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Reproductive state leads to intraspecific habitat partitioning and survival differences in greater sage-grouse: implications for conservation

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Abstract

Context. Inter- and intraspecific habitat partitioning is widespread across taxa, yet limited information is available on differences in intraspecific habitat selection by same-sex individuals among differing reproductive states. Understanding habitat selection by conspecifics of different reproductive states may help optimise conservation efforts, particularly for gallinaceous bird species such as greater sage-grouse (*Centrocercus urophasianus*), which are long-lived but have only moderate reproductive rates.

Aims. We predicted that habitat use differed between grouse under different reproductive states and that reproductive investment decreased survival of adults in summer.

Methods. We compared habitat characteristics used by brood-rearing and broodless female sage-grouse and evaluated the influence of reproductive investment and habitat use on survival of adult females.

Key results. We found that brood-rearing and broodless female sage-grouse partitioned habitat at micro- and macrohabitat scales. Broodless females were more likely to survive the summer.

Conclusions. Our findings suggest reproductive state variability in habitat selection by female sage-grouse. Broodless females were roosting and foraging in concealed habitats with intermediate visual obstruction and annual vegetation productivity, but less food forb availability compared with early and late brood-rearing females. In contrast, brood-rearing females likely selected more herbaceous understoreys to predictably maximise foraging opportunities and promote growth of their chicks, which appeared to mitigate the influence of reproductive costs on summer survival, particularly during the late brood-rearing period.

Implications. Survival of adult females is critical for population persistence of sage-grouse and other long-lived Galliformes, yet conservation efforts generally focus on habitats used during nesting and brood-rearing. Our results suggest that habitat partitioning is a potential risk-aversion strategy where individuals across different reproductive states likely select habitats to maximise their survival. Conservation efforts should focus on conserving habitats used by both brood-rearing and broodless sage-grouse to ensure population persistence.

Additional keywords: behavior, breeding status, reproduction.

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Introduction

Species that occupy heterogeneous landscapes utilise a spectrum of habitats throughout their life-cycles, potentially making inference about habitat use and identifying important habitats for conservation difficult (Donovan and Thompson 2001). Assessing interspecific and intraspecific habitat partitioning between species and among conspecifics may clarify inferences about habitat selection (e.g. Bañuelos *et al*. 2008; Alves *et al*. 2013); both inter- and intraspecific habitat partitioning are widespread across taxa and between sexes (Burger *et al*. 1977; Werner *et al*. 1977; Cumming *et al*. 1996). Several hypotheses have been proposed to explain sexual habitat segregation including the predation risk hypothesis developed for ungulate species (Bowyer 2004; Ruckstuhl 2007). The predation risk hypothesis proposes that males select riskier habitats that offer higher-quality forage, whereas reproductive females trade off forage quality to enhance offspring survival (Main and Coblentz 1996; Ruckstuhl 2007; Alves *et al*. 2013). Habitat-based segregation (Main and Coblentz 1996; Conradt 1999) may also apply to individuals of the same sex under different reproductive states, which must be accounted for when assessing individual variability of resource use (Bolnick *et al*. 2003). Because habitat choices often influence survival (Wilson and Nussey 2010), accounting for sex-specific or reproductive-state variability is necessary for identifying important habitats for conservation.

Reproductive costs imposed on individuals represent tradeoffs between current reproductive effort and future survival under limited energy constraints (Harshman and Zera 2007). These tradeoffs may occur in relatively long-lived species when reproducing individuals balance survival with rearing young to maximise lifetime reproductive success (Erikstad *et al.* 1998). Tradeoffs may also occur following reproductive attempts; the success of reproductive females depends on their own survival as well as offspring survival, whereas unsuccessful females must survive to reproduce in subsequent breeding periods to maximise lifetime reproductive success. Individuals in different reproductive states may utilise various habitats to mitigate these tradeoffs. For example, red deer (*Cervus elaphus*) (Alves *et al.* 2013) and noctule bats (*Nyctalus noctula*) (Mackie and Racey 2007) use different habitats under different reproductive states. In both species, non-reproductive females select different habitats or foraging resources than reproductive females. For species with high maternal parental investment, differences in habitat selection may result as differential responses to risk stimuli under distinct reproductive states (Frid and Dill 2002; Laundre *et al.* 2010). Females with young may be faced with balancing predation risk with foraging opportunities for the adult and dependent young (Main and Coblentz 1996; Ruckstuhl 2007); however, information on habitat partitioning across reproductive states is limited.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a species of great conservation concern (US Fish and Wildlife Service 2015), currently occupying ~668 000 km^2 of sagebrush (*Artemisia* spp.) across <60% of their historic range (Schroeder *et al.* 2004). Sage-grouse face significant threats from range-wide habitat loss and degradation (Connelly *et al.* 2004). Research has repeatedly documented sexual habitat partitioning in sage-grouse during different times of the year (see Connelly *et al.* 2011*a*), but habitat partitioning of females under different reproductive states has received little attention. Sage-grouse, unlike most other gallinaceous species, more closely align with a *K*-selection strategy because they are a relatively long-lived species with only moderate reproductive rates (Pianka 1970; Connelly *et al.* 2011*b*). Growth of sage-grouse populations is particularly sensitive to adult female survival (Johnson and Braun 1999; Schroeder *et al.* 1999; Taylor *et al.* 2012; Dahlgren *et al.* 2016) and range-wide nest success estimates for sage-grouse are generally low as approximately half of the females fail to produce a brood during most years (Schroeder *et al.* 1999; Connelly *et al.* 2011*b*). This is in spite of the fact that nest initiation rates are extremely high (>0.89: Taylor *et al.* 2012). Because adult female survival is critical to sage-grouse persistence, conservation actions that promote adult female survival across all reproductive states may be most beneficial to sage-grouse populations (Taylor *et al.* 2012; Dahlgren *et al.* 2016). Survival of adult female sage-grouse is typically lowest during the breeding season (Moynahan *et al.* 2006; Baxter *et al.* 2013; Blomberg *et al.* 2013) and research has suggested that reproductive investment is negatively correlated with annual adult survival (Blomberg *et al.* 2013).

