

Quantifying overlap and fitness consequences of migration strategy with seasonal habitat use and a conservation policy

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Abstract. Our study aimed to delineate seasonal habitats and assess differential fitness related to migration strategy and seasonal habitat use of greater sage-grouse (*Centrocercus urophasianus*, hereafter “sage-grouse”). In addition, we evaluated benefits gained for sage-grouse through the implementation of the Wyoming Core Area Strategy relative to protection of habitat and differences in nest, brood, and annual female survival. We compared the proportion of seasonal habitats that were within or outside Core Areas as delineated with 75% and 95% kernel density contours (KDE). The proportion of summer and winter habitats (95% KDE) that overlapped Core Areas was 0.69 of summer and 0.50 of winter habitat within a Core Area. We found no differences in nest or brood survival among migration strategies or within and outside Core Areas. However, females that did not migrate out of their respective winter habitat had lower risk of death, which highlighted year-round benefits of winter habitat. Females had lower risk of death during winter with the lowest risk occurring during winter in Core Areas. Higher temperature and lower snow water equivalent during the breeding season and fall were detrimental to female survival, whereas neither had an effect on winter survival. Although Core Areas encompassed a large proportion of winter habitat, our results indicate that Core Areas (as delineated) were not the most direct way to protect winter habitat for sage-grouse. During winter, sage-grouse gathered within habitat conducive to winter survival, indicating that disturbances within these winter habitats may have broad consequences for sage-grouse populations.

Key words: annual survival; climate effects; conservation policy; greater sage-grouse; migration strategy; reproductive success; seasonal habitat; winter habitat; Wyoming Sage-Grouse Core Area Strategy.

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INTRODUCTION

Distinct seasonal ranges provide habitat functions for migratory animals throughout crucial life stages including birth and rearing (Kozakiewicz 1995). Many migratory species utilize distinct

seasonal habitats that have been shown to provide greater reproductive rates or adult survival (Lima and Dill 1990, Alerstam et al. 2003, Schekkerman et al. 2003, Hebblewhite and Merrill 2009, 2011). For species sensitive to habitat degradation, understanding the spatial arrangement of

seasonal habitats and demographic consequences associated with use of those habitats is essential to provide adequate conservation measures. Often conservation measures favor some seasonal habitats relative to others, which results in disproportional conservation by life history stage. Habitat available to and used by greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) in winter months has the potential to influence the viability of sage-grouse populations. Sage-grouse typically have high overwinter survival (Beck et al. 2006, Baxter et al. 2013, Blomberg et al. 2013, Smith et al. 2014), but winter survival may be negated by severe winter weather conditions (Moynahan et al. 2006, Anthony and Willis 2009). Survival of adult female sage-grouse has the greatest potential to influence population growth in local and range-wide sensitivity and viability analyses (Johnson and Braun 1999, Taylor et al. 2012). In addition, research has identified avoidance responses by sage-grouse where winter habitat overlaps anthropogenic development (Doherty et al. 2008, Carpenter et al. 2010, Smith et al. 2014, Holloran et al. 2015). For these reasons, habitat used by sage-grouse during the winter should receive special attention as priority areas for conservation. Currently, conservation measures for sage-grouse have been focused on breeding season habitats delineated by buffer areas around communal male display grounds (Connelly et al. 2011, Doherty et al. 2016).

Inter-seasonal movement of sage-grouse is variable with some individuals moving large distances between breeding and winter habitats (Beck et al. 2006, Bruce et al. 2011, Fedy et al. 2012, Pratt et al. 2017). Winter habitat typically includes lower elevation areas with continuous patches of sagebrush, lower snow depths, and gentle southerly-facing slopes (Eng and Schladweiler 1972, Doherty et al. 2008, Carpenter et al. 2010, Connelly et al. 2011). Individual sage-grouse exhibit different migration strategies, where some individuals migrate to distinct breeding habitats and others occupy smaller areas year-round (i.e., partially migratory populations; Chapman et al. 2011, Fedy et al. 2012, Pratt et al. 2017). This suggests there may be trade-offs among different migration strategies for sage-grouse. The evolution of partial migration in many bird species is considered a mechanism to optimize individual fitness (Cohen 1967, Ricklefs 2000). Migratory individuals may

have greater reproductive success than non-migratory individuals, because they move to capitalize on better habitat for nesting and brood-rearing. In contrast, non-migratory individuals that utilize similar habitats year-round may benefit from higher annual survival than migratory individuals, which may lead to longer lifespan and compensated productivity in suboptimal habitat.

Life history strategies should optimize the reproductive output of a species; thus, various migratory strategies should exhibit benefits of either increased survival and/or greater reproductive success of individuals (Clark and Ehlinger 1987, Wilson 1998). Winter habitats are of utmost importance for sage-grouse, because compared to other seasonal habitats, functional winter habitat has a smaller spatial footprint more susceptible to degradation (Smith et al. 2014, 2016). In 2008, Wyoming enacted a Core Area Strategy to minimize impacts and limit development to areas with the greatest breeding densities of sage-grouse (State of Wyoming 2008). However, the focus of the Wyoming Core Area Strategy on breeding habitat carried an underlying assumption of providing protection to other seasonal habitats, which were not explicitly quantified. The Core Area Strategy set aside 31 distinct Core Areas encompassing 24% of Wyoming, which contain >30% of the breeding sage-grouse in the world (State of Wyoming 2008, 2011, U.S. Fish and Wildlife Service 2015). This policy is an example of conservation triage to gain benefits for sage-grouse while also conserving large areas of sagebrush known to be used by sage-grouse during one life history stage—breeding. However, their utility in conserving habitats for other life stages such as wintering habitat appears to be a function of their size, with larger Core Areas protecting more wintering habitat for grouse populations than smaller Core Areas (Smith et al. 2016). Our primary goals were to (1) delineate winter use areas and evaluate the overlap of these winter use areas with current Core Areas, (2) delineate winter use areas during winters with lower- and higher-than-average snow water equivalent (SWE [kg/m^2]; SWE is a common measurement of snowpack), and (3) compare fitness metrics (nest, brood, and adult survival) between migratory and non-migratory sage-grouse. We hypothesized that females localized to winter habitat year-round would benefit from higher annual survival,

whereas females that migrated would have higher reproductive rates at the expense of their survival. As a secondary goal, we evaluated the effect of climatic variables (temperature [TEMP], precipitation [PPT], and SWE) on annual female survival to account for variability in annual survival.

