INFLUENCE OF VEGETAL MOISTURE CONTENT AND NEST FATE ON TIMING OF FEMALE SAGE GROUSE MIGRATION[1]

RICHARD A. FISCHER[2] AND KERRY P. REESE
Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83843

JOHN W. CONNELLY
Idaho Department of Fish and Game, 1345 Barton Rd., Pocatello, ID 83204

Many North American Tetraoninae exhibit migratory behavior (Hoffman and Braun 1975, Herzog and Keppie 1980, Cade and Hoffman 1993, Schroeder and Braun 1993), either as partial (only some individuals migrate) or differential (age or sex classes differ in timing and/or distance) migrants between seasonal habitats (Terrill and Able 1988). Tetraoninae may migrate because of elevational or seasonal differences in habitat availability and selection, or fidelity to seasonal-use areas (Herzog and Keppie 1980, Schroeder and Braun 1993), and these migrations are typically < 100 km one-way.

Sage Grouse (*Centrocercus urophasianus*) are mainly herbivorous birds that occupy sagebrush (*Artemisia* spp.) dominated habitats of western North American shrub-steppe deserts. Sage Grouse populations are either migratory or nonmigratory, presumably depending on moisture content of vegetation, vegetal cover, elevation, and proximity of seasonal habitats (Dalke et al. 1963, Wallestad 1975, Connelly et al. 1988). Forbs are the major component of adult and juvenile Sage Grouse summer diets, but sagebrush is also used in varying quantities (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994). Sage Grouse most likely obtain the majority of their water from vegetation, because free-standing water is not readily available (Dalke et al. 1963, Klebenow 1982), or when available is only occasionally used (Connelly and Doughty 1989). Sage Grouse inhabit areas having low annual precipitation (approximately 18–50 cm), the amount of which may influence their migratory behavior. Wallestad (1975) reported on nonmigratory populations where annual precipitation was relatively high (35 cm), and where seasonal ranges were contiguous or proximal (i.e., seasonal movements > 16 km were uncommon), allowing most individuals to find required habitats within a relatively small annual range. In contrast, the ecology of migratory populations is more complex because individuals must cope with long-distance movements to suitable seasonal ranges (Dalke et al. 1963, Berry and Eng 1985, Connelly et al. 1988, Wakkinen 1990). Although Sage Grouse do not undertake migrations at a scale similar to some avian species such as Anseriformes (Bellrose 1980), Neotropical migratory Passeriformes (Finch and Stangel 1993), or Charadriiformes (Krementz et al. 1994), their movements still meet most ecological definitions of migration (e.g., Sinclair 1983).

Connelly et al. (1988), Wakkinen (1990), and Robertson (1991) investigated the ecology of a migratory Sage Grouse population inhabiting a xeric environment (≤ 25 cm annual precipitation) in southeastern Idaho. Grouse used contiguous areas for wintering, breeding, and nesting but moved as far as 82 km to summer range at either higher or lower elevations. Grouse return to winter range beginning in late fall (Robertson 1991). Movements to summer range presumably occur because Sage Grouse breeding and nesting ranges lack mesic habitats, such as wet meadows and riparian areas, that provide succulent vegetal foods for birds throughout summer (Autenrieth 1981, Connelly et al. 1988). Although reports of distance moved from breeding to summer ranges are common, little information regarding relationships between timing of these movements and vegetal characteristics or environmental factors are available. Nest fate also may influence the ability of females to initiate migration to summer range because successful females may delay migration (Schroeder and Braun 1993).

Migratory birds may rely on exogenous (environmental) factors (Terrill 1990), endogenous circannual rhythms (Berthold 1990, Gwinner 1990), or a combination of both (Krementz et al. 1994) for migrational timing cues. Sage Grouse appear to initiate migration to summer range at different times within and among years (Connelly et al. 1988), suggesting the cue for migrational timing may be influenced by exogenous factors. However, no empirical data exist to document timing and progression of plant desiccation, how weather variables might influence desiccation, or how migrational timing may be influenced by plant moisture content. We hypothesized that (1) cumulative annual precipitation and temperature influence timing of spring and summer vegetal desiccation, (2) vegetal moisture content would be higher in plants collected at sites used by Sage Grouse than at random sites, and (3) annual timing of Sage Grouse migration is related to vegetal moisture content and nest fate.

TABLE 1. Mean monthly maximum temperatures (°C) for 1959–1989 and 1990–1992, and cumulative precipitation (cm), at site 25 km northwest of the study area, southeastern Idaho (data from Agric. Eng. Dep., Univ. Idaho).

