

# Do greater sage-grouse exhibit maladaptive habitat selection?

AARON C. PRATT† AND JEFFREY L. BECK 

*Department of Ecosystem Science and Management, University of Wyoming, Laramie, Wyoming 82071 USA*

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**Abstract.** Maladaptive habitat selection, where animals select habitat with reduced fitness potential or avoid otherwise suitable habitat, exacerbates the threat of population decline for species vulnerable from habitat loss and fragmentation. The greater sage-grouse (*Centrocercus urophasianus*) is a species of conservation concern for which research has identified scenarios where populations may be under the influence of maladaptive habitat selection. Our objective was to evaluate whether sage-grouse selected habitat relative to habitat quality (i.e., ability to provide for higher survival or reproductive success), and to identify any habitat characteristics where they were not matching selection with costs and benefits, during the nesting, brood rearing, adult breeding, adult summer, and adult winter seasons. We measured an overall apparent adaptive relationship between habitat selection and survival for brood, adult breeding, and adult winter habitat. There was an overall apparent maladaptive relationship for nest and adult summer survival. Of 25 specific habitat characteristics that influenced sage-grouse reproductive success or survival, 13 (52%) had an apparent adaptive selection relationship, 10 (40%) had an apparent maladaptive relationship, and 2 (8%) were either inconclusive or not strongly selected. Surprisingly, most (8 of 10) of the habitat characteristics we observed that were selected contrary to apparent costs or benefits were associated with environmental variables (i.e., topography and vegetation). Relative to possible maladaptive selection and anthropogenic disturbance, grouse selected for areas of higher mortality risk near minor roads during the breeding season and grouse did not select for non-irrigated agricultural disturbance which had lower mortality risk. However, after accounting for the effects of habitat selection on all demographic rates that determine fitness, these apparent maladaptive selection effects were probably not biologically significant. The strongest evidence we observed for maladaptive habitat selection associated with anthropogenic land use was during summer when grouse were selecting for the edge of irrigated hayfields where there was higher mortality risk. To ensure the success of sage-grouse conservation actions, we encourage further investigation identifying the mechanisms behind observed cases of apparent maladaptive selection or identifying any fitness benefits that grouse are gaining from selecting risky areas.

**Key words:** *Centrocercus urophasianus*; ecological traps; greater sage-grouse; habitat selection; perceptual traps; reproductive success; survival.

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† **E-mail:** apratt3@uwyo.edu

## INTRODUCTION

The classic model of animal distribution assumes variability in habitat quality will lead individual animals to choose the best unoccupied site (Pulliam and Danielson 1991). The assumption that individuals will select habitat that

maximizes their fitness is reasonable if habitat selection is adaptive, and they can investigate and choose from an adequate number of sites when deciding where to live. Stated another way, high-quality habitat, or habitat that supports greater fitness, should have a higher probability of use than lower-quality habitat, or habitat that

supports lower fitness. If individuals are to select the highest quality habitat available, then they must identify cues for necessary resources to support successful reproduction and reduce risk of mortality (Williams and Nichols 1984, Kristan 2003). Situations where animals are not able to properly identify these features can result in an ecological trap (first identified by Dwernychuk and Boag 1972). An ecological trap occurs where an individual preferentially selects habitat that reduces its fitness (Robertson and Hutto 2006). In this case, the individual perceives habitat features as being high quality when they are not. More recently, the concept of a perceptual trap has been described (Patten and Kelly 2010). Perceptual traps are scenarios where an individual preferentially avoids habitat that would increase its fitness (or undervalued resources; Robertson and Chalfoun 2016). In this case, an individual perceives habitat features as risky when they are not. A central concept to these ideas is the misperception by the animal of the habitat features that influence fitness resulting in maladaptive selection (Schlaepfer et al. 2002, Robertson and Hutto 2006).

Impacts of anthropogenic disturbance on habitat selection and fitness are well documented for many wildlife species (Johnson et al. 2004, 2005, Sawyer et al. 2006, Kight and Swaddle 2007, Gilbert and Chalfoun 2011, Buchanan et al. 2014). Therefore, it is not surprising that ecological and perceptual traps are mainly a result of reactions to anthropogenic activity (Remeš 2000, Battin 2004, Bock and Jones 2004, Robertson and Hutto 2006, Patten and Kelly 2010). A population with adaptive habitat selection will remain stable unless habitat becomes limited by habitat loss or fragmentation (Pulliam and Danielson 1991). In contrast, a population under the influence of ecological and perceptual traps will tend toward rapid population decline unless the population can adapt quickly to its changing environment (Donovan and Thompson 2001, Kokko and Sutherland 2001). Therefore, there are potentially profound consequences for population persistence if the dynamic under which a population operates is not identified. Traditionally, habitat selection by animals across the landscape is assumed to follow fitness benefits such that habitats with high preferential selection lead to population increases in species whereas avoidance of

habitats leads to population declines. For example, resource selection maps are used by land managers and policymakers to guide conservation and regulatory actions, but these may have limited success if habitat selection does not lead to fitness benefits in predictable ways. If habitat selection is maladaptive, proper conservation actions will be dependent on identifying the areas of maladaptive habitat use and the reasons why (Robertson et al. 2013).

The greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") is a species of conservation concern that has received several petitions to be listed under the U.S. Endangered Species Act of 1973 (Stiver 2011). These petitions have cited habitat loss and fragmentation as a primary threat, and the 2010 finding considered the listing of sage-grouse as warranted (USFWS 2010). Because of increased conservation actions and regulations, the sage-grouse was no longer warranted for listing in 2015 (USFWS 2015). However, if sage-grouse populations are influenced by ecological and perceptual traps, then there is a greater risk of population decline than what may be realized. Significant threats of habitat loss and fragmentation to sage-grouse are from land surface disturbances such as agricultural development (e.g., Smith et al. 2016), energy development (e.g., Kirol et al. 2015), mineral development (e.g., Pratt and Beck 2019), residential development (Connelly et al. 2004), livestock grazing (e.g., Beck and Mitchell 2000), and fire (e.g., Lockyer et al. 2015). Sage-grouse is a species with strong habitat selection tendencies relative to environmental and anthropogenic landscape features, which also influences its survival. There have been studies that have combined resource selection models with fitness metrics to define habitat quality for sage-grouse during various life stages (Aldridge and Boyce 2007, Atamian et al. 2010, Dzialak et al. 2011, Smith et al. 2014, Kirol et al. 2015, Gibson et al. 2016a). Firstly, in these studies, it was demonstrated that there are possible scenarios where ecological (i.e., selected sink habitat) and perceptual (i.e., unselected source habitat) traps caused sage-grouse to not match selection with fitness consequences (Aldridge and Boyce 2007, Kirol et al. 2015). In each study, anthropogenic disturbance influenced selection and contributed to reduced survival or reproductive success.

Secondly, through our research, we wanted to contribute a more thorough investigation of the overall response of selection relative to habitat quality throughout the annual cycle and identify the specific habitat characteristics that may contribute to sage-grouse not matching selection with fitness benefits. In addition, we wanted to account for possible secondary fitness benefits, or higher subsequent demographic rates, from using risky habitats. For example, it is possible that a female may choose to nest in risky habitat if there is a higher chance for brood survival (Gibson et al. 2016a).

Our research objective was to evaluate whether sage-grouse selected habitat relative to habitat quality for the combinations of the most critical demographic rates and seasonal habitat requirements (i.e., nest, brood, adult breeding, adult summer, and adult winter survival; Connelly et al. 2011, Taylor et al. 2012), and to identify any specific habitat characteristics that were selected contrary to the survival and reproductive costs or benefits associated with those characteristics. We completed four steps to address this objective. First, we used habitat-specific survival models to identify which specific habitat characteristics most influenced survival and reproductive success and predicted overall habitat quality across our study area based on the relative success (i.e., mortality risk) estimated from model coefficients. Secondly, we measured selection relative to overall habitat quality predicted during the first step. Thirdly, we measured selection relative to the individual habitat characteristics that most influenced grouse success to identify any specific variables selected contrary to survival and reproductive costs or benefits. Finally, because using riskier habitats could provide secondary fitness benefits, we measured the effect of habitat use during a season on all of the other demographic rates, and an index of fitness, for those habitat characteristics that were apparently selected maladaptively. We expected sage-grouse to adaptively select overall habitat quality, but that this selection may not necessarily be a strong relationship because of potential maladaptive selection of specific habitat characteristics. We also expected maladaptive selection that resulted in lower fitness to be associated with anthropogenic disturbance because these disturbances are recent and rapid changes to the

landscape that could create mismatches between the cues grouse use to evaluate habitat quality and the realized costs or benefits of using disturbed habitat (Battin 2004).

## METHODS

### Study area

Our study included sage-grouse location and demographic data from sagebrush habitats in the Bighorn Basin of north-central Wyoming and extreme south-central Montana, USA. Our study area consisted of three research sites that were approximately associated with the Carbon Sage-Grouse Core Conservation Area in Montana (State of Montana 2015), the Shell Sage-Grouse Core Area in Wyoming (State of Wyoming 2015), and the Hyattville and Washakie Sage-Grouse Core Areas in Wyoming (State of Wyoming 2015). Sage-grouse winter habitat was mostly located in Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) at lower elevations, whereas summer habitat was mostly located in either mountain big sagebrush (*A. t. vaseyana*) at higher elevations or in irrigated hayfields or pastures at lower elevations. Breeding habitat occurred at a wide range of elevations with nests ranging between 1210 m and 2600 m. Anthropogenic disturbance was not widespread across the study area but was abundant in localized areas in all three sites (Table 1). Agricultural fields (row crops, hayfields, and pastures) were the most common disturbance and were located along the major floodplains. More detailed study area descriptions and figures are found in Pratt et al. (2017) and Pratt and Beck (2019).

### Data collection

During 2011–2015, we captured, aged (yearling or adult; Eng 1955), and marked female sage-grouse with very-high frequency (VHF) radio transmitters (22-g necklace-mounted VHF transmitter Model A4060, Advanced Telemetry Systems, Isanti, Minnesota, USA) or with Global Positioning System (GPS) equipped Platform Transmitter Terminals (22-g Solar Argos/GPS PTT-100, Microwave Telemetry, Columbia, Maryland, USA or Model 22 GPS PTT, North Star Science and Technology, King George, Virginia, USA). We collected grouse locations according to season and monitored survival and reproductive

Table 1. Anthropogenic surface disturbance (%) within five seasonal greater sage-grouse study areas (size) in Bighorn Basin, Montana and Wyoming, USA, 2011–2015.

