate. Because some of the missing birds probably were still alive and some probably were actually dead, the true mortality lies somewhere between.

Within a year, crude mortality tended to be highest in the second quarter (April – June; Fig. 17). This peak corresponds to the breeding season of the Greater Prairie-Chicken, when males are on the booming grounds every day (and therefore vulnerable to predators because of their noisy displays out in the open), and females are vulnerable because they are incubating and rearing broods. Mortality declined in the summer and fall (third and fourth quarters), and began to increase again in winter (first quarter).

Fig. 17. Crude mortality by quarter-year for Greater Prairie-Chickens in 1997 – 1999. Estimates are percentages of birds dead and / or missing (see text) of all birds known alive during the quarter. The "true" mortality lies between the lines.
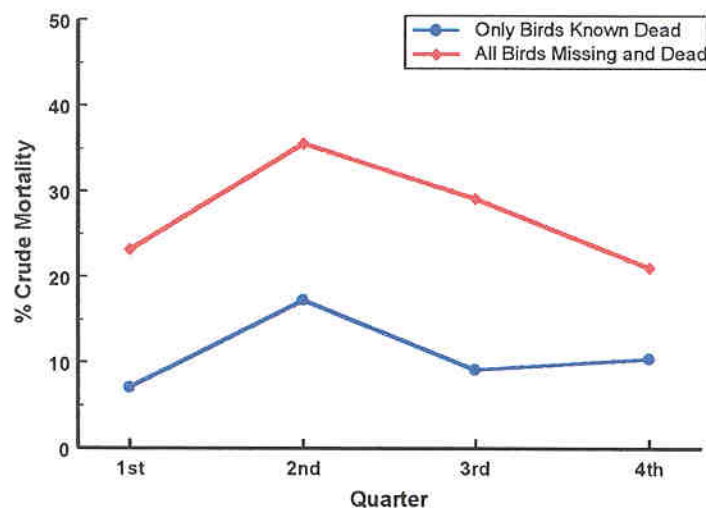

In general, our estimates of survivorship for the entire year probably fall within the range of expected values (40 – 60%) for Greater Prairie-Chicken.

Survivorship in Burned and Unburned Areas

Although the prairie-chickens may be more vulnerable during the breeding season, a confounding factor is that in the study area the breeding season is also the time of year when there is the least amount of cover for the birds from predators. As described in previous sections, much of the study area is burned, usually in March or early April. The grass rapidly begins to re-grow, providing greater cover as the season progresses.

By month, the average crude mortality declines fairly steadily from May – September (using only data from 1998 and 1999; Fig. 18), in general accordance with the quarterly decline in Fig. 17. The decline in seasonal mortality may be partially attributable to the re-growth of vegetation.

Fig. 18. Average crude mortality by month for the period May – September, for the years 1998 and 1999 only.
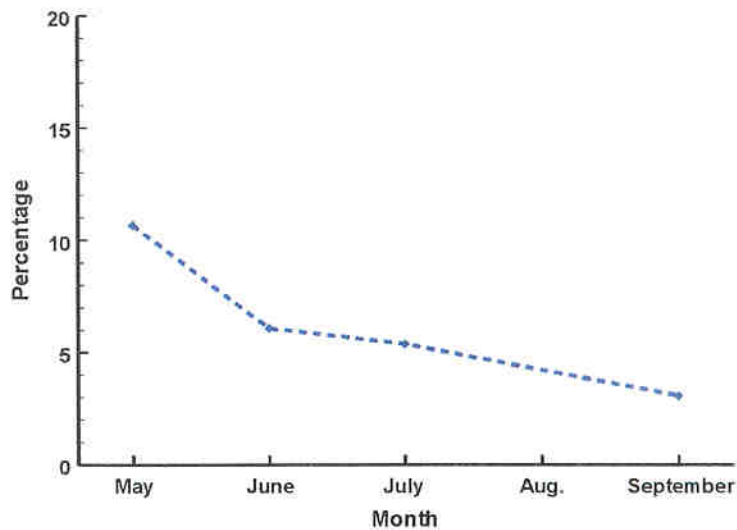
The mortality on burned areas for the same period tended to be lower, although the difference was not statistically significant (Fig. 19). The apparent difference is greatest in May and June, when the contrast in the amount of cover is greatest between the burned and unburned rangelands. By September, the mortality was the same in both areas.

Fig. 19. Crude mortality rate of Greater Prairie-Chickens on burned and unburned areas in 1998 and 1999. The mortality was calculated as the number of dead birds only as a proportion of the number of locations on burned and unburned lands. Because this number is very low, values were multiplied by 10.
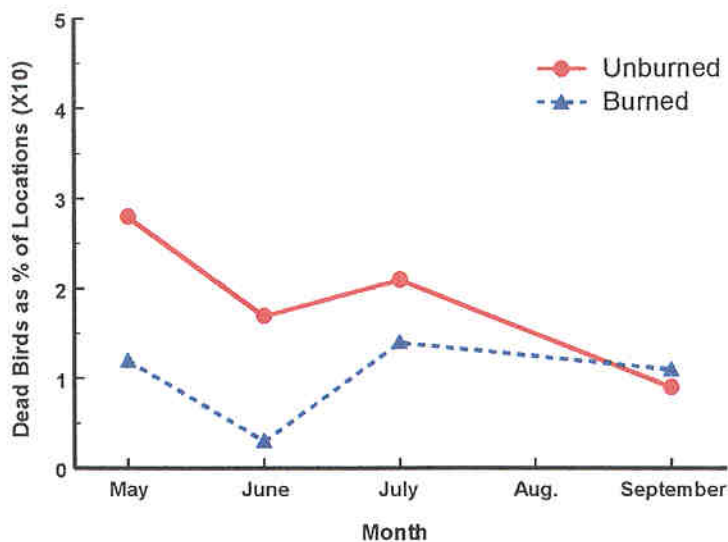
Although this result, having apparently greater mortality in the unburned areas where there is more cover, may seem counter-intuitive, it may be a direct consequence of the concentration of the prairie-chickens in unburned areas (see page 31). Because the birds are concentrated in the relatively small unburned areas, both mammalian and avian predators may be able to locate them more effectively. Although the prairie-chickens in the burned areas may have less cover, because the amount of area is substantially larger and the prairie-chicken density lower, the birds may be less likely to be detected and killed. In addition, as mentioned in the previous section, the predators themselves, especially mammalian predators, may be concentrated in the unburned areas to find their own cover.

The decreasing difference in mortality between the burned and unburned rangelands as the season progresses suggests that the birds are able to avoid predators equally well on the burned and unburned areas later in the season. This may be because they are less concentrated in the unburned lands, and the predators themselves may also disperse across the larger area including the (now re-grown) burned areas. This further supports the idea that the concentration of the prairie-chickens into unburned areas early in the breeding season may be detrimental to their populations.

Nest Success

We located 70 nests in the four springs of the project, 1997-2000. This included 12 nests in 1997; in 1998 we located 26 nests; in 1999 we located 24; and in 2000 we located eight (Table 3).

Nest success can be measured in several ways. "Raw nest success" is the number of nests that were successful out of all nests found. Although this number is easy to calculate, it counts equally a nest found on the first day of egg laying and one found late in incubation. In this example, the nest found early has a much greater likelihood of being unsuccessful than the one found late, because the one found late has already survived nearly to hatching. To account for this, we also used the Mayfield nest success calculation (Mayfield 1961). The Mayfield method accounts for nests found at different stages. The Mayfield nest success estimate will almost always be less than the raw nest success estimate, but is a more realistic value for nest success.

The raw nest success for the four years was nearly 33%, but the Mayfield nest success estimate was only 24% (Table 3).

Table 3. Successful and unsuccessful nests, raw nest success, and Mayfield nest success, by year, for 70 nests.

| Period	No. Successful Nests	No. Failed Nests	Raw Nest Success (%)	Mayfield Nest Success (%)
1997	1	11	8.3	10.5
1998	10	16	38.5	30.3
1999	10	14	41.7	31.2
2000	2	6	25.0	12.9
1997-2000	23	47	32.9	24.3

The Mayfield nest success estimates followed a fairly consistent pattern among the years: it was either around 30% (in 1998 and 1999) or around 10% (1997 and 2000). It is unclear what may have caused the differences in nest success.

The estimate of about 25% nest success for the four-year period is about the level expected of most ground-nesting grassland birds. It is not clear whether this level of nest success would allow the population to remain stable. Many other factors, especially chick / poult survival and recruitment and survival of adult hens, are also important demographic parameters regulating the Greater Prairie-Chicken population.

Nest Relationship to Burns
The Greater Prairie-Chickens did not place their nests as frequently on burned areas as on unburned rangelands by a large margin, with only 11 of 68 nests placed on burned areas over the four springs of the project (Fig. 20).

Fig. 20. Percentage of nests on burned and unburned rangelands. Data are for 68 nests from 1997 – 2000.
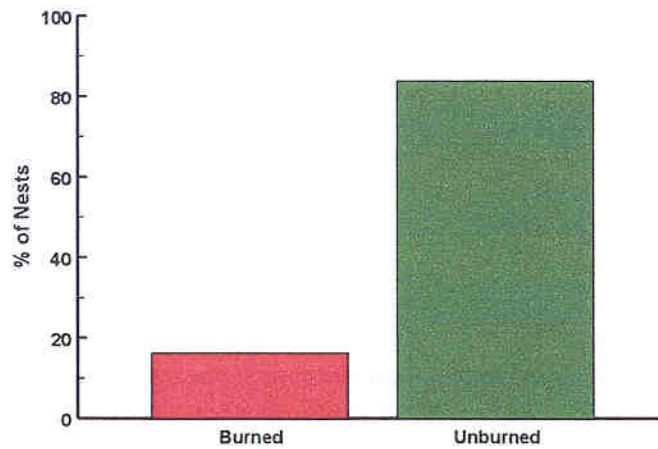
There is seasonality to the placement of the nests on burned and unburned areas, however. Of 50 nests from 1998 and 1999, only 6% of nests found before 20 May each year (approximately the midpoint of the nesting season) were located on burned lands, but of nests found after 20 May, 44% were located in burned rangelands, and the difference in seasonality is significant ($\chi^2 = 16.09$, 1 df, $P < 0.001$; Fig. 21). Nests found after 20 May were likely re-nest attempts after a first nest had failed.