Identifying habitats used by brood-rearing and females without broods (hereafter broodless) is important when prioritising habitat for sage-grouse; however, most research has focussed on nesting or brood-rearing habitats (e.g. Hagen *et al.* 2007; Connelly *et al.* 2011*a*), leaving a knowledge gap regarding habitat selection by broodless females. Some research suggests that broodless females generally move to mesic sagebrush habitats earlier in the summer than females with broods (Gregg *et al.* 1993). Earlier and longer-distance movements by broodless females compared with brood-rearing females is likely explained by limited mobility of young chicks that are not capable of flight until ~2 weeks after hatch (Wallestad 1971). Because broodless females are more mobile they likely select habitats to minimise predation risk and maximise foraging opportunities and select distinct locations for roosting and diurnal foraging to minimise these risks (Dumroese *et al.* 2015). Reduced movements by adult females with broods may indicate that habitat choice is especially critical during this time to maximise chick growth while simultaneously minimising predation risk (Drut *et al.* 1994; Gregg and Crawford 2007; Huwer *et al.* 2008; Blomberg *et al.* 2012; Guttery *et al.* 2013).

Macrohabitat- (Shepherd *et al.* 2011; Kirol *et al.* 2015) and microhabitat-scale (Gregg *et al.* 1993; Bunnell *et al.* 2004) habitat selection has been assessed for broodless females, but we are unaware of any studies that have evaluated microhabitat selection by brood-rearing and broodless female sage-grouse simultaneously. Differences in selection among brood-rearing and broodless females of other grouse species (e.g. Bañuelos *et al.* 2008) highlights the importance of understanding habitat partitioning across different reproductive states and how this might relate to adult female survival during the same period.

In our study, we compared potential differences in habitat selection by brood-rearing and broodless female sage-grouse roosting locations during the breeding season. We predicted that brood-rearing females would occupy more open sagebrush habitats with greater forb availability to meet the nutritional requirements of dependent chicks. We predicted that broodless females would occupy denser sagebrush habitats for roosting because their increased mobility facilitates movement between distinct roosting and foraging locations. Research has demonstrated that both reproductive costs and habitat use may influence survival of female sage-grouse (Blomberg *et al.* 2013; Kirol *et al.* 2015). Thus, we also evaluated survival of adult females in summer relative to reproductive costs and evaluated whether survival was also associated with habitat use. We predicted that reproductive costs would influence female survival in summer and brood-rearing females occupying more open sagebrush habitats would experience greater mortality risk than broodless females occupying areas with potentially greater concealment cover.

Materials and methods

Study area

Our study area was located in portions of Fremont and Natrona counties, in central Wyoming, USA (42.63°N, 107.92°W) encompassing ~3098 km^2. Elevation ranged from 1644 to 2439 m and included ~81% Federal, 7% State, and 12% privately administered lands. Annual precipitation ranged from ~13.3 to 33.7 cm (NOAA 2016). Vegetation communities in the study area were dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) at higher elevations, with inclusions of basin big sagebrush (*A. t. tridentata*), black sagebrush (*A. nova*), greasewood (*Sarcobatus vermiculatus*), and silver sagebrush (*A. cana*). The major land use in the area was livestock grazing.

Capture and monitoring

We captured and radio-marked female sage-grouse near leks in spring 2011–13 by spot-lighting and hoop-netting (Giesen *et al*. 1982; Wakkinen *et al*. 1992). We used roosting locations of radio-marked females captured in spring to capture and radio-mark additional females in August each year. We attached radio-transmitters (22 g, Model A4060; Advanced Telemetry Systems Inc., Isanti, MN, USA; <3% body mass) to females with a PVC-covered wire necklace. We began locating female sage-grouse weekly during late April each year with R-1000 hand-held receivers and 3-element antennas (Communication Specialists, Orange, CA, USA). We used fixed-wing aircraft flights to locate individuals not located from ground searches. All sage-grouse were captured, marked, and monitored in accordance with approved protocols (Wyoming Game and Fish Department Chapter 33-801 permit and University of Wyoming Institutional Animal Care and Use Committee protocol 03132011).

We monitored all females weekly irrespective of nesting or brood status from 1 May through 15 August of each year. Consequently, if a female was not documented on a nest or a nesting female was unsuccessful (i.e. failed to hatch at least one egg: Rotella *et al*. 2004), we continued to monitor the female and considered that individual to be broodless unless a renesting attempt was documented. We located nests of radio-marked females by triangulating the signal until the female was spotted or when the location was isolated to a single nest shrub or shrub patch. Once a female was determined to be nesting, we monitored the nest weekly until the female was no longer located in the area to determine nest fate. We monitored nests from a distance of ≥30 m and left the area in an erratic pattern to reduce the potential of the researcher to influence nest predation (i.e. leaving a scent trail to the nest: Kirol *et al*. 2012). For successfully hatched nests we determined whether the female was with a brood by visual observations of chicks or brooding behaviour by the female (Kirol *et al*. 2012). If no brooding behaviour was detected during two successive telemetry visits, we estimated the date of brood loss as the midpoint between the last date when the female was determined to be with a brood and the first visit when a brood was not detected. We further assessed brood fate by night-time spotlight counts at ~35 days after hatching and considered broods successful when at least one chick was present with the hen at this time (Walker 2008; Kirol *et al*. 2015).