Disturbance (%)	Nest (2348 km <sup>2</sup> )	Brood (2347 km <sup>2</sup> )	Breeding (2954 km <sup>2</sup> )	Summer (3421 km <sup>2</sup> )	Winter (5381 km <sup>2</sup> )
All†	6.5	6.2	6.3	7.4	9.2
High	0.5	0.6	0.6	0.6	0.9
Low	5.9	5.5	5.6	6.7	8.3
RdMaj	0.2	0.2	0.2	0.2	0.2
RdMin	0.3	0.3	0.3	0.3	0.3
AgAll	4.6	4.2	4.3	5.7	7.2
Field	3.2	3.1	2.9	4.0	5.6
AgOth	1.5	1.2	1.3	1.7	1.7

† See Table 2 for description of disturbance types.

success according to established protocols described in Pratt et al. (2017) and Pratt and Beck (2019). Sage-grouse capture and monitoring were approved by University of Wyoming Animal Care and Use Committee (protocols 03142011 and 20140228JB00065) and were completed under permits from Wyoming Game and Fish Department (Chapter 33 Permit 800) and Montana Fish, Wildlife and Parks (Scientific Collector's Permits 2013-072, 2014-037, and 2015-76). We rarified locations from GPS-marked grouse to the sampling intensity of VHF-marked grouse. Each nest location was only used once in the adult breeding season analysis. Average location sampling for VHF-marked grouse was one location every 7, 16, 22, and 26 d of exposure for broods, adults during the breeding season, adults during summer, and adults during winter, respectively.

#### *Spatial predictor variables*

We considered several predictor variables for habitat-specific mortality risk and resource selection modeling that were based on topography, vegetation, and anthropogenic land surface disturbance (Table 2). Topographic variables included compound topographic index (soil wetness index; Gessler et al. 1995), heat load index (amount of radiation index; McCune and Keon 2002), slope, and vector ruggedness measure (topographic roughness index; Sappington et al. 2007) calculated from a 10-m digital elevation model (EROS 2016b) and ArcGIS 10.0 (ESRI 2011). We calculated compound topographic index and heat load index using the geomorphology and gradient metrics toolbox (Evans et al. 2014), and we calculated vector ruggedness

measure using the terrain ruggedness tool (Sappington 2012). The vegetation metrics included variables of percent cover representing the ground (bare ground), herbaceous (annual grass and herbaceous cover), and shrub layers (big sagebrush, non-sagebrush [not *Artemisia* spp.], and total shrub cover). We also utilized shrub height, probability of black sagebrush presence (*A. nova*), and probability of juniper (*Juniperus* spp.) presence. Because there was not adequately available (either did not exist or only partial coverage of study area) spatial data for our desired vegetation variables, we predicted them for our study area by using random forest regression or classification (Breiman 2001) with remotely sensed spatial predictor data (surface reflectance imagery, climate measures, topographic metrics, vegetation indices, and soil metrics) and field measurement plots (30-m resolution; see Pratt 2017 for details). We also utilized categorical land cover data from National Land Cover Database (NLCD; 30-m resolution; Homer et al. 2015) to represent forest and wetlands (mostly riparian associated with major floodplains in our study area). Our final vegetation variable was the soil-adjusted vegetation index (SAVI; Qi et al. 1994), which represents vegetation greenness. We calculated SAVI from a median surface reflectance image (30-m resolution; Landsat 8 Operational Land Imager; EROS 2016a) from Landsat images associated with the nearest first day of the month (2013–2015) for June (17 May–16 June; 17 April–16 May images would have been included but they were too cloudy), for breeding season analysis, and for August/September (17 July–16 September), for summer season analysis. We digitized anthropogenic disturbance using the

Table 2. Variables used for measuring greater sage-grouse habitat-specific nest, brood, and seasonal adult mortality risk in Bighorn Basin, Montana and Wyoming, USA, 2011–2015.

Code	Description
Topographic	
CTI	Compound topographic index <sup>†</sup>
HLI	Heat load index <sup>†</sup>
Slope	Slope (%) <sup>†</sup>
VRM	Vector ruggedness measure <sup>†</sup>
Vegetation	
Herbaceous/Ground	
AnnG	Annual grass cover (%) <sup>†</sup>
Bare	Bare ground (%) <sup>†</sup>
Herb	Herbaceous cover (%) <sup>†</sup>
Shrub	
ArC	Big sagebrush cover (%) <sup>†</sup>
BSaP	Black sagebrush (probability of presence) <sup>†</sup>
JunP	Juniper (probability of presence) <sup>†</sup>
NSaC	Non-sagebrush shrub cover (%) <sup>†</sup>
ShC	Shrub cover (%) <sup>†</sup>
ShH	Shrub height (cm) <sup>†</sup>
Land cover	
Fore	Forest land cover <sup>‡</sup>
Wetl	Wetland land cover <sup>‡</sup>
Vegetation index	
Savi	Soil-adjusted vegetation index <sup>†</sup>
Disturbance	
All	All anthropogenic surface disturbance <sup>‡</sup>
High	All high-intensity disturbance (e.g., major road, active mining, residence) <sup>‡</sup>
Low	All low-intensity disturbance (e.g., 2-track trail, reclaimed mine, field) <sup>‡</sup>
RdMaj	High-intensity major roads (e.g., bladed dirt/gravel and paved) <sup>‡</sup>
RdMin	Low-intensity minor roads (e.g., 2-track trail) <sup>‡</sup>
AgAll	All agricultural disturbance (e.g., access road, building, reservoir, field) <sup>‡</sup>
Field	Irrigated field <sup>‡</sup>
AgOth	Any non-irrigated agricultural disturbance <sup>‡</sup>

<sup>†</sup> Calculated as mean and standard deviation at multiple spatial extents (radius = 50, 100, 200, 400, 800, 1600, and 3200 m).

<sup>‡</sup> Calculated as proportion of area and distance (m) to variable using a decay function at the same multiple extents.

World Imagery basemap (0.3-m resolution) within ArcGIS 10.0 (ESRI 2011). We classified disturbance into two categories based on whether it was an active higher-intensity (e.g., gravel/paved road, active mining, residence) or a lower-intensity (e.g., 2-track trail, reclaimed mine, field) disturbance. Roads were classified as major (bladed dirt/gravel and paved) or minor (2-track trail). We classified disturbance from agricultural practices as irrigated hayfields/pastures and all other forms of disturbance. These classifications were based on our observations that irrigated fields were frequently used as summer habitat by grouse in our study area, but there was no apparent benefit from other forms of disturbance from agriculture.