Date	Mean monthly maximum temperatures (°C)				Cumulative precipitation (cm)			
	31-year mean	1990	1991	1992	31-year mean	1990	1991	1992
April	12.9	18.0	13.4	18.7	7.3	6.0	4.4	2.0
May	19.0	19.3	17.3	25.4	10.6	9.2	9.6	2.8
June	24.6	26.1	24.6	27.4	13.7	11.4	12.5	6.5
July	30.4	31.9	32.5	29.2	15.1	12.9	13.9	7.3
August	29.3	30.3	31.9	31.8	16.6	14.7	15.8	7.5

STUDY AREA AND METHODS

We studied Sage Grouse during 1990–1992 on a 20,000-ha portion of the 240,867-ha Big Desert, in Blaine and Butte counties on the Upper Snake River Plain, southeastern Idaho (43°24′N, 113°07′W). Peak precipitation typically occurred from April through June, although there was considerable seasonal and annual variation. Hironaka et al. (1983) classified the Big Desert as a Wyoming big sagebrush (*A. tridentata wyomingensis*)/bluebunch wheatgrass (*Agropyron spicatum*) habitat type. Wakkinen (1990) and Fischer (1994) provide detailed descriptions of the Big Desert study area.

We captured Sage Grouse by spotlighting at night on and near leks during March and April, 1990–1992 (Giesen et al. 1982, Wakkinen et al. 1992). One hundred and sixteen females were captured and fitted with solar or battery-powered, poncho-mounted (Amstrup 1980) transmitters. The transmitter and poncho weighed approximately 20 g, which was ≤ 2% of female body mass.

We intensively monitored females during the nesting season, using a portable scanning receiver and four-element Yagi antenna, to determine whether or not individual females nested (Connelly et al. 1993) and the success of documented nests (Fischer et al. 1993). After the nesting season, we attempted to locate females at least biweekly (April–July), both from the ground and from fixed-wing aircraft. Radio-telemetry data were used to identify timing of Sage Grouse migration to summer range. We considered the nest as point-of-origin of summer migration for nesting hens and lek-of-capture as point-of-origin for non-nesting females or females whose nesting attempts were not identified. Each location was plotted on 7.5-minute topographic maps and recorded as Universal Transverse Mercator grid coordinates. For nesting hens, we calculated Euclidean distance from nest to all subsequent locations after nesting ceased. For all other females, we calculated the Euclidean distance from lek-of-capture to all subsequent locations. We arbitrarily decided that migration was initiated when a bird had moved ≥ 5 km from her respective point-of-origin because the mean (± SE) lek-to-nest distance for Sage Grouse females in the Big Desert was 3.4 ± 0.4 km (range 0.02–20.95 km; $n = 94$), and 76% of females nested within 5 km of lek of capture (Fischer 1994).

To document timing of migration from breeding/nesting habitat during spring and summer, we parti-tioned location data *a priori* into seven two-week intervals, from 15 April to 30 July. At least 32 radio-marked females returned to the study area during consecutive years with functioning transmitters and, of these birds, only those located after 15 June were included in analyses. Although we attempted to locate all birds during each time-interval, this was precluded because birds occupied an area over 4,000 km². We assumed that radio-marked birds on the study area during the eight weeks prior to 15 June, that could not be located after that date, moved from the study area to an unknown summer range. This assumption could potentially bias our results as these females could have died or experienced radio failure. However, we believe that most birds that disappeared did migrate because > 80% of those were unsuccessful nesters (R. A. Fischer, unpubl. data).

If a bird was not located during a time-interval, but was located ≥ 5 km from point-of-origin in a subsequent time-interval, we assumed the bird initiated migration during the interval following the last location in the study area. Within each time-interval, we calculated the cumulative percentage of females that initiated migration. We used an analysis of variance on ranks (Conover and Iman 1981) of intervals (1–7) to examine if female grouse initiated migration at the same time each year.

Monthly precipitation and temperature data were obtained from a National Oceanic and Atmospheric Administration weather station in similar habitat approximately 25 km northwest of the study area. We examined annual cumulative precipitation (by month) to explore possible influences on vegetal desiccation among years as an index of availability of moisture to vegetation. We arbitrarily selected January of each year to begin cumulative annual precipitation. We also examined mean monthly maximum temperatures each year (1 April–31 August) to make qualitative comparisons among years.

