

# Movements and Survival of Juvenile Greater Sage-Grouse in Southeastern Idaho

JEFFREY L. BECK,<sup>1,2</sup> Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844, USA

KERRY P. REESE, Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844, USA

JOHN W. CONNELLY, Idaho Department of Fish and Game, Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA

MATTHEW B. LUCIA,<sup>3</sup> Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844, USA

## Abstract

Low recruitment has been suggested as a primary factor contributing to declines in greater sage-grouse (*Centrocercus urophasianus*) populations. We evaluated movements and survival of 58 radiomarked juvenile greater sage-grouse from 1 September ( $\geq 10$  weeks of age) to 29 March ( $\geq 40$  weeks of age) during 1997–1998 and 1998–1999 in lowland and mountain valley study areas in southeastern Idaho, USA. Juvenile sage-grouse captured in the mountain valley area moved an average of 2.2 km (20%) farther ( $\bar{x} = 13.0$  km,  $SE = 1.2$  km) from autumn to winter ranges than juvenile grouse captured in the lowland area ( $\bar{x} = 10.8$  km,  $SE = 1.2$  km). Ten of 11 deaths occurred from September to December. Fifty percent of deaths in the lowland population were attributable to human-related mortality including power-line collisions and legal harvest, while 33% and 17% of deaths were attributable to mammalian predators and unknown cause, respectively. All deaths in the mountain valley population were attributed to avian or mammalian predators. Survival was relatively high for birds from both populations, but was higher across years in the lowland ( $\hat{S} = 0.86$ ,  $SE = 0.06$ ,  $n = 43$ ) than in the mountain valley population ( $\hat{S} = 0.64$ ,  $SE = 0.13$ ,  $n = 14$ ). In our study juvenile sage-grouse that moved farther distances to seasonal ranges experienced lower survival than juveniles from a more sedentary population. Moreover, high juvenile survival in our study suggests that if low recruitment occurs in sage-grouse populations it may be due to other factors, especially poor nesting success or low early chick survival. (WILDLIFE SOCIETY BULLETIN 34(4):1070–1078; 2006)

## Key words

*Centrocercus urophasianus*, greater sage-grouse, Idaho, juvenile survival, power-line collisions, predation, seasonal movements.

Greater sage-grouse (*Centrocercus urophasianus*) historically occupied sagebrush (*Artemisia* spp.) rangelands in at least 13 states and 3 Canadian provinces and now occur in 11 states and 2 provinces (Schroeder et al. 2004). Range-wide, populations declined 3.5% per year from 1965 to 1985, and 0.4% per year from 1986 to 2003 (Connelly et al. 2004). These declines are attributed to loss, degradation, and fragmentation of sagebrush–steppe habitat resulting from long-term impacts, including agricultural expansion (Swenson et al. 1987), drought (Connelly and Braun 1997), fire (Connelly et al. 2000b, 2004), invasive species (Connelly et al. 2004), and livestock-related activities (Beck and Mitchell 2000, Crawford et al. 2004). Continuing changes to sage-grouse habitats include communication towers, mining and energy developments, roads, power lines, fences, reservoirs, and urbanization (Braun 1987, 1998, Connelly et al. 2004). These changes have affected brood-rearing habitats, potentially driving population declines through low survival of juveniles (Connelly and Braun 1997, Beck et al. 2003, Crawford et al. 2004).

Estimates of sage-grouse chick (0–10 weeks of age) and juvenile (10–40 weeks of age) survival are limited and have

