Brood Break-up and Juvenile Dispersal of Lesser Prairie-chicken in Kansas

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ABSTRACT -- Natal dispersal is critical for genetic interchange between subpopulations of birds and little is known about the timing and extent of lesser prairiechicken (Tympanuchus pallidicinctus) dispersal movements. We monitored movements of 51 transmitter-equipped female lesser prairie-chicken known to have hatched a nest. Average minimum daily brood movements differed (t = -2.94, df = 829, P < 0.01) between the early (273 m; 0 to 14 days post-hatch) and late (312 m; 15 to 60 days post-hatch) brood rearing periods. We captured 71 juvenile lesser prairie-chicken from 10 broods at 3 to 11 days post-hatch and marked them with passive integrated transponder (PIT) tags. We subsequently captured 41 chicks from 20 different broods and fitted them with necklace-style transmitters. Transmitter-equipped brood hens and individual chicks were monitored daily and the average date of brood break-up was 13 September (85 to 128 days post-hatch). Both males and females exhibited bimodal dispersal movements in the fall and spring. Autumn dispersal movements peaked between late October and early November for both sexes. Spring dispersal movement of males peaked during late February. Female dispersal movements in the spring peaked in late March and

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were much more extensive than fall dispersal movements. Natal dispersal distance for all marked males averaged 1.4 km (SE = 0.2, n = 9). The approximate dispersal distances of three transmitter-equipped females ranged from 1.5 to 26.3 km. Because of greater dispersal distances, females will contribute more to genetic exchanges between fragmented subpopulations. To ensure genetic connectivity, we recommend that a distance of less than 10 km be maintained between lesser prairie-chicken subpopulations through protection or establishment of suitable habitat.

Key words: brood break-up, dispersal, Kansas, lesser prairie-chicken, *Tympanuchus pallidicinctus*.

Lesser prairie-chicken (*Tympanuchus pallidicinctus*) occupies xeric grasslands in Kansas, Oklahoma, Texas, New Mexico, and Colorado (Hagen 2005). Its numbers have declined range-wide since the 1800's (Braun et al. 1994) and its occupied range has decreased by an estimated 92% (Taylor and Guthery 1980). Most of the population decline has been attributed to habitat deterioration and conversion of grasslands to intensive row crop agriculture. In Kansas, the lesser prairie-chicken still occupies habitat in 31 of 39 counties of its historical distribution (Jensen et al. 2000), but most of the original habitat is heavily fragmented by agriculture and development.

Movement of birds between subpopulations is critical to the persistence of the metapopulation and maintaining genetic variability (Greenwood 1980, Hanski and Gilpin 1997). Most genetic interchange between subpopulations likely comes from natal dispersal. Natal dispersal is the movement of an animal from its point of origin to the place where it reproduces or likely would have reproduced had it survived and found a mate (Howard 1960, Greenwood 1980). Natal dispersal is even more critical to genetic interchange for lek mating species such as the lesser prairie-chicken because adult males have extremely high fidelity to display sites and few males typically do most of the breeding (Bouzat and Johnson 2004). In addition to maintaining genetic variability, dispersal movements likely buffer mortality within small or sink-like subpopulations (Pulliam 1988). Thus, knowledge of natal dispersal distances can aid in identification of critical habitat fragments that ensure gene flow between subpopulations. However, only Copelin (1963) has reported approximate dispersal distances (fall capture site to lek site) for juvenile lesser prairie-chicken. Copelin's (1963) estimates might not provide a good estimate of natal dispersal due to movements prior to initial capture and lower search effort at long distances from the initial capture sites. Thus, little information is available on juvenile dispersal of lesser prairie-chicken and no estimates of sexspecific natal dispersal distances have been reported. This information is useful in understanding how genetic exchanges occur between fragmented subpopulations.

Our objectives were to 1) identify the timing of brood break-up, 2) identify the timing of natal dispersal, and 3) estimate natal dispersal distances for male and female lesser prairie-chicken.

