NATAL DISPERSAL AND LEK FIDELITY OF SAGE GROUSE

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ABSTRACT.—Natal dispersal and lek fidelity (attendance within and between years) of Sage Grouse (*Centrocercus urophasianus*) were studied on Cold Spring Mountain, northwestern Colorado, from July 1981 through May 1984. Female Sage Grouse followed the typical avian pattern of dispersing farther than males. However, there was no difference between proportions of male and female yearling grouse attending the lek closest to their juvenile banding location. Fifteen percent of all individually marked juveniles (24/157 birds) were known to have attended leks as yearlings. There was no difference between yearling and adult lek attendance rates for either sex; however, females attended leks less often than males. Yearling females, but not yearling males, visited 2 or more leks more often than adults. These differences may be related to yearlings' inexperience with breeding or to a strategy to enhance reproductive success. *Received 9 July 1984, accepted 6 March 1985.*

DISPERSAL has a major role in population regulation (Lidicker 1962, Krebs et al. 1976) and distribution (Taylor and Taylor 1977). It also may have a role in the evolution of song dialects (Baker and Mewaldt 1978), mating systems (Greenwood 1980), and the stability of local populations (Reddingius and den Boer 1970). Despite its potential importance, studies of avian dispersal are few; most research has investigated fall movements, not movement from natal to initial breeding areas. There have been even fewer studies of dispersal of avian species that may show exceptions to the general pattern of greater female than male dispersal. Greenwood (1980) proposed that both female-biased dispersal and monogamy *can* be a consequence of a resource-defense mating system. Bird species with lek mating systems may be exceptions to Greenwood's hypothesis because males do not appear to defend resources required by females.

If there is a relationship among the intensity and direction of sexual selection, mating systems, and natal dispersal patterns (Oring and Lank 1982), then Sage Grouse (*Centrocercus urophasianus*) are an ideal species in which to study dispersal because they exhibit some of the greatest variation in male mating success among lekking species (Payne 1984: 8). Here we describe natal dispersal and lek fidelity (attendance within and between years, and movements between leks) of a population of Sage Grouse in northwestern Colorado. We examined female Sage Grouse to determine whether they follow the typical avian pattern of dispersing farther than males. We also present data on the natal philopatry of yearling grouse (birds 8–10 months old) and relate their patterns of dispersal and lek fidelity to recent hypotheses concerning lek mating systems.

STUDY AREA AND METHODS

The study was conducted on Cold Spring Mountain (2,622 m) in northwestern Moffat County, Colorado and adjacent parts of Wyoming and Utah from July 1981 through June 1983 and on 3 days in April and May 1984. The study area is semiarid sagebrush (*Artemisia* spp.) rangeland with interspersed quaking aspen (*Populus tremuloides*) and pinyon pine (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) stands, and meadows. Lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*) occur above 2,620 m on Middle Mountain (2,904 m) and Diamond Peak (2,909 m) near the Wyoming border. Sage Grouse studies have been conducted on the area since 1978. From 120 to more than 300 juvenile Sage Grouse have been banded during July and August each year.

In 1981 and 1982, juvenile grouse were captured and individually marked with numbered aluminum bands and unique combinations of colored plastic bands. Drive traps, a bumper-mounted cannon net,

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and spotlighting with long-handled nets were used to capture grouse (Giesen et al. 1982). Captured birds were classified to sex and age by wing molt and primary length (Beck et al. 1975). Lek searches were made at least 5 days/week during late March through May 1982 and 1983 for birds individually banded during those springs and in previous summers. Lek searches also were made on 3 days in 1984 (22 April, 8 and 9 May) to observe changes in the leks where birds displayed during 1982 to 1984. We recorded observations of marked birds on leks and calculated straight-line dispersal distances between the juvenile banding location and the lek on which the bird was observed displaying (attended) as a yearling. The banding location was used as an approximation of a juvenile's natal area since most juveniles were marked before long-distance (>2 km) movements took place (Wallestad 1971; unpubl. data). For birds that attended more than one lek, the lek attended most frequently or where mating occurred was used in calculating dispersal distances.