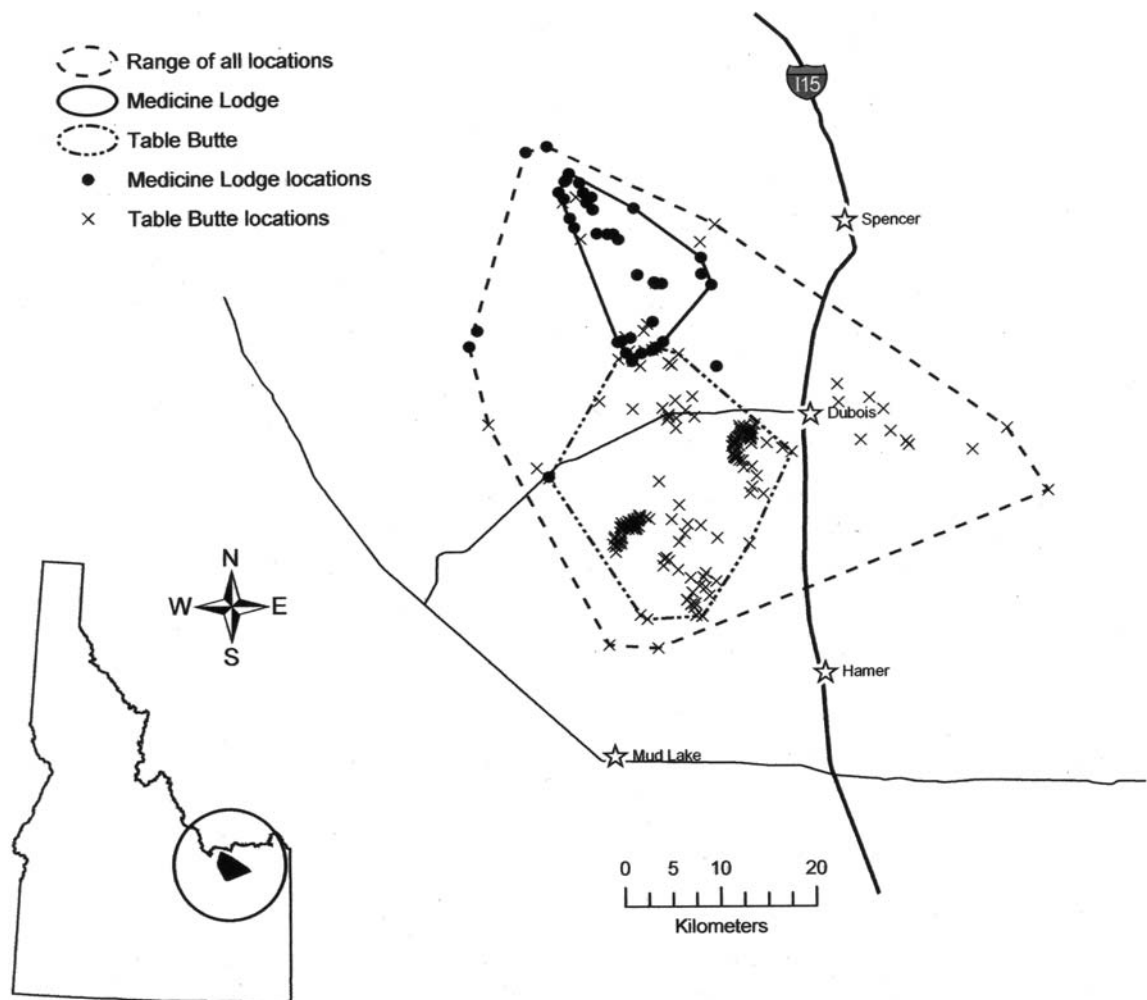
not been based on standardized time periods, thus making comparisons difficult. Crawford et al. (2004) averaged partial estimates from 3 studies to compute a mean survival rate of 10% for juvenile sage-grouse from hatching to the first potential breeding season. Survival of juveniles from hatching to autumn was 38% in Wyoming, USA (June 1963). Chick survival between hatching date and 50 days after hatching (7 weeks of age) was estimated to be 33% in Washington, USA (Schroeder 1997) and 18% in Alberta, Canada (Aldridge and Brigham 2001). In contrast, survival rates for chicks from all North American grouse species range from 50% to 60% from hatching to autumn (Bergerud 1988).

Sage-grouse populations inhabiting mountain valley and lowland habitats experience differences in topography and precipitation (Connelly et al. 1988, 2003a), and these differences may correspond to greater distances moved between seasonal ranges for certain age and sex classes (Connelly et al. 1988). For example, in southeastern Idaho, USA, movements of male sage-grouse from a mountain valley population from winter to summer range were greater than for females from the mountain valley population or females or males from lowland populations (Connelly et al. 1988). In addition, risk of predation may increase as offspring move away from natal areas (Larsen and Boutin 1994). Therefore, we hypothesized that juvenile sage-grouse moving further distances from summer brood-rearing areas

<sup>1</sup> E-mail: jl\_beck@yahoo.com

<sup>2</sup> Present address: Colorado Division of Wildlife, Grand Junction, CO 81505, USA

<sup>3</sup> Present address: Teton Regional Land Trust, Driggs, ID 83422, USA



**Figure 1.** Juvenile greater sage-grouse study areas and range of all locations, southeastern Idaho, USA, 1997–1999. Medicine Lodge and Table Butte study area boundaries based on minimum convex polygons placed around 88% and 90% of juvenile sage-grouse locations, respectively, in these areas from 1 Sep–29 Mar, 1997–1998 and 1998–1999. Range of all locations was delineated with a 100% minimum convex polygon around all juvenile sage-grouse locations from 1 Sep–29 Mar, 1997–1998 and 1998–1999.

to winter ranges may experience higher mortality than those juveniles remaining closer to brood-rearing areas in winter. To address these questions, we investigated movements and survival rates of juvenile sage-grouse occupying mountain valley and lowland habitats (Connelly et al. 1988, 2003a) to better understand survival of different age classes of greater sage-grouse in southeastern Idaho.

We defined juveniles as birds from 10 weeks of age until entering their first breeding season in March (approx. 40 weeks of age). We based our definition on the fact that young males outweigh young and adult females by 10–12 weeks after hatching and weights of young female and adult female sage-grouse are nearly equal by October (Patterson 1952, Dalke et al. 1963). Our objectives were to 1) assess space use and seasonal movements of juvenile greater sage-grouse in mountain valley and lowland populations, 2) document mortality patterns for juvenile greater sage-grouse in mountain valley and lowland populations, 3) estimate survival rates of juvenile greater sage-grouse in mountain valley and lowland populations, and 4) evaluate relationships

between seasonal movements and survival rates of juvenile sage-grouse.