METHODS

Phase I (1997-1999) of our research was initiated on a 5,700-ha sand sagebrush prairie fragment (study site I) in southwestern Kansas just south of the Arkansas River in Finney County. During Phase II (2000-2002), an adjacent study site (study site II) of approximately the same size was added and work continued on both sites through spring 2003. At the nearest point, the two sites were 3.2 km apart and both were surrounded almost entirely by center-pivot irrigated cropland. Both sites were owned privately and used primarily for livestock grazing and mineral exploration/production.

We captured female lesser prairie-chicken on leks in the spring by using walkin funnel traps (Haukos et al. 1990, Schroeder and Braun 1991). Females were marked with an individually numbered aluminum leg band (size 12) and an 11-g necklace-style transmitter (RI-2B; Holohil Systems Ltd., Carp, Ontario, Canada) with a 1 year expected battery life. All birds were released on-site immediately following transmitter attachment. We located nests by approaching females when telemetry locations remained unchanged for greater than three consecutive days. We estimated the fate of each nest upon reinspection of the site immediately following female departure or death.

During Phase I, females that successfully hatched a nest were approached at night with spotlights at 3 to 11 days post-hatch. If chicks were present, they were captured with a long-handled net and individually marked with a passive integrated transponder (PIT) tag (Jamison 2000). When females were captured with the brood, a soft release was attempted by using an opaque-bisected release pen (Jamison 2000). If the female was not captured with the brood, the chicks were released near the capture location.

During Phase II, the same procedures were used to capture chicks but captures were not attempted until 30 to 40 days post-hatch. All captured chicks were marked with individually numbered aluminum leg bands (size 12) and birds exceeding 150 g were equipped with a 2-g necklace-style transmitter (BD-2C; Holohil Systems Ltd., Carp, Ontario, Canada) with a 60 day expected battery life. Chicks were released at their capture location immediately following handling. Beginning at approximately 55 days post-hatch, the same procedures were used to capture additional birds and all previously transmitter-equipped chicks. At this time, all captured chicks were fitted with an 11-g necklace-style transmitter and beginning midway through the 2000-field-season, blood samples were collected from each bird. Blood samples were submitted to a genetics lab (Zoogen

Incorporated, Davis, California) where chromosome analysis of blood cells was used to identify each bird's sex (Van Tuinen and Valentine 1983). Captures of previously marked chicks on lek sites during subsequent years also were used to verify the sex of birds that were not classified by chromosome analysis. The age of chicks not associated with a transmitter-equipped female was estimated from body measurements (Pitman et al. 2005).

We used a truck-mounted null-peak telemetry system to monitor transmitterequipped females with broods and individual chicks (Phase II) daily, until death of the bird, dispersal outside of the study sites, or transmitter failure. We triangulated the location of birds by using azimuth bearings recorded from known tracking stations. We searched all suitable habitats within a 120-km radius of our study sites for dispersing transmitter-equipped chicks from a Cessna 150 aircraft by using aerial telemetry equipment. In the final year of our project (2002-2003), we located transmitter-equipped birds daily through mid-August. From mid-August to the following March, we monitored birds at approximately monthly intervals from a Cessna 150 aircraft.

We used distances between daily locations of females with chicks as an estimate of brood movements. We used a t-test for unequal variance (Ott 1993) to compare minimum daily brood movements between the early (0 to 14 days post-hatch) and late (15 to 60 days post-hatch) brood rearing periods. The timing of brood break-up was estimated by monitoring broods containing transmitter-equipped females and chicks, and estimated for each radio-marked chick. We defined the time of brood break-up as the first of three consecutive days when the distance between a female and her chick exceeded 200 m. We chose this distance because it approximated the amount of error associated with locations collected from the null-peak telemetry system used during our study. We compared the mean date and age when transmitter-equipped male and female chicks separated from their broods by using a t-test for unequal variance (Ott 1993).