Habitat sampling and analysis

We evaluated vegetative and ground cover microhabitat parameters at randomly selected brood-rearing locations (early and late brood-rearing periods), summer broodless female locations, and random locations along two perpendicular 30-m transects centred at each grouse and random location aligned in cardinal directions. We measured microhabitat variables that have been shown to be important predictors of microhabitat selection by sage-grouse in other studies (e.g. Hagen *et al*. 2007; Kirol *et al*. 2012; Dinkins *et al*. 2016) (Table 1), as well as variables that we suspected to be biologically relevant. We defined the early brood-rearing period as the 2-week period following nest hatch (Bergerud and Gratson 1988; Thompson *et al*. 2006), and estimated microhabitat characteristics at two locations during 2011 and one location during 2012 and 2013 for each brood-rearing female during this period. For late brood-rearing (2–5 weeks after hatching), we recorded habitat characteristics at two locations in 2011 and one location in 2012 and 2013 when chicks were estimated to be between 20 and 35 days of age. We sampled no more than two locations for each broodless female during each year. We separated brood-rearing between early and late periods because chicks are not capable of flight until ~2 weeks after hatch (Wallestad 1971), resulting in more restricted movement during that time. Broodless female locations were sampled between late June and July each year. Sampling was conducted as soon as possible after each telemetry visit, but no later than two weeks after the individual was located. We estimated herbaceous and ground cover attributes using the Daubenmire (1959) technique in 20×50 cm quadrats ($n = 17$ quadrats location^{-1}) placed at predetermined locations along both 30-m transects. We recorded shrub canopy cover with the line intercept method and computed percentage cover for each shrub species (Canfield 1941; Wambolt *et al*. 2006). We recorded shrub density by counting shrubs rooted within 1-m belt transects positioned along the right side of each 30-m transect. Visual obstruction was measured using a Robel pole (dm: Robel *et al*. 1970) placed in the centre of each location and measurements were recorded from a distance of 5, 10, and 15 m at 1-m height from each cardinal direction. We measured the droop height of current and residual perennial grasses in each 20×50 cm quadrat and the height of the tallest leader, excluding inflorescences, for each shrub encountered along each 30-m line transect. We examined microhabitat at paired random locations constrained by a random distance (100–500 m) and direction from each sage-grouse use location (Aldridge and Boyce 2008), during the same day that use locations were sampled.

We were interested in potential differences in selection by sage-grouse under different reproductive states compared with available habitat. We first used multinomial logistic regression models using function 'multinom' in package 'nnet' in R (Venables and Ripley 2002; R Core Team 2015), where resource use was identified as microhabitat sampling locations for radio-marked early brood-rearing, late brood-rearing, or broodless female sage-grouse, and resource availability was defined as random microhabitat sampling locations. Multinomial logistic regression is useful for modelling habitat selection when there are >2 response categories. This method allowed for simultaneous comparisons of microhabitat selection by early brood-rearing, late brood-rearing and broodless females relative to available habitats in a single model with the same predictor variables across reproductive states. Similar approaches have been used to assess the influence of habitat predictors on nesting and brood-rearing sage-grouse (Dinkins *et al*. 2014) and brood-rearing and broodless capercaillie (*Tetrao urogallus cantabricus*) (Bañuelos *et al*. 2008).

Table 1. Variables used in model selection to evaluate greater sage-grouse microhabitat selection in central Wyoming, USA, 2011–13

Ground cover and herbaceous canopy cover were estimated from 17 Daubenmire (0.1 m^2) quadrats at each location

Variable names	Description
Ground cover (%)	
Bground[A]	Mean bare ground from Daubenmire quadrats
Cactus[A]	Mean cactus cover from Daubenmire quadrats
Crypto[A]	Mean biological soil crust cover from Daubenmire quadrats
Gravel[A]	Mean gravel cover from Daubenmire quadrats
Litter	Mean litter from Daubenmire quadrats
Height and visual obstruction	
BsageH[A,B,C]	Mean big sagebrush height (cm) for each plant along two perpendicular 30-m transects
ShrubH[A,B,C]	Mean total shrub height (cm) from each plant along two perpendicular 30-m transects
PerGrassH	Averaged maximum perennial grass droop height (cm) from Daubenmire quadrats
ResGrassH	Averaged maximum residual grass droop height (cm) from Daubenmire quadrats
VO[B]	Visual obstruction estimated from Robel pole (dm)
Herbaceous canopy cover (%)	
AnGrass[A]	Mean annual grass cover from Daubenmire quadrats
PerGrass[A]	Mean perennial grass cover from Daubenmire quadrats
ResGrass[A]	Mean residual grass cover from Daubenmire quadrats
FoodF[A,C]	Mean food forb cover from Daubenmire quadrats
NFoodF	Mean non-food forb cover from Daubenmire quadrats
SpeciesR	Mean food forb species richness from Daubenmire quadrats
Shrub characteristics	
Bsage[A,B,C]	Mean big sagebrush cover (%) measured from two perpendicular 30-m transects
BsageD	Big sagebrush density (plants m^{-2}) measured along two perpendicular 30-m transects
Shrub[B,C]	Mean total shrub cover (%) estimated from two perpendicular 30-m transects
ShrubD[1]	Total shrub density (plants m^{-2}) measured along two perpendicular 30-m transects

[A] Variables were not brought forward following initial screening.

[B] Quadratic transformations assessed.

[C] Standard deviation assessed with two perpendicular 30-m transects for cover and height.

Prior to model selection, both non-informative variables with 85% confidence intervals of parameter estimates overlapping 0 (Arnold 2010) and single-variable models that had Akaike's information criterion adjusted for small sample size (AICc: Burnham and Anderson 2004) values higher than the intercept-only model were removed. We computed Pearson's correlation matrix to test for collinearity among predictors and removed the less predictive of two correlated variables based on AICc when correlation coefficients (r) were $\geq |0.6|$. We explored all combinations of the remaining variables that were brought forward following initial variable screening procedures (Burnham and Anderson 2002). The model with the lowest AICc score was identified as being the best fit model; however, models within 4 AICc of the top model were considered competitive (Arnold 2010). After the best model(s) were identified, we used binomial generalised mixed models with package 'lme4' (Bates *et al*. 2015) using predictor variables from competitive multinomial logistic regression models to evaluate reproductive states individually. Resource use was defined as either early brood-rearing, late brood-rearing, or broodless female microhabitat sampling locations and resource availability was defined as random locations. All models included individual as a random intercept term to account for potential differences in microhabitat selection by year and repeated sampling of microhabitat locations for each individual.

We used a second set of binomial generalised mixed models to identify habitat selection across reproductive states using remotely sensed products at the macrohabitat scale. This was necessary to test our predictions that adult female survival was related to both reproductive costs and the habitats used over the entire summer season to match our adult female survival analysis period. Note that we were unable to collect microhabitat information at every female telemetry location across the summer season. We developed a single model for each reproductive state using an integrated normalised difference vegetation index (INDVI; 250-m resolution) generated for each year as the sole predictor variable. INDVI provides a metric of growing season production of vegetation and has been linked to plant nutritional quality and insect abundance (Pettorelli *et al*. 2005, 2011). Normalised difference vegetation index (NDVI) has been positively associated with sage-grouse summer habitat selection and population productivity (Blomberg *et al*. 2012; Dinkins *et al*. 2014). Resource use was identified as early brood-rearing, late brood-rearing, or broodless female locations and resource availability was defined as available locations. Available locations were generated at a rate of five times the number of used locations for each reproductive state and were restricted to a 90% fixed kernel surrounding all summer locations (default bivariate kernel smoothing parameter: Worton 1989; Calenge 2006), representing a population level design (Type 1 Design *sensu* Thomas and Taylor 2006).