### Study Areas

Medicine Lodge, the mountain valley study area (Fig. 1), consisted of 157 km<sup>2</sup> in Clark County, Idaho (44°18'N, 112°27'W). Approximately 50% of the area was privately owned, 46% was managed by the Bureau of Land Management, and 4% by the state of Idaho. Elevations range from 1,664 to 2,282 m above mean sea level with topography of moderate to high relief. Main topographical features include creek drainages, basalt outcroppings, mountain ridges, and peaks. Livestock ponds, wet meadows, springs, seeps, and creeks were common. Vegetation was dominated by mountain big sagebrush (*Artemisia tridentata vaseyana*) at higher elevations in the north, xeric sagebrush composed of Wyoming big sagebrush (*A. t. wyomingensis*) and basin big sagebrush (*A. t. tridentata*) on deeper soils in the south, and little sagebrush (*A. arbuscula*) on ridgetops with underlying shallow soils throughout Medicine Lodge. Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus*

**Table 1.** Area and patch metrics for cover types important to greater sage-grouse, Medicine Lodge and Table Butte, southeastern Idaho, USA, 1997–1999.

Location	Patch metric			
	Area (%)	Mean area (km <sup>2</sup> )	Density (No./km <sup>2</sup> )	Perimeter: area ratio
Medicine Lodge				
Agriculture	6	1.78	3	100
Grassland	1	0.05	22	448
Little sagebrush	15	0.18	84	418
Mountain big sagebrush	33	0.92	36	424
Xeric big sagebrush <sup>a</sup>	43	1.28	34	476
Total (%)	98 <sup>b</sup>			
Table Butte				
Agriculture	28	14.05	2	58
Grassland	23	0.39	6	378
Xeric big sagebrush <sup>a</sup>	48	1.81	27	448
Total (%)	99 <sup>c</sup>			

<sup>a</sup> Basin and Wyoming big sagebrush as well as threetip sagebrush in Table Butte.

<sup>b</sup> Remaining cover (2%) composed of forest, riparian, and other shrubs.

<sup>c</sup> Remaining cover (1%) composed of low-intensity urban, riparian, and other shrubs.

*contorta*) stands occurred at higher elevations (Table 1). Portions of the area were previously strip-sprayed to remove sagebrush and planted with crested wheatgrass (*Agropyron cristatum*). Predominant land use was livestock grazing.

Table Butte, the lowland study area (Fig. 1), consisted of 451 km<sup>2</sup> in Clark (77%) and Jefferson (23%) counties, Idaho (44°06'N, 112°24'W). These lands were owned and managed by the Bureau of Land Management (57%), private landowners (39%), and the state of Idaho (4%). Elevations range from 1,463 to 1,812 m, and topography is of low relief with outcrops of basalt scattered throughout the landscape. Free water was scarce. The surrounding private land was predominately crop agriculture dominated by alfalfa and potato production. A xeric sagebrush community composed of Wyoming big sagebrush, basin big sagebrush, and some threetip sagebrush (*A. tripartita*) covered most of the unfragmented rangelands (Table 1). A portion of the area burned in the early 1990s and was dominated by seeded crested wheatgrass. Conservation Reserve Program lands bordered alfalfa fields in the northeastern portion of Table Butte. Livestock grazing and cropland agriculture were the dominant land uses.

The climate of both study areas was continental, characterized by cold winters and hot summers. We obtained climatic data from a weather station at the United States Sheep Experiment Station in Dubois, Idaho (1,664 m; 44°15'N, 112°12'W; Fig. 1; Western Regional Climate Center 2005). Average monthly temperatures from September to March were 1.3°C in 1997–1998 and 1998–1999, similar to the 30-year (1971–2000) average of 0.1°C. September–March cumulative precipitation was 13 cm during 1997–1998 and 14 cm during 1997–1998, slightly drier than the 16-cm, 30-year average.

Coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), common

ravens (*Corvus corvax*), golden eagles (*Aquila chrysaetos*), soaring hawks (*Buteo* spp.), and weasels (*Mustela* spp.) were common predators of sage-grouse in both study areas and are recognized as primary predators of sage-grouse elsewhere (Schroeder and Baydack 2001). There was much less cropland, no low-lying power lines, and relatively few pasture fences in Medicine Lodge compared to Table Butte. Grouse in Table Butte were more likely to be exposed to agricultural hazards such as agrochemicals (Blus et al. 1989), farm machinery, fences, power lines, and vehicles, as well as domestic dogs and cats.

## Methods

### Capturing and Marking

We captured and radiomarked 11 yearling and 14 adult female greater sage-grouse in March and April on 7 leks in and adjacent to both study areas to facilitate capturing of juveniles during summers 1997 and 1998. Females breeding on these leks commingled, but separated following nesting to rear broods. We captured and marked juveniles from the first week of August through the first week of October, but we did not capture during full moons or the 1-week mid-September hunting season. While capturing and handling birds, we followed animal welfare protocols of Gaunt and Oring (1997) and the University of Idaho Animal Care and Use Committee (protocol No. 5039).

We used a spotlighting technique (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003b) to trap sage-grouse. We used roosting locations of radiomarked yearling and adult females as well as observations of sage-grouse broods in evening hours to locate juveniles during the trapping period. We restrained all captured grouse in burlap sacks to reduce stress. To reduce hen-brood separation, we held all captured birds in partitioned cardboard boxes or burlap sacks and released birds together at the point of capture.

We assigned captured sage-grouse to age and gender categories based on mass (Dalke et al. 1963), plumage characteristics (Bihle 1993), and length of primary feathers (Beck et al. 1975, Idaho Department of Fish and Game 1989). We weighed each juvenile and, depending on mass, fitted individuals with 15- or 18-g necklace-mounted, battery-powered radiotransmitters with built-in mortality sensors (Advanced Telemetry Systems, Inc., Isanti, Minnesota) and an Idaho Department of Fish and Game numbered aluminum leg band. Radiotransmitters were ≤3% of the body mass of each juvenile grouse.