Variables were measured at multiple, circular spatial extents around locations with radii that started at about twice location error (i.e., 50 m for nest locations, 100 m for brood and breeding locations, and 400 m for summer and winter locations) and systematically increased by doubling in size until the radius of circular analysis extents reached 3200 m. Within these extents, we calculated the mean and standard deviation (SD) for each continuous topographic and vegetation variable. For the categorical land cover variables and for the categorical disturbance variables, we calculated the proportion (prop.) of the landscape within each circular extent. In addition, for the categorical variables we measured Euclidean distance to the nearest feature, as well as,

distance scaled between zero (away) and one (near) with a decay function ( $e^{-d/\alpha}$ ,  $d$  = distance; e.g., Aldridge et al. 2012) where  $\alpha$  was set to the same values as our analysis extent radii. The distance decay variables allowed for non-linear relationships. We standardized all variables, so observations had a mean equal to zero and SD equal to one so model coefficients were directly comparable.

### *Mortality risk*

We evaluated the effect of spatial predictor variables on mortality risk for nests, broods, and seasonal adult survival using mixed-effects Cox proportional hazards regression, which uses the variation in exposure time to a mortality event relative to covariates (Cox 1972; *coxme* R package, Therneau 2015; R version 3.4.1, R Core Team 2016). The values for the spatial covariates were averages for each experimental unit (i.e., each nest, brood, or adult-season combination). For the nest mortality-risk analysis, covariates were measured within concentric analysis extents surrounding each nest location. For the brood mortality-risk analysis, covariates were measured in circular analysis extents surrounding brood locations and averaged for each individual brood. For the adult seasonal mortality-risk analyses, covariates were measured within the circular analysis extents surrounding the relevant seasonal locations and averaged over the lifetime of each individual female. Therefore, covariates were time independent and represented the average habitat use for each experimental unit. We implemented several steps to screen variables for model selection. We first determined which random effects should be included by comparing null models with all possible combinations of random effects from individual, bird age, transmitter type, research site, and year using Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002; *AICcmodavg* R package, Mazerolle 2017). We only included one measurement extent for each variable, so we used single-variable models with  $AIC_c$  to select the most predictive extent. To avoid multicollinearity, we carried forward top-performing variables while removing those that were correlated ( $|r| \geq 0.6$ ) from further consideration. We then created a global model of all remaining variables and employed a backward

variable-selection procedure by systematically removing the least significant variable (i.e., largest  $P$  value) until all remaining variables had a  $P$  value  $\leq 0.1$  and there was a minimum of ten events per fixed-effect variable (Harrell et al. 1984). We interpreted  $P$  values  $\leq 0.1$  as moderate evidence and  $P$  values  $< 0.05$  as strong evidence of an effect on mortality risk. We removed any variables from further consideration if they demonstrated coefficient instability or sign switching when moderately correlated variables ( $0.3 \leq |r| < 0.6$ ) were removed from the final model. We checked that the proportional hazards assumption was met, which is represented by a slope not different from zero for Schoenfeld residuals (Schoenfeld 1982).

### *Resource selection*

To first evaluate population resource selection relative to overall habitat quality, we mapped relative mortality risk across our study area based on coefficients from the final mortality-risk models. We mapped mortality risk at 30-m resolution and binned into five quantiles (1–5 from lowest to highest relative mortality risk). We then used this as an explanatory variable in our second-order (i.e., selection within the range of sage-grouse in the Bighorn Basin; Johnson 1980) resource selection model comparing grouse-use locations to available locations (Manly et al. 2002). We generated 20 times the number of available locations as use locations because this was an adequate (Pratt and Beck 2019) number of available locations to ensure convergence of estimated parameter coefficients (Northrup et al. 2013). Available locations were restricted to each research site. The extents of the research sites were delineated from minimum convex polygons of use locations with areas of non-habitat masked out (i.e., closed canopy, developed [residential, impervious road, etc.], and non-terrestrial land covers, 2011 National Land Cover Database; Homer et al. 2015). We modeled relative probability of selection with generalized estimating equations (PROC GENMOD, SAS 9.4, SAS Institute 2012). We accounted for repeated observations from the same individual by assigning use and available locations into clusters, and by selecting between independent and compound-symmetric correlation structures to estimate robust standard errors (Koper and

Manseau 2009, Fieberg et al. 2010). After first measuring selection of overall habitat quality predicted by our mortality-risk model, we then measured selection relative to each of the individual landscape characteristics most influential to survival that were included in the final mortality-risk model. We followed the same process as the overall habitat quality model, but instead of only one explanatory variable representing overall predicted mortality risk we incorporated all the explanatory variables in the final mortality-risk model. Finally, we graphed standardized coefficients (with 95% confidence intervals) from our mortality-risk and selection models to compare each landscape characteristic's influence on mortality risk and resource selection and interpreted this relationship relative to a theoretical perfect matching of habitat selection to survival costs or benefits (Fig. 1). In these graphs, positive values along the  $x$ -axes represented greater mortality risk and positive values along the  $y$ -axes represented greater resource selection. Variables that fell within the upper-left or lower-right quadrants represented an apparent adaptive relationship between selection and survival and we considered it strong evidence for this relationship if 95% confidence intervals overlapped the  $1: -1$  line (Fig. 1A). Variables that fell within the upper-right or lower-left quadrants represented an apparent maladaptive relationship between selection and survival and we considered it strong evidence if 95% confidence intervals did not overlap any axes.