Lek attendance was calculated as the number of days that a bird was observed on a lek divided by the total days that males or females, depending on the sex of the particular bird, were observed on the lek multiplied by 100. Attendance was corrected for birds captured during each spring breeding season (26 adult males, 5 adult females, 5 yearling males) by subtracting the number of days of the respective sex's days of lek attendance prior to the bird's capture from the denominator. For example, adult male #9947 was captured and banded on Gee Flats Lek on 11 April 1983 after 6 days of lek observations during which males were seen. Therefore, the total days that males were seen on Gee Flats (37) minus the days prior to banding (6) equaled the number of days (31) in the denominator. Lek attendance for bird #9947 was 18 days seen on the lek ÷ 31 = 58%. Total recruitment, defined as the number of birds entering the breeding population, was estimated by dividing the number of marked yearlings seen on leks each spring by the total number of juveniles banded the previous summer. Recruitment was adjusted for known mortality by subtracting hunter harvest and known predation from the number of banded juveniles. Recruitment rates of yearling grouse to each lek were first divided by the number of potential recruits (the number of juveniles assigned to a natal-area lek) to correct for differential marking, then expressed as grouse per hour to correct for differing observation times at leks, and, finally, divided by the maximum number of males observed on leks to express recruitment rates on a per-male basis. References to "grouse·h^{-1}·$male^{-1}$" refer to this relative recruitment rate. The natal-area lek of a juvenile grouse was defined as the lek closest to the capture location of the bird.

Estimates of the percentage of marked grouse returning to their natal-area lek as yearlings may have been biased by unequally distributed summer banding efforts and lek observations in spring. Therefore, we present natal-lek attendance rates for only 2 leks (Gee Flats, Beaver Basin) around which we banded at least 50 juveniles whose capture location was closer to one of these leks than to any other lek (i.e. juveniles that were assigned one of these leks as their natal-area lek). All other leks on the study area either had no juveniles assigned to them or were observed on only a few mornings late in the breeding season. Statistical tests were considered significant at the 0.05 probability level; all tests were 2-tailed.

RESULTS

Natal dispersal.—There were no differences in dispersal distances from natal to breeding areas between 1982 and 1983 for either males or females (Kruskal-Wallis test, $P > 0.1$); consequently, data from both years were combined. The rate of resighting of males and females was similar since the sex ratio (males/females) of juveniles at banding was nearly equal (0.94 in 1981 and 0.87 in 1982; $\chi^2 = 2.76$, $P = 0.09$) and almost equal numbers of marked individuals of each sex were seen each spring on leks (3 females and 2 males in 1982, 9 females and 10 males in 1983).

Dispersal distances of yearling females (median = 8.8 km) were greater than those of yearling males [median = 7.4 km; Mann-Whitney *U*-test, $P = 0.02$, $n = 24$ (12 males, 12 females)]. However, male and female yearling Sage Grouse did not differ (Fisher's exact test, $P > 0.1$) in tendency to attend the lek closest to the location of their banding as juveniles (natal-area lek). Here we have assumed that any bias caused by unequally distributed banding efforts and lek observations was similar for both males and females. Recruitment to natal-area leks varied between 53% (8/15, Gee Flats) and 100% (6/6, Beaver Basin) for leks where we believed we banded an adequate sample of juveniles (see Methods). Of the 3 remaining yearlings seen on leks, 2 attended Sugarloaf Lek (a non-natal lek for these birds because we did not band any juveniles nearby) and 1 attended Swede Flats Lek, which was observed on only 2 mornings. Overall, 15 yearlings attended the lek closest to their initial capture site, 2 yearlings went to the next closest lek (Sugarloaf), and 7 yearlings attended the second closest lek (their natal-area lek was Beaver Basin, but they went to Gee Flats). Our low sample size, band-

TABLE 1. Sage Grouse lek observations, Cold Spring Mountain, Moffat County, Colorado, March–May 1982 and 1983.

	Gee Flats	Beaver Basin	Sugarloaf[a]	Whiskey Draw[a]	Swede Flats[a]	Cold Spring[a]
1982						
Number of males						
$\bar{x}$ (SD)	13 (7)	26 (9)				
Max *n* (date)	30 (13 Apr)	39 (26 Apr)				
Total days[b]	27	23				
Number of females						
$\bar{x}$ (SD)	23 (23)	20 (22)				
Max *n* (date)	66 (8 Apr)	82 (21 Apr)				
Total days[b]	21	20				
Observation time (h)	27.2	21.1				0.5
1983						
Number of males						
$\bar{x}$ (SD)	22 (15)	30 (8)	15 (8)	12 (7)	16 (7)	4 (1)
Max *n* (date)	42 (23 Apr)	39 (7 May)	26 (10 Apr)	20 (20 May)	21 (25 May)	5 (25 May)
Total days[b]	37	9	31	13	2	2
Number of females						
$\bar{x}$ (SD)	9 (11)	7 (5)	10 (18)	1 (2)	3 (1)	0
Max *n* (date)	42 (23 Apr)	14 (7 May)	88 (10 Apr)	8 (28 Apr)	3 (25 May)	0
Total days[b]	35	8	26	4	2	0
Observation time (h)	29.4	5.7	18.9	3.7	1.3	0.75

[a] Sugarloaf, Whiskey Draw, and Swede Flats leks were found in 1983. Cold Spring Lek had no birds in 1982. Two other leks had no birds in 1982 or 1983.