### Monitoring

We located radiomarked grouse by radiotelemetry and visual observations of the birds or by circling the estimated location indicated by the loudest signal strength (Springer 1979). We also made relocations from a fixed-wing aircraft twice each year to find marked birds that could not be located from the ground. Birds that were found during aerial flights were also relocated by ground searches. We recorded the Universal Transverse Mercator (UTM) coordinates (datum, NAD27; projection, UTM Zone 12) at each

location with a Global Positioning System unit or by examining United States Geological Survey 7.5-minute topographical maps. We documented fate (alive or dead) for each bird based on pulse signals. When pulse signals indicated mortality, we collected forensic evidence to identify cause of death (Thirgood et al. 1998).

### **Space Use and Movements**

We conducted home-range analyses in ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California, 1992–2002) to delineate study area boundaries. We assigned juvenile sage-grouse to study areas based on their location at the time of capture and grouped all locations following capture into respective study areas. We used the Home Range extension for ArcView (Rodgers and Carr 2002) to select 90% of all sage-grouse diurnal locations from 1 September to 29 March, 1997–1998 and 1998–1999 in each study area with the harmonic mean method (Dixon and Chapman 1980) and then placed a minimum convex polygon (Mohr 1947) around those locations using the Animal Movements Program extension for ArcView (Hooge and Eichenlaub 1997). We used a 100% minimum convex polygon to delineate the area all grouse used from 1 September to 29 March, 1997–1998 and 1998–1999.

We clipped 30-m-resolution vegetation coverage grids from Idaho Gap Analysis Program (Scott et al. 2002) to the 90% minimum convex polygon for each study area. We reclassified the vegetation in each study area as agriculture, forest, grassland, low-intensity urban, little sagebrush, mountain big sagebrush, riparian, other shrubs, and xeric big sagebrush (basin and Wyoming) cover types. The subsets of cover types we selected were important for sage-grouse relative to space use in the study areas. We used Frag Stats 3.3 (McGarigal and Marks 1995) to evaluate fragmentation metrics at the cover-type scale, including patch density, mean patch area, and perimeter-to-area ratio of patches for agriculture, grassland, little sagebrush, mountain big sagebrush, and xeric big sagebrush.

We designated seasons as summer (Jun–Aug), autumn (Sep–Nov), winter (Dec–Feb), and spring (Mar–May; Leonard et al. 2000). We did not include capture locations or locations where dead grouse were located in our movement analyses and only considered birds with at least 2 locations in each season. To evaluate movement distances, we used ArcView 3.3 to create polygons around locations for birds with  $\geq 3$  seasonal locations, or lines joining locations for birds with 2 seasonal locations in autumn or winter and then computed centroids for each polygon or line to represent the average of seasonal locations for each grouse. We computed linear distances (km) grouse moved between autumn and winter ranges with UTM coordinates for each seasonal centroid. We located Medicine Lodge birds monitored for movement distances an average of 3.2 times on autumn ranges (range = 3–4) and twice each on winter ranges. We located Table Butte birds an average of 7.5 times on autumn ranges (range = 3–12) and 2.7 times on winter ranges (range = 2–4).

We used analysis of variance (ANOVA) to model 6

alternative hypotheses related to grouse movements from autumn to winter ranges (Proc GLM; SAS Institute 2001). Explanatory variables supporting our hypotheses included gender, year, study area, and the gender  $\times$  year interaction. Prior to modeling, we assessed normality and equal variance in the seasonal-movement response data with appropriate plots and found these data met the assumptions of ANOVA (Proc UNIVARIATE and Proc GLM; SAS Institute 2001).

We evaluated the strength of evidence for each ANOVA model with Akaike's Information Criterion for small samples ( $AIC_c$ ; Hurvich and Tsai 1989). We computed maximized log-likelihood values for each model as

$$\log_e [L(\hat{\theta})] = -\frac{n}{2} \log_e (\hat{\sigma}^2)$$

where  $\hat{\sigma}^2$  is the sum of the squared residuals/ $n$  (Burnham and Anderson 2002:63). Differences between  $AIC_c$  for each model and the best model ( $\Delta AIC_c$ ) provided a ranking of our models, and Akaike weights ( $w_i$ ) allowed us to assess the weight of evidence in favor of each model. We ranked the relative importance of variables using methods described by Burnham and Anderson (2002:167–169).

### **Survival**

We evaluated juvenile sage-grouse survival for the 30-week period extending from 1 September to 29 March in 1997–1998 and 1998–1999. On average, we monitored grouse from the Table Butte study area 6.3 times (range = 1–15) and grouse from the Medicine Lodge study area 3.5 times (range = 1–7) during the 30-week period over each year. We censored grouse (Hosmer and Lemeshow 1999) if their radiotransmitters were lost or quit functioning and we right-censored them if they survived past 29 March. Each year survival of right-censored birds was confirmed with aerial flights conducted shortly after 29 March.

We evaluated survival by year (1997 and 1998), gender (male and female), and study area. We estimated survival with the Kaplan–Meier product-limit estimator (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989). We computed the variance for survival estimates following Greenwood (1926) and compared survival rates between groups with a log-rank test (Cox and Oakes 1984:105).