During 1990, we conducted a pilot study to examine the feasibility of estimating percentage of moisture in forb and sagebrush plants at bird locations throughout the study area. When a radio-marked bird was located and flushed, we established transects in cardinal directions from the flushing location. For each transect, we clipped all above-ground growth of the forb closest to the plot-center that was known to be consumed by grouse (Klebenow and Gray 1968). We then identified the closest sagebrush shrub on each transect and stripped

TABLE 2. Mean (± SE) percent sagebrush and forb moisture, and percent of female Sage Grouse migrating from the Big Desert study area, southeastern Idaho, 1990–1992.

Date	Percent sagebrush moisture			Percent forb moisture			Percent migrating					
	1990 (n = 23ᵃ)	1991 (n = 107)	1992 (n = 17)	1990 (n = 23)	1991 (n = 108)	1992 (n = 16)	1990 S (11)ᵇ	1990 U (25)	1991 S (11)	1991 U (32)	1992 S (7)	1992 U (25)
15 May	—	—	65.6 ± 1.9	—	—	75.4 ± 1.4	0.0	28.0	9.1	43.8	14.3	16.0
31 May	63.6ᶜ	69.0 ± 1.2	54.0 ± 1.9	71.7ᶜ	77.8 ± 1.6	63.1 ± 4.0	0.0	36.0	9.1	46.9	28.6	40.0
15 June	65.6 ± 1.8	64.1 ± 0.6	54.0 ± 2.9ᵈ	70.0 ± 1.6	73.6 ± 0.8	52.9 ± 2.6ᶜ	0.0	48.0	18.2	53.1	71.4	80.0
30 June	60.3 ± 2.3	60.2 ± 0.6	—	63.2 ± 2.3	69.6 ± 0.5	—	36.4	76.0	27.3	56.3	100	92.0
15 July	51.7 ± 2.8	50.7 ± 0.6	—	46.7 ± 3.1	53.8 ± 1.6	—	90.9	100	54.2	90.6		92.0
31 July	—	54.1 ± 2.1	—	—	51.8 ± 5.3	—			72.7	100		

ᵃ Number of sites sampled.
ᵇ Number of females followed; some females followed for two or more consecutive years. S = successful, U = unsuccessful.
ᶜ Only two sites sampled; SE not reported.
ᵈ Sampling began and ended earlier this year because of extremely dry conditions. By mid-June most above-ground growth of forbs was either dead or dying.

all leaves from 2 branches within reach of an adult Sage Grouse (i.e., ≤ 50 cm from ground). During 1991, we collected forb and sagebrush samples at grouse-use and random sites using the same techniques as in the 1990 pilot study; vegetation often was repeatedly sampled at use-sites during subsequent two-week intervals following flushing at that location. Because < 25% of the radio-marked grouse remained in the study area after 1 June 1992, we collected vegetation only at random sites that year.

Vegetation samples from each transect were stored separately in air-tight plastic bags of known weight and then frozen for 1–6 weeks. In the laboratory, sealed bags were weighed to the nearest 0.01 g. To calculate percent moisture of each plant material, samples were removed and dried (48 hr at 100 °C), and then weighed again. We calculated percent moisture for each sample and pooled data from the four transects at a location.

We calculated the percentage of successful and unsuccessful females that initiated migration and mean percent vegetal moisture content for each time interval (as defined for migration). We used a Spearman rank correlation (Zar 1984) to test the possible relationship between vegetal moisture content and timing of migration (percent of females migrating during each interval).

RESULTS

We collected 1,088 vegetation samples (544 forb, 544 sagebrush) at 59 grouse-use and 38 random sites on the study area; 23 use sites during 1990, 36 use and 20 random sites in 1991, and 18 random sites in 1992. During 1991, moisture content of forbs at use and random sites was similar (Mann-Whitney $U = 9$, $P = 0.89$); sagebrush moisture content was also similar between sites (Mann-Whitney $U = 10$, $P = 0.67$). Higher temperatures and lower precipitation were most apparent during spring 1992 (Table 1), resulting in vegetation desiccation occurring approximately 30 days earlier in the growing season than in 1990 or 1991 (Table 2).

From 1990 to 1992, movement data were collected for 98 female Sage Grouse. Unsuccessful females initiated migration earlier than successful females ($F_{1,97} = 9.59$, $P = 0.003$; Table 2). The percentage of females migrating from the study area was negatively correlated ($r_s = -0.83$, $P < 0.001$) with vegetal moisture content during the 3 years. The majority of birds began migrating from the study area each year during the interval when moisture amounts in vegetation declined to approximately ≤ 60% water.