Adult female survival

We evaluated adult female survival relative to reproductive status, total reproductive effort, brooding effort, and distance moved between subsequent relocations. We defined reproductive status as the behaviour (nesting, brood-rearing, roosting) during the previous telemetry visit. Total reproductive effort was defined as the estimated number of weeks spent incubating and brood-rearing, whereas brooding effort was the number of weeks spent brood-rearing following a successful nesting attempt during the previous telemetry visit, respectively. Total reproductive effort and brooding effort represented the cumulative effects of reproductive activities that could not be captured with reproductive status during the previous week. That is, we expected that cumulative effects of nesting and brood rearing activities may better explain mortality risk rather than the reproductive status of an individual during the previous monitoring interval. We truncated total reproductive effort and brooding effort to reflect uncertainty in brood retention following night-time spotlight counts at 35 days (five weeks) after hatching. Chicks often become more visible as they grow; however, brood flocking behaviour makes parental assessment difficult after ~5 weeks (Dalke *et al*. 1963; Dahlgren *et al*. 2010). Therefore, the maximum value of total reproductive effort of ~9 weeks was reflective of the incubation period for successful nests (27 days; 25–29-day incubation period: Schroeder Young and Braun 1999) plus the estimated age when night-time spotlight counts were conducted (35 ± 0.3 (s.e.) days after hatching). Average distance moved was estimated as the linear distance between consecutive relocations. We assessed brood movement because more mobile broods could have increased exposure to predators or experienced greater movements due to insufficient local food resources (Drut *et al*. 1994; Gibson *et al*. 2017).

We used mixed-effects Cox's proportional hazards regression (Cox PH: Cox 1972) using function 'coxme' in package 'coxme' in R (Therneau 2015; R Core Team 2015) to identify relationships between predictor variables and sage-grouse reproductive seasonal survival with the counting process (Andersen and Gill 1982; Therneau and Grambsch 2000). Year was included as a random effect in all models. The counting process accounts for time-dependent and discontinuous hazard intervals, and allows baseline hazards to vary with time (Allison 2010). Cox PH assisted in assessing variables that had the greatest influence on adult survival (Hosmer and Lemeshow 1999). To align with our observation intervals that were ~7 days, we modelled weekly female survival from nesting (1 May) through 15 August during each year for all females (~15-week survival period: Winterstein *et al*. 2001). We used left and right censoring to properly incorporate individuals entering and leaving the study at different times (Winterstein *et al*. 2001). If a female was never located on a nest, we used the average day of nest initiation for each year as the day that individual entered the sample. We estimated mortality dates from the last known telemetry monitoring interval, and used the midpoint between the last two locations (most recent location determined alive and date when located dead) as the estimated mortality date. Individuals that did not die during the study were right censored.

We used AICc (Burnham and Anderson 2002) to evaluate model support for Cox PH models. We assessed correlation between covariates and did not allow variables to compete in the same model when $r \geq |0.6|$. We brought forward variables when single-variable models showed an improvement over the null model and explored all variable combinations of non-correlated variables to evaluate model support. Once we identified the most predictive model explaining female survival relative to reproductive investment, we included INDVI and interaction terms of the main effects to assess model improvement over the reproductive model. We assured that proportional hazards assumptions were met by examining Schoenfeld residuals for each covariate in the top model (Schoenfeld 1982).

Results

We sampled 233 female sage-grouse plots (68 early brood-rearing, 49 late brood-rearing, 116 broodless female), and 233 random microhabitat plots for 133 radio-marked female sage-grouse from 1 May to 15 August 2011–13. We monitored 32, 80, and 101 individuals during 2011, 2012, and 2013, respectively. Microhabitat plot sampling dates ranged from 14 May to 5 July for early brood, 12 June to 20 July for late brood, and 30 June to 27 July for broodless females. The percentage of broodless females (i.e. females that failed to hatch a nest or lost their chicks before 5 weeks of age) during 2011, 2012, and 2013 breeding seasons ranged from 69.5 to 82.6%. Average weekly movement distance between estimated relocations was 1518 ± 116 m (s.e.) for brood-rearing females and 1539 ± 78 m (s.e.) for broodless females.

Habitat selection

Eight multinomial logistic regression models, including nine variables, were competitive, explaining microhabitat selection across all sage-grouse reproductive states (Table 2). We used all variables across competitive models to evaluate microhabitat selection for each reproductive state individually. Shrub canopy cover variables included big sagebrush density (individual plants m^{-2}) and shrub cover variability. Big sagebrush density was positively associated with early brood-rearing selection, and a marginal predictor of late brood-rearing and broodless female microhabitat selection (Tables 3, 4). Shrub cover variability (%) was positively associated with late brood-rearing, but uninformative for early brood-rearing and broodless female microhabitat selection (Tables 3, 4). The ground cover variable litter (%) was positively correlated with broodless female selection, but was uninformative for early and late brood-rearing selection. Horizontal visual obstruction variables included visual obstruction, perennial grass height, and residual grass height. Visual obstruction as a quadratic term was positively correlated with early brood-rearing and broodless females, but was a marginal predictor for late brood-rearing (Tables 3, 4, Fig. 1*a*). Perennial grass height was positively associated and residual grass height negatively associated with early brood-rearing, but both predictors were uninformative for late brood-rearing and broodless females

Table 2. Top and competing multinomial logistic regression models and model fit statistics best explaining sage-grouse selection for early-brood, late-brood, and broodless female microhabitat in central Wyoming, USA, 2011–13

K, number of parameters; ΔAICc, change in Akaike's Information Criterion score from the top model; w_i, Akaike weights

