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Source: Wildlife Biology, 19(4) : 347-357

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/13-001

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Wildl. Biol. 19: 347-357 (2013)
DOI: 10.2981/13-001
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Original article

Intraseasonal variation in survival and probable causes of mortality in greater sage-grouse *Centrocercus urophasianus*

Erik J. Blomberg, Daniel Gibson, James S. Sedinger, Michael L. Casazza & Peter S. Coates

The mortality process is a key component of avian population dynamics, and understanding factors that affect mortality is central to grouse conservation. Populations of greater sage-grouse *Centrocercus urophasianus* have declined across their range in western North America. We studied cause-specific mortality of radio-marked sage-grouse in Eureka County, Nevada, USA, during two seasons, nesting (2008-2012) and fall (2008-2010), when survival was known to be lower compared to other times of the year. We used known-fate and cumulative incidence function models to estimate weekly survival rates and cumulative risk of cause-specific mortalities, respectively. These methods allowed us to account for temporal variation in sample size and staggered entry of marked individuals into the sample to obtain robust estimates of survival and cause-specific mortality. We monitored 376 individual sage-grouse during the course of our study, and investigated 87 deaths. Predation was the major source of mortality, and accounted for 90% of all mortalities during our study. During the nesting season (1 April - 31 May), the cumulative risk of predation by raptors (0.10; 95% CI: 0.05-0.16) and mammals (0.08; 95% CI: 0.03-013) was relatively equal. In the fall (15 August - 31 October), the cumulative risk of mammal predation was greater ($M_{(mam)} = 0.12$; 95% CI: 0.04-0.19) than either predation by raptors ($M_{(rap)} = 0.05$; 95% CI: 0.00-0.10) or hunting harvest ($M_{(hunt)} = 0.02$; 95% CI: 0.0-0.06). During both seasons, we observed relatively few additional sources of mortality (e.g. collision) and observed no evidence of disease-related mortality (e.g. West Nile Virus). In general, we found little evidence for intraseasonal temporal variation in survival, suggesting that the nesting and fall seasons represent biologically meaningful time intervals with respect to sage-grouse survival.

Key words: cause-specific mortality, Centrocercus urophasianus, cumulative hazard function, greater sage-grouse, hunting, predation, survival

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Received 3 January 2013, accepted 2 May 2013

Associate Editor: R.J. Gutiérrez

Survival of breeding-aged individuals is a fundamental component of avian population dynamics and, by extension, understanding the mechanisms that affect survival is important for grouse conservation. For species with relatively low intrinsic population growth rates, or in populations with generally low reproductive output, adult survival can be a major determinant of population growth (Sæther & Bakke 2000). For grouse species or populations that exhibit such characteristics, reduction in adult survival is likely to be detrimental to population persistence (Blomberg et al. 2012). Factors that influence survival are often complex, and survival may vary through time, space and among individuals. Often,

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multiple sources of mortality may contribute to observed rates of survival, and understanding cause-specific mortality allows for partitioning of these sources of variation in survival.

To accurately estimate survival and quantify mortality risk from competing sources in a marked population, one must account for 1) staggered entry of individuals into the sample of marked animals, and 2) variable mortality risk during the study period (i.e. staggered exit), each of which lead to variability in sample size among sampling intervals (Heisey & Fuller 1985, Pollock et al. 1989, Heisey & Patterson 2006). These considerations are particularly important when mortality is temporally dynamic because mortality estimates are likely to be biased towards factors that occur when a greater number of individuals are available to die (Heisey & Patterson 2006).

Greater sage-grouse *Centrocercus urophasianus* (hereafter sage-grouse) are the largest grouse species in North America, and are endemic to sagebrush *Artemisia* spp. ecosystems in the western United States and Canada. Conservationists have expressed concern over the population status of sage-grouse since at least the early 20th century (Hornaday 1916). Recent declines have resulted in considerable interest in sage-grouse ecology (Knick & Connelly 2011). Taylor et al. (2012) showed that survival of adult female sage-grouse was a major determinant of population growth for most populations. Sage-grouse die for many reasons, including predation (Hagen 2011), collision (Stevens et al. 2012), disease (Walker & Naugle 2011), human harvest (Sedinger et al. 2010, Reese & Connelly 2011) and exposure to toxins (Blus et al. 1989). Many studies have evaluated sources of variation in sage-grouse survival (e.g. Zablan et al. 2003, Moynahan et al. 2006, Blomberg et al. 2013), and several authors have quantified cause-specific sources of mortality (Connelly et al. 2000, Beck et al. 2006). However, no sage-grouse studies have accounted for the aforementioned assumptions that are required to properly evaluate competing sources of cause-specific mortality in sage-grouse.