[b] Includes only days when observers were present at leks.

ing biases, and the similarity of non-natal-lek attendance precluded attempts to determine if yearlings usually traveled to the next nearest lek when they did not attend their natal-area lek.

Determination of a juvenile's natal-area lek could have been biased by long-distance brood movements into an area closer to a non-natal lek. We do not believe that this possible bias affected our results for two reasons. First, of the 24 yearlings, 4 would have had to move over 4 km from their capture site to have their assigned natal lek switched, while the remaining 20 yearlings would have had to move at least 7 km to have their natal lek switched. Data from other studies indicate that brood movements ≥7 km prior to early September are unlikely (Wallestad 1971, Connelly and Markham 1983). Second, our data suggest that sites where juvenile grouse were captured and marked were close to each bird's nest site. Eighteen radio-marked juveniles on our study area had relatively small home ranges prior to 5 September each fall [grouse locations (n = 241) averaged <2.2 km from capture sites], and 1 radio-marked juvenile remained <2.1 km from its nest site until 12 September 1982 (Dunn and Braun MS). Only 5 of 157 juveniles were banded afer 11 September.

Recruitment.—Eight known leks were on the study area. In 1982 and 1983, grouse were not observed on 2 previously used leks. Recruitment observations were made on 2 active leks in 1982 and 6 in 1983 (2 leks were found late in May 1983 and observed on only 2 days; Table 1). Direct recruitment rates of yearlings were 12% (5/41) for 1982, 16% (19/116) for 1983, and 15% (24/157 individually marked juveniles) pooled.

Recruitment among leks was examined with data from 1983 because in 1982 all 5 yearling grouse with known recruitment attended Gee Flats Lek. In 1983, most yearling grouse were recruited at Beaver Basin (6 grouse; 5.0×10^{-4} grouse·h^{-1}·male^{-1}) and Gee Flats leks (9 grouse; 5.3×10^{-5} grouse·h^{-1}·male^{-1}). Four yearlings attended Sugarloaf Lek, but no juveniles were banded nearby. This sequence of leks (Beaver Basin to Gee Flats and Sugarloaf) did not follow any trend among leks in maximum num-

TABLE 2. Sage Grouse lek attendance (%), Cold Spring Mountain, Moffat County, Colorado, March–May 1982 and 1983.

Sex and parameter	Age (yr)[a]				All adults
	1	2	3	4	
Male attendance					
$\bar{x}$	33	46	51	63	43
SD	28	31		42	26
Range	2–50	3–74		16–96	3–96
n	19[b]	6	1	3[c]	52
Female attendance					
$\bar{x}$	11	5		6	8
SD	6	3			6
Range	3–25	3–9			3–29
n	12	12		1	30

[a] Adults of unknown age were excluded from the age columns, but included under all adults. Adults are birds 2 years or older.

[b] Seven yearlings that were initially banded in spring 1982 or 1983 are included with 12 males initially banded as juveniles and later observed as yearlings.

[c] One of the 3 birds was a "dominant" male (1 of 2 birds seen mating) on Gee Flats Lek in 1982, but was present for only 6 days in 1983. This bird was over 4 years old and may have died in early spring 1983, leading to the 16% attendance estimate.

ber of attending males (Table 1). These data suggest that there was no relationship between yearling recruitment and relative size of a lek. Because there were too few data to test statistically, we examined other Sage Grouse data to test the related prediction that relatively more birds (females, in the next case) attended leks with larger numbers of males.

Maximum numbers of males and females attending leks in North Park, Jackson County, Colorado during 1974–1979 (C. E. Braun unpubl. data) were analyzed to determine if more females per male recruit to leks with larger maximum numbers of males. Research methods in North Park were similar to those used in this study: intensive counts (>8 counts/lek in any year) were made at 21 leks during periods including the peaks of male and female lek attendance. Using these data, the maximum number of attending females per male was not correlated with the maximum number of attending males ($r = -0.16$, $P > 0.5$).

