

PARTIAL MIGRATION IN A POPULATION OF GREATER PRAIRIE-CHICKENS IN NORTHEASTERN COLORADO

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ABSTRACT.—Seasonal movements of radio-marked Greater Prairie-Chickens (*Tympanuchus cupido*) were examined in northeastern Colorado during 1986–1989. Many birds migrated between breeding and winter areas; all appeared to display fidelity to both breeding and winter sites. The average date of migration from winter to breeding areas was 20 February for males and 27 March for females. The average date of migration from breeding to winter areas was 4 July for females and 28 July for males. Much of the variability in timing of migration from breeding areas for females was related to brood status; average date of migration was 10 June for females without broods and 26 August for females with broods. Average migration distance between winter and breeding ranges differed significantly by sex: 9.2 km for females and 2.7 km for males. When migration samples were expanded to include distances between breeding and late summer ranges (as suggested by timing of movements), females migrated an average distance of 10.6 km, while males migrated 2.9 km. Seasonal movements of Greater Prairie-Chickens appear to represent a partial migration with both obligatory and facultative components. Received 3 June 1991, accepted 23 February 1992.

MIGRATION has been defined as “a regular round trip within a life-span of the individual” (Sinclair 1983:241), while patterns of migration have been categorized as “annual,” “partial,” or “differential” (Terrill and Able 1988). Species of Tetraoninae are particularly variable with respect to migration patterns. While some species such as Willow and Rock ptarmigan (*Lagopus lagopus* and *L. mutus*) may be annual migrants in certain regions (Weeden 1964, Irving et al. 1967), most are considered either nonmigrants or partial migrants with only some individuals migrating. However, extensive research on movements of Blue Grouse (*Dendragapus obscurus*; Wing 1947, Mussehl 1960, Zwickel et al. 1968), Spruce Grouse (*D. canadensis*; Herzog and Keppie 1980, Schroeder 1985), White-tailed Ptarmigan (*Lagopus leucurus*; Hoffman and Braun 1975), and Common Capercaillie (*Tetrao urogallus*; Rolstad 1989) indicate that patterns of partial migration may be the rule rather than the exception, particularly among females.

Explanations for partial migration include seasonal and/or sexual differences in habitat selection, and dispersal differences due to ag-

gressive interactions, breeding success, and/or heritability (Lack 1944, Biebach 1983, Smith and Nilsson 1987). For example, Blue Grouse migration has been attributed to elevational and/or seasonal differences in habitat selection (Wing 1947, Mussehl 1960, Zwickel et al. 1968), and Spruce Grouse migration appears to be related to fidelity to specific winter and breeding areas, and to variability in dispersal movements during their first spring (Herzog and Keppie 1980, Schroeder 1985, 1988). Despite similarities in patterns of movement for Blue Grouse, Spruce Grouse, White-tailed Ptarmigan, and Common Capercaillie, possible explanations for movement have not been thoroughly examined in other species of Tetraoninae.

Greater Prairie-Chickens (*Tympanuchus cupido*) are among the most mobile of the species in the Tetraoninae, with seasonal movements up to 170 km (Hamerstrom and Hamerstrom 1949). Early reports indicated that Greater Prairie-Chicken movements were particularly extensive among females and typically related to seasonal differences in habitat selection (Schmidt 1936, Hamerstrom and Hamerstrom 1949) and regional food availability, such as the abundance of acorns (*Quercus* spp.; Cooke 1888, Gross 1930, Leopold 1931). However, Gross (1930) suggested that introduction of corn throughout the range of Greater Prairie-Chick-

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ens resulted in the elimination of their migratory tendencies. Despite numerous anecdotal reports about Greater Prairie-Chicken movements, a thorough examination of their seasonal pattern of movement has not been undertaken.

We examined patterns of movement in a population of Greater Prairie-Chickens in north-eastern Colorado during 1986–1989. The study area had both winter and breeding populations of prairie-chickens throughout, and there was no *a priori* reason to expect large movements between winter and breeding ranges by members of the population. Seasonal movements were investigated with respect to three questions: (1) Do Greater Prairie-Chickens migrate between winter and breeding areas? (2) Do females migrate farther and more frequently than males? (3) Do movements occur in response to habitat, weather, and nest failure?