We evaluated weekly survival and cause-specific mortalities of radio-marked sage-grouse during two seasons: nesting (1 April - 31 May) and fall (15 August - 31 October). We selected these two seasons because we observed reduced seasonal survival rates during these periods relative to other times of the year (Blomberg et al. 2013), and we had detailed data during these two intervals. Our specific objectives were to 1) characterize sources of variation in survival within each seasonal period, 2) classify probable causes of sage-grouse mortalities, and 3) evaluate the relative risk to grouse from each mortality source.

Material and methods

Study area

Our study area encompassed approximately 6,500 km^2 in Eureka County, Nevada, USA (40°15'N, -116°30'E). This system contains landscape and habitat features typical of the American Great Basin. Shrub steppe communities were dominated by sagebrush species with Wyoming big *A. tridentata wyomingensis* and black sagebrush *A. nova* found at low elevations (< 2,000 m a.s.l.), and mountain big *A. tridentata vaseyana* and low sagebrush *A. arbuscula* found at high elevations. Other common shrub species within these communities included common snowberry *Symphoricarpos albus*, western serviceberry *Amelanchier alnifolia*, bitterbrush *Purshia tridentata*, basin big sagebrush *A. tridentata tridentata*, rabbitbrush *Chrysothamnus* spp. and greasewood *Sarcobatus vermiculatus*. Single-leaf pinyon pine *Pinus monophylla* and Utah juniper *Juniperus osteosperma* were common in our study area, but tended to be found as bands in mid-elevations between the two communities. Large-scale wildfires have converted much sagebrush steppe into grasslands dominated by invasive cheatgrass *Bromus tectorum* and planted exotic crested wheatgrass *Agropyron cristatum*. Topography was intermittent rugged mountain ranges and hills separated by broad xeric valleys. Sage-grouse were generally distributed across all sagebrush habitats during the nesting season, but during the dry fall season, moisture largely restricted them to either high-elevation mountain big sagebrush habitats or low-elevation agricultural areas (primarily irrigated pastures) adjacent to shrub steppe (Blomberg et al. 2013).

Predator communities in our study area were diverse. The most common mammalian predators were coyote *Canis latrans*, bobcat *Lynx rufus*, American badger *Taxidea taxus* and grey fox *Urocyon cinereoargenteus*. Common avian predators included golden eagle *Aquila chrysaetos,* prairie falcon *Falco mexicanus*, great-horned owl *Bubo virginianus*, northern goshawk *Accipiter gentilis*, Cooper's hawk *A. cooperii*, red-tailed hawk *Buteo jamaicensis*, ferruginous hawk *B. regalis* and northern harrier *Circus cyaneus*.

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Field monitoring

We captured male and female sage-grouse during the spring breeding season around leks, and during the fall in high-elevation seasonal habitats using standard nightlighting techniques (Connelly et al. 2003). During 2008-2012, we captured birds from 1 March to 15 May and from 28 August to 26 September. Sage-grouse were aged as subadult (< 1 year old) or adult (> 1 year old) based on feather characteristics (Crunden 1963), and were banded with both a uniquely numbered aluminum leg band (National Band and Tag, Newport, Kentucky; size 14 for females, size 16 for males) and a 3-character plastic color band (Spinner Plastics, Springfield, Illinois). We fitted sage-grouse with a 22 g necklace-style radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, model A4060) having a 'mortality switch' that doubled the signal pulse following eight hours of inactivity. Our monitoring of males during the spring was typically more sporadic than for females, and we were interested in the effect of nesting status on subsequent survival, so we only included females in analyses of nesting season data. However, we included both sexes in the analysis of fall-season survival when male live/dead status was recorded more regularly. All capture and monitoring of sage-grouse was approved by the University of Nevada Reno Institutional Animal Care and Use Committee (Protocol Numbers A05/06-22).

We analyzed data collected during 2008-2012 for the nesting seasons, and during 2008-2010 for the fall seasons. During the fall, we checked radio-signals for mortality pulse rate at least once every one to three days. Every three days during the nesting season, we also attempted to visually locate females to record nesting status (described in Blomberg et al. 2013). We typically used handheld receivers and three-element Yagi antennas; however, when necessary, we searched for missing birds from fixed-wing aircraft. Individual status was recorded as live/dead based on signal pulse rate, and upon indication of mortality, we located the transmitter to confirm mortality and estimate cause of death. We assumed predation when we found a carcass with muscle tissue clearly removed from bones, or when we found no carcass, but found remains (feathers, bone) that suggested predation (e.g. broken bones, teeth or claw marks on feathers). When we found no evidence of predation associated with a carcass, or when we presumed predation occurred and substantial tissue still remained, we collected and froze all remains for necropsy and disease testing. Necropsy and disease testing were conducted at Oregon State University's Veterinary Diagnostic Laboratory within the College of Veterinary Medicine. For assumed predation events, we also attempted to distinguish between mammalian and avian predators based on specific characteristics of remains. We assumed raptor predation in cases where contour feathers were cleanly plucked (Errington & Hamerstrom 1936), and were in a relatively neat pile at the kill site (i.e. a plucking mound). In contrast, we assumed mammalian predation in cases where feather vanes were crushed or sheared, and feathers were widely scattered around the kill site. These criteria were consistent with those used by Thirgood et al. (1998) to establish identity of predators of red grouse *Lagopus lagopus scoticus*. We also considered additional predator signs at the kill site, such as tracks or scat to evaluate causes of mortality; however, we considered such evidence to be of secondary value. Aluminum leg bands and radio-collars were stamped with telephone numbers to facilitate harvest reporting by hunters. The hunting season occurred 25 September - 9 October each year.