Fig. 21. Proportion of 50 nests from 1998 and 1999 located on burned and unburned rangelands. Nests were separated into two categories depending on whether they were found before or after 20 May of each year, the approximate middle day in the nesting season.
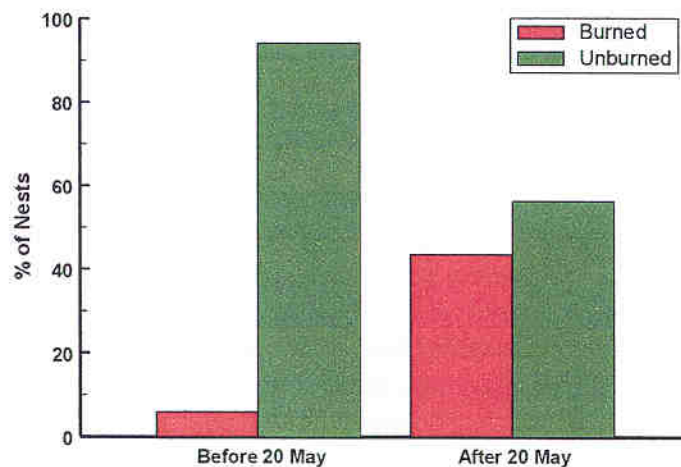
Because the grassland rapidly re-grows following a late-winter / early spring burn, by late May or June the contrast in amount of vegetation cover between the burned and unburned areas was probably much lower than before 20 May. Prairie-chicken hens seeking a nest site with sufficient cover may have been unable to find a suitable site early in the season, but after 20 May, areas that had been burned may have provided sufficient cover. This may account for nearly half of the later nests being located in the burned areas. However, note that even with nearly half the nests on burned areas, because the amount of burned rangeland was much larger (about two-thirds of the area was burned; see above), the density of nests on unburned areas was more than twice as high as on burned areas (1.7 vs. 0.7; that is, 56% of nests on 33% of land vs. 44% of nests on 67% of land). Therefore, although the prairie-chicken hens after 20 May were placing more nests on burned ground than earlier in the season, they still chose unburned lands in substantially greater proportion.

Although the prairie-chicken nests were more frequently located on unburned lands, nest success did not differ between nests located on burns and those on unburned land ($\chi^2 = 0.007$, 1 df, P = 0.935; Table 4). In fact, the raw nest success was exactly the same, 40%, on unburned and burned lands. The Mayfield nest success estimate differed only slightly (and non-significantly) between the two areas.

Table 4. Successful and unsuccessful nests, raw nest success, and Mayfield nest success, by on burned and unburned areas, for 50 nests from 1998 and 1999.

Period	No. Successful Nests	No. Failed Nests	Raw Nest Success (%)	Mayfield Nest Success (%)
Burned	2	3	40.0	32.4
Unburned	18	27	40.0	30.5

This lack of difference in nest success between burned and unburned areas conforms with the lack of difference in predator numbers during the nesting season (page 60). If predators are not concentrated in the burned areas in late May – early June, but are instead fairly evenly distributed between the two types of areas, their effect on nest success may be roughly the same between the two areas.

*Incubation Behavior and Time of Day of Nest Predation*

Data loggers were placed in seven nests, four in 1998 and three in 1999. Of these seven, three hatched (all in 1998) and four failed (one in 1998 and all three in 1999).

We were concerned that placement of the loggers in the nests might reduce nest success, either through abandonment by the hen because of the strange object in her nest, or through increased predation caused by the presence of the logger somehow making the nest more easily detected. However, because the hatching success rate was three of seven nests (a raw nest success rate of 43%), a rate as high or higher than for nests without the

loggers, we are confident that placement of the data loggers did not greatly affect the outcomes of the nests.

An example of data logger results can be seen in Fig. 22. These data were obtained from the successfully hatched nest of Hen 153 during May and early June 1998.

Fig. 22. Plotted output from data logger in nest, showing placement and removal date and time.

Nest of Hen 153
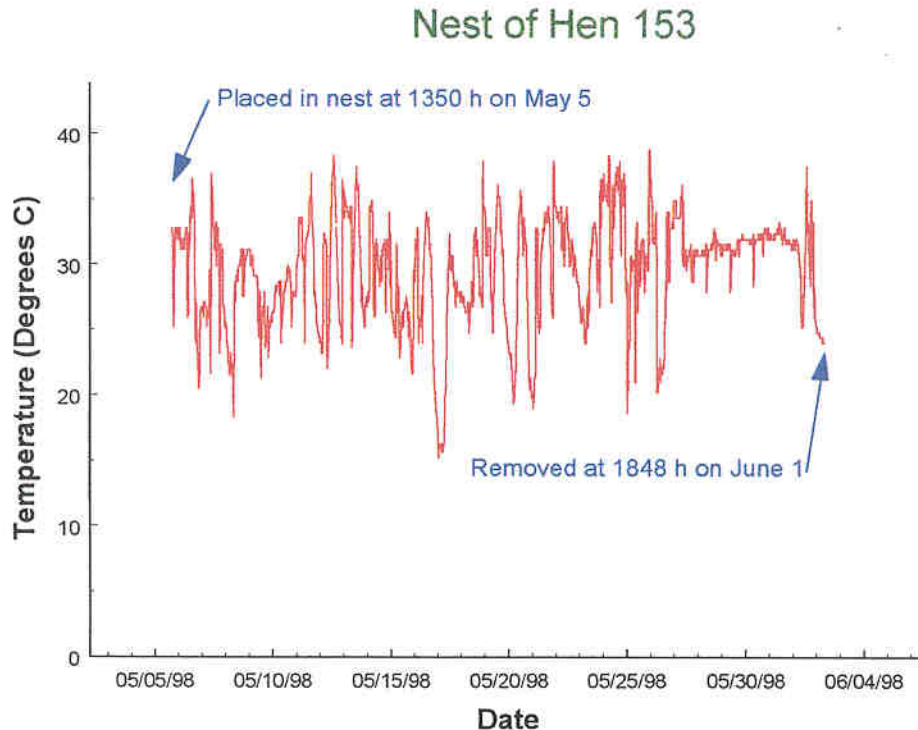
The graph shows the long period of incubation from 5 May 1998, when the logger was deployed, to about 28 May 1998. During that period, the temperature in the nest fluctuated between about 20° and 37° C (about 60° and 100° F). Temperature fluctuations probably represent periods when the hen was away from the nest for feeding.

Beginning on 28 May and extending through 5:47 h CDT on 1 June, the temperature in the nest remained much more constant, at about 31° C. It is likely that this was the time when the eggs began to pip and hatch, and the hen remained very attentive on the nest, not even leaving to feed. Finally, at 5:47 h on 1 June, the temperature again began to fluctuate again. We determined later that day that the hen and chicks had left the nest. It is likely that she and her brood left the nest at 5:47 h, when the temperature began to fluctuate. Sunrise on 1 June 1998 was at 6:08 h CDT; it is apparent that the hen and her brood probably left the nest with the first light. Similar interpretation can be made on the data from the six other data loggers deployed in nests.

The data collected at two of the nests is atypical of that of the other five, although it is still useful. The data logger was in the nest of Hen 57 for only a little over 24 hours before the nest was depredated. In addition to this short time, it appears from the data that the eggs were already pipping, because they do not show the normal fluctuations. The data from the logger placed in the nest of Hen 173 also appear to be aberrant, in that the temperature is unusually low (Table 5). When recovered, this logger had become wet within its wrappings, and although it still functioned, its readings may not be correct.

The overall average temperature of the other five loggers (excluding the ones from the nests of hens 57 and 173) was 31.9° C, with an average maximum of 39.5° C and an average minimum of 19.9° C (Table 5). This does not seem to differ much from the average of the successful or of the unsuccessful nests.

Table 5. Summary statistics for data logger output from successful and unsuccessful nests for the entire nest period (period the logger was deployed).

Bird / Nest No.	Mean Temp.	Variance	Min. Temp.	Max. Temp.
SUCCESSFUL NESTS				
153	29.6	16.8	15.2	38.8
103	33.5	17.4	17.9	42.9
127	34.2	2.6	26.3	39.2
Average	32.4	12.3	19.8	40.3
UNSUCCESSFUL NESTS				
166	29.8	7.7	19.0	38.8
176	32.2	14.2	21.3	37.9
57* only pipping	35.5	1.3	24.8	36.6
173 ** wet?	27.8	1.6	21.3	30.3
Average of 166 and 176	31.0	11.0	20.2	38.4
AVERAGE OF ALL NESTS	31.8	8.8	20.8	37.8
AVERAGE OF 5 NESTS (without 57 and 173)	31.9	11.7	19.9	39.5

Because the hen appears to incubate without leaving during the final two or three days before the chicks leave the nest (in successful nests), the temperature remains more constant during that period (Table 6). During the final 48 hours before the chicks left the nest, the average temperature was higher and the variance much lower than that during the entire incubation period.

Table 6. Summary statistics for data logger output for the last 48 hours before chicks left the nest for the three successful nests.

Bird / Nest No.	Mean Temp.	Variance	Min. Temp.	Max. Temp.
153	32.0	0.3	28.3	33.2
103	35.8	7.8	25.6	39.2
127	34.2	1.4	27.9	37.0
AVERAGE	34.0	3.2	27.3	36.5

Brood-leaving occurred an average of 1.2 hours from sunrise or sunset (-0.4, 1.1, 3.0 hours), with two of the three successful broods leaving the nest within an hour of dawn (Table 7). The other left the nest three hours before sunset. Predation events averaged 2.5 hours from sunset or sunrise (2.8, 0.8, 4.45, 1.9). Only one predation event occurred less than an hour from sunset, and one occurred nearly 4.5 hours after sunrise. Day length on 15 May at this location is about 14 hours. Therefore, since no brood-leaving occurred farther from sunrise or sunset than three hours, broods appear not to leave nests during the middle eight hours of the day. Likewise, since no depredation occurred more than 4.5 hours from sunrise or sunset, the predation does not seem to occur in the middle five hours of the day.

These two facts suggest that birds and predators are not active during midday, as would be expected. (This can also be seen for the prairie-chickens in the section beginning on page 46.) This indicates that nests were probably depredated during the active part of the day for predators and that chicks left the nest during the active part of the day for the birds.

Table 7. Deployment dates for all data loggers, the time chicks left the nest or the nest was depredated, and the time of sunrise and sunset for all seven data logger deployments.

Bird / Nest No.	Date Logger Placed in Nest	Date Brood Left Nest or Nest was Depredated	No. Days Logger Was in Nest	Time Brood Left Nest or Nest was Depredated	Time of Sunrise or Sunset (CDT)
SUCCESSFUL NESTS					
153	5 May 1998	1 June 1998	28	5:47	6:08
103	19 May 1998	17 June 1998	30	7:14	6:06
127	22 June 1998	4 July 1998	13	17:49	20:48
UNSUCCESSFUL NESTS					
57	14 May 1998	15 May 1998	1	9:08	6:18
176	27 April 1999	16 May 1999	20	19:38	20:26
166	13 May 1999	25 May 1999	13	10:38	6:11
173	5 May 1999	29 May 1999	25	18:42	20:36

The temperature within the nest of Hen 153 over about a 50-hour period beginning at 18:00 h on 5 May 1998 and ending at about 20:00 h on 7 May 1998 can be seen in Fig. 23. This period covers two nights (sunset to sunrise) and two days (sunrise to sunset).