Lek fidelity.—Lek attendance data for 1982 and 1983 did not differ (t-test without data from birds seen both years, $P > 0.1$), so the data were combined (Table 2). Within each age class (yearling or adult), females had a lower attendance rate than males [ANOVA, Duncan's multiple range test (DMRT), $P < 0.05$]. There was no difference between yearling and adult attendance rates for either females or males (ANOVA, DMRT, $P > 0.05$).

Twenty-five marked Sage Grouse (20 males, 5 females) were seen on leks during two or more breeding seasons during 1982–1984. Of these, 3 males (15%) and 2 females (40%) changed leks attended between years. No movements between leks (interlek movements) were known to have been made in 1982, but 14 of 91 (15%) individually identified grouse were seen at more than one lek in spring 1983. Interlek movement rates generally decreased with increasing distance between leks when movement rates were compared between different pairs of leks (Table 3). Yearling females made more interlek movements than adults (22%, 2/9 for yearlings; 7%, 2/28 for adults; G test, $P < 0.01$); however, there was no difference between proportions of yearling and adult males visiting two or more leks (33%, 3/10 for yearlings; 16%, 7/44 for adults; G test, $P > 0.3$).

DISCUSSION

In birds, females generally move greater distances than males between natal areas and initial breeding sites (reviewed by Greenwood 1980). Explanations for the sex bias in dispersal have been based on the type of mating system (Greenwood 1980, Dobson 1982, Moore and Ali 1984) and the promotion of optimal inbreeding (Shields 1982, Bateson 1983). Our results support Greenwood's (1980: 1154) statement that greater male dispersal is not an automatic consequence of polygyny (contrary to the prediction of Dobson 1982); instead, females of a polygynous species will disperse farther than males when males partition resources prior to the selection of mates (resources needed to acquire mates). In Sage Grouse this may mean the establishment of lek territories, or a positional hierarchy, in which males make a high reproductive and energetic investment, while females, without this constraint, may choose a mate among leks and territories within leks. Specific territories or positions within a lek may be a "resource" needed by males to acquire mates, if territories provide females with a means to assess the quality of a male (Emlen and Oring 1977). Females may be traveling

TABLE 3. Interlek movements of Sage Grouse, Cold Spring Mountain, Moffat County, Colorado, March–May 1983.

	Interlek movement					
	Gee Flats to Sugarloaf	Sugarloaf to Gee Flats	Whiskey Draw to Beaver Basin	Gee Flats to Beaver Basin	Sugarloaf to Whiskey Draw	Beaver Basin to Gee Flats
Interlek movements (*n*)	11	7	1	1	1	1
Sum of observation time on both leks (h)	48.3	48.3	35.1	35.1	22.6	9.4
Interlek movements/hour of observation time (in decreasing order)	0.23	0.15	0.11	0.09	0.04	0.03
Distance between leks (km)	7.5	7.5	10.9	13.1	12.2	13.1

among leks to compare potential mates, and this, rather than male philopatry, may be the basis for the dispersal bias.

Superimposed on this defense of a "resource" by males, Greenwood (1980) proposed that males attempting to breed for the first time will establish territories in their natal areas because of familiarity with the locality and other male competitors, and because of a tendency among females to breed with similar, but not *too* similar, males (optimal inbreeding, Shields 1982). These latter aspects of the sex bias in dispersal remain relatively unknown. Juvenile Sage Grouse may become familiar with lek sites and other competitors during fall migration and winter. Three radio-marked juvenile males spent at least 2 weeks near Beaver Basin Lek in early November 1982, and all radio-marked grouse spent at least 2 months in winter 1983 within 5 km of Gee Flats or Sugarloaf Lek.

Although biased by differences in banding effort near each lek, probably over half of all yearling grouse attended their natal-area lek, suggesting that Sage Grouse may be philopatric. The validity of our assumptions about assigning grouse to natal-area leks may influence philopatry estimates and should be investigated further. The philopatry hypothesis will require larger sample sizes for adequate testing; unfortunately, dispersal studies require long-term research to acquire sufficient sample sizes (see Keppie 1979, Jamieson and Zwickel 1983, Zwickel 1983).