### *Fitness index*

To measure the effect of selection of specific landscape features on overall fitness, we calculated a relative fitness index based on a simple deterministic population growth (which is an outcome of fitness) model according to the following equation:

$$\lambda = (BS \times SS \times WS) + (NS \times CS \times CF),$$

where BS was adult survival during breeding season, SS was summer survival, WS was winter survival, NS was nest survival, CS was brood survival, and CF was a constant correction factor to account for other vital rates not included in the model. This formula is equivalent to a 1-stage projection matrix (Lefkovich 1965) representing a birth-pulse model with a pre-breeding census

and with the first half of the formula consisting of probability of survival and the second half consisting of fecundity (Caswell 2001, Morris and Doak 2002). The constant correction factor accounted for vital rates with unknown values such as nest initiation, reneating, clutch size, number of chicks fledged, and juvenile survival (Taylor et al. 2012). The constant correction factor was calculated based on population averages for the other equation elements so that  $\lambda = 1$ . Therefore, a relative fitness index of  $\lambda > 1$  represented above-average fitness because calculated vital rates would contribute to above-average population growth and  $\lambda < 1$  represented below-average fitness. We defined breeding season survival as the probability of an adult surviving 89 d, summer survival as the probability over 89 d, and winter survival as the probability over 127 d which were the median season lengths observed in our study area (Pratt 2017). We defined nest survival as at least 1 egg hatching after 26.5 d of incubation, and we defined brood survival as at least 1 chick surviving to 35 d posthatch, which coincided with our field brood counts (Pratt and Beck 2019). We estimated these vital rates according to grouse use of a specific seasonal habitat characteristic by adding the variable in question to the final mortality-risk models. For example, to calculate brood survival relative to shrub cover at nests we added this variable to the final brood mortality-risk model to predict brood survival.

## RESULTS

When modeling habitat-specific mortality risk and resource selection, we used data collected from 321 female sage-grouse captured in the Big-horn Basin during 2011–2015 (Table 3). Significant random effects for mortality-risk modeling included transmitter type and research site for nesting analysis, bird age and research site for brood-rearing analysis, year for adult breeding analysis, year and research site for adult summer analysis, and year and research site for adult winter analysis. The probability of nest survival was 0.316 (95% CI = 0.191–0.532) for grouse equipped with GPS transmitters and was 0.406 (95% CI = 0.283–0.604) for grouse with VHF transmitters. The probability of brood survival was 0.637 (95% CI = 0.467–0.870) for yearling