Fig. 23. Detail of data logger output from Hen 153. This is a portion of the graph shown in Fig. 22. Values recorded at night are in blue; days in dark red. "F" marks times when the hen was likely away from the nest and foraging.
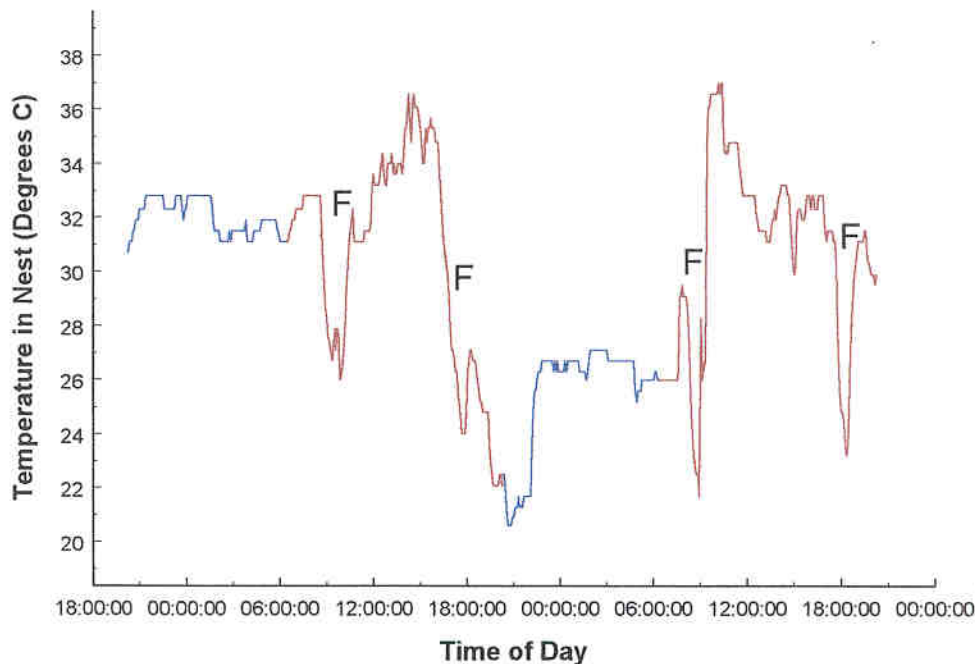
Night-time nest temperatures tended to be much more stable than daytime temperatures. The night of 6-7 May 1998 (second blue region) was somewhat less stable than the first night. The temperature averaged much lower, too. This is probably a result of where the data logger was placed in the nest, and may not indicate the actual average temperature within the nest.

Daytime temperatures were much more variable, and tended to be higher than the nighttime temperatures. Of course, this is probably an affect of the higher ambient daytime temperature. Most notable about the daytime pattern, however, are large dips in the nest temperature in early morning and in the evening, marked with "F" on the graph. It is likely that these temperature decreases occurred when the hen was off the nest for feeding. When she returned and again began incubating, the temperature returned to higher levels. The temperature dip in the early night of the second day may have been an effect of where the hen had moved the data logger within the nest. Because the logger is a foreign object, she likely was trying to remove it and had placed it near the edge of the nest where temperatures were cooler.

The four feeding bouts marked with the letter "F" averaged 2.35 hours in length (range 2.08 to 2.58 hours). The morning and evening bouts did not differ much in length;

the two morning bouts were 2.08 and 2.58 hours, and the two evening bouts were 2.50 and 2.25 hours. The two morning bouts began over an hour after sunrise (about 6:27 CDT at that time of year), at 8:37 and 7:52 h. The two evening bouts ended over an hour before sunset (about 20:17 CDT at that time of year), at 18:12 and 19:07 h. Of course, it takes some time for the eggs to begin cooling once the hen leaves the nest, and some time for them to warm up once she returns, so the exact minute she departed and returned to the nest was probably a few minutes before these times. These results suggest the hen was spending about 10 hours during the day on the nest, and all 10 hours of night, for a total of 20 hours per day.

During midday, temperatures tended to fluctuate more than at night. This is likely because the ambient temperature was closer to the temperature at which the hen was trying to maintain the eggs, and she may have spent some time moving about the nest, or, during midday, even standing and shading the eggs to prevent their overheating.

These results are preliminary, a result of analysis of only a small sample of data available from only seven data logger deployments. Further analysis is necessary, and additional data logger deployments in nests are also desirable.

Movements and Home Range Size

Although Greater Prairie-Chickens most often now live in fragmented habitats, divided by cultivated fields, roads, or woodlands, it is useful to understand their movements and range requirements in a homogenous, unbounded habitat (i.e., in an unlimited area of suitable habitat where they can go and do as they please). Of course, movements and home ranges are dependent on local habitat and conditions (Burger 1988). Home ranges vary according to the distribution of cover, location of suitable lek sites, and availability of food supplies in each season. For example, agricultural land may provide waste grain as a winter food source, but obtaining it may require extensive movement. Although the home range and movements are affected by these factors, analysis of their range in a homogeneous habitat should provide a baseline measure of home range requirements.

Until the advent of transmitters for radio tracking in a form small enough to be carried by even so large a bird as a Greater Prairie-Chicken (800 – 1100 g) in the 1960s, study of movements and home ranges relied on band recoveries, fortuitous sighting of marked birds, or actually following flocks through a day (e.g., Hamerstrom and Hamerstrom 1949). These methods allowed study of only very short-term, short-distance movements (following of birds), or obtained sparse data (band recoveries).

In the era of radio telemetry studies, the small amount of non-fragmented habitat remaining has allowed few studies of Greater Prairie-Chickens or other prairie grouse to be carried out in homogeneous habitat. Robel et al. (1970) used radio telemetry to track Greater Prairie-Chickens on a site in central Kansas, that was also generally homogeneous and unbounded. Our objectives were to examine movement patterns at several time scales (within a day, over a season, and over the life span of the prairie-chickens), and to estimate home range sizes (area) in a homogeneous and unbounded habitat, such as the Greater Prairie-Chicken may have occupied previous to the time of European colonization and the sod-busting of the Great Plains.

Hourly Movements

At haphazardly chosen intervals through the year, field technicians followed a randomly-selected individual prairie-chicken for an entire day. Locations were recorded every half-hour, with some locations recorded more frequently when a bird had moved some distance.

Data were used only from individuals which were tracked at least every half hour from within one hour after sunrise to within one hour before sunset. Because sunrise and sunset vary through the year, we obtained a variable number of locations per bird-day of tracking, from 20 to 30. We used data from 32 individuals that had a complete set of data, 22 males (17 adults and five juveniles) and 10 females (eight adults and two juveniles). Distances were calculated between consecutive locations.

Three-Day Movements

Aside from all-day tracking efforts used to describe the hourly movements, we attempted to obtain locations at three day intervals for use in three-day movement analysis. However, this interval varied from one to 525 days, depending on how readily a bird could be relocated. Because the distances moved during widely varying intervals are not comparable, we used only locations from non-overlapping three day intervals. (That is, if a bird were tracked on days 1, 2, 3, 4, 5, 6, and 7, the three-day intervals between days 2 and 5 or 3 and 6 were not usable because they overlap. These seven locations would allow only two three-day intervals, between days 1-4 and 4-7.) This produces equal-length intervals over which distances were calculated between consecutive locations. We will hereafter refer to these movements as "three-day movements." For the three-day movement analysis we selected only individuals with greater than 25 locations, and used only the first location of the day if a bird was tracked more than once on any day.

We used only individuals for which there were at least four three-day tracking intervals in a season. This allowed a data set of 617 usable tracking events. The values for one bird in one season[5] were averaged, resulting in 99 bird•season combinations. Of these, 77 were of males and 22 of females, with only one of the females in Fall and one in Winter. The 99 bird•season combinations were unevenly divided among the four seasons, with a large majority (81) in Spring and Summer, 10 in Fall and eight in Winter. Likewise, the large majority of individuals were adults, with 19 juvenile bird•season combinations and 14 of unknown age class.

Home Range and Maximum Distance Moved

For the home range analyses we only included birds with greater than 50 locations. These locations could be on a lek, on a nest (for hens only), or elsewhere—that is, all locations. We used only birds captured and for which tracking was begun in March, April, or May of the years 1997, 1998, or 1999. This produced a set of 45 individuals: 12 females (six adult, two juvenile, and four unknown) and 33 males (17 adults, 14 juvenile, and two unknown). The range in number of locations for individual birds was from 52 to 328 locations, with a total of 5211 locations for all 45 birds combined. The number of days a bird was tracked, between its first and last locations, ranged from 53 to 857 days

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[5] Seasons with capital letters ("Spring" as opposed to "spring") are defined on page 8.

(about two years, four months). The maximum distance over seasons moved was measured as the greatest distance between any two locations for an individual.

Analysis

Home range areas were calculated using HRE: The Home Range Extension for ArcView (Beta Test Version 0.9, July 1998; Rodgers and Carr 1998). We used the Minimum Convex Polygon (MCP) of 98% of points, median centered. Only individuals with at least 50 tracking locations were included in the analysis, as recommended by Seaman et al. (1999).

Although kernel smoothing methods for determination of range area have been shown to be less biased for measuring the home ranges of some species (for example, bears; Seaman and Powell 1996), kernel smoothers are problematic with prairie-chicken data, even when the number of locations greatly exceeded the minimum of 50 recommended to achieve reasonable results (Seaman et al. 1999). Because of the highly focused use by Greater Prairie-Chickens of one area (around the lek) during much of the year (one male chosen haphazardly to be an example, tracked 207 times over 516 days, was located more than 200 m from the lek only 24 times), kernel methods with usual estimates of the smoothing parameter h underestimate the area actually used by the birds. Visual comparison of MCP and various kernel methods (fixed and adaptive; using several methods for determining the value of h) always showed that the kernel method underestimated the area used by the prairie-chickens, unless the value of h was manually set unusually high, several times the value estimated using least-squares cross validation. In those cases, where h was set high, the kernel methods clearly over-estimated the area used by the birds by smoothing in large portions of the unoccupied surrounding area. MCP, although not ideal, produced a more consistent home range covering the actual locations used by the birds. In addition, it is not our purpose to identify a center of activity for the prairie-chickens, as can be done using kernel density estimators. The activity of the birds is always centered on the lek and therefore already known. Instead, we are here interested in the extent of the area used by the birds through their life spans.

The range estimated by the MCP tends to increase as the sample size increases (Jennrich and Turner 1969), although when the true range is a convex polygon, it approaches asymptotically the true home range size as sample size increases (Anderson 1982). Although MCP may overestimate the size of a range if there are lacunae within it (Boulanger and White 1990), careful comparison of the actual distribution of the locations with the extent of the MCP can identify any lacunae. Once a lacuna is identified, the locations can be divided into subgroups (hereinafter called "activity centers" following the terminology of Boulanger and White 1990) and an MCP obtained for each. In general, because our study area was homogeneous, there is little reason to expect that home ranges would not be convex polygons, although in some cases the birds did move between two or more areas leaving gaps and lacunae. In our analysis, home ranges were split into two or more activity centers if the two nearest-neighbor points were farther apart than either was from the farthest member of their cluster. The bird was then determined to have moved its home range, not just enlarged it.