METHODS

Study site

Our study included sage-grouse location and demographic data collected in central and southwestern Wyoming during 2008–2015 from five distinct study regions (Table 1). We collected data in Atlantic Rim, Stewart Creek, and Southwest Wyoming during 2008–2011 and the Bighorn Basin and Jeffrey City during 2011–2015. All study regions were within the semidesert grass-shrub zone and were characterized by sagebrush steppe habitats. Elevations ranged from 1300 to 2850 m. Most of the land in each study region was federally administered. Livestock grazing was the dominant land use across all regions. Other major land uses included oil and gas extraction and mining.

Vegetation within all study regions was dominated by big sagebrush (*Artemisia tridentata*); Wyoming big sagebrush (*A. t. wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common shrub species followed by black (*Artemisia nova*) and/or low (*Artemisia arbuscula*) sagebrush. Other common shrub species included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), Gardner's saltbush (*Atriplex gardneri*), greasewood (*Sarcobatus vermiculatus*),

Table 1. Summary of female sage-grouse summer and winter locations, 2008–2014, used to create kernel densities, 2008–2015.

Study region	Years	No. bird locations		
		Summer	Winter	Total
Atlantic Rim	2008–2011	1832	338	2170
Bighorn Basin	2011–2015	3071	666	3737
Jeffrey City	2011–2015	1043	127	1170
Southwest Wyoming	2008–2011	1046	207	1253
Stewart Creek	2008–2011	700	150	850
Total of all studies	2008–2015	7692	1488	9180

Note: Sage-grouse were located in five distinct study regions throughout Wyoming, USA.

and rabbitbrush (*Chrysothamnus* and *Ericameria* spp.). Stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at higher elevations.

Bird monitoring

We captured and radio-marked female sage-grouse at night using spotlights, all-terrain vehicles, and hoop nets (Giesen et al. 1982, Wakkinen et al. 1992), and marked them with 17.5- or 22-g (<1.5% body mass) necklace radio collars (model RI-2D; Holohil Systems, Carp, Ontario, Canada, or model A4060; Advanced Telemetry Systems, Isanti, Minnesota, USA). A small portion of females ($n = 31$) in the Bighorn Basin region and all of the females ($n = 32$) from the Jeffrey City region were equipped with 32 g (<3.0% body mass) rump-mounted Global Positioning System (GPS) transmitters (PTT-100 Solar Argos/GPS PTT; Microwave Telemetry, Columbia, Maryland, USA, or Model 22 GPS PTT; North Star Science and Technology, King George, Virginia, USA). Females were captured either near lek locations in spring or near roost locations of other radio-marked females in late summer each year. We aged females at the time of capture as yearlings or adults (≥ 2 years of age) based on established protocols (Eng 1955, Dalke et al. 1963). All animal capture and monitoring was conducted under Wyoming Game and Fish Department Chapter 33 permits (permit numbers 33-572, 33-657, 33-699, 33-800, 33-801) and Institutional Animal Care and Use protocols for University of Wyoming (protocol numbers 03032009, 03142011, 20140228JB00065, 03132011, and 20140128JB0059) and Utah State University (protocol number 1357).

We primarily used ground-based tracking to record locations during breeding season (May–July) and fall (August–November), aerial flights during winter (December–February), and both ground-based tracking and aerial flights in the spring (March–April) for very high frequency (VHF)-marked sage-grouse. We located VHF-marked sage-grouse throughout the year with one to two locations per week during breeding season and monthly during fall, winter, and spring. All GPS-marked birds had location data rarified to reflect the sampling intensity of the VHF-marked birds. Thus, we used two locations per week during the breeding season and three locations per bird each winter with one location in December,

January, and February. Approximately 77.5% of winter locations from the Bighorn Basin were collected from aerial surveys. Aerial survey location error was estimated by comparing GPS locations from aerial survey data to on the ground locations of dummy collars placed for calibration or radio collars recovered from grouse that died during the winter (i.e., fixed locations). Both VHF and GPS transmitters were equipped with motion sensors to determine death, allowing us to document mortality when visual observations were not possible.

For VHF-marked females, we visually located nests and broods to monitor survival using established protocols (see Dinkins et al. 2014a, b, Kirol et al. 2015). Nest and brood success were defined as at least one hatched egg or one surviving chick, respectively. Brood success was monitored until chicks of VHF-marked and GPS-marked females were 50 or 35 d of age, respectively. We visually inspected broods of VHF-marked and GPS-marked females twice at night when the chicks were estimated to be 35 and 36 d of age. For VHF-marked females, brood failure between 36 and 50 d was recorded by not detecting a chick or brooding behavior (clucking or feigning injury) on two consecutive monitoring visits. Exposure to brood loss was appropriately truncated to the last day seen (see brood survival analysis below). Brood loss was assumed when we did not detect evidence of a brood during two consecutive telemetry visits, or there were no chicks detected during 35- to 36-d brood checks (Kirol et al. 2015).