Model	Model fit statistics			
	K	ΔAICc	w_i	Deviance
BsageD + ShrubSD + VO + VO^2 + Litter + NFoodF + SpeciesR	24	0.00	0.19	915.74
BsageD + ShrubSD + VO + VO^2 + NFoodF + SpeciesR	21	0.11	0.18	922.49
ShrubSD + VO + VO^2 + Litter + NFoodF + SpeciesR	21	0.30	0.16	922.68
BsageD + ShrubSD + VO + VO^2 + PerGrassH + NFoodF + SpeciesR	24	1.79	0.08	917.53
ShrubSD + VO + VO^2 + NFoodF + SpeciesR	18	2.00	0.07	930.93
BsageD + ShrubSD + VO + VO^2 + PerGrassH + ResGrassH + NFoodF + SpeciesR	27	2.20	0.06	911.21
BsageD + ShrubSD + VO + VO^2 + PerGrassH + ResGrassH + Litter + NFoodF + SpeciesR	30	3.03	0.04	905.22
BsageD + ShrubSD + VO + VO^2 + PerGrassH + Litter + NFoodF + SpeciesR	27	3.33	0.04	912.33
Null	3	167.71	0.00	1128.11

Table 3. Parameter estimates with 90% confidence intervals (LCL and UCL) from binomial generalised mixed models evaluating sage-grouse early brood, late brood, and broodless female habitat selection relative to random habitats in central Wyoming, USA, 2011–13

Parameter	Early Brood versus Random			Late Brood versus Random			Broodless versus Random		
	Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL
Microhabitat selection									
Intercept	–5.453	–	–	–3.363	–	–	–4.444	–	–
Shrub cover variables									
BsageD	0.453	0.093	0.813[A]	–0.375	–0.896	0.147	–0.101	–0.435	0.232
ShrubSD	0.020	–0.008	0.048	0.075	0.039	0.111[A]	0.002	–0.029	0.033
Ground cover variables									
Litter	0.003	–0.014	0.020	–0.008	–0.029	0.013	0.016	0.001	0.030[A]
Horizontal visual obstruction variables									
VO	1.841	0.752	2.929[A]	–0.049	–0.851	0.752	1.615	1.008	2.222[A]
VO^2	–0.251	–0.415	–0.087[A]	0.054	–0.045	0.153	–0.124	–0.192	–0.056[A]
PerGrassH	0.095	0.020	0.170[A]	–0.076	–0.179	0.027	0.028	–0.030	0.086
ResGrassH	–0.082	–0.150	–0.014[A]	0.037	–0.044	0.118	–0.035	–0.085	0.016
Herbaceous canopy cover variables									
SpeciesR	0.495	0.077	0.913[A]	1.601	1.087	2.115[A]	–0.360	–0.778	0.057
NfoodF	–0.180	–0.290	–0.070[A]	–0.111	–0.221	–0.001[A]	0.033	–0.021	0.087
Macro habitat selection									
Intercept	–4.673	–	–	–6.264	–	–	–2.673	–	–
INDVI	0.0276	0.012	0.043[A]	0.060	0.049	0.072[A]	0.030	0.023	0.036[A]

[A] 90% confidence intervals that do not include zero.

Table 4. Mean microhabitat characteristics and standard errors (in parentheses) of sage-grouse early brood, late brood, broodless and random locations in central Wyoming, USA, 2011–13

Characteristic	Early Brood	Late Brood	Broodless	Random
Shrub canopy cover (%)				
BsageD	1.5 (0.1)	1.1 (0.1)	1.3 (0.1)	1.3 (0.1)
ShrubSD	22.1 (1.4)	30.4 (2.8)	24.8 (0.9)	19.8 (0.5)
Ground cover (%)				
Litter	42.0 (2.3)	38.9 (2.8)	49.1 (1.6)	36.5 (1.2)
Horizontal visual obstruction				
VO (dm)	2.7 (0.1)	3.6 (0.3)	3.7 (0.2)	2.2 (0.1)
PerGrassH (cm)	16.4 (0.5)	16.6 (0.8)	17.6 (0.6)	15.2 (0.3)
ResidGrassH (cm)	13.1 (0.5)	14.1 (0.9)	15.4 (0.6)	14.7 (0.4)
Herbaceous canopy cover (%)				
SpeciesR	0.8 (0.1)	1.1 (0.1)	0.5 (0.1)	0.5 (0.0)
NFoodF	1.3 (0.3)	1.8 (0.4)	3.6 (0.4)	2.8 (0.3)

(Table 3, 4). Herbaceous ground cover variables included species richness and non-food forb cover. Species richness was positively correlated with early brood and late brood, but was marginally correlated with broodless female microhabitat selection (Tables 3, 4, Fig. 1*b*). Early and late brood habitat selection were negatively correlated with non-food forb cover, and marginally correlated with broodless female microhabitat selection (Tables 3, 4, Fig. 1*c*). INDVI was positively correlated with early brood, late brood, and broodless female habitat selection at the macrohabitat scale (Table 3, Fig. 3*a*).

Survival

Initial variable screening indicated that distance moved between relocations had less model support than the null model (Table 5). Total reproductive effort and brood-rearing effort were highly correlated ($r = 0.86$) and were not allowed to compete in the same model. The most predictive reproductive effort model of adult