RESULTS

Hourly Movements

Because day length varies greatly from season to season, with approximately five hours more daylight at summer solstice than winter solstice at the latitude of our study site, prairie-chicken hourly movements (that is, movements within a single day) must be compared only within seasons. In Fall, Winter, and Spring, Greater Prairie-Chicken hourly movements generally followed a pattern of greatest movement in early morning, declining steadily until early afternoon, remaining low for about two hours, then increasing until dark (Fig. 24). There were some differences, however. In Spring and Fall the movement distances and patterns were very similar, but in Winter the birds tended to move greater distances in midday and afternoon (that is, the midday trough was not as low) than in the other two seasons, although they still moved less than in the morning or evening. Summer activity, however, showed a very different pattern, although this may be a partial artifact of small sample size; there were only four birds followed all day in the Summer, two males and two females. The Summer pattern shows an increase in movement during the morning, peaking near the time the movements reached a low point in the other three seasons. In Summer, activity dropped off by mid-afternoon, and did not increase in evening. In Summer, the two males showed a peak of movement distances around noon, whereas the females showed a peak of movement distances in late afternoon (Fig. 25).

Fig. 24. LOWESS smooths of hourly movements in Spring, Summer, Fall, and Winter.
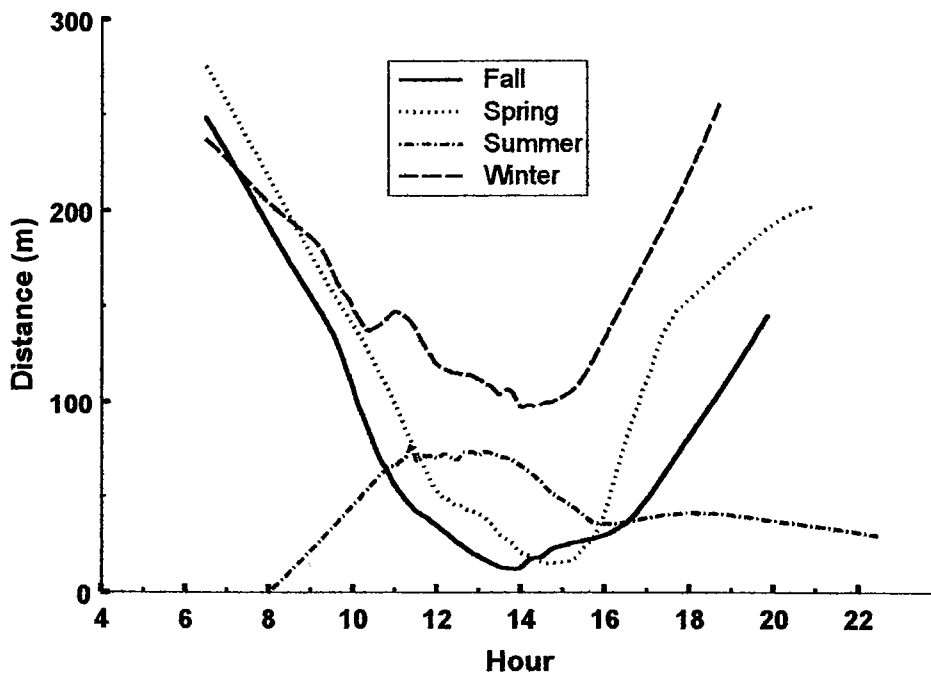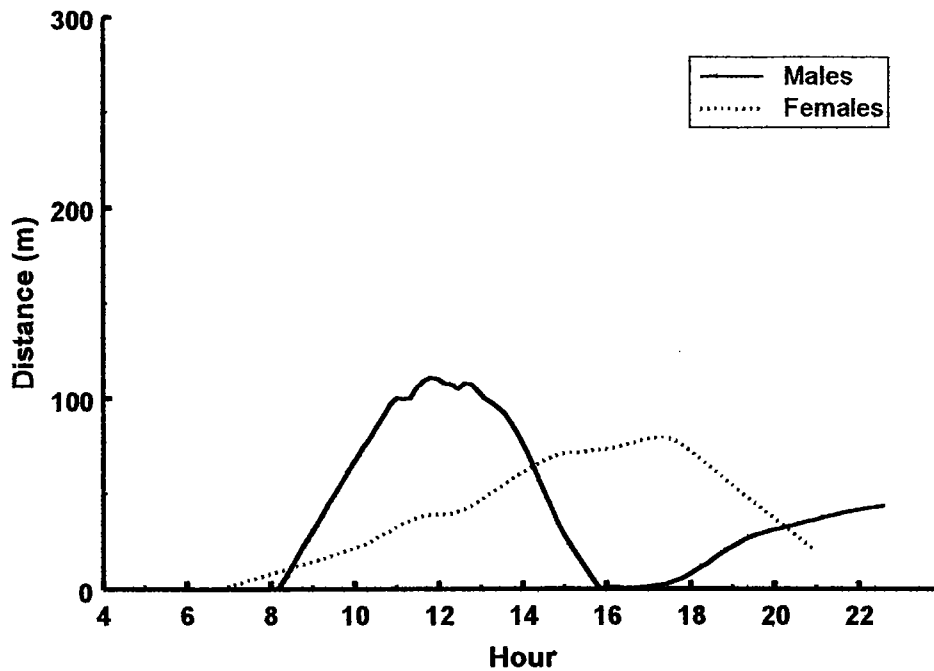
Fig, 25. LOWESS smooths of hourly movements in Summer only of two males and two females.

Comparing male and female movement distances in Fall and Winter showed little difference between the sexes, especially after late morning. In early morning, the females tend to move slightly less than males in both of these seasons, but the pattern is similar to that seen in Fig. 24. A small sample size of hens (one) precludes making comparisons between the sexes in Spring.

Three-day Movements

Movements by individuals throughout the year averaged 429 m per three-day period, with a minimum of 0 m (bird was at the same point on consecutive locations) and a maximum of 1706 m. Of course, these distances refer only to birds that were located three days apart; some individuals may have moved much greater distances but were not located again.

Three-day movement distances varied significantly between seasons (Fig. 26, Table 8). Spring (average 289 m) and Summer (391 m) movements differed strongly from Fall (839 m) and Winter (845 m) movements, with the latter being two to three times greater than Spring and Summer movements. Spring and Summer movement distances, although significantly different, did not differ greatly in magnitude. Fall and Winter movement distances did not differ.

Table 8. Pairwise separate variance t-tests, using square-root transformed data. ns = not significant at P < 0.05; * = P < 0.05 and P > 0.01; ** = P < 0.01 and P > 0.001; *** = P < 0.001. Degrees of Freedom (DF) in parentheses.

Season	Summer	Fall	Winter
Spring	* (76.3)	*** (16.1)	*** (12.6)
Summer		** (13.1)	** (10.2)
Fall			ns (15.8)

Fig. 26. Box plots of (untransformed) distance in m moved, by season. Numbers above each box plot are sample sizes.
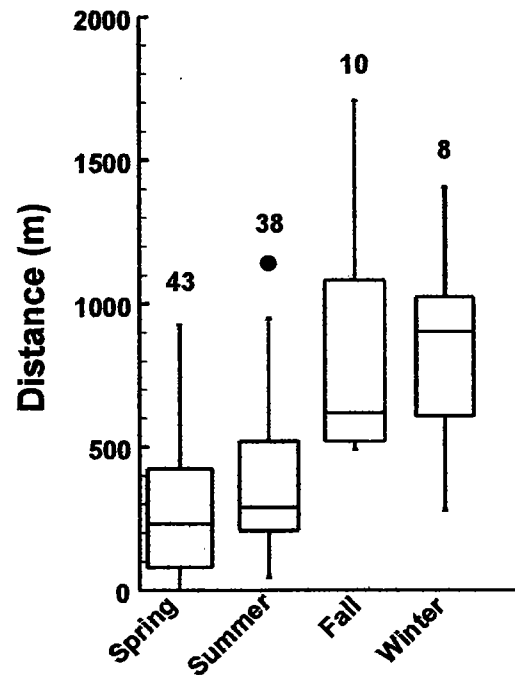

Because data were usable from only one female each in Fall and Winter, comparisons between the sexes could only be made for Spring and Summer (Fig. 27). In Spring, males moved an average of 190 m and females an average of 422 m, although this difference was not significant (using square-root transformed data, separate variance t = -2.0, df = 5.8, P = 0.096), and may be a result of the small sample size of females.

In Summer, on average the males moved greater distances (434 m) than the females (241 m), and the difference was significant (using square-root transformed data, separate variance t = 2.7, df = 31.0, P = 0.010).

Fig. 27. Box plots of (untransformed) distance moved, by sex. A. Spring; B. Summer. Numbers above each box plot are sample sizes.
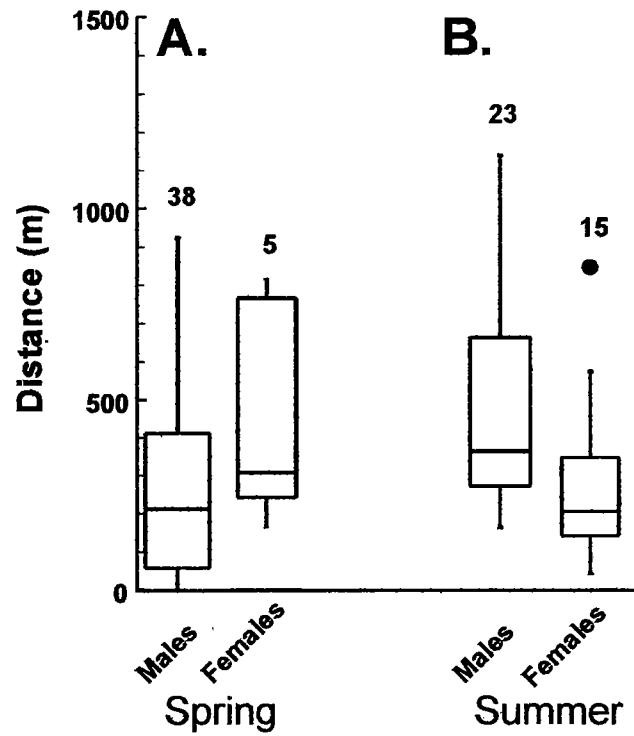
Because the number of females was small, comparison of age classes was restricted only to males. Even within males, too few Fall juveniles were available to allow comparisons, so all comparisons were made using Spring, Summer, and Winter males. There was no significant difference in the distance moved between the adults (306 m) and juveniles (300 m; see Fig. 28), although the range of distances moved (0 – 1138 m for adults; 0 – 1405 m for juveniles) was greater for juveniles. Likewise, none of the pairwise comparisons between seasons was significant .

Fig 28. Box plots of (untransformed) distance moved (m), males only, comparing adults vs. juveniles. Numbers above each box plot are sample sizes.
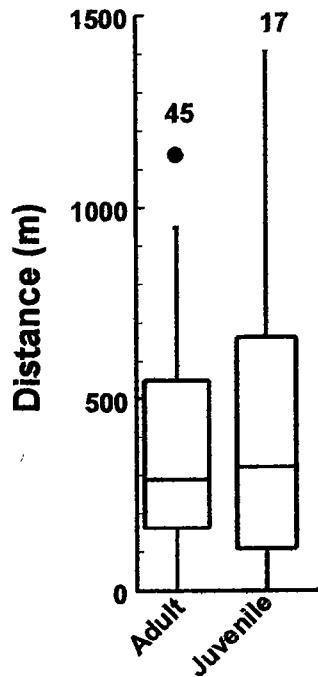
Potential Biases in Home Range Measures

There are several potential sources of bias in the home range and maximum distance moved measures. Because the entire life span of all birds is not known, the range size and distance moved for those birds that were lost may be actually much larger than measured. In addition, the time span over which the birds were tracked varies. Finally, some birds tracked were found dead, while others were lost and never rediscovered. The birds not found dead may have simply moved away, and therefore the actual area used by the birds (their range size) may be much larger than measured.