Winter and summer habitat analysis

We delineated seasonal use areas by generating kernel density estimations (KDE) using all recorded sage-grouse locations during summer (May–July) and winter (December–February; Table 1). We mapped seasonal habitats for sage-grouse as 75% and 95% KDE contours with ArcMap version 10.0. Winter habitats were mapped as (1) aggregates of all winters and (2) stratified as winters with above- and below-average SWE. We evaluated the overlap of sage-grouse winter and summer habitats with Wyoming Core Areas and 75% and 100% core regions. Wyoming Core Area boundaries were obtained from the Wyoming Game and Fish Department. Core regions were generated by Doherty et al. (2011) as theoretical areas for sage-grouse conservation based on 8.5 km radius buffers around leks, which

represent the smallest area necessary to conserve 75% and 100% of breeding sage-grouse.

Sage-grouse use within Core Areas and core regions was calculated as proportion of overlap. We divided the area of sage-grouse use—stratified as summer, winter, and year-round (75% and 95% KDEs)—by the area within Core Areas and core regions (75% and 100%). To calculate proportional overlap of individual Core Areas, we summarized overlap with 75% KDEs, because almost all 95% KDEs of sage-grouse use intersected multiple Core Areas. We used 95% KDE to summarize total proportional overlap of all Core Areas combined. When a 75% KDE of winter or summer habitat overlapped more than one Core Area, we calculated proportional overlap using the entire sage-grouse habitat KDE relative to each Core Area. This yielded the relative overlap of total sage-grouse use to individual Core Areas. We also calculated the ratio of proportional overlap between summer and winter use within Core Area and 75% and 95% core regions to illustrate relative differences in sage-grouse use of Core Areas and core regions between summer and winter.

To identify potential shifts in winter habitats, we stratified winters as higher- or lower-than-average SWE for each winter habitat KDE. Stratification of winters with above-average SWE was $>50 \text{ kg/m}^2$ in the Atlantic Rim region, $>30 \text{ kg/m}^2$ in the Bighorn Basin region, $>30 \text{ kg/m}^2$ in the Jeffrey City region, $>23 \text{ kg/m}^2$ in the southwest Wyoming region, and $>32 \text{ kg/m}^2$ in the Stewart Creek region. We obtained SWE data from Daymet, which provides daily weather data at 1 km^2 spatial resolution (Thornton et al. 1997, 2014). We extracted SWE using ArcMap version 10.0 and R (version 3.0.2; R Core Team 2015) as bimonthly (January and February) average values for each distinct winter habitat KDE.

Survival analysis

We evaluated annual female survival and reproductive success with Cox proportional hazard (Cox PH) models using function `coxph` in the survival package (version 2.37-4) in R (version 3.1.3). Cox PH is an appropriate analysis for survival data collected from telemetry, because Cox PH is a time-to-event analysis that accounts for individuals having different exposure time to mortality (Cox 1972). Cox PH also accommodates staggered entry and censoring of individuals in or out of the

dataset. Parameter estimates from Cox PH were presented as the risk of female death, nest failure, or brood failure. Greater risk was associated with positive parameter estimates. Each variable in Cox PH models is assumed to have proportional hazard across time (proportional hazard assumption; Hosmer and Lemeshow 2000). We tested the proportional hazard assumption for all variables using function `cox.zph` in the survival package (Therneau and Grambsch 2000).

We conducted three separate survival analyses: (1) annual adult female, (2) nest, and (3) brood. These analyses were focused on comparing demographic benefits or consequences of migrating away from winter habitats (migratory status) or staying within winter habitats year-round (annual residency). This required us to classify each sage-grouse as migratory or non-migratory. We only included data from birds with at least one summer and one winter location, which allowed us to classify them as migratory or non-migratory. Distinct winter habitats ($n = 12$) from our winter habitat evaluation (75% KDE) were used as strata with the “strata” command in the “coxph” function, which fits separate baseline hazard functions for each strata. This accounted for inherent differences in annual female, nest, and brood survival.

Each female’s summer and winter locations were used to create variables describing migration and annual residency. A minimum convex polygon (MCP) was constructed for each female’s summer use (May–July) using ArcMap. Fall locations were not used due to greater location error. We measured the minimum Euclidean distance between winter use locations (1–3 locations per winter) and the edge of that bird’s summer MCP (migration distance). We created a categorical migration variable (migratory status) by classifying females with migration distance >10 km as migratory (Connelly et al. 2000). In addition to migration distance and migratory status, we quantified the proportion of a female’s summer MCP overlapping a winter habitat KDE ($PROP_{WIN}$). We created a categorical variable (annual residency) comparing females that stayed in winter habitats year-round to females that had <5% of their summer MCP overlapping a winter KDE. Both $PROP_{WIN}$ and annual residency were intended to assess whether demographic rates were different in winter habitats used for breeding compared to summer-only areas.

Annual female survival was analyzed with the Anderson-Gill formulation of Cox PH (Anderson and Gill 1982), which fits both fixed (time-independent) and time-dependent covariates (Hosmer and Lemeshow 2000). Time-dependent variables were included by constructing time intervals between visits for each unique individual (Therneau and Grambsch 2000). We used monthly time intervals with mortalities assigned to the month when the death occurred. Fixed variables included migration distance, migratory status, $PROP_{WIN}$, and annual residency. Time-varying variables included the age of the female (AGE; yearlings were reclassified as adults after their second summer), locations within or outside of a Core Area (CORE), season, average maximum monthly TEMP, total monthly PPT, and average monthly SWE. The season variable (WINTER) compared survival in the winter (December–February) to the remainder of the year. In addition to comparing survival within and outside of Core Areas, we included $CORE \times WINTER$ as an interaction to assess whether survival within or outside of Core Areas was different relative to the winter or remainder of the year. Climatic variables were obtained from Daymet (Thornton et al. 1997, 2014). We incorporated pairwise interactions to assess the potential of divergent survival relative to being in Core Areas or annual residency. Thus, we included $CORE \times PROP_{WIN}$, $CORE \times$ annual residency, migration distance \times annual residency, and migration status \times annual residency. Climatic variables were only examined as interactive effects with seasonal survival ($TEMP \times WINTER$, $PPT \times WINTER$, and $SWE \times WINTER$), which allowed us to evaluate climate effects during the winter separately from climate effects during the remainder of the year.