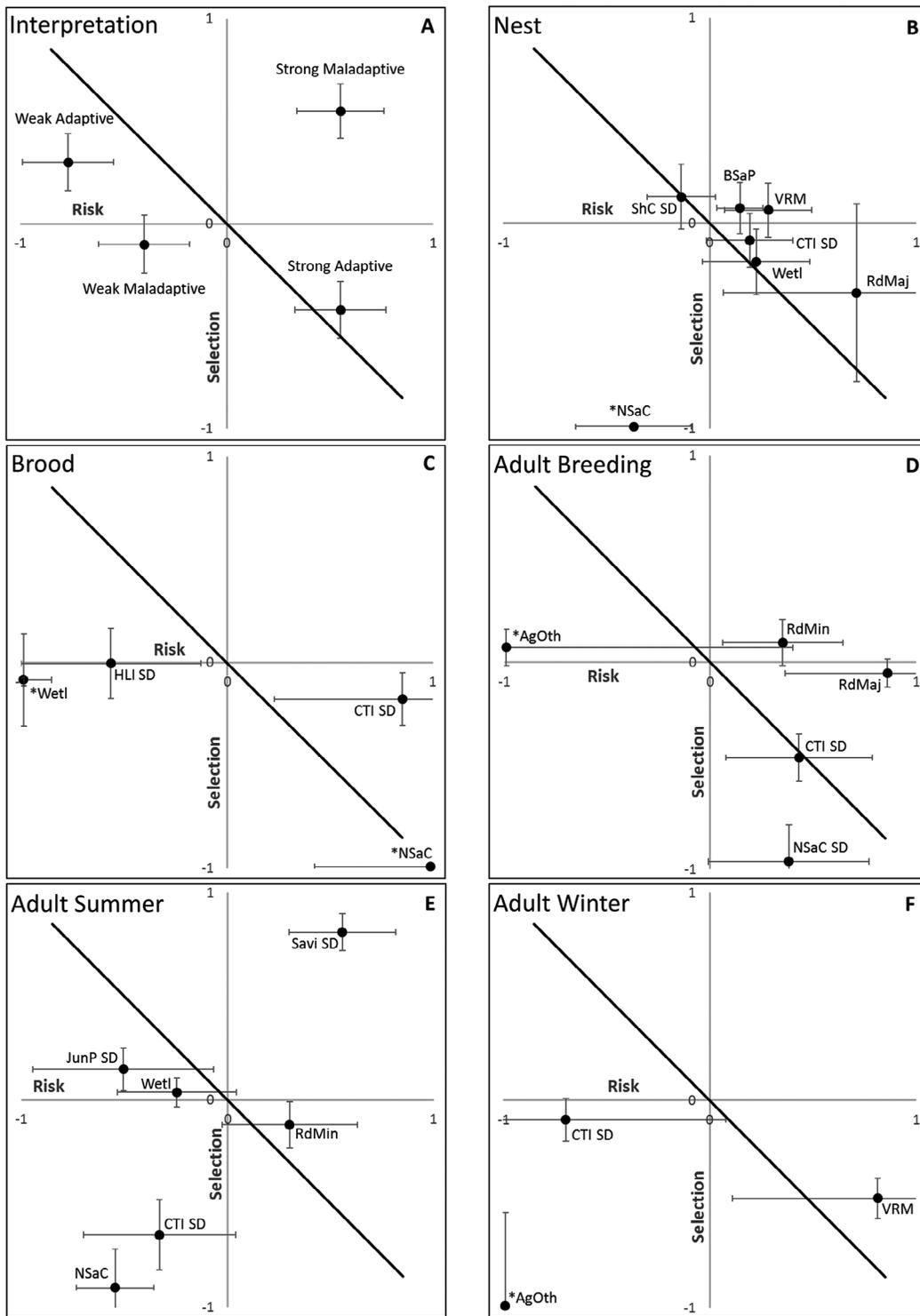


Fig. 1. Interpretations of selection for habitat variables (see Table 2 for variable descriptions) relative to mortality risk and resource selection.  $x$  and  $y$  coordinates are standardized coefficients (with 95% confidence intervals)

(Fig 1. *Continued*).

from habitat-specific mortality risk and resource selection models, respectively. Diagonal line represents a perfect adaptive relationship between selection and apparent survival costs or benefits. Strong and weak evidence is based on overlap of confidence intervals with axes and the adaptive relationship line (A). Standardized coefficients for nest (B), brood (C), and adult seasonal (D–F) mortality risk and resource selection for greater sage-grouse in Bighorn Basin, Montana and Wyoming, USA, 2011–2015. Asterisk identifies a point that is off the chart area. If confidence interval is not shown, then it also is off the chart area.

Table 3. Sample sizes used for modeling habitat-specific mortality risk and resource selection for greater sage-grouse in Bighorn Basin, Montana and Wyoming, USA, 2011–2015.

Analysis	Sage-grouse	Broods	Mortality events	Locations
Nest	246		207	378
Brood	128	157	48	754
Adult breeding	285		62	1978
Adult summer	289		77	1696
Adult winter	220		31	1365

grouse and was 0.776 (95% CI = 0.694–0.868) for adult grouse. Our final nest mortality-risk model indicated strong evidence for increased nest failure risk for birds that nested in areas with black sagebrush, less non-sagebrush shrub cover, more topographic ruggedness, and more disturbance from major roads (Table 4). There was moderate evidence for increased risk with more variability in soil moisture, less variability in shrub cover, and more wetland. There was evidence that sage-grouse were choosing riskier areas when selecting nest sites (Table 5). This was a result of avoiding non-sagebrush shrub cover, and by not avoiding black sagebrush and topographic ruggedness (Fig. 1B). Our final brood mortality-risk model indicated strong evidence for increased brood failure risk with more variability in soil moisture, less variability in heat load, more non-sagebrush shrub cover, and less wetland (Table 4). There was evidence that sage-grouse were selecting for brood-rearing areas relative to predicted brood success (Table 5).

Our final adult breeding season mortality-risk model indicated strong evidence for increased adult mortality risk in areas with more variability in soil moisture and with more disturbance from major roads and in closer proximity to

minor roads (Table 4). There was moderate evidence for increased risk with more variability in non-sagebrush shrub cover and less disturbance from agricultural practices (i.e., not irrigated fields). Overall, there was evidence that sage-grouse were selecting habitat during breeding season relative to predicted adult survival (Table 5). However, there was moderate evidence that female sage-grouse were selecting for proximity to minor roads where there was higher mortality risk (Fig. 1D). Our final adult summer season mortality-risk model indicated strong evidence for increased adult mortality risk with less variability in juniper presence, less non-sagebrush shrub cover, and more variability in vegetation greenness (Table 4). There was moderate evidence for increased risk with less variability in soil moisture, less wetland, and more minor roads. There was evidence that sage-grouse were selecting for riskier areas when selecting summer habitat (Table 5). This was a result of avoiding non-sagebrush shrub cover and variability in soil moisture, and by selecting for more variability in vegetation greenness (Fig. 1E). Our final adult winter season mortality-risk model indicated strong evidence for increased adult mortality risk in areas with more topographic ruggedness and with less disturbance from agricultural practices (i.e., not irrigated fields; Table 4). There was moderate evidence for increased risk with less variability in soil moisture. There was evidence that sage-grouse were selecting for less risky areas relative to survival when selecting winter habitat (Table 5). Even so, they were not selecting for more disturbance from agricultural practices that were apparently providing a survival benefit (Fig. 1F).

Of the 25 specific habitat characteristics that influenced sage-grouse success, 13 (52%) had at least weak evidence for an apparent adaptive relationship, 10 (40%) had at least weak evidence

Table 4. Variable type, measurement extent, estimated standardized coefficients ( $\beta$ ), and standard errors (SE) for variables in habitat-specific mortality risk and resource selection models for greater sage-grouse in Bighorn Basin, Montana and Wyoming, USA, 2011–2015.