METHODS

We selected a 301-km² study area centered 10 km northeast of Eckley, Colorado (40°11'N, 102°22'W). The area was grassland dominated by sand sagebrush (*Artemisia filifolia*) and small soapweed (*Yucca glauca*) intermixed with irrigated cropland, primarily corn (Schroeder and Braun 1992b). Forty-one to 47 leks were active (>1 male) during each breeding season. Trapping was concentrated in a core area of approximately 75 km². Trapping in winter at feeding sites with walk-in traps baited with corn and in spring at leks with walk-in traps and cannon nets resulted in capture of 243 Greater Prairie-Chickens (Schroeder and Braun 1991).

All captured birds were banded with a numbered aluminum band and a unique combination of three colored plastic bands. Birds were classified according to feather appearance and wear (Ammann 1944) as: yearlings, 5 to 17 months old (1 November of first year to 31 October of second year); and adults, greater than 17 months old (after 31 October of second year). Battery- and solar-powered radio transmitters were attached to poncho-type markers (Amstrup 1980) and placed on 111 female and 34 male Greater Prairie-Chickens. Radio masses were 1.8 to 2.3% of each bird's body mass at the time of capture.

Seasons were defined *a priori* as breeding (15 February to 30 June), late summer (1 July to 15 August), autumn (16 August to 31 October), and winter (1 November to 14 February) based on breeding behavior and daily movement (Robel et al. 1970). Breeding, nesting, and hatching usually occur during the breeding season and brood break-up during autumn.

Radio-marked Greater Prairie-Chickens were located using a portable receiver and three-element Yagi antenna. Observations of each bird were made daily

(≤4 days between sightings for all birds) between 1 March and 15 August and weekly during other times of year. There were three types of exceptions: (1) birds that moved long distances resulting in their departure from the study area; (2) birds that were dead with their transmitters temporarily buried in soil and/or vegetation; and (3) birds that disappeared either due to movement, transmitter failure, or both. Aerial searches were conducted two to three times each year to locate missing transmitters.

Locations for each sighting were obtained by visual observation (all nest sites) or by triangulation; three or more azimuths were obtained within 1.5 km of target transmitters and at angles-of-incidence between 35° and 145°. All locations were recorded with Universal Transverse Mercator (UTM) coordinates (Zone 13, nearest 10-m interval). Ninety percent of locations derived by triangulation were within 250 m of actual locations (Schroeder 1991).

We defined winter-breeding migration as movement from winter to breeding areas and breeding-winter migration as movement from breeding to winter areas, regardless of specific time. Migration distance was estimated as the distance between the breeding season location (lek for males and nest for females) and mean X- and Y-coordinates for at least four locations during winter. Although 17 of 21 males were observed on only one lek during the breeding season, the four exceptions were observed on a single lek at least 75% of the time (Schroeder and Braun 1992a); these "primary" leks were used as breeding season locations. Additional distances were estimated using mean locations in late summer and autumn seasons as intermediate points between breeding and winter areas; this helped identify the specific time of migratory movements.

Svedarsky (1988) attributed long movements of Greater Prairie-Chickens, particularly females, to their previous nest failure and/or interactions with predators; he suggested that movements were frequently nomadic in response to disturbance. Consequently, site fidelity between consecutive years was examined for both sexes to distinguish between regular migrations and nomadic movements. Nomadic birds may not return to the same sites in consecutive years.

Dates were estimated only for distinct movements of at least 5 km, clearly not part of the normal home range. Since some migratory movements may be less than 5 km, this procedure was necessary to estimate time of migration, not the likelihood of migration. This procedure resulted in little ambiguity; birds often moved from the study area (>10 km) within 36 h of being observed on or near their nest site, or on their winter area. In these cases, time of movement was estimated based on search intensity (time between searches). For example, if a telemetry search failed to result in detection of a bird later found off the study area, we assumed the bird had migrated at the midpoint in time between the last successful search and the first unsuccessful search.

We used multiresponse permutation procedures (MRPP; Zimmerman et al. 1985, Biondini et al. 1988) to statistically compare distributions of distances and dates. We compared variances with F_{\max} -tests and means with t -tests (SAS Institute 1985). Direction of movement was examined with a chi-square goodness-of-fit test using eight 45°-categories (Cain 1989, Bergin 1991).

RESULTS

Site fidelity.—Of six radio-marked males monitored during at least two consecutive breeding seasons, all attended the same lek; the winter area for one male was more than 5 km from its breeding area (returned to same lek three consecutive years). An additional 10 banded males without radios were also observed on the same lek in consecutive years.