Analysis

We conducted two separate analyses as part of this research; a known-fate survival analysis (Sandercock 2006) to evaluate sources of individual and temporal variation in weekly survival, and a cumulative incidence function model (Heisey & Patterson 2006) to assess the relative risk of cause-specific sources of mortality. We conducted both analyses because the former allowed greater flexibility in evaluating sources of variation in mortality rates (1 - survival), whereas the later allowed us to directly compare relative risks among mortality factors. Because of the large temporal gap between the nesting and fall seasons (1 June - 14 August) and varying number of years of data available for analysis, we conducted separate analyses for each season.

Known-fate survival analysis

We first summarized live/mortality pulse rate signals into weekly encounter histories for each season, and estimated survival rates during weekly intervals using the known-fate module (a modified Kaplan-Meier analysis) of Program MARK (White & Burnham 1999). We tested for potential sources of temporal and/or individual variation in survival using a set of a priori general linear models. Temporal effects that were evaluated included annual, weekly and bi-

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weekly variation, as well as models where we considered linear and quadratic time-varying trends on weekly survival. Individual effects included individual age (subadult $<$ 1 year old, adult $>$ 1 year old) and sex (male vs female; fall only). Individuals that were captured as subadults, but monitored for $>$ 1 year, were classified as adults in subsequent years. We also considered an interaction effect between age and sex in the fall analysis.

For the nesting season, we evaluated whether females experienced greater mortality risk while incubating eggs compared to other periods. This question was confounded by survival, however, because females that survived an entire interval had an inherently longer time to be detected on a nest. For this reason, we only considered the effect of nesting status in week t on survival during week t+1, and included nesting status as a time-varying individual covariate.

We hypothesized that the timing of raptor migration may influence mortality in our system during the fall (Robinson et al. 2009). We obtained raptor migration data from HawkWatch International (http://www.hawkwatch.org) for their raptor migration site in the Goshute Mountains, located at a similar latitude and approximately 175 km east of our study site. We realize that data collected at this distance may not accurately reflect raptor abundance within our study site. However, we assumed raptor migration would follow a similar timing because both locations were at similar latitudes, and therefore, the Goshute Mountain data provided a useful approximating index to raptor migration within our study area. These data consisted of daily counts of individual raptors, by species, and were collected by HawkWatch personnel between 15 August and 5 November each year. For this analysis, we considered migration timing for all raptors, all *Accipiter* spp., all *Buteo* spp. and golden eagles only. We first adjusted raw counts to correct for daily variation in the number of observers or total hours of observation in a given day. We used the GENMOD procedure with a specified Poisson distribution in SAS (SAS Institute, Cary, North Carolina) to regress the daily count for each raptor group on the number of observers and total hours of observation recorded for that day. We calculated daily residual scores for each species or species group based on these regressions, and used these values as corrected estimates of daily passage rates. To evaluate correlations between timing of raptor migration and sage-grouse survival, we calculated mean weekly passage rates for each raptor group, and used these values as weekly group covariates in our survival analysis. Thus, we were able to test for potential effects of timing (within year) and magnitude (among years) of raptor passage rates on sage-grouse survival. Finally, we also examined the possibility of reduced survival during the 15-day sage-grouse hunting season by evaluating models where survival was constrained to be different during weekly intervals that overlapped the hunting season.

In each analysis, we evaluated support for individual and temporal covariates by comparing them to an intercept-only 'null' model (i.e. no meaningful variation in weekly survival) using an information theoretic approach (Burnham & Anderson 2002). Using Akaike's Information Criterion adjusted for small sample size (AIC_c), we considered any model within 2.0 ΔAIC_c of the best model to be competitive, but also assumed that those models that did not outcompete the null model did not explain any meaningful variation in weekly survival rates. We used model-averaging for all survival estimates $\pm$ SE, and calculated parameter coefficients (β) along with 85% confidence intervals (Arnold 2010), and considered covariate effects to be meaningful when 85% confidence intervals did not overlap 0.0, consistent with recommendations made by Arnold (2010). We report all parameter estimates (e.g. weekly survival) $\pm$ SE, unless otherwise indicated.