Nest and brood survival were analyzed with Cox PH models as cumulative exposure time enumerated from VHF-marked and GPS-marked sage-grouse. This formulation of Cox PH only allows fixed variables, which included migration distance, migratory status, $PROP_{WIN}$, annual residency, and CORE. Similar to the annual female survival analysis, we included interaction terms to assess potential divergence in survival relative to being in a Core Area or annual residency ($CORE \times PROP_{WIN}$, $CORE \times$ annual residency, migration distance \times annual residency, and migration status \times annual residency).

We used function `model.sel` in the MuMIn package (version 1.13.4) to compare all survival models with Akaike's information criterion corrected for small sample sizes (AIC_c) and Akaike weights (ω_i ; Burnham and Anderson 2002). All variables were screened to identify informative variables by conducting single variable Cox PH analyses, then eliminating any variable with a parameter estimate that had 85% confidence intervals (CIs) that overlapped zero as suggested by Arnold (2010). As the final modeling step, we compared all combinations of additive models with the informative variables. We considered all models within 4 ΔAIC_c of the top selected model competitive (Burnham and Anderson 2002). Multicollinearity was avoided by not including covarying variables ($r > |0.65|$) and/or variance inflation factor (VIF) < 10 in the same Cox PH model.

RESULTS

Winter and summer habitat

During 2008–2015, we used 9180 locations from 585 individual female sage-grouse to construct kernel density contours (75% and 95% KDE; Table 1). Kernel densities overlapped eight Core Areas of varying size (Fig. 1). Winter location error was estimated as 1693 m (standard error [SE] = 377 m) for the southwest region, 490 m (SE = 177 m) for the Atlantic Rim and Stewart Creek regions, and 169 m (SE = 25 m) for the Bighorn Basin region. All GPS-marked bird locations had error < 20 m. Winters with above- and below-average SWE had vastly overlapping KDE; thus, we only report on KDE for all winter locations combined (Fig. 1).

The proportion of sage-grouse habitat (95% KDE) overlap with Core Areas was substantial with 0.69 of summer and 0.50 of winter habitat within Core Areas (Table 2). However, proportion of sage-grouse habitat (95% KDE) overlap with 100% core regions (i.e., theoretical areas of sage-grouse conservation) was 0.95 and 0.91 of summer and winter, respectively (Table 3). This indicates that winter habitat was primarily nested within estimated breeding habitat (core regions); however, the Core Area Strategy disproportionately overlapped with summer habitats compared to winter habitats. Within individual Core Areas, proportional overlap of summer habitat with Core Areas ranged from 0.42 to 0.98, whereas

proportional overlap of winter habitat with Core Areas ranged from 0.12 to 0.74. In general, there was less overlap of winter habitats with each Core Area with the exception of Greater South Pass (Table 2). We did not find a consistent relationship between summer and winter habitat overlap with Core Areas (i.e., high summer overlap did not necessarily coincide with relatively higher winter overlap). Ratios of summer to winter habitat overlap also indicated high variability (range: 0.94–3.67) in protection provided by Core Areas for summer and winter habitats (Table 2).

Survival analysis

During 2008–2015, 374 female sage-grouse were included in our annual survival analysis. We found 81 females (21.7%) had at least one location outside Core Areas, 23.5% of nests were outside Core Areas, and 26.8% of broods were outside Core Areas during at least one relocation event. We documented 155 sage-grouse mortalities that occurred during the breeding season ($n = 84$; April–July), fall ($n = 36$; August–November), and winter ($n = 35$; December–March). There were 426 nests and 183 broods included in our nest and brood survival analyses. Estimated nest survival for all nests was 35.6% (SE = 0.03; 95% CI = 30.2–41.8), and estimated brood survival was 67.3% (SE = 0.04; 95% CI = 59.9–75.5). We did not detect multicollinearity (VIF < 2), and all Cox PH models adhered to the proportional hazard assumption.

For the annual female survival analysis, there were three competitive models within 4 ΔAIC_c of the top model that included combinations of AGE, TEMP \times WINTER, SWE \times WINTER, PROP_{WIN}, and CORE \times WINTER (Table 4). However, we only discuss the top model, because it included all of these variables. The null model was not competitive ($\Delta AIC_c = 71.96$; Table 4). Both SWE \times WINTER and PROP_{WIN} were informative parameters with 85% CI not overlapping zero; however, parameter estimates for both were considered marginal with 95% CI that overlapped zero (risk score 0.98 [95% CI: 0.95–1.01] and 0.68 [95% CI: 0.44–1.05], respectively). All other parameter estimates had 95% CI that did not overlap zero. Yearling female sage-grouse had lower risk of death compared to females ≥ 2 years of age (risk score 0.07 [95% CI: 0.01–0.48]). The TEMP \times WINTER and SWE \times WINTER interactions indicated that higher TEMP and lower SWE during the breeding