Nest locations of individual hens between consecutive years were an average of 0.83 km \pm SE of 0.19 km ($n = 8$) apart; two of these hens wintered in areas that were more than 20 km from their breeding areas. These distances were not different (MRPP-test, $P = 0.599$) from distances ($\bar{x} = 0.81 \pm 0.11$ km, $n = 10$) between first nests and second nests within the same year. Thus, distances between consecutive nests were the same statistically for nests within years as they were for nests between years.

Distances between mean locations for consecutive winter ranges were relatively small ($\bar{x} = 1.08 \pm 0.33$ km, $n = 7$ females and 2 males); five of these birds had moved more than 5 km between winter and breeding areas (four moved >20 km). Five of seven females returned to within 1 km of their previously occupied winter area despite the possible disturbance of predators at their destroyed nest sites (including two females moving >20 km). Overall, there were no observations of radio-marked birds changing (>5 km apart) either their winter or breeding sites between consecutive years.

One adult female that moved 26 km returned to the same winter area she occupied as a yearling. This observation was significant for three reasons: (1) her first movement between winter and nesting areas may have represented dispersal (marked as a yearling); (2) her subsequent return to the same general winter area may indicate that migration movements may retrace dispersal movements; and (3) she wintered in the same general area in which numerous females spent the breeding season.

Timing of movement.—Dates of winter-breed-

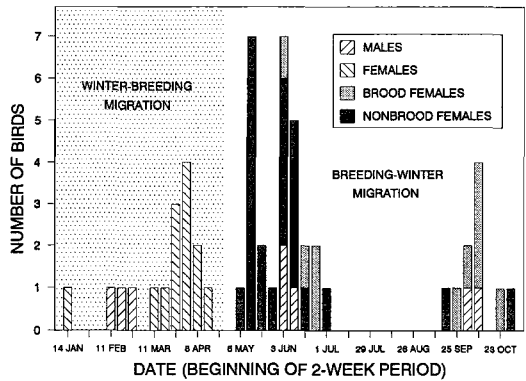


Fig. 1. Distribution of dates for distinct movements by Greater Prairie-Chickens in northeastern Colorado, 1986-1989.

ing migration were earlier (MRPP-test, $P = 0.002$, $t = 4.518$, $P = 0.001$) for males ($\bar{x} = 20$ February ± 4 days, $n = 3$) than females ($\bar{x} = 27$ March ± 6 days, $n = 13$; Fig. 1). Dates of breeding-winter migration did not differ (MRPP-test, $P = 0.520$; $t = 0.792$, $P = 0.464$) between males ($\bar{x} = 28$ July ± 30 days, $n = 5$) and females ($\bar{x} = 4$ July ± 10 days, $n = 33$). The tendency for males to move early to their respective leks was expected since leks were frequently active by mid-February.

Breeding-winter movements by females appeared to be bimodal (Fig. 1). Much of the variability in movement was associated with their brood status. The mean date of migration from breeding areas was 10 June ± 9 days ($n = 23$) for females without broods and 26 August ± 19 days ($n = 10$) for females with broods (MRPP-test, $P = 0.001$; $t = 3.693$, $P = 0.003$). Similarly, 4 of 25 females (12%) migrating during May-August, and 6 of 8 females (75%) migrating during September-October had broods ($X^2 = 9.989$, $P = 0.002$). Exceptions to the general pattern of female movement usually were females with late reneesting attempts (late migration) or females that lost their broods relatively soon after hatching (early migration).

Due to speed and distance of many movements, actual observations were difficult to obtain. One female completed a 26-km migration between her depredated nest and her winter range in a maximum of 71 h. Another female completed a 24-km migration between her winter range and breeding area in a maximum of 137 h.

Many birds that apparently migrated died prior to being observed during the winter or

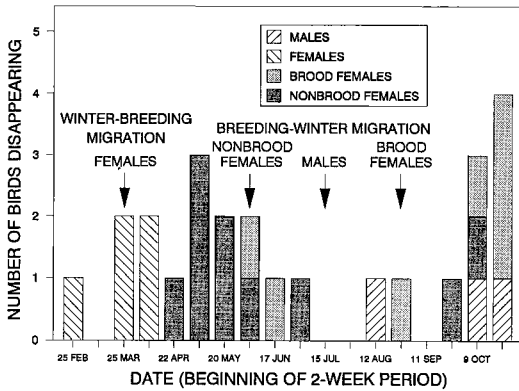


Fig. 2. Distribution of disappearance dates in relation to average date of migration (arrows) for Greater Prairie-Chickens in northeastern Colorado, 1986-1989.

breeding seasons. Consequently, breeding-winter distances were divided into breeding-late summer and late summer-winter components. These distances were estimated only for females followed throughout all seasons to provide additional information on specific timing of movements. Of 38 distances recorded, all of those greater than 10 km ($n = 5$) were observed during the breeding-late summer period.