## **Results**

### **Capturing and Marking**

We captured and radiomarked 58 juveniles during 1997 and 1998. Twenty-six juveniles were radiomarked in 1997 (14 M and 12 F) and 32 (16 M and 16 F) in 1998. Of the radiomarked juveniles, we captured 15 (26%) in Medicine Lodge (3 in 1997 and 12 in 1998) and captured 43 (74%) in Table Butte (23 in 1997 and 20 in 1998).

### **Space Use and Movements**

Xeric big sagebrush was the dominant cover type in each study area (Table 1). Patches of agricultural cover were nearly 8 times larger on average in Table Butte than in Medicine Lodge (Table 1). Patch density was highest for

**Table 2.** Summary of model fit statistics from ANOVA modeling to select the best approximating model explaining autumn to winter movements (km) of 24 greater sage-grouse (Medicine Lodge,  $n = 5$ ; Table Butte,  $n = 19$ ) in southeastern Idaho, USA, 1997–1998. Models are listed according to the model that best fit the data and ranked by  $\Delta AIC_c$ , the difference between the model with the lowest Akaike's Information Criterion for small samples ( $AIC_c$ ) and the  $AIC_c$  for the current model. The number of parameters ( $K$ ), estimated residual variance ( $\hat{\sigma}^2$ ), value of the maximized log-likelihood function ( $\log(L)$ ), and Akaike weights ( $w_i$ ) for each model are also presented.

Model	$K^a$	$\hat{\sigma}^{2b}$	$\log(L)^c$	$\Delta AIC_c$	$w_i$
Null <sup>d</sup>	2	21.05	-36.56	0.000	0.378
Gender	3	19.13	-35.42	0.337	0.320
Study area	3	20.26	-36.11	1.715	0.161
Year	3	21.04	-36.55	2.611	0.103
Gender + Year					
+ Gender $\times$ Year	5	18.08	-34.74	5.111	0.029
Global <sup>e</sup>	6	17.11	-34.08	7.400	0.009

<sup>a</sup> Estimable parameters include the intercept and estimated residual variance  $\hat{\sigma}^2$ .

<sup>b</sup>  $\hat{\sigma}^2$  = residual sum of squares/ $n$ .

<sup>c</sup>  $\log(L) = -n/2 \times \log_e(\hat{\sigma}^2)$ .

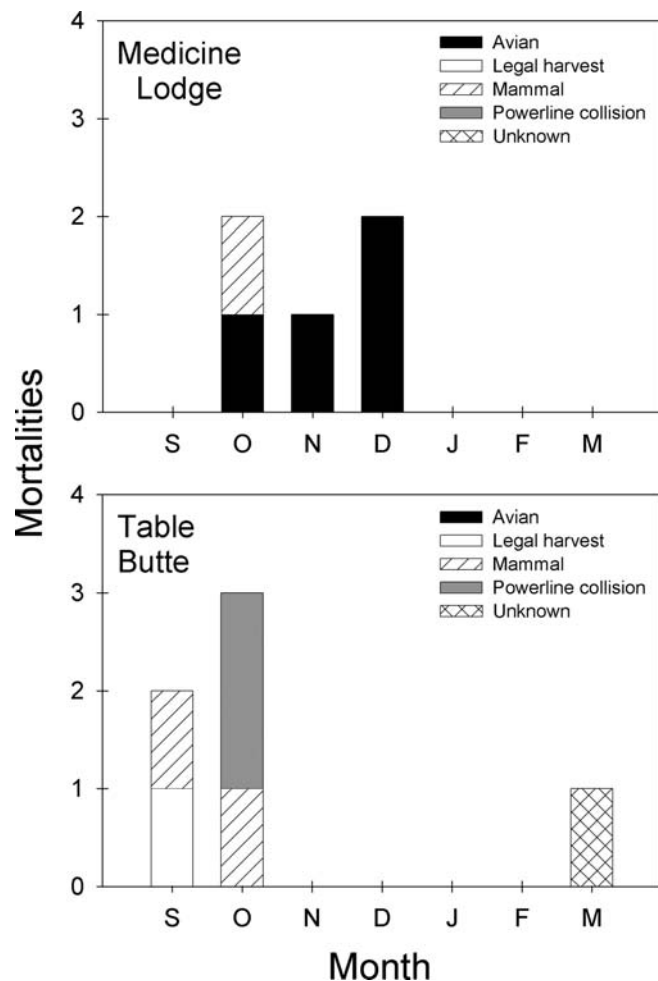
<sup>d</sup> The null model is the model without explanatory variables.

<sup>e</sup> Global model = Gender + Study Area + Year + Gender  $\times$  Year.

little sagebrush in Medicine Lodge and for xeric sagebrush in Table Butte. Xeric big sagebrush provided patches of cover with more complex or elongated boundary shapes than other cover types in both study areas based on largest perimeter-to-area ratios (Table 1).

We delineated a 100% minimum convex polygon for the area used by all sage-grouse from 1 September to 31 March, 1997–1998 and 1998–1999, based on 317 diurnal locations of grouse following capture and located through aerial and ground monitoring (Fig. 1). Of these locations 50 were from 13 birds in Medicine Lodge and 267 were from 40 birds in Table Butte. We delineated the Medicine Lodge study area boundaries from 44 of 50 locations (88%) from 13 birds (Fig. 1). This delineation reflects removal of 1 outlier location for a male that made a long-distance movement between 17 November and 11 December 1998 only to return within 6 days (17 Dec) to associate with 3 other radiomarked grouse and remain on winter range. We delineated the Table Butte study area with 241 of 267 locations (90%) from 40 birds (Fig. 1). Movement analyses were based on 234 locations in autumn and 74 locations in winter, which corresponds to 97% of all locations from August to March. Three grouse captured in Table Butte (2 F and 1 M) crossed Interstate 15 to access habitat in Fremont and eastern Clark counties. We located these birds at 11 times (4% of all Table Butte locations) from 1 November to 22 December in 1997 and 1998 (Fig. 1).