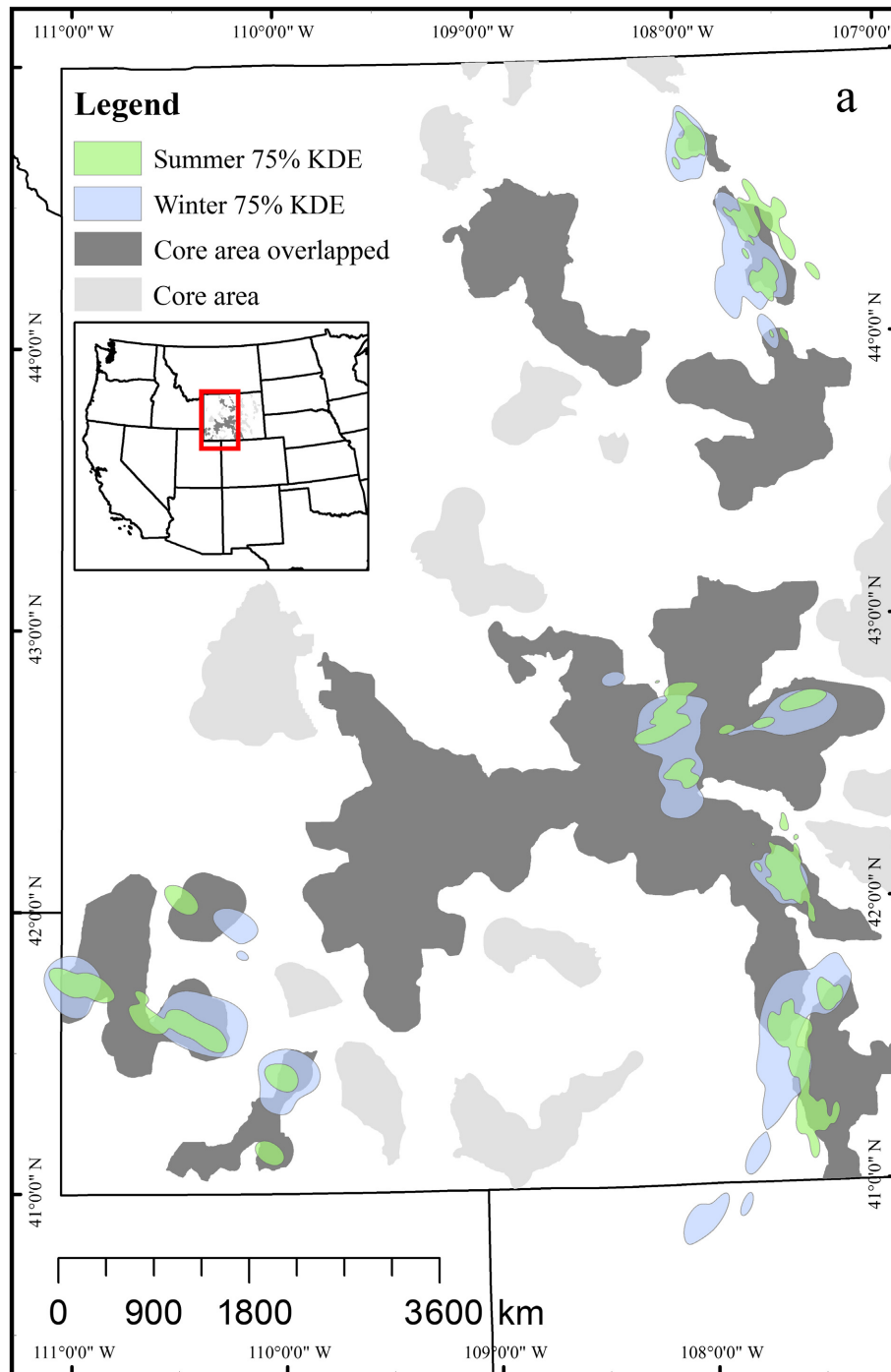
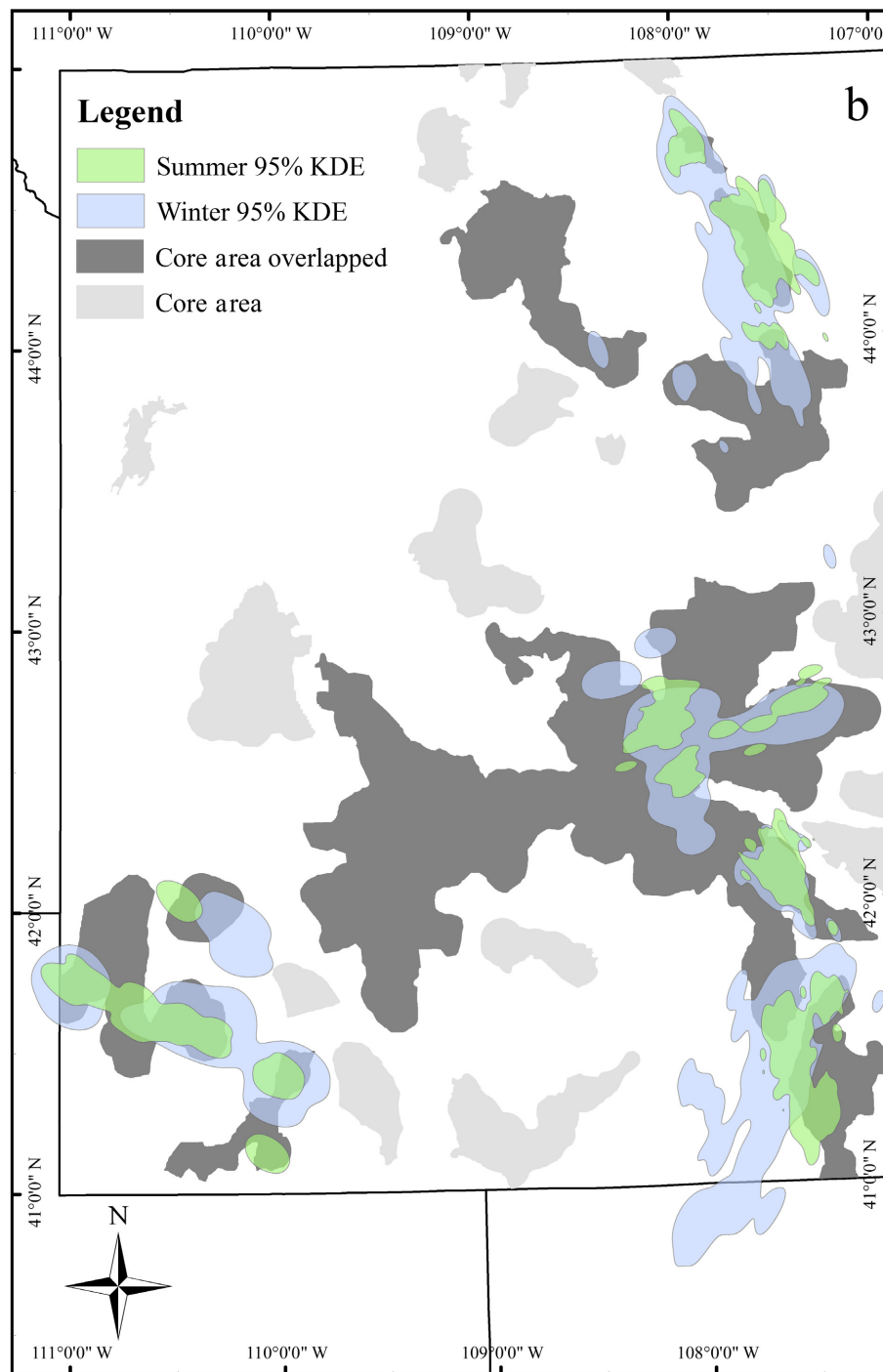