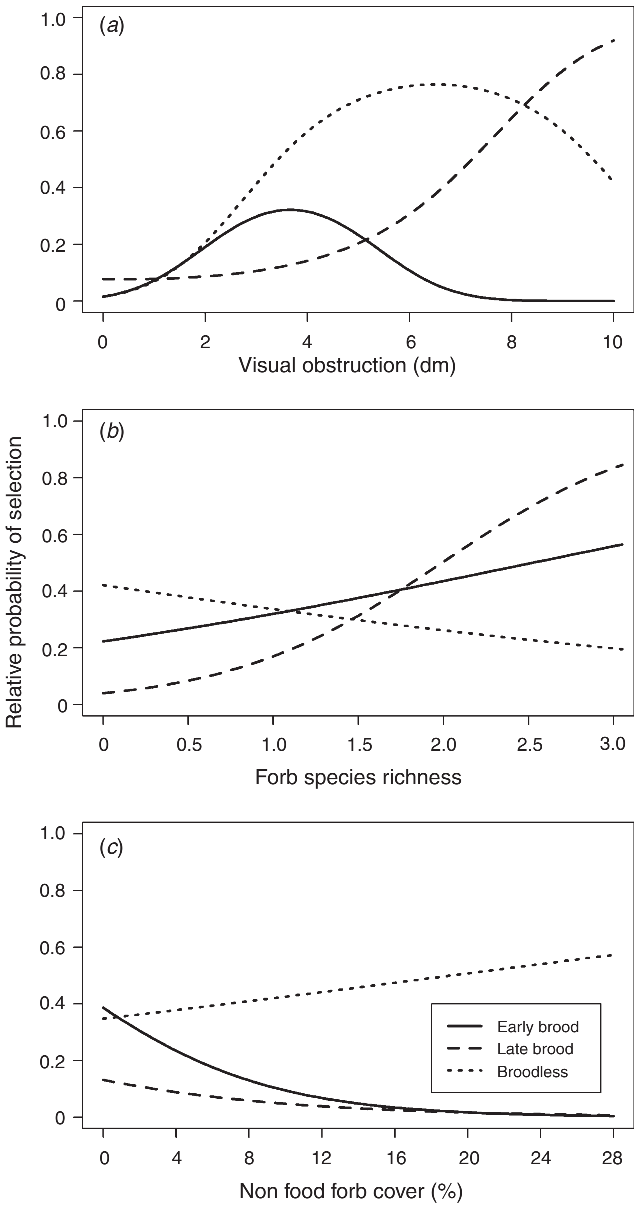

Fig. 1. Relative probability of selection of early-brood, late-brood, and broodless female summer habitats as a function of (*a*) visual obstruction, (*b*) forb species richness, and (*c*) non-food forb cover in central Wyoming, USA, 2011–13.

female survival to 15 weeks included the single variable that estimated total reproductive effort (Table 5). For every 1-week increase in reproductive effort, the adult female hazard rate increased by ~20.7% (Fig. 2). Inclusion of INDVI and the interaction between total reproductive effort and INDVI improved model fit relative to the model that only contained total reproductive effort (Table 6). Both total reproductive effort ($\hat{\beta}_1 = 0.089 \pm 0.03$, s.e.) and INDVI ($\hat{\beta}_1 = 0.086 \pm 0.03$, s.e.) were negatively associated with female summer survival. However, the interaction term between total reproductive effort and INDVI ($\hat{\beta}_1 = -0.002 \pm 0.001$, s.e.), indicated that mortality risk associated with INDVI varied with total reproductive effort. For predictions, we partitioned total reproductive effort into reproductive states by averaging the number of days spent in total reproductive activity for each group during the study (early brood = 5.0 ± 0.06 weeks, late brood = 8.2 ± 0.06 weeks, broodless = 1.2 ± 0.05 weeks) (Fig. 3*b*). We used model coefficients to predict mortality risk across the range of INDVI values for each reproductive state. Visual interpretation of prediction plots suggested that INDVI had little influence on survival of early brood-rearing females, late brood-rearing females had lower mortality risk in areas with greater INDVI, and broodless females had greater mortality risk in areas with greater INDVI.

Discussion

Our study used a relatively long-lived gallinaceous species to assess conspecific habitat partitioning. We evaluated the influence of reproductive state on partitioning of habitat and whether habitat partitioning was consequential to adult female survival. We found that female sage-grouse partitioned habitat across reproductive states at both micro- and macrohabitat scales. During the same period, adult female survival was negatively related to reproductive effort and an index of annual productivity – females that were rearing chicks were ~20.7% more likely to die when brood-rearing for an additional week. Adult female survival was also negatively related to plant productivity; however, we found evidence that survival associated with productivity varied with reproductive investment. Differences in habitat use among individuals in other tetraonid species have been documented (Bañuelos *et al.* 2008; Blanco-Fontao *et al.* 2013) and some macrohabitat-scale research suggests that habitats used by reproductive female sage-grouse differ from those used by non-breeding individuals (Shepherd *et al.* 2011; Kirol *et al.* 2015). However, information identifying differences in microhabitat selection between brood-rearing and broodless female sage-grouse is lacking. Further, survival consequences of habitat partitioning by reproductive and broodless female sage-grouse has not been assessed in the context of different habitat use. Yet, reduced adult female survival relative to reproductive investment has been documented in other sage-grouse populations (Moynahan *et al.* 2006; Sika 2006; Blomberg *et al.* 2013; Dinkins *et al.* 2014). Here we suggest that differences in adult survival under different reproductive states are also partially explained by differences in habitats used by brood-rearing and broodless females.

Early brood-rearing females selected microhabitats with greater density of big sagebrush, intermediate visual obstruction, greater perennial grass height, less residual grass height, greater food forb species richness, and less non-food forb herbaceous cover. The importance of structure, cover, and food for early brood-rearing sage-grouse has been well documented and are consistent with our findings that early brood-rearing females selected areas of intermediate sagebrush cover with greater herbaceous understoreys during nesting and brood rearing (Sveum *et al.* 1998; Connelly *et al.* 2000; Bunnell *et al.* 2004; Hagen *et al.* 2007; Doherty *et al.* 2010; Kirol *et al.* 2012) to meet the nutritional requirements of chicks (Johnson 1987; Johnson and Boyce 1990; Barnett and Crawford 1994; Dumroese *et al.* 2015), while providing structural cover for concealment

Table 5. Model fit statistics from single variable, reproductive investment, and reproductive investment plus environmental models from the model building procedure used to assess adult female survival to 15 weeks in central Wyoming, USA, 2011–13

K, number of parameters; ΔAICc, change in Akaike's Information Criterion score from the top model; w_i, Akaike weights

Model	Model fit statistics			
	K	ΔAICc	w_i	Deviance
Single Variables				
Total reproductive effort	2	0.00	0.73	–179.07
Brood-rearing effort	2	3.94	0.10	–181.04
Reproductive status	3	4.66	0.07	–180.39
Null	1	4.82	0.07	–182.48
Distance moved	2	6.40	0.03	–182.27
Reproductive Variables				
Total reproductive effort	2	0.00	0.65	–179.07
Total reproductive effort + Reproductive status	4	3.61	0.11	–178.87
Brood-rearing effort	2	3.94	0.09	–181.04
Reproductive status	3	4.66	0.06	–180.39
Null	1	4.82	0.06	–182.48
Brood-rearing effort + Reproductive status	4	6.44	0.03	–180.28
Reproductive + Environmental Variables				
Total reproductive effort + INDVI + Total reproductive effort × INDVI	4	0.00	0.84	–174.38
Total reproductive effort	2	4.43	0.09	–177.60
Total reproductive effort + INDVI + big sagebrush	4	5.36	0.06	–179.07
Null	1	10.17	0.01	–182.48