We modeled distances moved from autumn to winter ranges for 5 grouse (2 F and 3 M) captured in Medicine Lodge and 19 grouse (9 F and 10 M) captured in Table Butte. The best-supported models explaining juvenile sage-grouse movements from autumn to winter ranges were the gender, null, and study area models (Table 2). Relative importance of explanatory variables supporting our seasonal movement model was gender (0.358), study area (0.170), and year (0.141). While on average juvenile males ( $\bar{x} = 12.6$



**Figure 2.** Mortality by cause and month for juvenile greater sage-grouse, Medicine Lodge and Table Butte, southeastern Idaho, USA. Mortalities are monthly totals from Sep–Mar, 1997–1998 and 1998–1999.

km, SE = 1.1,  $n = 13$ ) moved 2.8 km farther from autumn ranges to winter ranges than juvenile females ( $\bar{x} = 9.8$  km, SE = 1.6,  $n = 11$ ), ranges in distances of male and female movements from autumn to winter ranges were 3.3–19.4 km and 2.3–18.9 km, respectively. Juvenile sage-grouse captured in Medicine Lodge moved an average of 2.2 km farther ( $\bar{x} = 13.0$  km, SE = 1.2,  $n = 5$ ) from autumn to winter ranges than juvenile grouse captured in Table Butte ( $\bar{x} = 10.8$  km, SE = 1.2,  $n = 19$ ). The difference in movement distances between study areas is meaningful even though ranges of movements at the 2 study areas overlapped. Movement distances of birds at Medicine Lodge ranged from 9.2 to 16.7 km and at Table Butte ranged from 2.3 to 19.4 km, but 32% (6/19) of movements of Table Butte birds were less than the minimum movement distance of birds at Medicine Lodge. Movement distances from autumn to winter ranges were similar between 1997 ( $\bar{x} = 11.3$  km, SE = 1.1,  $n = 19$ ) and 1998 ( $\bar{x} = 11.0$  km, SE = 2.4,  $n = 5$ ).

### Mortality and Survival

One female from Medicine Lodge died within 1 day of capture in 1997; following a necropsy, we determined this

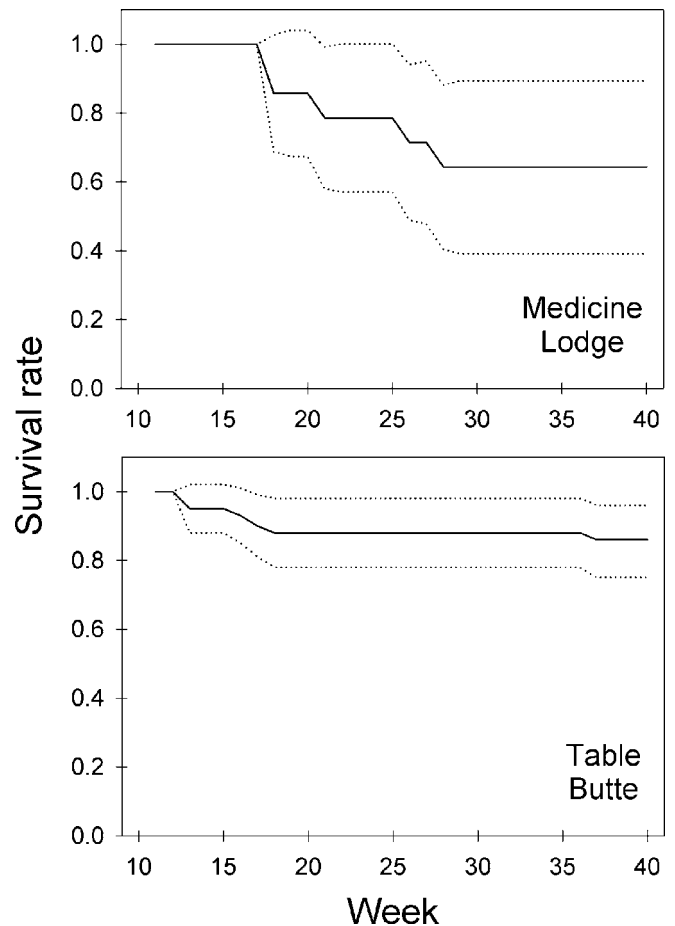
bird died from capture-related stress and was thus not considered in survival analyses. One male captured in Table Butte in 1998 lost his radiocollar 6 weeks after he entered the study on 1 September and was censored. Of the remaining 56 birds, 11 (20%) died from 1 September to 31 March, 1997–1998 and 1998–1999 (Fig. 2). The remaining 45 birds (Medicine Lodge = 9; Table Butte = 36) survived and became subadult sage-grouse. Mortality by study area was 5 of 14 (36%) in Medicine Lodge and 6 of 43 (14%) in Table Butte. Two deaths occurred in September (18%), 5 in October (46%), 1 in November (9%), 2 in December (18%), and 1 in March (9%; Fig. 2). All mortalities in Medicine Lodge were attributed to natural predators (avian = 80%; mammal = 20%), while mortality associated with human activities (legal harvest = 17%; power-line collisions = 33%) accounted for 50% of mortalities in Table Butte. All mortalities associated with human activities in Table Butte occurred during September and October (Fig. 2). The remaining deaths in Table Butte were attributable to mammalian predation (33%) and unknown cause (17%; Fig. 2). Of total mortalities avian predation was the cause of death for 36% of grouse, followed by mammal predation (27%), power-line collisions (18%), legal harvest (9%), and unknown cause (9%; Fig. 2).