Cumulative incidence function model

Our second objective was to evaluate the relative risk to sage-grouse from differing sources of mortality (e.g. mammal vs raptor predation). Heisey & Fuller (1985) developed a modified Kaplan-Meier approach to estimate cause-specific mortality risk in a staggered entry design. In our study, individuals entered the sample in staggered intervals because they were radio-marked at different times, and the timing of different sources of mortality was not evenly distributed across sampling intervals (Fig. 1), so our data were appropriate for a staggered entry approach. We used the package wild1 in Program R (R Development Core Team 2011) to estimate nonparametric cumulative incidence functions, which describe the cumulative risk of cause-specific sources of mortality M(k) (e.g. human harvest) during successive study intervals (Heisey & Patterson 2006). This approach also allowed us to estimate the cumulative risk of mortality M(t) defined as the sum of each individual risk function, including mortalities that could not be attributed to a specific cause. This cumulative mortality risk should have

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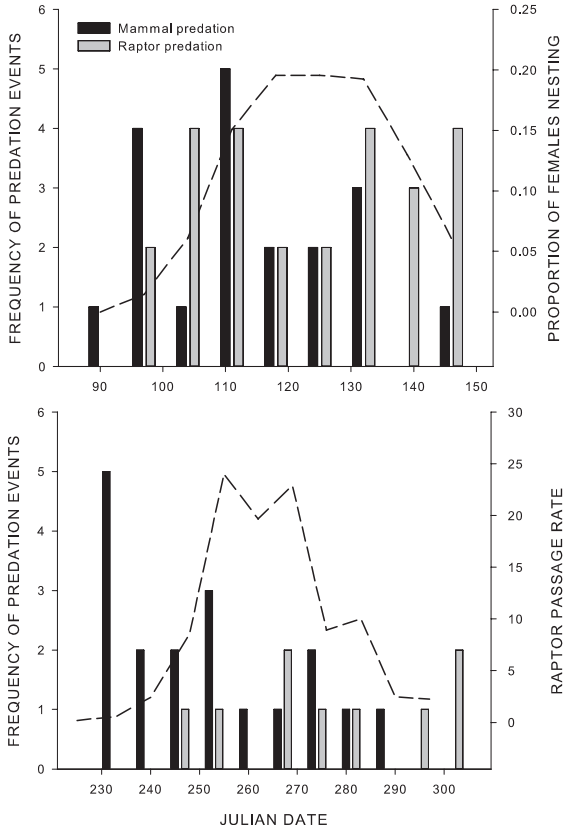


Figure 1. Distribution of sage-grouse predation events by predator type during the nesting and fall periods in Eureka County, Nevada. The proportion of radio-marked females known to be on a nest and the timing of annual raptor migration during the fall are identified by dashed lines and secondary y-axes. Raptor migration timing was estimated using data from the HawkWatch International Raptor Migration Study Site in the Goshute Mountains, located approximately 175 km east of our study site. Julian date 90 = 29 March and Julian date 230 = 16 August.

been the complement to overall fall survival probability based on known-fate estimates, that is $M(t) \sim 1 - \Phi_{(fall)}$, although we expected slight differences due to variation among the analytical methods. We calculated cumulative incidence functions for each weekly interval, and assessed risk individually for mammalian predation, raptor predation and mortality associated with human harvest (fall only). During each season, we also included a final 'unknown' category when we could not establish cause of mortality. In cases where cause could not be established, or when predator type was not clear, we included mortalities in the unknown category. Because these instances represented a relatively small proportion of total mortalities during our study, our estimates of predation risk should be viewed as conservative. Incorporation of an unknown risk category allowed for M(t) to reflect more accurately the survival of our sample.

Results

We monitored 203 individual female sage-grouse during the nesting season between 2008 and 2012, and 132 individual females and 41 individual male sage-grouse during the fall between 2008 and 2010. Of these individuals, 74 were classified as subadults during one nesting season, and 26 were classified as subadults during one fall season. We investigated 87 mortalities of radio-marked sage-grouse, which are summarized in Table 1. The most common source of mortality was predation, which accounted for 90% (N = 78) of all mortalities (see Table 1). During the nesting season, we classified 25 predation events as mammalian, 19 predations as raptors and four of unknown predator class. During the fall, we classified 18 predation events as mammalian, nine predation events as raptors and three of unknown predator class. Hunters legally harvested and reported two female and two male sage-grouse during the fall, and an additional female was determined through necropsy to have been shot and not recovered by the hunter. We classified four additional fall mortalities as unknown, two of which were not recovered quickly enough to establish cause of death, but evidence at the mortality site was consistent with either predation or scavenging. One bird was recovered with broken neck vertebra, and may have collided with a nearby (~ 20 m) barbed-wire fence. Finally, we observed a female sage-grouse on 2 October 2009 that was unable to fly and was recovered dead four days later before her mortality sensor activated. She was either predated or scavenged following death, but we could not establish the cause of her flightless condition; therefore, we classified her cause of mortality as unknown. This female and four others tested negative for West Nile Virus.