To evaluate these potential sources of bias, we plotted range size against two measures of length of time a bird was tracked: number of tracking records and number of days between first and last tracking (tracking span). Regression of range size against number of records was not significant ($R^2 = 0.064$; $F = 2.92$ with 1, 43 df; $P = 0.095$; Fig. 29). Regression of range size against number of days between first tracking and last tracking was significant ($R^2 = 0.428$; $F = 32.16$ with 1, 43 df; $P < 0.001$; Fig. 30), indicating that range size increased with increasing time. However, most of the increase came in the first year a bird was tracked. A LOWESS smooth (Fig. 30) of the same data shows that after about one year, range size did not appear to increase further. Therefore, although there may be a tendency for range size to increase over short time spans, our having data of varying time span probably does not cause biases in our estimate of range size over the longer term.

Fig. 29. Regression of $\log_{10}$ (range size) against $\log_{10}$ (number of tracking records). The regression was not significant.
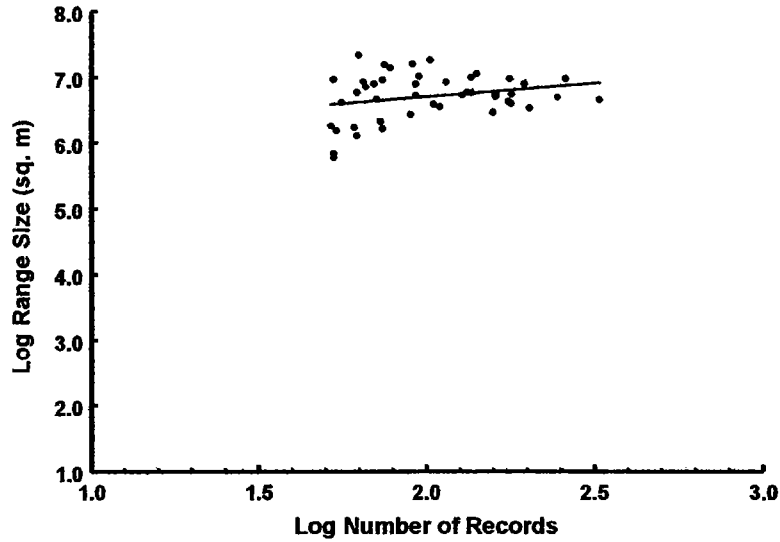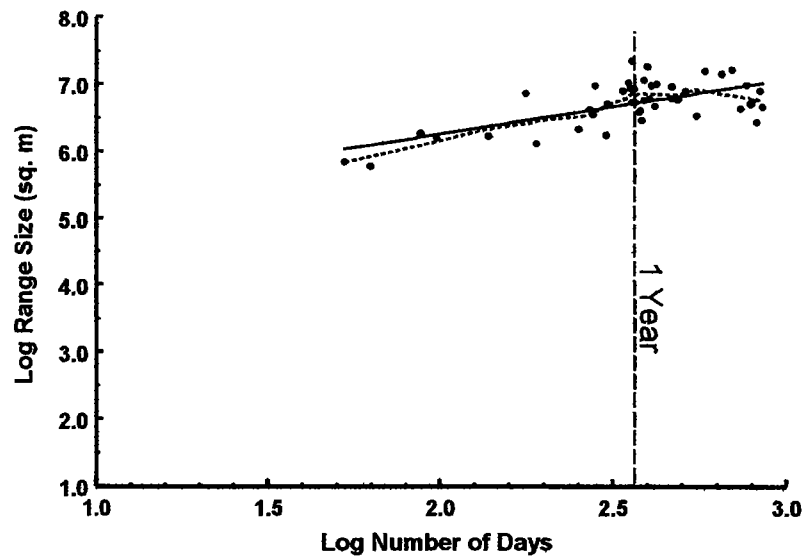

Fig. 30. Regression of $\log_{10}$ (range size) against $\log_{10}$ (time span between first and last location). The regression was significant. The LOWESS smooth (f = 0.5) of the same data shows no increase after about one year (vertical line).

One additional measure useful in evaluating whether our data are biased is whether those individuals for which we had a known final location (i.e., when the bird was found dead) have a smaller range than those which were lost or disappeared. Birds which disappeared may have been individuals that wandered more than those we tracked to the end of their life, and therefore might be expected to have a larger home range. The difference in home range size between those found dead and those that disappeared, however, was not significantly different (Mann-Whitney $U = 246$, $P = 0.613$).

Home Range Size

The home ranges of the 45 birds averaged 6.7 km^2, with the median slightly lower (5.5 km^2). The range was from 0.6 to 21.7 km^2. The largest range was one that was split into two activity centers. The largest range with only one activity center was 17.9 km^2.

Females tended to have larger home ranges than males (Fig. 31), although the difference was not significant (Mann-Whitney $U = 254$, $P = 0.15$). The average for females (8.6 km^2) was about 46% larger than that of males (5.9 km^2). The largest home range was of a female, and the smallest was of a male. Of the five largest, three were of hens, but of the five smallest, two were also of hens.

Fig. 31. Box plots of (untransformed) range size (km^2) by sex. Numbers above each box plot are sample sizes.
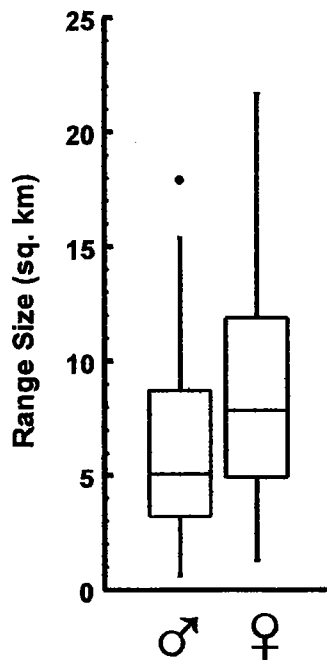
Significantly more females have split ranges (where the bird moves some distance between two, clearly-defined activity centers) than males ($\chi^2 = 14.8$, df $= 1$, $P < 0.001$). Half of the females (six of 12; one of these actually had a three-way split) had more than one activity center, but only one male of 33 (3%) did.

There does not appear to be a clear pattern to the movements by the birds among activity centers. The following list describes the movements among activity centers for the six hens with more than once activity center:

Hen 165: Moved to new area for winter. Returned "home" in early spring.

Hen 103: Moved to new area to nest, then back "home" after breeding season.

Hen 166: After nesting moved to new area.

Hen 178: Had three activity centers. Four nesting attempts, one successful in 1999 and three failed attempts in 2000; all were in the same activity center. After nesting, moved to a new area (west) for fall 1999, returned "home" for early winter, moved to second new area (southeast) for late winter (2000), returned "home" to nest (2000).

Hen 10: Moved to new area for the fall, returned "home" for the winter.

Hen 87: After breeding season moved to new area for early fall. Went back "home" for winter and early spring. Returned to new area for nesting and stayed there through fall.

This series of movements among activity centers does not form a pattern. While some may be associated with breeding activity and others with seasonal movements, there is no consistency among the movements. Some could be called seasonal, but not in all cases; some could be associated with breeding, but not in all cases.

Range sizes between adult and juvenile males was not significantly different, nor was it different for adult and juvenile females. Because larger birds may be more dominant, we also analyzed range size as a function of body mass for males. If the larger birds were more dominant, whether because they were simply larger or because they were older as well, one would expect the range size to decrease with increasing body mass. However, regression of range size on body mass was not significant.

Maximum Seasonal Distance Moved

On average, birds moved about 5 km from one corner of their home range to the farthest point over the span of seasons (the entire time the bird was tracked; Table 9). The minimum, however, was only about 1 km, and the maximum was over 15 km. Females moved farther than did males (Mann-Whitney $U = 313$, $P = 0.003$), on average, about twice as far (8 vs. 4 km). The minimum and maximum movement distances by hens were also about twice those of males.

Table 9. Maximum movement distances over life span (the entire time the bird was tracked) in km.

	All	Males	Females
Mean (km)	5.0	3.9	8.0
Median (km)	4.0	2.7	6.0
Minimum (km)	1.1	1.1	1.9
Maximum (km)	15.3	9.3	15.3
N	45	33	12

The difference between maximum movement distances by males and females is more dramatic when represented graphically (Fig. 32). Half of the females had a maximum movement distance greater than all but a few males.

Fig. 32. Maximum distance moved (km) by sex.
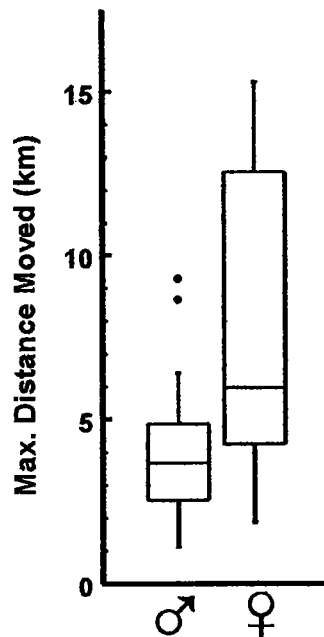
DISCUSSION

Greater Prairie-Chicken movements form patterns at three scales: within a day, over seasons, and over the life span of the individuals birds. Burger (1988) and the work presented here are the only studies to examine movements over the shortest of these, hourly movements within a day. Burger (1988), however, analyzed hourly movements only for hens in a fragmented landscape. His results are not directly comparable with ours, because he reported only the hourly movement distance, and did not show how movements varied within the day.

In general, the hourly movement patterns tend to show activity that is similar to those expected of most birds, or even most diurnal wildlife: greater activity (indicated by greater movement distances) in morning and evening, with a midday lull. Hamerstrom and Hamerstrom (1949) followed flocks of Greater Prairie-Chickens in Wisconsin and noted a similar movement pattern, with movement in morning from the feeding area to a midday loafing area, then back to the feeding area in evening shortly before going to roost.

These patterns were consistent, even with varying day length among the seasons, although the overall amount of activity varied somewhat, with greater movements

especially at midday during Winter. Burger (1988) also showed that hourly movement distances were greatest in fall-winter (corresponding to our Winter and a small portion of late Fall). Hamerstrom and Hamerstrom (1949) found that in spring, males were always closely associated with leks, and therefore their movements were generally short (also see below).

During Summer, however, both males and females showed a notably different pattern (Fig. 25). In general, hourly movements in Summer were not as large, even at their greatest, as movements in the other seasons. In fact, Summer hourly movements were always less than those during the least active time of day in Winter. Summer males showed activity primarily in morning, but not early morning, and without the usual peak in evening. This may be a result of their not being associated with a lek (which consumes their attention in morning and evening each day) or any other breeding activity at that time of year and therefore not commuting between the lek site and feeding or loafing sites. In summer, their primary activity is to feed themselves, which may require less effort in that relatively abundant time of year.