We identified the timing of sex-specific natal dispersal for transmitterequipped lesser prairie-chicken chicks by using a dispersal index (Small and Rusch 1989). This index equals the linear distance between the first and fifth location in a set of five consecutive daily locations. For each chick, we calculated a dispersal index for each consecutive five-day interval beginning on 1 August. The index was assigned to the date corresponding to the mid-point of each set. The mean index values on these dates were plotted to identify the approximate periods of dispersal for males and females, respectively. The dispersal index was calculated for transmitter-equipped females through early May. We were unable to record five consecutive daily locations for any juvenile male following mid-March. Thus, we were not able to calculate the dispersal index for juvenile males beyond that time.

Natal dispersal distances were calculated separately for juvenile male and female lesser prairie-chicken. Birds captured at lek sites were scanned with a PIT-

tag reader to determine if they had been marked as chicks. For males PIT-tagged in Phase I, natal dispersal was the distance from hatch to the lek of capture the following spring. For males equipped with transmitters in Phase II, dispersal distance was the distance from hatch to the spring lek site where the bird was observed most frequently. We compared dispersal distances of PIT-tagged and transmitter-equipped males by using a t-test for unequal variance (Ott 1993). Female natal dispersal distances were only observed for transmitter-equipped birds in Phase II of our project because no PIT-tagged females were ever recaptured. Female natal dispersal distance was the distance from hatch to the first observed nest site. Because the hatch location was unknown for some chicks, an approximate dispersal distance also was estimated. Using this method, dispersal was the distance between the chicks location at approximately 60 days post-hatch and the lek most attended or the first observed nest site for males and females, respectively.

RESULTS

We captured and equipped 226 females with transmitters during our six-year study. We located 209 nests from these transmitter-equipped birds and determined fate for 196 nests. Fifty-one of these nests (26.0 %) were known to have produced at least one chick. During Phase I, we captured 71 chicks from 10 broods and implanted each chick with a PIT-tag. Five chicks died during capture and marking or as result of these procedures shortly after release. The remaining 66 chicks showed no adverse effects from marking at the time of release. During Phase II, we captured 34 chicks from 16 broods with transmitter-equipped brood hens and seven chicks from four broods with unmarked hens. We used chromosome analysis of blood cells or subsequent captures at lek sites to identify the sex of 31 of these chicks (19 male and 12 female).

Average minimum daily brood movements differed ($t_{829} = -2.94$, P < 0.01) between the early ($\bar{x} = 273$ m, SE = 10.5, n = 393) and late ($\bar{x} = 312$ m, SE = 7.9, n = 773) brood rearing periods with longer movements more frequently occurring during the late brood rearing period (Fig. 1). Brood break-up was determined for nine chicks (three male and six female) in six broods in which the brood hen also was equipped with a transmitter. The date these nine chicks separated from the brood hen averaged 13 September (range = 21 August to 6 October) and did not differ between juvenile male and female birds ($t_4 = 1.27$, P = 0.27). Juvenile age at the time of brood break-up averaged 101 days (range = 85 to 128 days) and was also similar between male and female birds ($t_4 = 0.94$, P = 0.40). An additional unmarked brood containing a transmitter-equipped juvenile male had not dissolved prior to 2 October when the chick was depredated at 113 days post-hatch. Three of the monitored broods contained two transmitter-equipped chicks each and both



Figure 1. Percentage of minimum daily brood movements observed in each distance category for lesser prairie-chicken during early (0 to 14 days post-hatch; n = 393) and late (15 to 60 days post-hatch; n = 773) brood rearing periods in southwestern Kansas, 1997 to 2002.

chicks left the brood simultaneously in only one instance. The two chicks in each of the other two broods broke away from the brood hen at intervals of 20 and 25 days. We documented brood mixing for 2 of 41 (4.9%) transmitter-equipped chicks from two different broods at 36 and 37 days post-hatch. These chicks remained with their unmarked broods through brood break-up.

Dispersal indices revealed a bimodal dispersal pattern between August and May for both juvenile males (n = 12) and females (n = 10) (Fig. 2). The timing of autumn dispersal movements peaked between late October and early November for both sexes. However, distinct sexual differences were apparent during the spring dispersal period with peak movements occurring during late February for males and late March for females (Fig. 2). The dispersal index was similar during fall and spring for juvenile males, but the female index was much greater during the spring dispersal period.