We did not have a sufficient sample of birds to test for differences in survival between years at Medicine Lodge. However, we found no difference in survival between years at Table Butte ( $\chi^2_1 = 0.03$ ,  $P = 0.862$ ); we used this evidence to pool data within study areas across years. We found no difference ( $\chi^2_1 = 0.15$ ,  $P = 0.699$ ) in survival between female ( $\hat{S} = 0.78$ ,  $SE = 0.08$ ,  $n = 27$ ) and male ( $\hat{S} = 0.82$ ,  $SE = 0.07$ ,  $n = 30$ ) juvenile sage-grouse. Survival was lower ( $\chi^2_1 = 3.12$ ,  $P = 0.077$ ) at Medicine Lodge ( $\hat{S} = 0.64$ ,  $SE = 0.13$ ,  $n = 14$ ) than at Table Butte ( $\hat{S} = 0.86$ ,  $SE = 0.06$ ,  $n = 43$ ; Fig. 3).

## Discussion

Once young sage-grouse reached 10 weeks of age, they experienced low to moderate mortality (14–36%) through March. Mortality in both study areas was concentrated in autumn with only 3 deaths occurring from December to March. Our estimates of juvenile sage-grouse survival are higher than estimates of survival for chicks from hatching to 7 weeks (Schroeder 1997, Aldridge and Brigham 2001), hatching through autumn (June 1963), and hatching until birds enter the breeding season (Crawford et al. 2004). A comparison of our results with previous estimates suggests high mortality of sage-grouse chicks (0–10 weeks of age) may have most influenced previous estimates of juvenile survival.

Population viability analysis for sage-grouse in North Park, Colorado, incorporating sensitivity and elasticity analyses of vital rates, indicated that adult and juvenile survival followed by adult and juvenile fecundity most limited population growth (Johnson and Braun 1999). Poor recruitment in prairie grouse may reflect low juvenile survival rates or reproductive potential (clutch size, nest



**Figure 3.** Kaplan-Meier product-limit survival curves with 95% confidence limits (dashed lines) for juvenile greater sage-grouse in Medicine Lodge and Table Butte, southeastern Idaho, USA. Survival rates are from 1 Sep (week 10) to 29 Mar (week 40), 1997–1998 and 1998–1999.

success, nest initiation rates, and reneating rates) for adult females.

Clutch sizes for sage-grouse average 6.6–9.1 eggs (Schroeder et al. 1999), reflecting a relationship between low adult mortality rates and low clutch size among North American grouse (Bergerud 1988). Average nest success (nests hatching  $\geq 1$  egg) for sage-grouse ranges from 15% to 86% (Schroeder et al. 1999). In southeastern Idaho percentage of females known to initiate nesting was 55% for yearlings and 78% for adults, nest success between age classes averaged 52%, and reneating rate for unsuccessful first nesters was 15% (Connelly et al. 1993). Reneating rates in areas with smaller populations were 36% in Alberta (Aldridge and Brigham 2001), and 82% for yearling females and 88% for adult females in Washington (Schroeder 1997). Likelihood of nest initiation averaged 80% (range = 63–100%) from 11 studies in Alberta, Canada; and Colorado, Idaho, Montana, Oregon, Utah, Washington, and Wyoming, USA, while likelihood of reneating averaged 29% (range = 9–87%) from 9 studies in Alberta, Colorado, Idaho, Oregon, and Washington (Connelly et al. 2004). These findings suggest reproductive success among female

sage-grouse is highly variable. Thus, nesting success or survival of chick sage-grouse may be the factors most limiting recruitment in sage-grouse populations and needs further study because it is clear that losses in productivity occur from nest initiation to 10 weeks of age. We did not investigate nest success or survival of chicks; therefore, we do not know whether recruitment was higher or lower for sage-grouse inhabiting the 2 study areas.

Adult sage-grouse have low overwinter natural mortality, with most mortality occurring in spring and summer (Connelly et al. 2000a). We likewise found low overwinter mortality of juvenile sage-grouse. Therefore, specific causes of mortality during spring and summer potentially could be influencing population declines of sage-grouse. Identification of these factors may provide managers with information to develop recommendations and strategies for increasing numbers of sage-grouse.

Exposure to wet and cold weather after hatching can limit survival of sage-grouse chicks (Patterson 1952), linking yearly survival to annual climate cycles. Predation, including that on nests, juveniles, and adults is the largest direct cause of prairie grouse mortality (Schroeder and Baydack 2001). Other factors responsible for juvenile mortality include accidents, hunting, disease, and parasites. Half of the deaths in the lowland population were attributable to human activities during September and October. In contrast, all deaths in the mountain valley population were related to predators from October to December when birds were moving to winter habitats. Sage-grouse in Medicine Lodge had lower survival and moved 20% farther from autumn ranges to winter ranges than birds in Table Butte, suggesting that mortality of juvenile sage-grouse in autumn may increase as distances moved between seasonal ranges increase, thereby increasing exposure to predators.