Hens as well have different activities and requirements in Summer than at other times of the year. The hens of course are restricted in their movement patterns by the requirements of breeding: incubation and brood-rearing. Because Greater Prairie-Chickens are precocial, once a hen's brood has hatched she may leave the nest site, but because the chicks do not fly until several weeks of age, her movements are restricted by the distance the chicks can walk. The increasing movement through the day, a pattern not seen for either sex at any other time of the year, may indicate that slow-paced feeding activity takes place primarily in morning and evening, while longer-distance movements, accomplished by walking, take place in midday. Burger (1988) found a significant difference in summer hourly movements between hens with and without broods in one of his study areas, but not the other.

Seasonal Movements

Three-day movements (as measured in this study), daily movements, and monthly home range sizes, as have been reported in previous studies, all likely measure the same underlying factor, the amount of movement by prairie-chickens over a time scale of a few days, within a season. Daily movement distances are likely most sensitive to short-term movements and monthly home ranges the least.

These measures, however, are not directly convertible one to another. Three-day movement distances cannot be converted for direct comparison to one-day (daily) movement distances by dividing by three, because it is unlikely that an individual bird would move in a straight line for three days. (It is equally unlikely that one-day movement distances actually represent the distance moved by a bird in one day.) However, both three-day and daily (one-day) movement distances likely represent relative amount of movement activity. Likewise, monthly home ranges cannot readily be converted to daily movements. Nonetheless, the magnitudes and directions of these three measures can allow useful comparisons between studies.

Lesser Prairie-Chickens, which live in more arid shortgrass prairies than Greater Prairie-Chickens, demonstrate greater movement distances on average than do the Greater Prairie-Chickens. Jamison (2000) reported Lesser Prairie-Chicken daily

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movement distances of between 435 m and 786 m, substantially above our estimate of 429 m over three-day intervals.

Robel et al. (1970) showed a pattern of daily distances by month through the year that is somewhat different from the pattern for our three-day movement distances by season (Fig. 26), finding the birds to move greatest distances in February, corresponding to the early part of our Spring season. Jamison (2000) also reported the longest movements in early Spring (March) for Lesser Prairie-Chickens. In contrast, Spring was the season when our birds moved their shortest distances. However, Hamerstrom and Hamerstrom (1949), and Robel et al. (1970) for Greater Prairie-Chickens, and Taylor and Guthery (1980) and Jamison (2000), for Lesser Prairie-Chickens, noted that movements during the months corresponding to our Summer season were the lowest and the Fall and Winter seasons were notably greater than Summer, which do correspond well with our results. Schroeder and Braun (1992) suggested that the prairie-chickens had moved less during late summer because of molting, which can reduce the birds' ability and propensity to fly.

Comparison of males and females showed the two sexes to generally reverse between Spring and Summer in amount of seasonal movement (Fig. 27), with males moving less in Spring and more in Summer. In Spring males of Greater Prairie-Chicken, as well as their congener Sharp-tailed Grouse (*Tympanuchus phasianellus*; Giesen 1997), generally spend most of their time at the lek, while females only visit the lek briefly. Therefore, it would be expected that the females might move more than the males. In contrast, in Summer males are freed from lek attendance, but females may be restricted in movement by nesting and brood maintenance. All 15 hens in this portion of the analysis were known to have nests and / or broods for at least a portion of the time from which their Summer data were collected.

The lesser movement by hens in summer is also supported by Burger (1988). In a fragmented habitat in Missouri, Burger (1988) observed movements by hens in Spring and Summer that were about half those in late Fall and Winter. Robel et al. (1970) and Riley et al. (1994; for Lesser Prairie-Chickens) also found that hen movements were less in Summer and early Fall than movement distances for males. Although Robel et al. (1970) showed that the females also moved less in late Winter / early Spring, in late Spring they showed a marked increase in movement distances. This probably corresponds to our showing a greater movement distance for females in Spring.

Three-day movements by males in our study were not significantly different between adult and juvenile birds (Fig 28), although the juveniles showed a greater range of movement distances. Robel et al. (1970) and Taylor and Guthery (1980; for Lesser Prairie-Chickens in winter) also found that the day-to-day movements of adults and juveniles were similar. Robel et al. (1970) did not show a greater variation by juvenile males in movement distances or monthly home range sizes. The greater range in movement distances, however, does support the contention that juvenile males are more mobile than adults. This is generally thought to be a result of the adults being already established in a territory on a lek, while juveniles are required to visit many areas seeking a lek on which to become established.

Home Range

The home range size for Greater Prairie-Chickens in the very homogeneous habitat of Osage County was generally quite large, averaging 6.7 km^2, although smaller than the 8.6

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km^2 reported by Burger (1988) in a large block of contiguous habitat (6.5 km^2 in size), and substantially smaller than the 25.5 km^2 he reported for an area with a mosaic of prairie patches and cultivation. Sharp-tailed Grouse, on the other hand, used home ranges far smaller than those for Greater Prairie-Chicken in our study, only averaging 1.9 km^2 (Giesen 1997 and authors cited therein).

Ryan et al. (1998), using the same study area as Burger (1988) also found that in a fragmented area, Greater Prairie-Chicken hens with broods used larger home range areas than in an area of contiguous habitat. These results suggest that home range requirements in a fragmented (mosaic) habitat may be greater than those in a homogeneous area. A fragmented area may require the birds to move greater distances to obtain all necessary resources (food, cover, nesting sites) than in a homogeneous one.

Greater Prairie-Chicken females tend to have larger home ranges than males, although the difference in this study was not significant. Schroeder and Braun (1992) found males to have a generally smaller home range size than did females in a fragmented habitat in Colorado, although, as with our study, the differences were not significant. They did find that females with broods tended to have smaller home ranges than females without broods. Giesen (1997) found no difference in home range size between the sexes of Sharp-tailed Grouse.

Greater Prairie-Chicken hens did show significantly greater maximum movement distances, and also moved between activity centers much more than did males. Female Greater Prairie-Chickens are thought to be the more mobile than males (Hamerstrom and Hamerstrom 1949; Schroeder and Braun 1993), with movements generally related to seasonal movements among habitats. Greater movements by hens, however, may not be to the their advantage; Burger (1988) showed that annual survival and reproductive success of female Greater Prairie-Chicken were negatively related to amount of movements by the birds. These movements by hens, however, may be important to the species by lowering inbreeding. Although males move little, large hen movements may mix genes among population groups and reduce the likelihood of parent – offspring or sibling breeding.

Schroeder and Braun (1992, 1993) did not find significant differences in home range size among age classes, although juveniles tended to have larger home ranges, as in our study. They attributed this to attempts by the juveniles to visit a series of leks until they found one at which they could become established.

Migration

In contrast to Schroeder and Braun (1993), we had no evidence of any migration. Almost all birds in our study remained in their home range until they died or were lost. A few hens did move between one activity center and then returned, but others moved to a new area and did not ever return to the original activity center, a movement that could not be called migration. Although it may be possible that some birds in our study that were lost (i.e., were never found dead) had actually migrated but died before they could return, we did not have instances of birds disappearing and then reappearing. Those birds that disappeared may have emigrated, but they did not migrate. We have had instances of birds that have disappeared and later reappeared, but none were among the birds in this study, and it does not appear to be a general pattern in our study area. Hamerstrom and Hamerstrom (1949) also point out that although they had a few birds that moved a great

distance, most did not. They suggested migratory movements by Greater Prairie-Chickens that might have taken place in the past were reduced with the introduction of cultivation to the Great Plains. Hamerstrom and Hamerstrom (1949) concluded that the usual habit of the Greater Prairie-Chicken is to spend most of its life in a relatively small area.

Movements in our study, although on the order of kilometers, were still small relative to migratory movements. Although our results do support greater movement by hens, movements among activity centers did not produce a clear pattern of birds seeking differential habitats among seasons. However, migratory or other long-range movements recorded by Hamerstrom and Hamerstrom (1949) and Schroeder and Braun (1993) may not be relevant in our area, because winter weather usually is not severe for extended periods. In addition, because the habitat in our study area was homogeneous over an extensive area, there may be little incentive for birds to move large distances seeking additional food sources such as waste grains.

CONCLUSIONS

Although the study area was not completely homogeneous either spatially or temporally, it is among the largest homogeneous areas, unfragmented by cultivation, woodlands, or highways, of remaining Greater Prairie-Chicken habitat, providing a largely unbounded habitat for the birds. In this area, the prairie-chickens occupy large home ranges, and can make lengthy movements, if not over a span of days, over the span of a year or a prairie-chicken's life. Home ranges in other habitats may be larger or smaller, depending on the various restrictions to movement and availability of food.

Movement patterns varied by hour and season, but little by sex and age class, except in Summer, when the biological roles of the sexes may fix their movement distances. Nonetheless, males exhibit less mobility than females, which may be a result of males being associated with territories on the leks.

The implications of this analysis for land managers and conservationists are that Greater Prairie-Chickens require extensive amounts of habitat. Although the average home range size in this study was less than 7 km^2, the average hen had a home range of around 9 km^2. To maintain a population of the birds would probably require a very large area, even though the individuals' home ranges overlap.

Predator Survey

Comparison of the number of predators recorded during the 1998 scent post surveys (all three seasons combined) with the surveys from the period from 1972 – 1981 can be seen in Fig. 33. However, please note that the surveys were not carried out at exactly the same locations (the earlier surveys were carried out near Bluestem Lake, 6 – 20 km away from the locations of the 1998 transects). In addition, the surveys from 1972 – 1981 were all carried out in September, whereas the 1998 surveys were carried out April, June and September.

Keeping this in mind, however, it appears that predator numbers in 1998 were generally as high or higher than the numbers recorded during the earlier period. Coyote numbers were the third highest value of any time during the 11 years surveyed (not including the 17-year gap between the 1981 and 1998 surveys; see Fig. 33). Skunk

numbers were possibly three times as high as in 1981, and raccoon numbers were possibly twice as high as during the earlier period. Opossum numbers were about as high as at any time during 1972 – 1981, but were not higher.