DISCUSSION

Percent moisture in plants on our study area available to Sage Grouse decreased from approximately 75% in May to < 60% by mid-June to early-July, when we ceased sampling. Moisture content of forbs and sagebrush was similar at grouse-use and random sites, suggesting that vegetal moisture on our study area was homogeneous. As vegetation desiccated, there were likely few sites on the study area where grouse could obtain adequate moisture from vegetation; the study area lacked wet meadows and riparian areas. The only sources of free water in or near the study area were wildlife water developments which were not readily

used by Sage Grouse during summer (Connelly and Doughty 1989). Most radio-marked Sage Grouse moved from the study area each summer to more mesic sites, usually near agricultural fields along traditional migration routes (Wakkinen 1990) or in the foothills of mountains that were interspersed with wet meadows and riparian areas. Grouse were commonly found in and adjacent to cultivated alfalfa. Alfalfa contains a mean of 74.7% moisture during full bloom (NAS-NRC 1958), which is similar to forb moisture on the study area prior to grouse migration.

We failed to reject the hypotheses that timing of Sage Grouse migration was related to vegetal moisture content or nest fate. Timing of both migration and vegetal moisture content varied among years. During drier years (1990 and 1992), grouse tended to initiate migration earlier in the summer. During 1991 (a wet year), ≥ 12% of females remained on the study area at least through late July. Our data indicated that there was a threshold of moisture content that provided a cue for birds to initiate summer migration. During all three years, the largest proportional increase in female migration occurred during the largest decline in vegetal moisture, when moisture amounts in vegetation declined to approximately 60% water. Although there was a strong correlation between moisture in vegetation and the onset of migration, our study design precluded us from ruling out possible endogenous factors. It is unlikely that endogenous factors (e.g., circannual rhythms) would be important migrational cues in such a relatively short-distance migratory bird, especially because of the variability in annual initiation of migration during our study. However, it is conceivable that physiological need for water, a potential endogenous cue, is triggered by an exogenous factor (declining moisture content in foods), that subsequently drives the need for birds to move to more mesic areas.

Schroeder and Braun (1993) found that successful Greater Prairie-chicken (*Tympanuchus cupido*) females migrated to summer range up to four months later than unsuccessful females. Successful female Sage Grouse also moved to summer range later than unsuccessful females, presumably because of brood care. However, during the extremely dry summer of 1992, even successful females initiated migration early in the summer. Although timing of migration varied among years, nest success was similar among years (R. A. Fischer, unpubl. data).

Our study indicates timing of plant desiccation can vary annually with precipitation. In most years, key Sage Grouse foods on our study area probably desiccate or fail to provide adequate moisture required by grouse regardless of spring/summer precipitation in this environment. Our data also indicate that during wet summers (i.e., 1991) fewer grouse moved to summer range. However, 34 years of precipitation data (1956–1989) suggest that there have been few years with precipitation that would have provided succulent vegetal growth throughout the summer sufficient to attenuate migrational behavior.

LITERATURE CITED

AMSTRUP, S. C. 1980. A radio-collar for game birds. J. Wildl. Manage. 44:214–217.

AUTENRIETH, R. E. 1981. Sage Grouse management in Idaho. Idaho Dept. Fish and Game, Boise. Wildl. Bull. 9.

BELLROSE, F. C. 1980. Ducks, geese, and swans of North America. Stackpole Books, Harrisburg, PA.

BERRY, J. D., AND R. L. ENG. 1985. Interseasonal movements and fidelity to seasonal use areas by female Sage Grouse. J. Wildl. Manage. 49:237–240.

BERTHOLD, P. 1990. Genetics of migration, p. 269–280. In E. Gwinner [ed.], Bird migration: physiology and ecophysiology. Springer-Verlag, New York.

CADE, B. S., AND R. W. HOFFMAN. 1993. Differential migration of Blue Grouse in Colorado. Auk 110: 70–77.

CONNELLY, J. W., AND L. A. DOUGHTY. 1989. Sage Grouse use of wildlife water developments in southeastern Idaho, p. 167–173. In G. K. Tsukamoto and S. J. Stiver [eds.], Symposium on wildlife water developments. Nevada Dept. Fish and Game, Reno, NV.

CONNELLY, J. W., R. A. FISCHER, A. D. APA, K. P. REESE, AND W. L. WAKKINEN. 1993. Renesting of Sage Grouse in southeastern Idaho. Condor 95: 1041–1043.

CONNELLY, J. W., H. W. BROWERS, AND R. J. GATES. 1988. Seasonal movements of Sage Grouse in southeastern Idaho. J. Wildl. Manage. 52:116–122.

CONOVER, W. J., AND R. L. IMAN. 1981. Rank transformation as a bridge between parametric and nonparametric statistics. Am. Stat. 35:124–133.