Weekly survival was correlated with year and individual age during the nesting season (Table 2). Adults had higher weekly survival ($\varphi = 0.99 \pm 0.01$) compared to subadults in their first breeding season ($\varphi = 0.98 \pm 0.01$). Model selection results also suggested annual variation in weekly survival rates. Although the range of weekly survival among years was relatively low (0.96 ± 0.02 - 0.98 ± 0.01), the total variation in nesting season survival ranged from a low of 0.72 ± 0.01 in 2008 to a high of 0.85 ± 0.01 in

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Table 1. Summary of cause-specific mortalities of radio-marked sage-grouse in Eureka County, Nevada, USA, by season, sex and age class. Harvest only occurred during the fall season. Male sage-grouse were not including in the nesting season analysis.

	Cause of mortality				
Sex/age class	Raptor	Mammal	Unknown predator	Harvest	Undetermined
Fall					
Adult female	5	14	1	3	2
Subadult female	2	2	1	0	1
Adult male	1	2	0	1	1
Subadult male	1	0	1	1	0
Total fall	9	18	3	5	4
Nesting					
Adult female	11	17	2	-	0
Subadult female	8	8	2	-	0
Adult male	-	-	-	-	-
Subadult male	-	-	-	-	-
Total spring	19	25	4	-	0
Total study	28	43	7	5	4

2012. We found no evidence to suggest differing survival between nesting and non-nesting hens. There was suggestive evidence that female survival declined slightly throughout the nesting season (see Table 2). However, inclusion of the linear trend did not improve model fit, and confidence intervals on the parameter coefficient overlapped 0.0 ($\beta = -0.07$; 85% CI: -0.16 - 0.02). Based on model-averaged parameter estimates, the overall probability of a female sage-grouse surviving the eight-week nesting season was 0.79 ± 0.01.

In the fall, weekly survival was correlated with individual age and increased slightly throughout the fall season (Table 3). We found that average weekly survival was higher for adults ($\varphi = 0.98 \pm 0.03$) compared to hatch-year birds ($\varphi = 0.95 \pm 0.04$). Model results also suggested that weekly survival increased progressively during the fall period, based on support for a linear trend ($\beta = 0.09$; 85% CI: 0.01-0.17). However, a model that did not contain the weekly trend was also competitive ($\Delta AIC_c = 0.37$). In general, weekly survival was relatively invariant during the fall season, as indicated by inclusion of the intercept-only null model in the competitive model set ($\Delta AIC_c = 1.21$), and a relatively small amount of variation between minimum and maximum weekly survival estimates within the fall period. Model-averaged estimates of weekly survival ranged from 0.97 ± 0.01 to 0.98 ± 0.01, and the overall probability of a sage-grouse surviving the 10-week fall season was 0.79 ± 0.03. We found no support for an effect of raptor migration timing on weekly survival rates for any raptor species group we considered, and found no support for reduced weekly survival during the hunting season (see Table 3).

During the nesting season, predation risk was similar between raptor and mammalian predators (see Fig. 1). The cumulative risk of a female being killed by a mammalian predator during the entire eight-week study interval was 0.10 (95% CI: 0.05-0.16), whereas the cumulative risk of raptor preda-

Table 2. Model selection results for known-fate analysis of weekly survival for radio-marked female sage-grouse during the spring nesting season (1 April - 31 May) in Eureka County, Nevada, USA, 2008-2012. Model selection notation follows Burnham & Anderson (2002). Age = subadult (< 1 year of age) vs adult (> 1 year of age). BiWeek = weekly intervals grouped into sequential two-week periods. Weekly trend = a linear trend applied across one-week intervals. Nest = weekly nesting status (observed on a nest vs not observed on a nest). AIC_c = Akaikie's information criterion corrected for small sample size. ΔAIC_c = change in AIC_c relative to the top model. w_i = Akaike weights. K = number of model parameters.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Year + Age	479.94	0.00	0.28	6	467.89
Year + Age + Weekly trend	480.57	0.63	0.20	7	466.51
Age	482.21	2.27	0.09	2	478.20
Year	482.53	2.60	0.08	5	472.50
Null	482.72	2.78	0.07	1	480.71
Weekly Trend	483.02	3.09	0.06	2	479.02
Year + Weekly trend	483.15	3.21	0.06	6	471.10
Year + (Weekly trend)^2	483.64	3.70	0.04	7	469.58
(Weekly trend)^2	483.84	3.90	0.04	3	477.83
Year + Nest	484.20	4.27	0.03	6	472.16
Nest	484.38	4.45	0.03	2	480.38
BiWeek	486.14	6.20	0.01	4	478.12
Year + BiWeek	486.18	6.24	0.01	8	470.10
Year + Week	490.38	10.44	0.00	13	464.19
Week	490.47	10.53	0.00	9	472.38