Fig. 33. Results of scent post surveys carried out by Wildlife Services near Bluestem Lake from 1972 – 1981 and for this study in 1998. No surveys were carried out in the area in 1982 – 1997, leaving a 17-year gap in the data. The number of predators is given per 1000 scent posts.
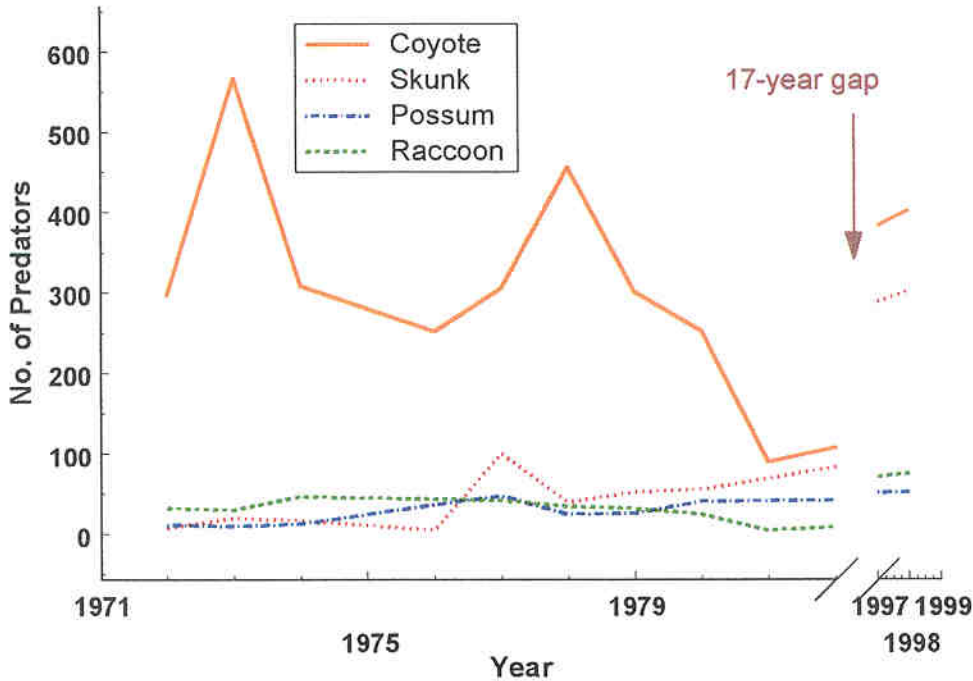

These results suggest that, although predation may be a factor contributing to the decline of the Greater Prairie-Chicken in Oklahoma, it is unlikely to be the only factor. Greater Prairie-Chicken numbers in the early 1970s were certainly higher than now, but the number of predators, especially coyotes, appears to have been as high or higher. Therefore, although several of the predator species have increased, it is unlikely to be the only cause of the decline in the prairie-chickens.

The number of predators generally showed an increase by season within 1998 (Fig. 34). Of the four species of predators, only one, opossum, did not increase steadily through the season, although the number of opossums was greatest in September. The rank of the predators did not change among the months except between opossum and raccoon in June. That is, coyotes were always the most abundant, skunks next, etc.

The pattern of increasing numbers of predators during the year is most likely a result of reproduction rather than immigration. As young of the year become more independent and mobile later in the season, the number of individuals recorded at the scent posts

increases. It is likely that mortality during fall and winter reduces the number of predators to start the next year at or near the April level.

Fig. 34. Number of predators / 1000 scent posts in each of the three surveys carried out in 1998.
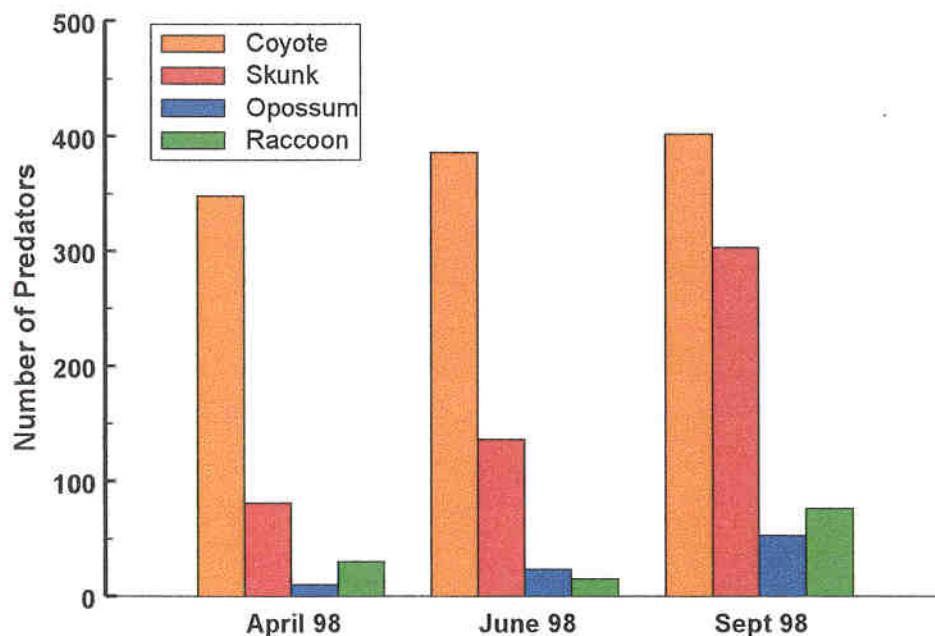
The surveys carried out in 2000 recorded only 36 predators during 165 scent post-nights, about 75% coyotes. Exactly the same number of predators (18) was recorded at scent posts on burned rangeland as on unburned. Obviously, this was not a significant difference (binomial test; $P = 0.5$).

There may have been no difference detected between the burned and unburned areas because of the time when the survey was carried out in 2000. The greatest contrast between the burned and unburned areas is immediately after the burn, which in the study area generally takes place in March or early April, and it is at that time that the greatest effect on the distribution of predators between the two areas would be expected. The survey was conducted at the end of May and the first week of June, at a time when the grass on the burned areas had already begun to re-grow. Any potential effect on the predator distribution caused by the lack of cover on the burned areas may have become too small to detect by June.

REV Survey

In conjunction with other researchers, we carried out a survey of blood samples for the presence of reticuloendotheliosis (RE). This portion of the project was conceived as a rangewide survey, and was to include samples from Lesser Prairie-Chicken; therefore

samples were collected from areas outside the study area. We used samples obtained in our study of Lesser Prairie-Chicken in western Oklahoma and eastern New Mexico, begun in 1999. Samples from outside our study were collected by collaborators John E. Toepfer (Wisconsin, Minnesota, North Dakota, and Nebraska), Larry M. Mechlin (Kansas and Missouri), and Roger D. Applegate (Kansas).

RE is a disease known to infect a number of bird species, including domestic chickens (*Gallus gallus*), ducks, quail, pheasants, and domestic turkeys (*Meleagris gallopavo*; Bagust 1993, Witter 1997). It has also been found to cause morbidity and mortality in captive Greater and Attwater's Prairie-Chickens (*Tympanuchus cupido attwateri*; Drew et al. 1998).

The two species of prairie-chickens (Greater Prairie-Chicken, including the Attwater's subspecies *T. cupido attwateri*; and Lesser Prairie-Chicken) have declined dramatically in numbers in recent years (Westemeier and Gough 1999), and it is not clear in many cases why the declines are occurring. Because of the serious effects of RE on captive Attwater's Prairie-Chickens (Drew et al. 1998), it is important to determine if RE might be a potential cause for the declines of prairie-chickens in areas with adequate remaining quality and quantity of habitat. Therefore, using samples collected in 1998, 1999, and 2000, we surveyed wild prairie-chickens across their ranges to determine if RE was present in the wild populations.

Reticuloendotheliosis

Reticuloendotheliosis is caused by a family of retroviruses, including REV-T, REV-A, spleen necrosis virus (SNV), chick syncytial virus (CSV), duck infectious anemia virus (Bagust 1993), and several non-classified viruses (Ritchie et al. 1994). The REV-T form appears to be responsible for the most acute oncogenicity in domestic chickens, while other viruses and strains in the group appear to be responsible for runting disease (poor growth, abnormal feathering, immunodepression) and chronic neoplastic disease (Witter 1997), which may also be lethal.

The viruses are found worldwide, although the disease seems to be more common in warm, humid climates (Bagust 1993). A survey in Japan (Sasaki et al. 1993) found RE in 26% of domestic chicken farms, and in 14% of the individual birds; in 15% of domestic pheasants (Phasianidae); but in <1% of mallards (*Anas platyrhynchos*). Antibodies were also detected in 34% of domestic chicken flocks and 12% of individual chickens in Korea (Seong et al. 1996). Surveys in the United States have found the virus or antibodies in 45% of flocks (Witter 1997).

Wild duck flocks may be a reservoir of RE (Wobeser 1997), but the disease was first identified in domestic turkeys (Bagust 1993). It has been recorded in galliforms in the wild only twice in Wild Turkeys (Ley et al. 1989, Hayes et al. 1992), and once in Attwater's Prairie-Chicken (Drew et al. 1998).

The virus can be transmitted from one individual to another (horizontally) by direct contact (Bagust 1993) and possibly by blood-sucking insects such as mosquitoes (Motha et al. 1984). It also may be transmitted vertically from the hen into egg albumen and thence to embryos (Bagust 1993). Age-related resistance to infection may prevent persistent viremia in domestic chickens exposed a few days after hatching. Domestic chickens and ducks infected at a few days of age show a high mortality rate, as high as 66-73% before 39 weeks of age, but birds infected as adults rarely are symptomatic

(Bagust 1993). The most notable effect of RE is the production of neoplastic lesions in the visceral organs of birds (Wobeser 1997). In Attwater's Prairie-Chickens, the lesions were described by Drew et al. (1998).

Collection of Samples and Analysis

In 1998, 1999, and 2000 we collected 354 samples from Greater Prairie-Chickens in seven states and 184 samples from Lesser Prairie-Chickens in three states (Table 10, Fig. 35). We collected about 1 cc of blood from the ulnar or jugular veins of birds that were captured in walk-in funnel live traps or at night using hand nets. Birds were captured for a variety of purposes including relocation projects, but most were captured to attach radio transmitters for radio-tracking projects. The greater number of males sampled reflects the fact that most trapping was on leks (booming or gobbling grounds), where males predominate. Samples were collected and placed in heparinized 2 cc tubes. We followed generally accepted procedures (Gaunt et al. 1999) for handling animals and obtaining samples. Because samples were collected during the execution of several disparate projects, the methods of handling were not the same for all samples. However, all samples met the minimum criteria for collection and storage that should allow detection of the RE viruses using the PCR test we used (see Analysis, below). Differences in the way samples were collected and stored are described below.

We collected samples twice at least one month apart, but up to 13 months apart, from 27 individual Greater Prairie-Chickens in Oklahoma to determine seasonal changes in prevalence of the disease if it were present.

Lesser Prairie-Chicken samples

Samples from Lesser Prairie-Chickens were collected in Kansas, Oklahoma, and New Mexico at 17 trap sites (Fig. 35). All samples were collected in 1999 and 2000 (Table 10), and were collected throughout the year, although the large majority were from March, April, and May of each year.

Except for 19 of the samples from New Mexico in 1999, all samples were frozen within four hours of being collected. The frozen samples were kept at -70° C or in household freezers at a temperature of about -18° C. The samples were maintained frozen until shipped to the TVMDL. The 19 New Mexico Lesser Prairie-Chicken samples were refrigerated for three months before being shipped to the lab for analysis.

As for Greater Prairie-Chicken, we collected samples twice at least one month apart but up to 11 months apart (1999 to 2000) from seven individual Lesser Prairie-Chickens in Oklahoma and five from New Mexico to determine seasonal changes in prevalence of the disease if it were present.

Analysis

All of the samples were shipped on dry ice to the TVMDL for analysis, and analyzed by personnel experienced with testing for RE viruses in Attwater's Prairie-Chickens. Samples were sent to the laboratory and analyzed in July of each year. Samples were generally analyzed in the year in which they were collected, although samples collected late in one year were kept until the following July.