After natal dispersal, birds are generally faithful to the initial breeding area in successive years (Greenwood 1980). Few investigators have discussed the establishment of and fidelity to lek territories by Sage Grouse. Studies by Jenni and Hartzler (1978) and Emmons and Braun (1984) examined the effect of variable lek attendance on a commonly used lek censusing technique (Patterson 1952). Wiley (1978) suggested that most females breed in their first year, while yearling males rarely mate, even though they are physiologically mature. Almost all matings are performed by adult males that return during successive years to the same lek and territory within the lek (Wiley 1978). Wiley's findings suggest that adult males may have a greater reproductive investment in their lek territories than yearling males. In this study, neither lek attendance nor percentage of individuals making interlek movements differed significantly between adult and yearling males; however, our sample sizes are small, and the data suggest a trend toward less lek attendance and more interlek movements by yearlings.

The reproductive success of male grouse that occupy territories at or near the mating center may be high (Davies 1978), although maintenance of these territories may be energetically expensive (Beck and Braun 1978). Males that regularly defend territories and progressively move them toward the mating center as opportunities arise may have greater reproductive success than males that are nonterritorial or visit several leks and establish only peripheral territories (Davies 1978). Average male reproductive success may be greatest when yearlings visit several leks to find one suitable for territory establishment and then retain territories on that lek until reaching the mating center as an adult.

The only other study of male Sage Grouse lek attendance (Emmons and Braun 1984) reported rates of 85% for 16 radio-marked yearlings and 92% for 17 radio-marked adults; these rates did not differ statistically. The difference

in lek attendance between studies may be due to Emmons and Braun's determination of lek attendance by triangulation of radio signals, which allowed them to identify grouse hidden in sagebrush near leks. In our study, grouse at the periphery of a lek and in heavy cover may not have been recorded as attending. However, physical presence near a lek does not necessarily mean that a bird held a territory on a lek. Throughout the breeding season and especially after mid-May, grouse were regularly seen sitting within 200 m of the periphery of Gee Flats Lek, but they were not counted as attending the lek because they were not seen displaying.

Yearling males may be moving among leks more frequently than other grouse because they are inexperienced at breeding and may need to investigate several leks before establishing a territory. Other studies also have suggested that yearling males make most interlek movements (Dalke et al. 1960). C. E. Braun and T. D. I. Beck (1976, unpubl. rept., Colorado Div. Wildl. Fed. Aid Proj. W-37-R-29) found 14 of 27 (52%) yearling and 7 of 48 (15%) adult males made interlek movements in North Park, Colorado. Emmons and Braun (1984) reported that male yearlings made more interlek movements than adult males (all 16 radio-marked yearlings visited two or more leks vs. 3 of 11 adults that switched). Studies of other lekking birds support this conclusion (Kruijt and Hogan 1967, Robel et al. 1970, Stiles and Wolf 1979: 57).

The lack of difference in lek attendance between yearling and adult females and the greater percentage of yearling (22%, 2/9) than adult females (7%, 2/28) attending two leks suggest that yearlings spend as much total time on two leks as adults spend on one lek. Yearling attendance and interlek movements may be greater than that of adults if yearlings need to examine several leks prior to mating because of inexperience or if they need to receive behavioral cues for mating by watching older females (Wiley 1978). Because there were no differences between yearling and adult females in lek attendance in this study, or in a study with radio-marked females (Petersen 1980), need for behavioral cues does not appear to lead to a lengthening of lek attendance by yearlings. The percentage of yearling vs. adult females engaging in interlek movements suggests that yearling females may actually be examining more leks than adults prior to mating. Petersen (1980) observed 2 of 14 (14%) yearling and 1 of 11 (9%) adult females attending two leks.

The percentage of all females visiting more than one lek has been used by Bradbury and Gibson (1983: 111–112, models 4, 7) to compare the predictions of two models for the evolution of male clumping in lek species (female preference and hot-spot models). Examined alone, the low percentage of all females visiting several leks in this study (11%, 4/37) would be best predicted by the female preference model, which suggests that most females should visit only one lek prior to mating. However, data on Sage Grouse from North Park, Colorado (C. E. Braun unpubl. data) and California (Bradbury and Gibson 1983) suggest that lek locations are often closer to each other than the average diameter of female home ranges, as predicted by the hot-spot model. Although these observations are not irreconcilable, they do point to a need for more study.

Another hypothesis for the initiation of male clumping on leks suggests that clumping is a means of increasing the range over which males may be heard or the amount of time during which display signals are produced (Bradbury and Gibson 1983: 111, model 2). The results of this study refute that hypothesis, at least for Sage Grouse, because it predicts that numbers of females must increase on a per-male basis with increasing lek size. Lek observations from Cold Spring Mountain and North Park indicate that, on a relative basis, there were not more females on leks with larger numbers of males.

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