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Table 3. Model selection results for known-fate analysis of weekly survival for radio-marked sage-grouse during the fall season (15 August - 31 October) in Eureka County, Nevada, 2008-2010. Model selection notation follows Burnham & Anderson (2002). Age = subadult (< 1 year of age) vs adult (> 1 year of age). Sex = male vs female. BiWeek = weekly intervals grouped into sequential two-week periods. Weekly trend = a linear trend applied across one-week intervals. Total raptor = weekly passage rate of all raptors recorded at the Goshute Mountain Raptor Migration site, after correcting for daily number of observers and total hours of observation. *Buteo* spp., *Accipiter* spp. and Golden eagle models represented weekly passage rates for each of these raptor species groups. Hunt = survival was modeled independently for hunting season and non-hunting intervals. AIC_c = Akaikie's information criterion corrected for small sample size. ΔAIC_c = change in AIC_c relative to the top model. w_i = Akaike weights. K = number of model parameters.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Age + Weekly trend	388.49	0.00	0.17	3	382.48
Age	388.86	0.37	0.15	2	384.86
Null	389.70	1.21	0.10	1	387.70
Weekly trend	389.72	1.23	0.09	2	385.71
Age + Year + Weekly trend	389.90	1.41	0.09	5	379.86
Fall	390.43	1.94	0.07	2	386.43
$(\text{Weekly trend})^2$	391.60	3.11	0.04	3	385.58
Golden eagle	391.61	3.12	0.04	2	387.61
Buteo spp.	391.64	3.15	0.03	2	387.63
Sex	391.66	3.17	0.03	2	387.66
Total raptor	391.67	3.18	0.03	2	387.67
Accipiter spp.	391.68	3.19	0.03	2	387.68
Sex + Weekly trend	391.69	3.20	0.03	3	385.68
Hunt	391.70	3.21	0.03	2	387.69
Year	392.06	3.57	0.03	3	386.05
Year + Weekly trend	392.17	3.68	0.03	4	384.15
Year + Hunt	394.05	5.56	0.01	4	386.03
Year + $(\text{Weekly trend})^2$	394.10	5.61	0.01	5	384.06
Sex + Year + Weekly trend	394.16	5.67	0.01	5	384.13
BiWeek	395.41	6.92	0.01	5	385.37
Year + BiWeek	397.91	9.42	0.00	7	383.84

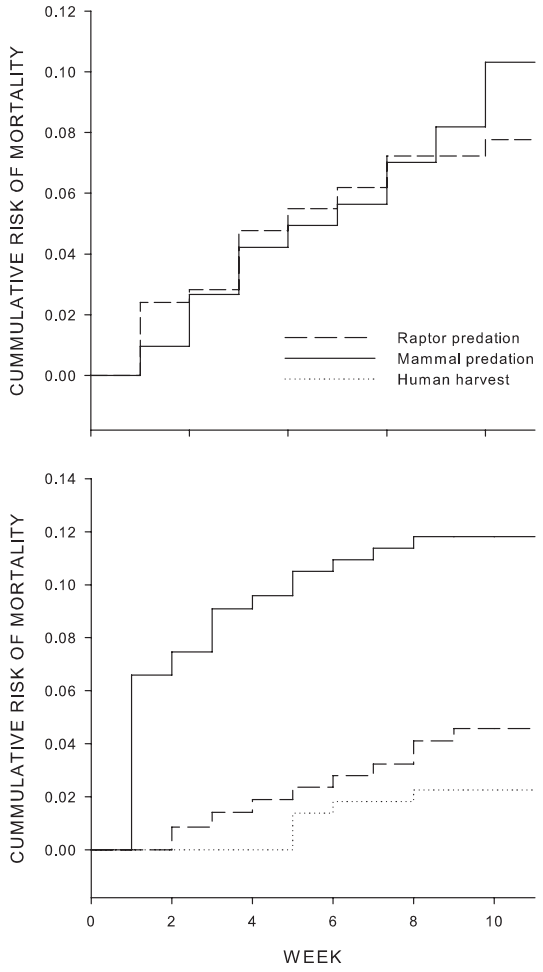


Figure 2. Cumulative incidence functions for competing risks of sage-grouse mortality during the nesting and fall periods in Eureka County, Nevada. Human harvest only occurred during the fall. Week 1 began on 1 April during the nesting season and on 15 August during the fall.