Fig. 1. Sage-grouse habitat use for summer and winter calculated as (a) 75% contour and (b) 95% contour of kernel density estimation (KDE) in Wyoming, USA. Inset map of the western United States. During 2008–2014, female sage-grouse locations during summer ($n = 7692$) and winter ($n = 1488$) were used to create kernel densities. Summer data were collected from April to August. Winter data were collected from December to February.



(Fig. 1. Continued)

Table 2. Overlap of female sage-grouse summer, winter, and annual use within eight Sage-grouse Core Areas in Wyoming (Core Area), USA.

Core Area	Contour (%)†	Bird use in Core Area (km ²)	Proportional overlap of bird use with Core Areas			
			Summer	Winter	Annual	Summer:winter
Fontenelle	75	136	0.62	0.39	0.48	1.59
Hyattville	75	460	0.51	0.47	0.43	1.09
Greater South Pass	75	2214	0.66	0.70	0.64	0.94
Sage	75	967	0.89	0.74	0.76	1.20
Shell	75	78	0.42	0.22	0.22	1.91
South Rawlins	75	364	0.44	0.12	0.20	3.67
Uinta	75	328	0.75	0.54	0.60	1.39
Washakie	75	45	0.98	0.50	0.56	1.96
All Core Area	75	4592	0.75	0.62	0.62	1.21
All Core Area	95	8476	0.69	0.50	0.51	1.38

Notes: During 2008–2014, female sage-grouse locations during summer ($n = 7692$) and winter ($n = 1488$) were used to create 75% and 95% contours of kernel density estimations of summer, winter, and annual use. Sage-grouse were located in five distinct study regions throughout Wyoming, USA.

† Contour of the kernel densities used to calculate overlap is denoted as 75% or 95%.

Table 3. Overlap of female sage-grouse use (75% and 95% contours of summer, winter, and annual kernel density estimation [KDE]) within core regions (75% and 100%).

Sage-grouse KDE (%)†	Core region (%)‡	Proportional overlap of bird use with breeding density			
		Summer	Winter	Annual	Summer:winter
75	75	0.86	0.85	0.83	1.01
75	100	0.97	0.98	0.97	0.99
95	75	0.80	0.71	0.71	1.13
95	100	0.95	0.91	0.91	1.04

Note: During 2008–2014, female sage-grouse locations during summer ($n = 7692$) and winter ($n = 1488$) were used to create 75% and 95% KDEs of summer, winter, and annual use. Sage-grouse were located in five distinct study regions throughout Wyoming, USA.

† Contour of the KDE used to calculate overlap is denoted as 75% or 95%.

‡ Core regions from Doherty et al. (2011), which were the minimum areas to conserve 75% or 100% of breeding sage-grouse within 8.5 km of leks.

Table 4. Top 10 models for annual female survival based on Cox proportional hazard (Cox PH) analyses.

Models	K	ΔAIC_c	ω_i
AGE + CORE × WINTER + PROP _{WIN} + TEMP × WINTER + SWE × WINTER†	9	0.00	0.48
AGE + CORE × WINTER + TEMP × WINTER + SWE × WINTER	8	1.00	0.29
AGE + PROP _{WIN} + TEMP × WINTER + SWE × WINTER	7	3.60	0.08
AGE + TEMP × WINTER + SWE × WINTER	6	4.73	0.04
AGE + CORE + PROP _{WIN} + TEMP × WINTER + SWE × WINTER	8	5.21	0.04
AGE + CORE + TEMP × WINTER + SWE × WINTER	7	6.03	0.02
AGE + CORE × WINTER + TEMP × WINTER	6	6.22	0.02
AGE + CORE × WINTER + PROP _{WIN} + TEMP × WINTER	7	6.32	0.02
AGE + TEMP × WINTER	4	9.80	0.00
AGE + PROP _{WIN} + TEMP × WINTER	5	9.87	0.00
Null $\Delta AIC_c = 71.96$			

Notes: Cox PH models included distinct winter habitats as strata. Models were compared with Akaike's information criterion (adjusted for small sample sizes; AIC_c) and Akaike weights (ω_i). Data were collected from 374 female sage-grouse in five distinct study regions throughout Wyoming, USA, during 2008–2015.