The three longest movements between late summer and winter areas (6-9 km) were recorded for females with broods. The only brood female that moved a long distance early in summer (23 km) lost her brood within two days of hatch (prior to movement). In general, movements between late summer and autumn ranges were relatively small (0-4 km) for all females. However, the four longest movements were by females with broods.

We also examined the dates of disappearance for radio-marked individuals that, subsequently, were not found (Fig. 2). Although some of these radios may have become disabled following mortality, the synchrony of disappearance dates with observed migration dates indicates that many radios may have been on birds that migrated but were not found. Thus, it is likely that estimates of migration tendencies and distances were low.

Distance of movement.—Distances between winter and breeding areas ranged between 0.6 and 40.0 km ($\bar{x} = 9.18 \pm 1.73$ km, $n = 38$) for females, and between 1.0 and 6.1 km ($\bar{x} = 2.74 \pm 0.44$ km, $n = 12$) for males. Although there was a suggestion that yearlings moved farther

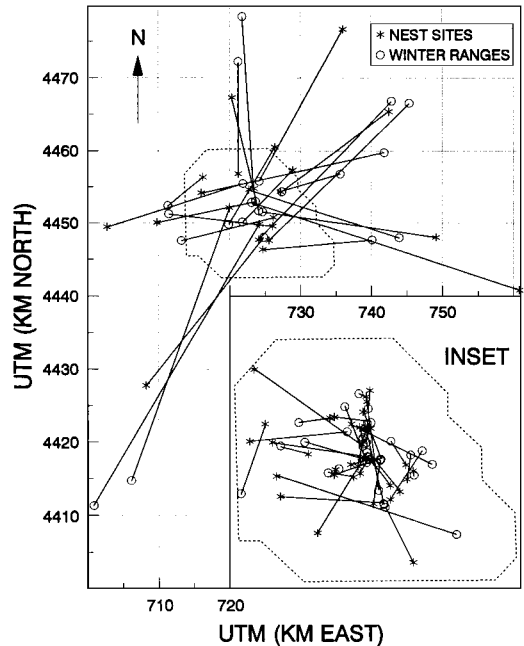


Fig. 3. Straight-line distances between estimated winter ranges (circles) and nest sites (asterisks) for 60 female Greater Prairie-Chickens captured on study area (dashed line) in northeastern Colorado, 1986-1989. Inset shows females with both winter ranges and nest sites on the study area.

than adults for both males (3.52 vs. 2.48 km) and females (14.39 vs. 8.20 km), these differences were not significant ($P = 0.501$ for females, $P = 0.289$ for males). With both ages combined, movements of females were longer ($P < 0.001$) and more variable ($P < 0.001$) than those of males. In addition, fewer male (0%) than female (31.6%) migrations crossed the study area boundary ($X^2 = 4.986$, $P = 0.026$).

Analysis of migration distances was conservative; only birds with known winter and breeding areas were included. Many birds that died prior to either the winter or breeding seasons were not included in the analysis, even though many had obviously made long migratory movements. Consequently, analysis of movement data was expanded to include additional birds based on locations between breeding and late summer areas. Females migrated an average distance of 10.58 ± 1.40 km ($n = 60$), while males migrated 2.86 ± 0.76 km ($n = 22$). Migration distances of females (Fig. 3) were longer ($P < 0.001$) and more variable ($P < 0.001$) than those of males (Fig. 4); both small

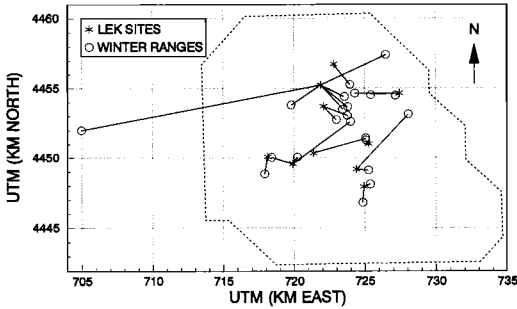


Fig. 4. Straight-line distances between estimated winter ranges (circles) and lek sites (asterisks) for 22 male Greater Prairie-Chickens captured on study area (dashed line) in northeastern Colorado, 1986-1989.