All samples were tested for the presence of RE integrated proviral DNA using polymerase chain reaction (PCR) methods as described by Aly et al. (1993). Positive and negative controls were used.

Results

Of the 538 samples from both species, only two were positive by PCR for a reticuloendotheliosis virus. Both were from Greater Prairie-Chickens from Osage County, Oklahoma, and were analyzed at the TVMDL in 1998. Because of the storage of these samples (they had been refrigerated, not frozen), they had degraded somewhat, and virus isolation could not be performed to verify the presence of the active virus.

Discussion

The positive results on two male Greater Prairie-Chickens in 1998 from Oklahoma add to the few reports of RE in free-ranging galliforms (Ley et al. 1989; Hayes et al. 1992; and Drew et al. 1998). Both positive birds were radio-tagged and were being radio-tracked on a regular basis. The first bird was sampled on 9 March 1998; the bird survived until at least 12 December 1998, when he was lost. The second bird was captured and sampled on 20 April 1998 and survived at least until 12 August 1998, when he was lost. Neither bird was found dead, but neither has ever been relocated. They may have wandered from our search region, or died (through disease, depredation, or other

Table 10. The number of samples collected from Greater and Lesser prairie-chickens, by state, year, and sex (M or F). The number of samples corresponds to the number of individual birds sampled except for Oklahoma, where 120 Greater Prairie-Chickens and 95 Lesser Prairie-Chickens were sampled (34 birds were sampled twice) and New Mexico where 74 Lesser Prairie-Chickens were sampled, with five being sampled twice.

| | Greater Prairie-Chicken | | | | | | | Lesser Prairie-Chicken | | | | |
| | 1998 | | 1999 | | 2000 | | Total | 1999 | | 2000 | | Total |
State	M	F	M	F	M	F		M	F	M	F	
Wisconsin[a]	12	6	18	2			38					
Minnesota[b]			18	10			28					
North Dakota[c]			10	8			18					
Nebraska[d]	4	8					12					
Missouri[e]			31	2			33					
Kansas[f]			30	48			78	3				3
Oklahoma[g]	14	11	73	26	21	2	147	42	3	37	20	102
New Mexico[h]								22	5	34	18	79
Total by sex	30	25	180	96	21	2		67	8	71	38	
Total by year	55		276		23		354	75		109		184

[a] Adams, Marathon, Portage, and Wood counties.
[b] Clay, Norman, and Polk counties.
[c] Grand Forks County.
[d] Garfield, Loup, and Rock counties.
[e] Barton, Dade, Pettis, and St. Clair counties.
[f] Greenwood, Morton, Lyon, and Waubansee counties.
[g] Beaver, Ellis, Harper, and Osage counties.
[h] Roosevelt County.

Samples were collected from Kansas, Missouri, and Oklahoma in 1998, 1999, and 2000 (Table 10). The samples were collected throughout the year, although the large majority were from March, April, and May of each year. They were taken from the ulnar vein. The samples were frozen whole in heparinized tubes except for 17 samples from Oklahoma in 1998. These samples were kept cool in a refrigerator at about 4° C for three to four months before being shipped to the TVMDL for analysis in July 1998. The remaining samples were kept frozen at -70° C in ultracold freezers or in household freezers at a temperature of about -18° C until being shipped to the TVMDL. Most of these samples were analyzed by the TVMDL in July and August of 1999. All samples collected in 2000 were analyzed at the TVMDL in July 2000.

Although it is unlikely, a small number of samples taken in Missouri may have been from birds that had been transplanted from Kansas in 1995.

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cause) and the radio tag left in a location or condition from which it could not be detected.

Given only two positive birds in this study, RE is not considered to be a major threat to prairie-chicken populations. However, the occurrence of two positive birds of 25 from Osage County, Oklahoma, in 1998 but no other positive birds from other areas or other years needs explanation.

The two positive results in the 1998 samples could be false positives. However, it is generally thought that degrading of the sample is more likely to yield false negatives than false positives.

It is also possible that the virus was present in 1998 but not in subsequent years. Possibly, all of the birds infected in 1998 had died or recovered from infection by 1999 or 2000, so no virus could be detected. Or the disease may enter the prairie-chicken population from a reservoir species, and conditions suitable for this, such as a high vector population, may not occur in all years. There may be considerable annual variation.

Additionally, the disease may have been present but not detected due to the timing of sampling. Drew et al. (1998) suggest that RE is usually fatal in prairie-chickens within 150 days of infection. If the disease normally follows a short course, it may be difficult to obtain samples from infected birds, because they do not survive very long. However, it is apparent that some Greater Prairie-Chickens may be infected yet survive at least for some time, since one of the birds that tested positive in 1998 survived at least nine months. As Bagust (1993) reported, domestic chickens infected as adults may be asymptomatic and survive the infection.

Landscape-scale differences in occurrence of possible reservoir species such as waterfowl, of possible vectors (mosquitoes), or prairie-chicken densities may interact to create large annual variation in the effects of these factors. Further data are needed to evaluate these possibilities and determine if infection rates vary among years. Knowledge of modes of transmission and possible reservoir species will be critical in the future for determination of disease control measures.

In addition, it could be useful to investigate whether individual prairie-chickens have antibodies to the REV viruses. The detection of antibodies may help to identify birds that have been exposed to the virus but carry proviral copies at numbers below threshold sensitivity of the PCR test. This could provide information about past exposure to the disease. At present a good serological test is not available for prairie-chickens.

The presence of REV in the wild populations of prairie-chickens should be carefully considered in any future relocation and reintroduction efforts. All individual birds being translocated should be tested for REV and no positive birds used in the translocation effort.

CONCLUSIONS

The cause or causes of the decline in population of the Greater Prairie-Chicken in Oklahoma remains elusive. It is likely that there is no single cause, but rather a suite of factors acting in concert, with interactions among the factors amplifying their effects in some years, but not in others.

Our work helps to eliminate some factors as causes of the decline and show some directions for future research. It appears that during the time period of our study, reticuloendotheliosis (caused by REV) was probably not a factor in the declines. Although we found RE to occur in the wild populations, it does not appear to be prevalent. There is annual variation in outbreaks of most wildlife diseases, however, and RE may be a factor in declines at other sites or in other years. In this study, however, it was rare.

Nest success over the four springs of our study was low in two years (1997 and 2000), but high in two others (1998 and 1999). Because Greater Prairie-Chickens are expected to have a nest success rate from 25-33%, in line with other species of ground-nesting grassland birds, these rates probably do not implicate low nest success as a cause of the decline in prairie-chicken population. Prairie-chickens generally have low nest success, but because they have large clutches (around a dozen eggs), relatively few successful nests are sufficient to maintain the population. Likewise, although survivorship appears to vary seasonally, overall it does not appear to be lower than expected for other populations of Greater Prairie-Chicken.

Although these factors do not appear to be unexpectedly high or low, our study does not eliminate the possibility that they may be contributing to the population decline of Greater Prairie-Chicken. Even if several factors are all within the expected range, their action in combination may have detrimental effects. For example, if survivorship and nest success were both near the lower end of the expected range, and predation near the high end of the expected range, the combination of these effects could be enough to cause the declines. Our study is not able to tease apart these factors.

Although prairie-chickens require great amounts of prairie for their home ranges, the Osage County study area seems to provide adequate habitat. However, other factors relating to that habitat may potentially be affecting the birds' populations, although our study was not able to demonstrate this. Especially of concern is the extensive amount of burning taking place on ranches each year in the Flint Hills of Kansas and Oklahoma, which may be a factor in the decline of the Greater Prairie-Chicken (Robbins et al., in press). The prairie-chickens were not randomly distributed across the study area, and in spring and early summer the birds clearly used unburned areas (for general / foraging use, nesting, and escape cover near booming grounds) preferentially over burned rangelands. Because of the small proportion of the range that remains unburned each year, the prairie-chickens become concentrated in the unburned areas. Their predators may also be concentrated in the same places. This concentration may make the birds more vulnerable to predators, which may learn to search in the unburned areas, or which may simply be in the unburned areas because they require cover themselves. Our study was not able to show increased predator numbers in the unburned areas, although the timing of our measurement of predator numbers may not have been appropriate to detect that difference. The burned and unburned areas are most clearly different in April,

immediately after most burning takes place. There was a tendency towards lower survivorship in the spring in the unburned areas, but this effect was not significant and may not be valid. Nonetheless, the burning of extensive ranges is clearly a factor affecting the distribution of the prairie-chickens in the study area, and therefore may have some effect on the birds, whether detrimental or not.

Although we studied 214 prairie-chickens over more than three years, this project can only help to elucidate some paths for future research that may be able to resolve the factors affecting the decline of the Greater Prairie-Chicken in Oklahoma. Once those factors have been analyzed and clarified, they may point to management options that could slow or reverse the decline.

RECOMMENDATIONS

Further research is needed before a management plan can be devised and implemented to reverse the declines of the Greater Prairie-Chicken in Oklahoma. This work should have a sharpened focus on a relatively few factors.

Comparison of Burned and Unburned Areas

- Carry out experiments on prairie-chicken abundance and distribution between burned and unburned rangelands. In conjunction with landowners in the area, select blocks to be burned and left unburned. Determine whether the distribution, number, survivorship, and nest success in these experimental blocks is affected. If a block is left unburned in a year, do the prairie-chickens move into it? Once it is burned again, do they move out? In this way a clear connection between burning and prairie-chicken population changes may or may not be established.
- Analyze landscape-level patterns of burned and unburned lands. What ratio of burned / unburned rangeland is ideal for the prairie-chickens? What pattern of habitat blocks is most appropriate, many small or a few large burned / unburned blocks? What temporal pattern of burning results in best habitat for prairie-chickens and most use of burned blocks? This should be accomplished using experimental plots, also in conjunction with the local landowners.
- Compare predator numbers on burned and unburned areas throughout the year. Surveys should be carried out monthly for at least two years, to determine if predators are concentrated in unburned areas during part of the year, as the prairie-chickens are. This may clarify the causes of lower survivorship, etc., if such effects are found in other comparisons.

Predation

- Use predator control or predator repellent experiments to determine the effect of predators on the prairie-chicken population. Such experiments could be carried out in conjunction with comparisons of burned and unburned areas.

Monitoring

- Detailed booming ground surveys should be carried out annually, to monitor the distribution of prairie-chickens over the whole area. The surveys should be carried out as well on other areas not included in the study area for this project, such as the Ted Turner ranch south of the study area. The roadside transect surveys carried out by the Oklahoma Department of Wildlife Conservation are useful for determining large-scale population changes, but for the purposes of the recommended projects, finely-detailed surveys are necessary.
- The extent and location of burns should be mapped each year, to aid in interpreting the results of the comparisons of burned and unburned areas. Because of the large area to be covered, this may perhaps be more readily, accurately, and inexpensively done using aerial photography.

Chick Survival

- Chick / poult survivorship was not addressed during the project. Because it is an important factor that may be critical to population changes, chick / poult survivorship must be evaluated.

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