† $AIC_c = 822.59$.

season and fall were detrimental to survival, while TEMP and SWE had no effect on survival in the winter (Fig. 2a–d). Females that had a greater proportion of their summer MCP in a winter habitat KDE (higher PROP_{WIN} values) had less risk of death (Fig. 2e). This finding supports the hypothesis that females remaining relatively more localized to a winter habitat year-round benefitted with higher annual survival. Finally, our CORE × WINTER interaction term suggested the lowest risk of death for sage-grouse was during the winter in Core Areas (Fig. 3). The mean risk of death during the winter outside of Core Areas was lower than the breeding season and fall but had overlapping 95% CI for risk of death (Fig. 3). Models describing differences in reproductive success did not perform better than their respective null models (Table 4). Thus, there was no evidence that nest or brood survival was higher for females that choose to migrate or move away from winter habitats. We did not find any evidence for differences in nest or brood survival within or outside Core Areas.

DISCUSSION

Conservation of seasonal habitats is of vital importance for stabilization of declining animal populations. The Wyoming Core Area Strategy seeks to limit negative impacts of human development in the highest quality habitat for sage-grouse by restricting surface disturbance within 6.4 km radius buffers around leks (Doherty et al. 2011). We found winter to be a time frame of high female survival compared to other times of the year, and winter habitats yielded relatively higher female survival during spring, summer, and fall compared to summer habitats that occurred outside of winter habitat KDEs. Other studies have documented high overwinter survival for sage-grouse (Beck et al. 2006, Connelly et al. 2011, Baxter et al. 2013, Blomberg et al. 2013, Smith et al. 2014), but no other study—to our knowledge—has found higher breeding season and fall survival in winter habitats. Yet, winter habitats have rarely been of primary concern when delineating conservation areas for sage-grouse at a large spatial scale, which likely reflects the difficulty in obtaining data on winter habitat use. Although breeding habitat—defined as the area within 8.5 km of a lek—was a good surrogate for delineating all seasonal habitats for sage-grouse, Core

Areas provided habitat protections disproportionately for summer habitats compared to winter. We suggest future conservation plans specifically incorporate mechanisms to include more winter habitat within conservation areas.

Small differences in demographic rates can lead to diverging life history traits, behavioral patterns, and species distributions (Clark and Ehlinger 1987, Roff 1992, Stearns 1992, Wilson 1998, Gotelli 2008, Burton et al. 2010). Differential annual survival and reproduction have been connected to development of partial migration in elk (*Cervus elaphus*; Hebblewhite and Merrill 2011), mule deer (*Odocoileus hemionus*; Nicholson et al. 1997), and European robins (*Erithacus rubecula*; Adriaensen and Dhondt 1990). Sage-grouse are well known to migrate to more productive areas while brood-rearing (Fischer et al. 1996, Gregg and Crawford 2009, Dinkins et al. 2014b). However, our results did not suggest migratory sage-grouse realized higher annual reproductive output. Females with lower mortality risk could compensate for low annual reproductive success by surviving more breeding seasons. Unfortunately, we were unable to assess differences in lifetime reproduction. A caveat to our analyses is winter habitats were treated as somewhat homogenous, which was not likely to be the case because some areas of winter habitat were likely more productive than others. Our analysis was intended to quantify potential reproductive differences at a broad scale. However, access to more productive areas may not require migration of >10 km. Seasonal habitat use for sage-grouse may be driven by site fidelity (Fischer et al. 1993, Holloran and Anderson 2005, Thompson 2012), which would foster lower risk of mortality and greater reproductive success due to a female's familiarity with a localized area. Other grouse species have been observed to learn seasonal migrations in relation to juvenile dispersal (Schroeder 1985, Cade and Hoffman 1993, Schroeder and Braun 1993, Alonso et al. 2000), which may help explain partial migration of these species.

Sage-grouse can be susceptible to extreme weather with deep snow during winter (Moynahan et al. 2006, Anthony and Willis 2009). However, we found that climatic variables influenced breeding season and fall survival but had no effect during winter. This likely indicates that our study regions had sufficient habitat to buffer sage-grouse during severe winters, or we did not