We calculated dispersal distances of juvenile lesser prairie-chicken for 4 of 67 birds PIT-tagged during Phase I (all four were males) and 14 of 41 (11 males and 3 females) transmitter-equipped birds during Phase II. None of the other PIT-tagged



Figure 2. Sex-specific dispersal indices, indicating the approximate timing of autumn and spring transience [distance (m) between the first and fifth location in a set of five consecutive locations] for juvenile lesser prairie-chicken. Indices were derived from transmitter-equipped males (n = 12) and females (n = 10) in southwestern Kansas, 2000 to 2002.

birds was captured and 25 of the remaining 27 transmitter-equipped birds did not survive until the spring breeding season. The other two transmitter-equipped birds were last detected on 11 September and 9 January due to either dispersal beyond our range of detection or transmitter failure. The mean natal dispersal distance for all marked males was 1.4 km (SE = 0.2) and did not differ ($t_z = 0.74$, P = 0.48) between PIT-tagged (1.5 km, SE = 0.3) and transmitter-equipped birds (1.2 km, SE = 0.3; Table 1). Five of seven transmitter-equipped males monitored during their first spring breeding season were recorded on multiple leks. We calculated dispersal distances for three female lesser prairie-chickens during Phase II. No female birds PIT-tagged during Phase I were ever recaptured. Two transmitter-equipped females dispersed 25.4 and 2.1 km to establish nests. The carcass of a third female was recovered on 10 April at a distance of 3.7 km from her location at 60 days post-hatch. An additional five chicks (two female and three male) equipped with transmitters during the 2002-brood-period were last located from the air on 14 March 2003. The two females were approximately 1.7 km and 18.1 km from their hatch location and the three males were all within three km of their hatch locations ($\bar{x} =$ $2,238 \,\mathrm{m} \pm 586$).

		Natal disp	ersal ^a		Approximate d	ispersal ^b
Gender	n	$\overline{x} \pm SE$	Range	n	$\overline{x} \pm SE$	Range
Male						
PIT	4	$1.5\pm\ 0.3$	0.9 to 2.3			—
TE	5	$1.2\pm\ 0.3$	0.6 to 2.1		_	_
Total	9	1.4 ± 0.2	0.6 to 2.3	11	1.2 ± 0.2	0.3 to 2.0
Female	2	NR ^c	2.1 to 25.4	3 ^d	$10.49\pm~7.94$	1.5 to 26.3

Table 1. Mean dispersal distances (km) of PIT-tagged (PIT) and transmitterequipped (TE) juvenile male and female lesser prairie-chicken in southwestern Kansas, 1997 to 2002.

^aDistance between the hatch location and the most visited spring lek site (male) or first nest location (female).

^bDistance between chick location at approximately 60 days post-hatch and most visited spring lek site (male) or nest location (female).

^cNR = not reported.

^dFor one female the distance was calculated from the 60 day post-hatch location to the 10 April location where the bird's carcass was recovered.

DISCUSSION

Brood break-up and dispersal signify the time at which chicks become independent from the brood hen. For fall-dispersing prairie grouse species, the autumn dispersal period is critical because it provides juvenile males time to prospect for advertising sites prior to winter (Bergerud and Gratson 1988). Previous grouse researchers have concluded that brood break-up and dispersal occur at distinctly different times (Godfrey and Marshall 1969, Bowman and Robel 1977). Similarly, the break-up of lesser prairie-chicken broods in Kansas and the onset of autumn dispersal were not simultaneous events. Break-up of broods occurred in mid-September and the timing was similar to the dates reported for other fall-dispersing grouse species (Godfrey and Marshall 1969, Rusch and Keith 1971, Bowman and Robel 1977, Schroeder 1986). Following brood break-up, the peak of autumn dispersal for juvenile lesser prairie-chickens was preceded by three to six weeks of more localized movements.