tion was 0.08 (95% CI: 0.03-0.13). We found no evidence that females were more susceptible to either competing mortality risks, and both risks appeared evenly distributed across the spring nesting period (Fig. 2). The cumulative risk of mortality during the entire nesting season, including sources of unidentified mortality, was 0.21 (95% CI: 0.16-0.26), which was consistent with our known-fate survival estimates for the same period ($\varphi = 0.79$; 95% CI: 0.77-0.81).

Predation by mammals represented the largest mortality risk to sage-grouse during the fall (see Fig. 1); cumulative hazard functions estimated the risk of mammal predation during the entire 11-week season to be 0.12 (95% CI: 0.04-0.19), and risk of mammalian predation was proportionally higher during the early portion of the season (see Fig. 2). Raptors were the second greatest risk, with a cumulative risk of 0.05 (95% CI: 0.00-0.10). In contrast to mammal predation, risk of predation by raptors was generally evenly spread across the fall season (see Fig. 2). Risk of human harvest was lower than either forms of predation risk ($M_{(hunt)} = 0.02$; 95% CI: 0.0-0.06), and occurred in conjunction with the annual sage-grouse hunting season (see Fig 2). After accounting for sources of unidentified mortality, the cumulative risk of mortality during the entire fall season was 0.23 (95% CI: 0.17-0.29), which was consistent with our estimate of cumulative survival based on the known-fate analysis ($\varphi = 0.79$; 95% CI: 0.73-0.85).

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Discussion

As in other studies of sage-grouse (Hagen 2011), predation was the largest source of mortality. During the fall, we found risk of predation by mammals to be greater than that of raptors, whereas during the nesting season, the two predation risks were more equivalent. In contrast, we found relatively little evidence to support high levels of other sources of mortality during either season. During the fall, the cumulative risk of predation was nearly three times greater ($M_{(pred)} = 0.17$) than all other sources of mortality combined (hunting, collision, undetermined; $M_{(other)} = 0.06$), and during the nesting season, the risk of predation was six times greater ($M_{(pred)} = 0.18$) than other sources ($M_{(other)} = 0.03$). Attaching radio-transmitters may influence mortality risk for some species (Barron et al. 2010). Gibson et al. (in press) found that radio-transmitters influenced male sage-grouse breeding behaviour, but survival did not differ between males marked with radio-transmitters and those marked with tarsal bands only. We therefore assumed radio-marking did not influence survival and bias our results during this study.

Unlike some other studies of radio-marked sage-grouse, we did not find substantive mortality risk other than predation. Connelly et al. (2000) reported that 15% of male mortalities and 42% of female mortalities were caused by hunting. Beck et al. (2006) classified causes of mortality for juvenile (subadult) sage-grouse at two study sites and reported that mammal and raptor predation accounted for 27% and 36% of mortalities, respectively; hunting mortality accounted for an additional 27%. Mortality associated with West Nile Virus has been substantial for some sage-grouse populations (Moynahan et al. 2006, Walker & Naugle 2011). However, we did not detect this virus during our study nor has it been documented previously from our study area (Blomberg et al. 2013). However, direct comparison between our results and those of others is problematic because we are the first to account for potential sampling bias when evaluating mortality risk in sage-grouse (Heisey & Fuller 1985, Heisey & Patterson 2006). In addition, some previous studies reported proportional rates of mortality based on small samples of recorded mortalities.

Regardless of methods, we expected variation among studies in sources of mortality, which may result from population-level variation in predator communities, human disturbance, habitat composition and other factors. Such variation among grouse studies is common. For example, Wolfe et al. (2007) documented a substantial number of collision-related mortalities for lesser prairie chickens *Tympanuchus pallidicinctus* in Oklahoma and New Mexico. In contrast, Hagen et al. (2007) did not document any collision mortality of lesser prairie chickens in western Kansas. For black grouse *Tetrao tetrix*, major mortality rates have been attributed to collisions (Miquet 1990), predation primarily by raptors (Angelstam 1984) and a mixture of raptor and mammalian predation (Warren & Baines 2002).

With a few exceptions, we found little evidence of temporal variation in survival during either the nesting or fall periods. Survival appeared to vary among nesting seasons, which was consistent with a larger analysis of female seasonal survival in this system (Blomberg et al. 2013). We also found that weekly survival increased throughout the fall, and this effect was consistent with higher predation by mammals during the early weeks of the fall period (see Fig. 2). The nesting and fall seasons likely represent biologically meaningful time intervals for sage-grouse in our study area, because rates of predation were relatively constant within these time intervals, whereas survival was higher during the summer and winter periods (Blomberg et al. 2013).