Variables	Measure	Extent (m) <sup>†</sup>	Mortality risk			Resource selection		
			$\beta$	SE	<i>P</i>	$\beta$	SE	<i>P</i>
Nest								
BSaP	Mean	50	0.146	0.057	0.010	0.073	0.064	0.249
CTI	SD	3200	0.193	0.106	0.069	−0.084	0.067	0.211
NSaC	Mean	400	−0.369	0.143	0.010	−1.556	0.155	<0.001
RdMaj	prop.	100	0.711	0.330	0.031	−0.339	0.221	0.125
ShC	SD	200	−0.138	0.085	0.100	0.128	0.081	0.114
VRM	Mean	800	0.283	0.108	0.009	0.063	0.068	0.352
Wetl	prop.	3200	0.225	0.132	0.089	−0.188	0.081	0.021
Brood								
CTI	SD	100	0.852	0.318	0.007	−0.177	0.065	0.006
HLI	SD	1600	−0.565	0.223	0.011	−0.004	0.087	0.965
NSaC	Mean	100	1.062	0.326	0.001	−1.854	0.223	<0.001
Wetl	prop.	800	−4.435	1.827	0.015	−0.083	0.114	0.465
Adult breeding								
AgOth	prop.	400	−9.034	4.814	0.061	0.072	0.045	0.112
CTI	SD	3200	0.431	0.181	0.017	−0.461	0.058	<0.001
NSaC	SD	200	0.382	0.199	0.055	−0.964	0.090	<0.001
RdMaj	prop.	100	0.860	0.254	<0.001	−0.053	0.035	0.132
RdMin	dist.	800	0.351	0.149	0.018	0.095	0.056	0.090
Adult summer								
CTI	SD	1600	−0.331	0.189	0.080	−0.650	0.087	<0.001
JunP	SD	1600	−0.506	0.224	0.024	0.149	0.053	0.005
NSaC	Mean	1600	−0.545	0.237	0.022	−0.906	0.096	<0.001
RdMin	prop.	1600	0.302	0.168	0.072	−0.119	0.056	0.035
Savi	SD	400	0.557	0.132	<0.001	0.810	0.046	<0.001
Wetl	prop.	400	−0.246	0.148	0.096	0.038	0.036	0.297
Adult winter								
AgOth	prop.	800	−58.41	21.791	0.007	−1.111	0.291	<0.001
CTI	SD	1600	−0.697	0.395	0.078	−0.094	0.053	0.077
VRM	Mean	400	0.813	0.359	0.024	−0.473	0.050	<0.001

Abbreviations: dist., distance; prop., proportion; SD, standard deviation.

<sup>†</sup> Extent for distance statistic is  $\alpha$  in the distance decay function.

for an apparent maladaptive relationship, and 2 (8%) were inconclusive or not strongly selected. Of the ten habitat characteristics where we documented at least a weak apparent maladaptive relationship, three (30%) were relative to topography, five (50%) were relative to vegetation, and two (20%) were relative to anthropogenic disturbance. We documented four habitat characteristics with significant evidence that they were selected contrary to the survival or reproductive costs or benefits associated with these characteristics. The first was grouse avoiding non-sagebrush shrub cover (within 400 m) when selecting nest sites when nests located in these areas were more likely to hatch (Figs. 1B and 2). Females

nesting in these areas were also associated with above-average overall fitness (Fig. 2). Second was grouse avoiding non-sagebrush shrub cover (within 1600 m) when selecting summer habitat when grouse that used these areas had higher survival (Figs. 1E and 3). Grouse using areas with moderate amounts of non-sagebrush shrub cover were associated with slightly higher overall fitness, but the summer survival benefits were counteracted by lower brood survival for grouse using the highest amounts of non-sagebrush shrub cover during summer (Fig. 3). Third was grouse selecting for higher variability in vegetation greenness (within 400 m) when selecting summer habitat when grouse that used these

Table 5. Estimated coefficients ( $\beta$ ), standard errors (SE), and 95% confidence intervals (CI) for greater sage-grouse nest, brood, and adult seasonal habitat selection relative to habitat quality (i.e., predicted mortality risk) in Bighorn Basin, Montana and Wyoming, USA, 2011–2015.

Analysis	$\beta$	SE	CI		P
			lower	upper	
Nest	0.073	0.034	0.007	0.139	0.031
Brood	-0.408	0.043	-0.492	-0.324	<0.001
Adult breeding	-0.205	0.046	-0.295	-0.115	<0.001
Adult summer	0.394	0.039	0.319	0.470	<0.001
Adult winter	-0.048	0.024	-0.095	-0.001	0.048

Note: Positive coefficient depicts selection for riskier areas.

areas had lower survival (Figs. 1E and 4). Grouse selecting these areas were also associated with below-average overall fitness (Fig. 4). The fourth habitat characteristic with an apparent maladaptive selection relationship was grouse avoiding non-irrigated agricultural disturbance (within 800 m) when selecting winter habitat when grouse that used these areas had higher survival (Fig. 1F). However, given that we documented very few individuals using areas with a substantial amount of disturbance, we are cautious of estimating demographic rates and believe we cannot conclude whether this is an example of maladaptive selection.

We documented four negative influences on survival from anthropogenic disturbance for three of the five demographic rates we investigated. Only one of these negative effects showed an apparent maladaptive selection relationship. This case of a weak apparent maladaptive selection relationship relative to disturbance was breeding adults selecting for proximity to minor roads where they were more likely to die (Figs. 1D and 5). Females in closer proximity to minor roads were also associated with lower nest success but higher brood success (Fig. 5). Overall, grouse using breeding habitat closer to minor roads had below-average overall fitness, but this effect was minimal (Fig. 5).

## DISCUSSION

One may assume that animals, including sage-grouse, select habitat that maximizes their

survival and reproductive success. This was the case for three (brood, adult breeding, and adult winter survival) of the five demographic rates and habitat requirements we investigated. However, this was not the case for nesting and adult summer habitat and survival where grouse selected more risky landscapes. We documented a specific habitat characteristic that was associated with an apparent maladaptive selection relationship for all five demographic rates, but more cases with strong evidence coincided with the two rates (i.e., nest and adult summer survival) that had the poorest overall apparent adaptive habitat selection relationship. Only about half of the specific habitat characteristics that influenced sage-grouse success had a clear apparent adaptive selection relationship.