The sex of spruce grouse (*Falcipennis canadensis*) chicks has been shown to influence the date of brood break-up with females leaving the brood later than males (Schroeder 1986). We failed to find such a relationship for lesser prairie-chicken in Kansas, but our sample sizes were small. Our results also suggested

that chick age was not the primary factor associated with brood-break up of lesser prairie-chicken because age varied substantially (85 to 128 days post-hatch) at the time of brood break-up. Bowman and Robel (1977) also failed to find evidence of age-specific brood break-up for greater prairie-chicken (*Tympanuchus cupido*) in Kansas. The age of chicks in their study ranged from 70 to greater than 84 days post-hatch (n = 11 chicks in four broods) at the time of brood break-up and they suggested that break-up of broods was under photoperiodic control. Godfrey and Marshall (1969) reported photoperiodic control or meteorological changes to be involved in the breakdown of ruffed grouse (*Bonasa umbellus*) broods. We have no evidence to suggest either of these environmental conditions were driving the timing of lesser prairie-chicken brood break-up.

The timing of autumn dispersal movements and sex-specific dispersal distances have been reported for several grouse species (Godfrey and Marshall 1969, Bowman and Robel 1977, Schroeder 1986, Small and Rusch 1989, Whitcomb et al. 1996). Bowman and Robel (1977) hypothesized that dispersal of juvenile greater prairie-chicken was not complete following brief initial dispersal in the fall. The occurrence of bimodal dispersal (autumn and spring) in several grouse species supported this hypothesis (Small and Rusch 1989, Small et al. 1993, Smith 1997, Caizergues and Ellison 2002, Warren and Baines 2002). Dispersal of juvenile lesser prairie-chicken in Kansas mimicked this bimodal pattern. Thus, autumn dispersal distances probably do not approximate true natal dispersal for lesser prairiechicken. Similarly, dispersal of juvenile greater prairie-chicken in Wisconsin is bimodal and spring dispersal movements are more extensive than more subtle autumn movements (Halfmann 2002). Final dispersal of juvenile greater prairiechicken occurs during February-March for males and March-early April for females (Halfmann 2002). Likewise, individuals of juvenile lesser prairie-chicken exhibit sexspecific periods of dispersal and complete their natal dispersal during the same time periods as greater prairie-chicken in Wisconsin.

Juvenile lesser prairie-chicken monitored in our study exhibited sex-specific natal dispersal distances with females dispersing farther than males. Eighteen studies of 10 grouse species have quantified sex-specific natal dispersal (Table 2). Five of these studies have solely used band recoveries at spring display sites to estimate natal dispersal distances. Dispersal distances might be underestimated in these studies because search efforts usually decline with distance from the original capture site (Lambrechts et al. 1999). However, the natal dispersal distance of male lesser prairie-chicken derived from PIT-tagged birds did not differ from that of transmitter-equipped birds during our study. Thus, our data suggested that recoveries of marked birds (banded or PIT-tagged) at spring display sites could be used to reasonably approximate natal dispersal distance of male lesser prairiechicken. Natal dispersal distance of male lesser prairie-chicken in Kansas (1.4 km) was similar to estimates derived from band recoveries in Oklahoma (less than 1.0 km; Copelin 1963). Natal dispersal distance of male lesser prairie-chicken also was