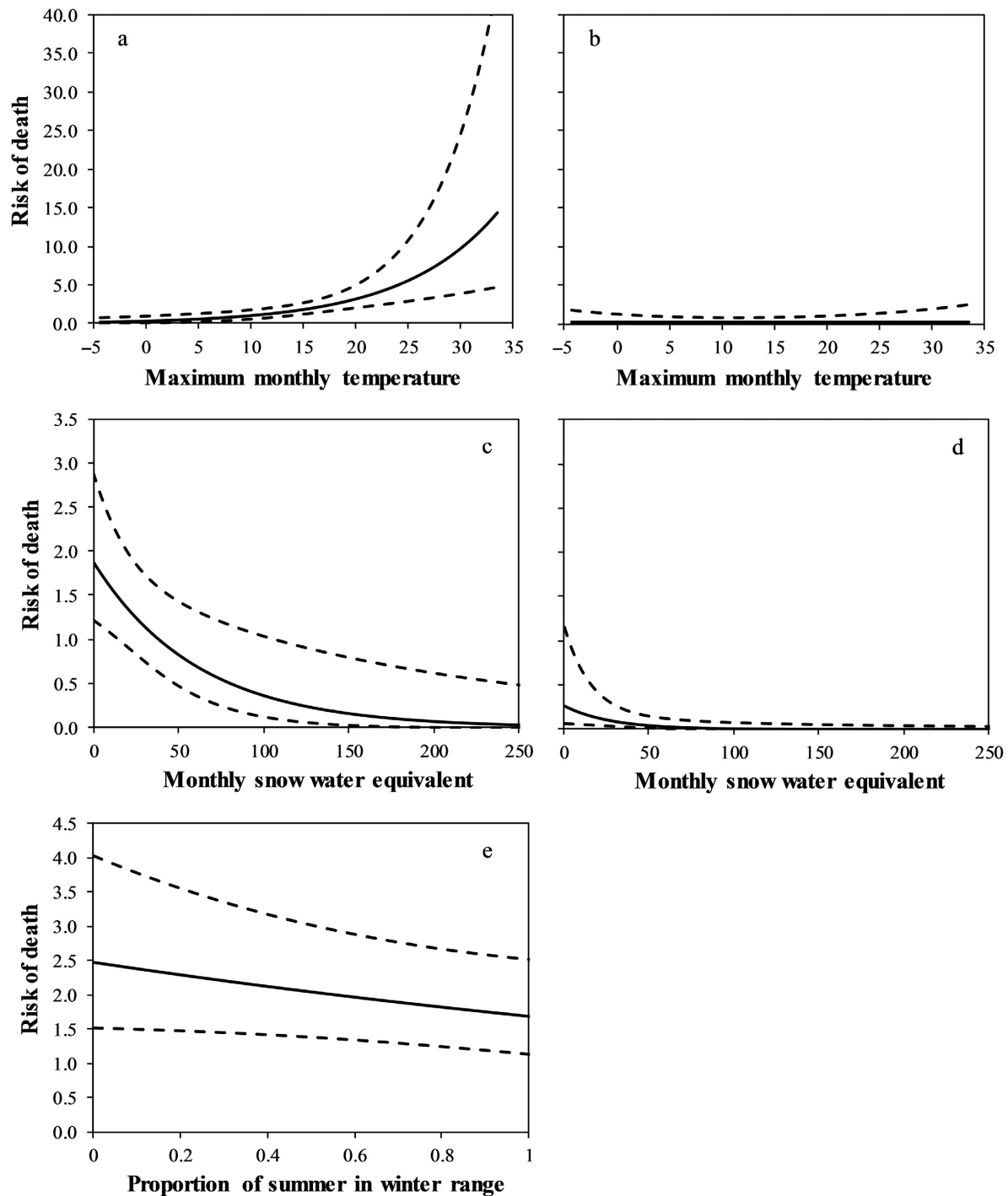


Fig. 2. Predicted effects ($\pm 95\%$ confidence interval [CI]) of (a) maximum monthly temperature (TEMP) during breeding and fall seasons, (b) maximum monthly TEMP during winter, (c) snow water equivalent during breeding and fall seasons, (d) snow water equivalent during winter, and (e) proportion of summer minimum convex polygon for each female within winter habitat ($PROP_{WIN}$) on annual female survival with 95% CIs. The y -axis was plotted as $\exp(\text{coefficient values})$, which was the risk of death. All other parameters were held at their mean values. Data were collected from 374 sage-grouse females from five distinct study regions throughout Wyoming, USA, during 2008–2015.

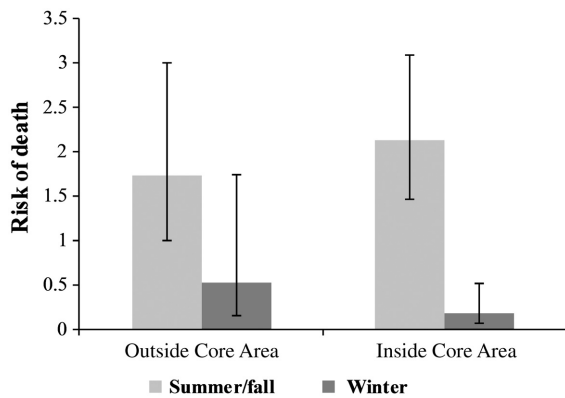


Fig. 3. Predicted risk of death ($\pm 95\%$ confidence interval) for adult females during the winter vs. the remainder of the year stratified by areas within and outside of Core Areas. The y -axis was plotted as $\exp(\text{coefficient values})$, which was the risk of death. All other parameters were held at their mean values. Data were collected from 374 sage-grouse females from five distinct study regions throughout Wyoming, USA, during 2008–2015.

observe a truly severe winter. Continued degradation and loss of winter habitat has the potential to increase negative effects on female survival during severe winters.

Our analyses did not find a difference in reproductive rates of grouse migrating to theoretically better breeding habitat. However, our mapping results demonstrated that net reproduction from all birds associated with a winter habitat magnifies the importance of maintaining high-quality winter habitat. In other words, birds breeding outside of winter habitats were reliant on winter habitats for winter survival; thus, degraded winter habitat could equate to loss of reproduction from a much larger spatial footprint. Sage-grouse were using a greater proportion of habitat outside of Core Areas in the winter, which indicates habitat surrounding Core Areas was important for sage-grouse during the winter. Sage-grouse avoid infrastructure in winter (Doherty et al. 2008, Carpenter et al. 2010, Smith et al. 2014, Holloran et al. 2015), and survival during winter is a function of the remaining habitat that grouse will use in developed sagebrush landscapes (Smith et al. 2014). In addition, sage-grouse were congregated during the winter and some females relied on winter habitat year-round, which indicates disturbances within winter habitats may

have much broader consequences for sage-grouse populations.

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