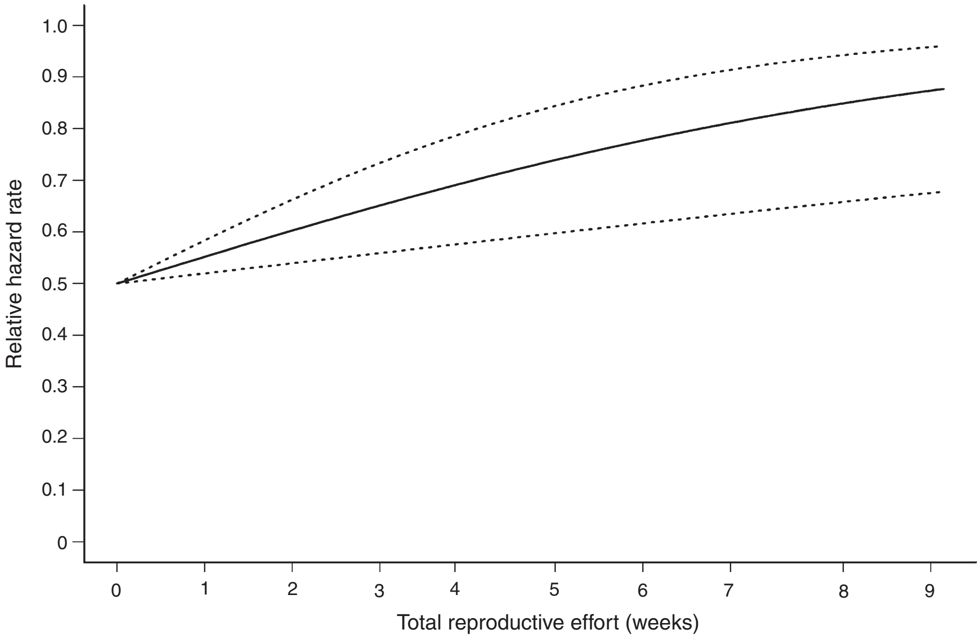

Fig. 2. Relative hazard rates for the most-supported model that included total reproductive effort (weeks) predicting adult female sage-grouse survival in central Wyoming, USA, 2011–13. Hazard rates were plotted with 90% confidence intervals (dashed lines).

from predators and thermal protection (Schroeder *et al.* 1999; Gregg and Crawford 2007; Kirol *et al.* 2012). As chicks grow, females with chicks generally move to more mesic habitats (i.e. late brood-rearing habitats) with resource-rich forbs (Wallestad 1971; Atamian *et al.* 2010). In our study, late brood-rearing females selected sagebrush habitats with greater variability in shrub cover, greater food forb species richness, and less non-food forb herbaceous cover when compared with available habitat. Hagen *et al.* (2007) reported that late brood-rearing females select for greater forb and grass cover, and use shrub cover in proportion to its availability, which is generally corroborated by our findings. At the macrohabitat

Table 6. Parameter estimates, risk ratios, and 90% confidence intervals (LCL and UCL) for variables in the final model used to assess adult female survival to 15 weeks in central Wyoming, USA, 2011–13

Parameter	Estimate	s.e.	Risk ratio	LCL	UCL
Total reproductive effort	0.089	0.026	1.093	1.047	1.140
INDVI	0.086	0.029	1.089	1.039	1.142
Total reproductive effort × INDVI	–0.002	0.001	0.998	0.996	0.999

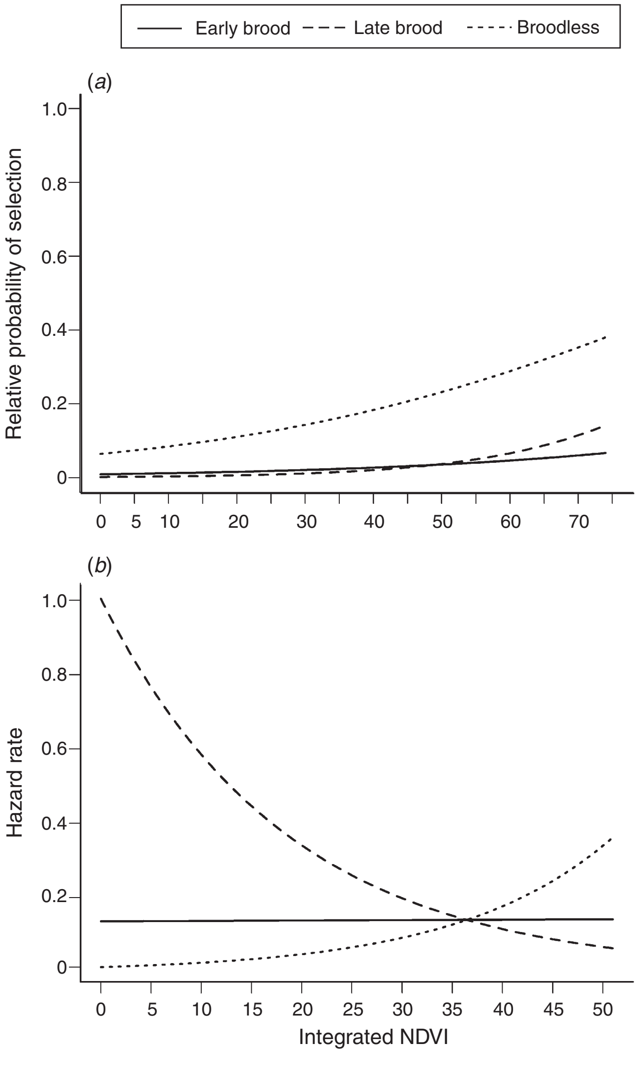

Fig. 3. Relative probability of selection of early-brood, late-brood, and broodless female summer habitats as a function of (*a*) INDVI, and (*b*) hazard rates relative to INDVI across reproductive states in central Wyoming, USA, 2011–13. We approximated each reproductive state by partitioning total reproductive effort into the average number of days spent in total reproductive activity for each group (early brood = 5.0 ± 0.06 weeks; late brood = 8.2 ± 0.06 weeks; broodless = 1.2 ± 0.05 weeks).

scale we found that as the brood-rearing period progressed, brooding females selected areas with greater INDVI values. This is also consistent with the findings of others (Dinkins *et al*. 2014).