DALKE, P. D., D. B. PYRAH, D. C. STANTON, J. E. CRAWFORD, AND E. F. SCHLATTERER. 1963. Ecology, productivity, and management of Sage Grouse in Idaho. J. Wildl. Manage. 27:810–841.

DRUT, M. S., W. H. PYLE, AND J. A. CRAWFORD. 1994. Technical note: diets and food selection of Sage Grouse chicks in Oregon. J. Range Manage. 47: 90–93.

FINCH, D. M., AND P. W. STANGEL [EDS.]. 1993. Status and management of Neotropical migratory birds. U.S. Dept. Agric. For. Serv., Gen. Tech. Rep. RM-229.

FISCHER, R. A. 1994. The effects of prescribed fire on the ecology of migratory Sage Grouse in south-

eastern Idaho. Ph.D. diss., Univ. Idaho, Moscow, ID.

FISCHER, R. A., A. D. APA, W. L. WAKKINEN, K. P. REESE, AND J. W. CONNELLY. 1993. Nesting-area fidelity of Sage Grouse in southeastern Idaho. Condor 95:1038–1041.

GIESEN, K. M., T. J. SCHOENBERG, AND C. E. BRAUN. 1982. Methods for trapping Sage Grouse in Colorado. Wildl. Soc. Bull. 10:224–231.

GWINNER, E. 1990. Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod, p. 257–268. In E. Gwinner [ed.], Bird migration: physiology and ecophysiology. Springer-Verlag, New York.

HERZOG, P. W., AND D. M. KEPPIE. 1980. Migration in a local population of Spruce Grouse. Condor 82:366–372.

HIRONAKA, M., M. A. FOSBERG, AND A. H. WINWARD. 1983. Sagebrush-grass habitat types in southern Idaho. Univ. Idaho For., Wildl., Range Exp. Sta. Bull. 35, Moscow, ID.

HOFFMAN, R. W., AND C. E. BRAUN. 1975. Migration of a wintering population of White-tailed Ptarmigan in Colorado. J. Wildl. Manage. 39:485–490.

KLEBENOW, D. A. 1982. Livestock grazing interactions with Sage Grouse, p. 113–123. In J. M. Peek and P. D. Dalke [eds.], Wildlife-livestock relationships symposium. Univ. Idaho For., Wildl., Range Exp. Sta., Moscow, ID.

KLEBENOW, D. A., AND G. M. GRAY. 1968. Food habits of juvenile Sage Grouse. J. Range Manage. 21:80–83.

KREMENTZ, D. G., J. T. SEGINAK, AND G. W. PENDLETON. 1994. Winter movements and spring migration of American Woodcock along the Atlantic coast. Wilson Bull. 106:482–493.

NATIONAL ACADEMY OF SCIENCES—NATIONAL RESEARCH COUNCIL. 1958. Composition of cereal grains and forages. Publ. 585, Washington, DC.

PETERSON, J. G. 1970. The food habits and summer distribution of juvenile Sage Grouse in central Montana. J. Wildl. Manage. 34:147–155.

ROBERTSON, M. D. 1991. Winter ecology of migratory Sage Grouse and associated effects of prescribed fire in southeastern Idaho. M.Sc. thesis, Univ. Idaho, Moscow, ID.

SCHROEDER, M. A., AND C. E. BRAUN. 1993. Partial migration in a population of Greater Prairie-chickens in northeastern Colorado. Auk 110:21–28.

SINCLAIR, A. R. E. 1983. The function of distance movements in vertebrates, p. 240–258. In I. R. Swingland and P. J. Greenwood [eds.], The ecology of animal movements. Clarendon Press, Oxford.

TERRILL, S. B. 1990. Food availability, migratory behavior, and population dynamics of terrestrial birds during the nonreproductive season. Stud. Avian Biol. 13:438–443.

TERRILL, S. B., AND K. P. ABLE. 1988. Bird migration terminology. Auk 105:205–206.

WAKKINEN, W. L. 1990. Nest site characteristics and spring-summer movements of migratory Sage Grouse in southeastern Idaho. M.Sc. thesis, Univ. Idaho, Moscow, ID.

WAKKINEN, W. L., K. P. REESE, J. W. CONNELLY, AND R. A. FISCHER. 1992. An improved spotlighting technique for capturing Sage Grouse. Wildl. Soc. Bull. 20:425–426.

WALLESTAD, R. O. 1975. Life history and habitat requirements of Sage Grouse in central Montana. Montana Dept. Fish and Game, Game Manage. Div., Helena.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.