either band recoveries (BR) c	or transmitt	ter-equ	uipped (TE	() birds.				
			Female			Male		
Species	Method	u	Mean	Max	u	Mean	Max	Reference
Tympanuchus pallidicinctus ^a	TE	5	NR ^b	21.0	10	1.4	2.3	Our study
Tympanuchus pallidicinctus $^{\circ}$	BR	5	< 3.0 ^d	< 6.0	27	$< 1.0^{d}$	< 4.0	Copelin 1963
Tympanuchus cupido	TE	88	6.9	70.0	71	2.3	17.2	Halfmann 2002
Lagopus lagopus ^a	TE	NR^b	11.4	NR	NR	2.6	NR	Smith 1997
Lagopus lagopus	TE	14	$2.0^{\rm d}$	10.0	21	< 0.5 ^d	< 1.0	Hudson 1992
Lagopus leucurus	BR	40	4.0 ^d	28.0	126	1.3 ^d	6.0	Giesen and Braun 1993
Centrocercus urophasianus	BR	12	8.8 ^d	NR	12	7.4 ^d	NR	Dunn and Braun 1985
Tetrao tetrix	TE	8	9.3	19.0	11	< 1.0	< 1.0	Warren and Baines 2002
Tetrao tetrix	TE	16	8.0 ^d	29.0	11	1.5 ^d	8.2	Caizergues and Ellison 2002
Dendragapus obscurus	TE	42	1.4 ^d	11.0	24	$^{\rm p}6.0$	2.6	Hines 1986
Dendragapus obscurus	BR	50	$2.0^{\rm d}$	10.0	49	1.1^{d}	9.1	Jamieson and Zwickel 1983
Falcipennis canadensis	BR	14	3.2	NR	16	2.3	NR	Robinson 1980
Falcipennis canadensis	TE	NR	5.0	NR	NR	0.7	NR	Schroeder 1986,
								Boag and Schroeder 1992
Bonasa umbellus	TE	7	NR	3.4	2	NR	0.8	Small and Rusch 1989
Bonasa bonasia ^c	TE	4	2.0	5.6	14	4.0	24.9	Montadert and Leonard 2005
Bonasa bonasia ^a	TE	4	4.2	6.8	б	2.7	5.7	Swenson 1991, Kämpfer-
								Lauenstein 1995, Fang and
								Yue-Hua 1997

94 Table 2. Estimates of mean and maximum (max) sex-specific juvenile dispersal distances (km) for 10 grouse species, by using "Natal dispersal is from the location of hatch to spring breeding site; all others calculated as the distance from initial summer capture site to spring breeding site. ^bNR= not reported.

^cDispersal distances calculated from fall and winter capture sites to spring breeding site; might not provide an accurate estimate of natal dispersal due to movements prior to initial capture.

^dDistances are medians; all others are means.

similar to seven of the nine grouse species for which an estimate has been reported (Table 2). Only juvenile dispersal distances of male greater sage-grouse (7.4 km; *Centrocercus urophasianus*; Dunn and Braun 1985) and hazel grouse (4.0 km; *Bonasa bonasia*; Montadert and Leonard 2005) were substantially greater than those observed for lesser prairie-chicken in Kansas.

The sex-specific natal dispersal distances observed in our study suggested that males contributed less than females to genetic exchanges between isolated populations because they generally remained within 2 km of their natal area. In a New Mexico lesser prairie-chicken population, most genetic variance was explained by differences within (96.4%), rather than among leks (3.6%) (Bouzat and Johnson 2004). These results along with observations of high lek fidelity (95%) by males within and across years led Bouzat and Johnson (2004) to conclude that female dispersal among lesser prairie-chicken leks might prevent local lek genetic differentiation at the mtDNA control level. We concurred with Bouzat and Johnson (2004) and suggested that mean natal dispersal distance of female lesser prairie-chicken could be used to identify the minimum acceptable distance between habitat fragments occupied by lesser prairie-chicken. In southwestern Kansas, natal dispersal averaged less than 10 km for female lesser prairie-chicken. When the distance between occupied habitat fragments exceeded this distance there was an increased risk of fitness effects due to genetic isolation. However, we only observed natal dispersal distances for two female lesser prairie-chicken and further research should focus on providing a more reliable estimate.

ACKNOWLEDGMENTS

Property access was provided by J. O. Cattle Company, Sunflower Electric Power Corporation, Thornton Cattle Company, Brookover Cattle Company, R. A. Greathouse, and the P. E. Beach family. The following assisted with field work: G. C. Salter, T. G. Shane, T. L. Walker Jr., and T. J. Whyte. Our study was supported by Kansas State University (KSU), Division of Biology; KSU Agricultural Experiment Station (Contribution 05-307-J), Kansas Department of Wildlife and Parks, Federal Aid in Wildlife Restoration Grants W-47-R and W-53-R; and Westar Energy, Inc. Finally, we thank D. A. Haukos and M. A. Schroeder for their comments, which substantially improved the quality of our manuscript.

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Received: 27 July 2005 Accepted: 15 September 2006

Associate Editor for Ornithology: Gregory A. Smith