To our knowledge no other investigators have examined the relationship between survival and distance of seasonal movements in sage-grouse. Although our sample sizes are not large, our results are consistent with similar studies. Caizergues and Ellison (1997) indicated that early spring generally is a period of high mortality in tetraonids at least in part because of high mobility of juveniles during this period. Male willow ptarmigan (*Lagopus lagopus*) experience a period of increased mortality in early spring when they move from winter habitat back to their breeding territories and subsequently must move to more protected areas during periods of inclement weather (Hannon et al. 2003). Other studies have reported on relationships of distance moved to other vital rates in grouse. Female greater sage-grouse subject to disturbance moved further and had a lower nesting propensity than birds in less disturbed habitats (Lyon and Anderson 2003). In contrast, Popham and Gutiérrez (2003) reported that successful nesting female sage-grouse in California, USA, nested farther from leks than unsuccessful females. In Colorado mean brood size and chick survival were lower for Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) occupying an area where broods moved an

average of 1.3 km from nest sites compared to a second study area where broods moved an average of 0.5 km from nest sites (Collins 2004).

## Management Implications

Low productivity and chick survival rates suggest recruitment is of great importance in maintaining sage-grouse populations (Connelly and Braun 1997, Crawford et al. 2004). We argue that understanding survival and mortality patterns of juvenile sage-grouse is critical because recruitment has the greatest effect on growth of sage-grouse populations. Managers and researchers should focus efforts on factors that influence sage-grouse production to include chick and juvenile survival. A common way production is indexed in sage-grouse populations is through ratios of juveniles to adult (including yearling) females obtained from the wings of hunter-harvested birds in autumn (Connelly and Braun 1997, Connelly et al. 2000c, Beck et al. 2003). These ratios have, at times, indicated stable to increasing populations when populations were declining, likely reflecting disproportionate harvest of adult females and juveniles near mesic areas (Beck et al. 2003). Additional work on evaluating production should complement our understanding of recruitment, which appears to be low in sage-grouse populations (Dunn and Braun 1985). Particular importance should be placed on studies evaluating chick and juvenile survival.

Both sage-grouse populations we studied were migratory, moving >10 km from autumn to winter ranges (Connelly et al. 2000c). Juveniles in a population that migrated longer distances to winter ranges experienced higher mortality rates than juveniles in a more sedentary population. Birds that migrate longer distances may have increased exposure risks to predation and other hazards (Caizergues and Ellison 1997). These risks can be mitigated by conserving and enhancing movement corridors and large unfragmented habitat patches. We believe our research suggests that implementation of this strategy is critical to promoting high survival among juvenile sage-grouse from migratory populations. Additional research to verify the relationship between migratory distance and juvenile survival across the range of the species is warranted.

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**Jeffrey L. Beck** (photo) is the sagebrush steppe wildlife research scientist for the Colorado Division of Wildlife. He earned B.S. and M.S. degrees in Wildlife and Range Resources from Brigham Young University and a Ph.D. in Forestry, Wildlife, and Range Sciences from the University of Idaho. His doctoral work focused on modeling nutritional carrying capacity for elk in the Jarbidge Mountains of northeastern Nevada. He was a habitat biologist for the Utah Division of Wildlife in southeastern Utah from 1996 to 1997. He completed postdoctoral work at the University of Idaho, where his work focused on evaluating habitat conditions and population parameters for greater sage-grouse and mountain quail populations in Idaho. He also completed a postdoctoral appointment at the University of Wyoming, where his work centered on developing and assisting in improving the rigor of monitoring protocols for management indicator species in the Rocky Mountain Region of the United States Forest Service. He is a certified wildlife biologist and has been a member of



The Wildlife Society (TWS) since 1992. His research interests include prairie grouse ecology and conservation, ungulate ecology and conservation, and monitoring wildlife populations. **Kerry P. Reese** is a professor of wildlife resources and head of the Department of Fish and Wildlife Resources at the University of Idaho. He received his B.S. degree in biology from Indiana University of Pennsylvania, M.S. in wildlife biology from Clemson University, and Ph.D. in wildlife science from Utah State University. A member of TWS since 1974, he is a past-president of the Idaho Chapter of TWS. His major research interests focus on avian ecology and management, especially of upland game birds. **John W. (Jack) Connelly** has been a principal wildlife research biologist with the Idaho Department of Fish and Game for the last 20 years. He recently completed a temporary assignment for the Western Association of Fish and Wildlife Agencies, where he served as Chief Scientist on the Range-Wide Greater Sage-Grouse Conservation Assessment. He received his B.S. in wildlife resources from the University of Idaho, and M.S. in wildlife biology and Ph.D. in zoology from Washington State University. He has been a member of TWS for 30 years, serving as president of the Idaho Chapter and Northwest Section. His professional interests include avian population ecology, harvest management, and pretty much anything related to grouse. **Matthew B. Lucia** is a land protection specialist and wildlife biologist for Teton Regional Land Trust in Driggs, Idaho. He received his B.S. degree from Utah State University. His career and research interests focus on habitat conservation and restoration, with a particular interest in riparian corridors and the shrub-steppe uplands of southeastern Idaho. He has been involved with TWS since 1993.

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