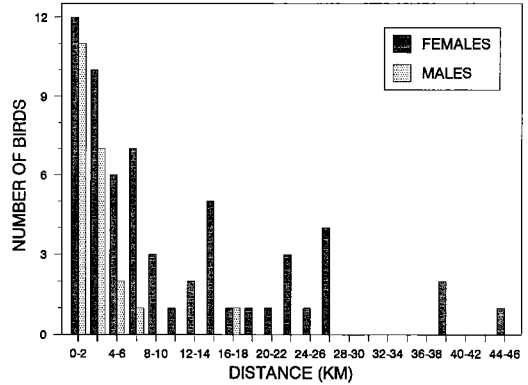


Fig. 5. Distributions of migration distances for 60 female and 22 male Greater Prairie-Chickens in northeastern Colorado, 1986-1989.

and large distances were common among females (Fig. 5). Twenty-one of 60 females (35.0%) and 1 of 22 (4.5%) males migrated farther than 5 km; this difference was significant ($X^2 = 8.230$, $P = 0.004$).

Direction of movement.—There was no obvious relationship between direction of movement and tendency to move north or south prior to particular seasons. Directions of movement for birds between winter and breeding areas were not different from random ($X^2 = 2.293$, $P = 0.942$, $df = 7$). Furthermore, many individuals occupied winter or breeding areas on the main study area as the result of relatively large migratory movements (Fig. 3); females often bypassed occupied habitats during the course of their movements.

DISCUSSION

Askins (1913) suggested that Greater Prairie-Chickens were nonmigratory. In contrast, several lines of evidence have been used to suggest that Greater Prairie-Chickens were historically annual migrants in portions of their original and acquired range (Gross 1930, Leopold 1931). Grange (1948:139) considered evidence for annual migrations prior to 1850 as "indisputable." First, seasonal increases and decreases in numbers were noted in both southern and northern parts of the range (Bogardus 1874, Cooke 1888, Banta 1892, Judd 1905, Webster 1912, Leopold 1931, Schmidt 1936, Stempel and Rodgers 1961, Spengler 1984). Second, evidence of biased sex ratios in resident and/or migratory populations has been used to demonstrate migratory tendencies (Cooke 1888, Leopold 1931, Schmidt 1936). Finally, large flocks of Greater Prairie-

Chickens have been observed making directional movements and/or were temporarily present in areas with no acceptable habitat (Gross 1930, Leopold 1931, Stempel and Rodgers 1961).

We found that Greater Prairie-Chickens in northeastern Colorado are partial migrants. Some individuals migrated substantial distances (up to 40 km) between seasonal ranges, while others were resident on relatively small areas (<5 km between winter and breeding areas). Similarly, banded individuals moved up to 170 km in Wisconsin (Hamerstrom and Hamerstrom 1949) and 30 km in Michigan (Ammann 1957), and radio-marked birds moved up to 12 km in Minnesota (Svedarsky 1988); numerous marked individuals moved shorter distances in each population.

In our study, females migrated farther and more frequently than males. Similar tendencies were noted for Greater Prairie-Chickens in Wisconsin (Hamerstrom and Hamerstrom 1949) and North Dakota (Toepfer and Eng 1988). Differential movement biased toward females is consistent with patterns of migration and/or dispersal for other grouse including Spruce Grouse (Herzog and Keppie 1980, Schroeder 1985, 1986), Blue Grouse (Hines 1986), Sharp-tailed Grouse (*Tympanuchus phasianellus*; Kobriger 1965), Sage Grouse (*Centrocercus urophasianus*; Beck 1977), White-tailed Ptarmigan (Hoffman and Braun 1975), Rock Ptarmigan (Weeden 1964), Willow Ptarmigan (Weeden 1964, Irving et al. 1967, Mossop 1988), and Black Grouse (*Tetrao tetrix*; Willebrand 1988). Although reasons for female-biased movement in Tetraoninae are not well understood, factors may include sexual differ-

ences in intraspecific competition (Herzog and Keppie 1980), habitat selection (Gross 1930, Schmidt 1936), and genetics (Keppie 1980, Schroeder 1988).