Habitat partitioning was evident between broodless and brood-rearing females. Broodless females only selected for greater litter and greater horizontal visual obstruction, whereas all other microhabitat features received only moderate support in our models. Broodless females showed contrasting selection patterns for big sagebrush density, food forb species richness, and non-food forb cover compared with early brood-rearing females. Habitat selection trends were more similar between broodless and late brood-rearing females; perhaps the most distinct differences in microhabitat between individuals in these reproductive states were selection for visual obstruction. Visual obstruction estimates total horizontal obstruction and includes all microtopographic and vegetation (e.g. shrub, grass, herbaceous) attributes that provide concealment cover for individuals. Furthermore, visual obstruction is strongly associated with above-ground vegetation biomass (Robel *et al*. 1970). Studies of sage-grouse during the nesting period have documented the importance of visual obstruction (Kirol *et al*. 2012; Dinkins *et al*. 2016). Similarly, early brood-rearing females were likely selecting areas with sufficient nutritional resources in a way that maximised structural concealment cover (i.e. intermediate herbaceous understorey and shrub overstorey cover).

Sage-grouse chicks almost exclusively consume insects and forbs during early brood-rearing, when nutritional requirements are high for growth and survival (Johnson 1987; Johnson and Boyce 1990; Gregg and Crawford 2007). Gallinaceous chicks likely feed throughout the day to meet their nutritional requirements (Maxson 1977), perhaps at a cost of increased predation risk to both adults and chicks. Similar to our study, Sika (2006) found that days spent brood-rearing were negatively associated with adult survival. Because exogenous resources are the dominant nutritional resources associated with sage-grouse reproductive effort and nesting success (Gregg 2006), reproductive costs likely do not influence survival outside of the reproductive season; rather, nutritional quality during the preincubation period may be most predictive of productivity (Barnett and Crawford 1994; Gregg 2006). Our findings support our predictions that adult survival was influenced by both reproductive behaviours and intraspecific habitat partitioning.

While we do not have data on predator communities in our study area, sage-grouse research has demonstrated that habitat selection is a balance between meeting biological or reproductive demands and avoiding predation through concealment or avoidance of riskier habitats (Hagen 2011; Dinkins *et al*. 2012). It reasons that increased conspicuousness during the brood-rearing reproductive state may be at the expense of increased predation risk in selected habitats. Our results suggest that females may be more vulnerable to predation as a function of habitat partitioning when brooding chicks. Brood protection and decreased vigilance during foraging may also partially explain increased female mortality due to predation. However, individuals that selected more productive sites, particularly late brood-rearing females, had greater survival in these more productive areas. We suspect that these areas maximised security cover and foraging opportunities for late brood-rearing females; yet, relationships between structural concealment and herbaceous cover in sagebrush communities are complex (Sowell *et al*. 2011; Camp *et al*. 2013). Unfortunately, the mismatch between sampling scales of our microhabitat (30 m) and remotely sensed INDVI (250 m) did not allow us to directly link microhabitat use to survival, indicating that further research is necessary to identify the mechanisms associated with this finding.

Nonetheless, previous research on other Galliformes supports our findings. Blanco-Fontao *et al*. (2013) suggested that habitat partitioning in greater prairie chickens (*Tympanuchus cupido*) resulted in females selecting more protein-rich diets in autumn compared with males, which likely selected habitats to reduce predation risk. Bunnell *et al*. (2004) examined microhabitat differences between brood-rearing and adult sage-grouse, but did not differentiate between males and broodless females, so their findings are difficult to compare with ours. Adults selected greater sagebrush height and less forb diversity compared with brood-rearing females (Bunnell *et al*. 2004). Because broodless females were not rearing broods, they were likely roosting and foraging in habitats that maximised concealment from predators (Lima 1985) while meeting their more basic nutritional needs. The same parent–offspring conflict (Trivers 1974) has been demonstrated in other tetraonids, with higher summer mortality of brood-rearing females and habitat partitioning by broodless females that exploit denser cover (Maxson 1978).

Ungulates provide a well documented case of habitat partitioning and suggest that, in some populations, males and females should be effectively managed as separate species (Conradt 1999; Bowyer 2004; Ruckstuhl 2007). Similarly, sufficient differences in habitat selection among tetraonid species (Bañuelos *et al*. 2008; Blanco-Fontao *et al*. 2013), including sage-grouse under different reproductive states, suggests that this principle should be applied when identifying the array of habitats used by both brood-rearing and broodless female sage-grouse. Sage-grouse habitat management generally focuses on nesting and brood-rearing habitats; however, habitat partitioning between brood-rearing and broodless females, as described here, suggests the need to re-evaluate strategies for sage-grouse habitat conservation. The success of reproductive female sage-grouse depends on their survival, to reproduce in subsequent breeding seasons, as well as the survival of their offspring. Therefore, adult survival is a critical component of sage-grouse population persistence. This is particularly true in years of poor population productivity when adult female survival may have the greatest influence on population demography (Taylor *et al*. 2012; Dahlgren *et al*. 2016). While it is evident that reproductive costs are high for sage-grouse, habitats used by individuals under different reproductive strategies may help to ameliorate these costs; conserving habitats used by all females during the breeding season should be a top priority for conservation efforts. In our study, ~3 of every 4 female sage-grouse were broodless, further highlighting the need to provide habitat for this important cohort of sage-grouse populations. Maintaining heterogeneous sagebrush landscapes that provide dense overstorey cover for broodless females interspersed with more open sagebrush habitats with concomitant herbaceous understoreys for foraging and brood-rearing is necessary to maintain the variability and juxtaposition of sage-grouse habitats necessary for all individuals within a population.

Conflicts of interest

The authors declare no conflicts of interest.

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