Adult sage-grouse were less susceptible to predation than subadults. Of previous studies that have examined survival of both age-classes in a single analysis, we found no reports of a positive association between age and survival. Baxter et al. (2008) and Moynahan et al. (2006) reported no age-related variation in survival in Utah and Montana, respectively. In contrast to our results, Zablan et al. (2003) reported higher survival rates for subadult sage-grouse of both sexes in Colorado. Also, in contrast to Zablan et al. (2003), we found no effect of sex on survival during the fall, although our sample of males was relatively small compared to our sample of females.

Survival of female sage-grouse in this system is reduced during the nesting season relative to winter or summer (Blomberg et al. 2013). However, within the nesting season, we did not find evidence that incubating female sage-grouse had reduced survival compared to females not known to be on a nest. In our study, we typically did not detect females on nests until after the onset of incubation. If females were equally susceptible to predation during other stages of nesting, such as while prospecting for nest sites or

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during egg laying, we were limited in our ability to detect such risks.

We found that weekly survival of sage-grouse was not correlated with timing of raptor migration during the fall. This result contrasts to a study of chukar *Alectoris chukar* conducted in western Utah, where 91% of known predation events were classified as raptor predation, and survival during the fall was reduced during the peak of raptor migration (Robinson et al. 2009). One possible explanation for the discrepancy between our two studies was that chukar, due to their smaller body size, are more vulnerable to a wider range of raptor species compared to sage-grouse. Although we observed predation of adult sage-grouse by raptors as small as Cooper's hawks, it has been generally assumed that large-bodied raptors such as golden eagles are the major source of raptor predation in sage-grouse (Schroeder & Baydack 2001). Given that predation risk from mammals was equal to, or greater than, that of raptors, little evidence for a negative association between raptor migration and sage-grouse survival was not surprising. However, we acknowledge that the raptor migration data we used was collected a substantial distance (~ 175 km) from our study area, and lack of support for a raptor migration effect may have reflected this separation. Also worth noting, is that we did not observe any instances of woodrat *Neotoma* spp. removal of radio-transmitters during our study, which was observed frequently during a study of chukar in western Utah (Larsen et al. 2008).

One potential limitation of our study is that we may have misclassified certain mortalities as mammalian predation that, in fact, represented scavenging by mammalian carnivores. However, we feel any error in this regard was minimal because we monitored birds with sufficient frequency to recover individuals prior to scavenging. Stevens et al. (2011) found that mean time to scavenging of female ring-necked pheasant *Phasianus colchicus* carcasses in sagebrush steppe habitats was 5.8 days, and reported a daily probability of initial scavenging of approximately 0.2. Based on these values and assuming a three-day sampling interval, a sage-grouse dying from non-predation mortality (e.g. collision) would have an approximately 0.51 probability of being scavenged prior to detection. We found three sage-grouse known to have died from causes other than predation or hunting during our study. A conservative estimate for misclassification would therefore be three mortalities misclassified as predation events that were in fact caused by other sources. Given the relatively large sample of total mortalities (N = 87) contained in our data set, we believe this potential error rate (~ 3.4%) is acceptable.

Hunting was probably a minor source of mortality in our study population. The nearest human population centers were relatively distant from our study area; driving distances from the cities of Reno and Elko, Nevada, were approximately 385 km and 145 km, respectively. However, fall sage-grouse habitats typically were accessible by road, and nearly all sage-grouse were found on public lands that were accessible to hunters. We also observed hunters in our study area during all years of our study. Our estimates of cumulative hazard risk for harvest-related mortality are analogous to an overall harvest mortality rate for this population, and included both harvest and crippling loss of shot sage-grouse. This harvest rate estimate (2%) was considerably lower than estimates from other sage-grouse populations, and accordingly harvest should operate in a compensatory manner (Sedinger et al. 2010, Reese & Connelly 2011). Moreover, survival did not decline during the hunting season relative to the rest of the fall period, so we infer that hunting was not adversely impacting the sage-grouse population in our study area.

Acknowledgements - we thank numerous field technicians and volunteers for assistance with sage-grouse capture and monitoring, and P. Wolff and C. Morris of the Nevada Department of Wildlife for assistance with necropsy processing. We thank HawkWatch International for making their raptor migration data available. C. Overton, R. Gutiérrez and K. Doherty provided comments that improved the manuscript. This work was supported jointly by the University of Nevada Reno Agricultural Experiment Station, the National Fish and Wildlife Foundation, the Nevada Department of Wildlife, the United States Bureau of Land Management and NV Energy Corp. Any use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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