Timing of migration of Greater Prairie-Chickens in northeastern Colorado was relatively complicated as breeding-winter movements occurred as early as late May. Timing of breeding-winter movements was bimodal; unsuccessful females moved during June and brood females typically moved during October–November. Although Greater Prairie-Chickens in other regions were observed moving as early as August (Leopold 1931), most movements were from October to November (Leopold 1931, Lehmann 1939, Hamerstrom and Hamerstrom 1949, Mohler 1952, Ammann 1957).

The early timing of most breeding-winter migrations by Greater Prairie-Chickens in northeastern Colorado was unusual. Most grouse species migrate during late summer or autumn (Irving et al. 1967, Zwickel et al. 1968, Hoffman and Braun 1975, Schroeder 1985, 1986). It is possible the bimodality in timing of migration by female Greater Prairie-Chickens (males showed a similar trend) may be due to molt of the flight remiges in summer. Females without broods migrate prior to molting, and females with broods may wait until after the molt before undertaking long movements. Similarly, the physiological cost of molting may force Lazuli Buntings (*Passerina amoena*) to interrupt their fall migration (Young 1991). The molt period may be important for prairie-chickens since their movements are often long, necessitating at least some flying. In contrast, Spruce Grouse have been observed completing substantial portions of their migratory movements by walking (Schroeder 1985).

Svedarsky (1988) suggested that many long movements by female Greater Prairie-Chickens may be due to disturbances by predators at nest sites. In contrast, although migrations of females in Colorado frequently occurred immediately following nest failure (Fig. 1), females moved to their previously occupied winter areas and returned to the same nesting areas in following years, despite nest failure. Furthermore, females producing broods also migrated, even though their movements were later during autumn or early winter. No females were observed reneesting following migration after the breeding-season loss of their nest or young brood.

Regional food availability (Cooke 1888, Gross 1930, Leopold 1931, Lehmann 1939, Hamerstrom and Hamerstrom 1949, Mohler 1952, Ammann 1957, Toepfer and Eng 1988) and/or weather (Leopold 1931, Hamerstrom and Hamerstrom 1949) have been suggested as explanations for migration of Greater Prairie-Chickens. Data from our study indicated that habitat and weather could be ruled out as adequate explanations for the observed movements, particularly those greater than 10 km: (1) the prevalence of early movements (most in midsummer) indicated that cold weather and/or snow were not major factors; (2) movements were typically in random directions, with birds as likely to move north as south prior to winter; (3) birds often migrated to areas that other birds vacated, while others remained on the same areas during both winter and breeding seasons; and (4) corn (typical winter food) was available throughout the region in both winter and breeding areas (Schroeder and Braun 1992b).

Little information is available on migration prior to 1900. Migratory movements may have been as long as 1,000 km before corn (typical winter food) was introduced throughout much of the Great Plains region (Cooke 1888); Hamerstrom and Hamerstrom (1949) suggested the tendency to migrate was reduced with increased availability of corn. However, planted food plots in Wisconsin failed to prevent birds from migrating from study areas prior to winter (Schmidt 1936).

One possible explanation for migration in Tetraoninae is that migratory movements mirror dispersal movements of birds from their first winter area to their first breeding area. Birds may disperse between their place of hatch and breeding area, while displaying fidelity to both their first winter and breeding areas (Herzog and Keppie 1980, Schroeder 1985, 1988, Hines 1986). Whether this dispersal tendency reflects a genetic predisposition to disperse or environmental pressure has not been determined (Greenwood and Harvey 1982).

Similarity between patterns of dispersal and migration in Greater Prairie-Chickens may be especially important given the context of historical observations of large-scale migrations. Many observations of migratory movements were recorded during periods of rapid range expansion (late 1800s). First, seasonal increases and decreases in numbers were observed in southern and northern parts of the range

(Grange 1948). These changes in numbers would be expected if Greater Prairie-Chickens were dispersing into previously unoccupied areas, particularly in the northern and western portions of their distribution. Second, evidence of biased sex ratios in resident and/or migratory populations has been used to demonstrate past migratory tendencies (Grange 1948). Dispersal into previously unoccupied range (during range expansion) would be observed as a female-biased pattern of movement, particularly since dispersal movements are female-biased (Hamerstrom and Hamerstrom 1949). Consequently, it may be possible that historical "migrations" of Greater Prairie-Chickens consisted of little more than local movements in response to habitat availability (<5 km movements) in combination with dispersal tendencies and fidelity to winter/breeding sites.

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