Ecological traps, when animals select for habitat where they perform poorly, have been proposed as an expression of maladaptive habitat selection (Robertson and Chalfoun 2016). Possible examples of ecological traps include Bell's sparrows (*Artemisiospiza belli*) that selected undisturbed habitats having lower nest success (Misenhelter and Rotenberry 2000) and indigo buntings (*Passerine cyanea*) attracted to artificial forest edges having lower reproductive success (Weldon and Haddad 2005). We documented four potential habitat characteristics that may pose as ecological traps for sage-grouse: black sagebrush and topographic ruggedness for nesting, minor roads for breeding season survival, and variability in vegetation greenness for summer survival. Similarly, Cutting et al. (2019) documented a higher preference in sage-grouse for low-elevation basin big sagebrush (*A. t. tridentata*) when selecting nest sites but these same areas had higher nest mortality risk. Perceptual traps, where animals avoid areas where they would perform well, have also been proposed as an expression of maladaptive habitat selection (undervalued resources; Robertson and Chalfoun 2016). Possible examples of perceptual traps include shorebirds (suborder Charadrii) avoiding nesting near man-made structures even though there was no effect on nest success (Wallander et al. 2006), and lesser prairie chickens (*Tympanuchus pallidicinctus*) avoiding powerlines and highways where there was no effect on nest success (Pruett et al. 2009). We documented six potential habitat characteristics that may pose as

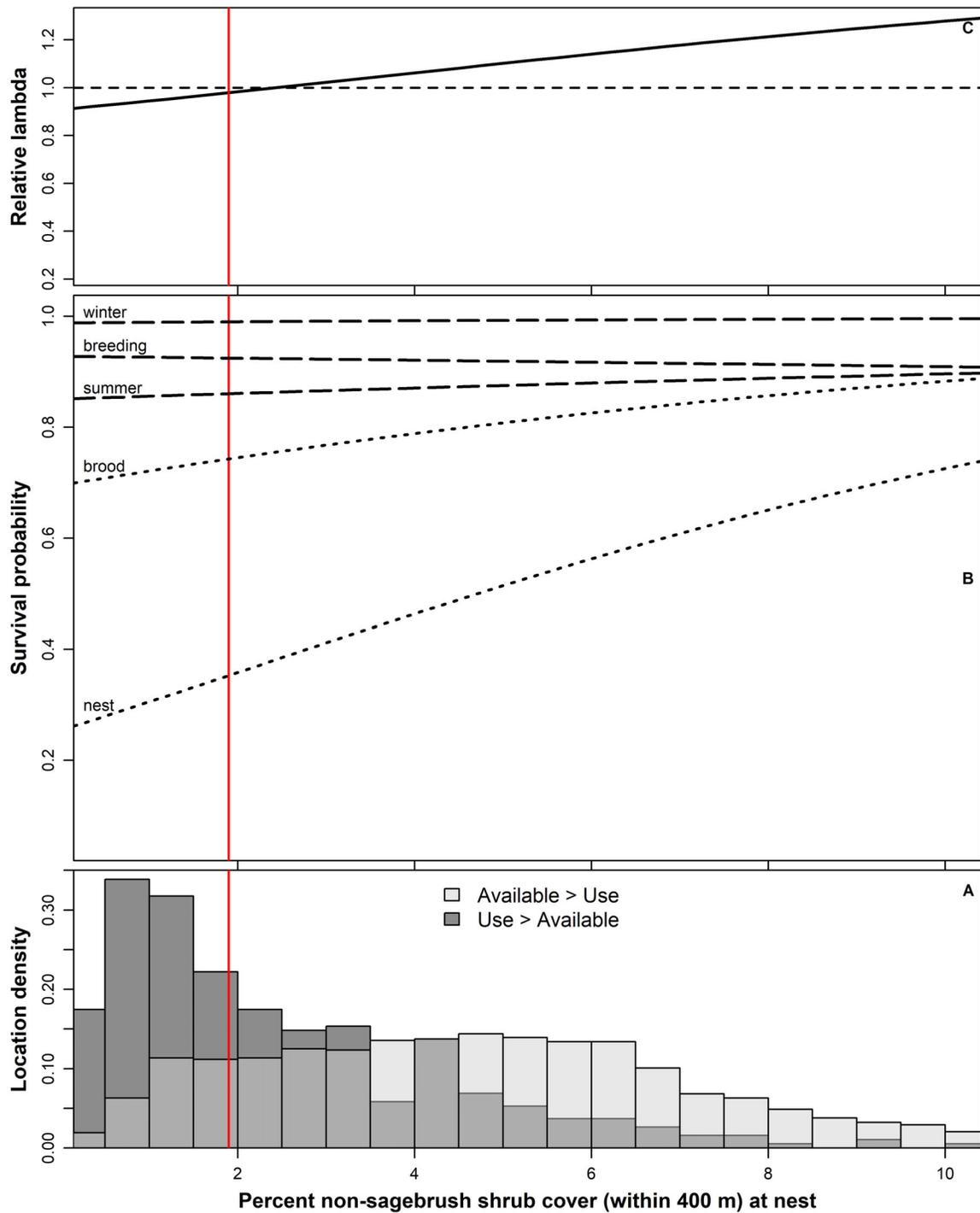


Fig. 2. Selection (A; available superimposed on use) by adult female greater sage-grouse relative to non-sagebrush shrub cover at nests and effects of this nesting habitat use on survival (B; dashed lines), fertilities (B; dotted lines), and relative fitness (C; dashed line represents population average) in Bighorn Basin, Montana and Wyoming, USA, 2011–2015. The x-axis limits represent the range of used habitat. The red vertical line is the median grouse-use location. The y-axes for graphs B and C are consistent among Figs. 2–5 for direct comparison.

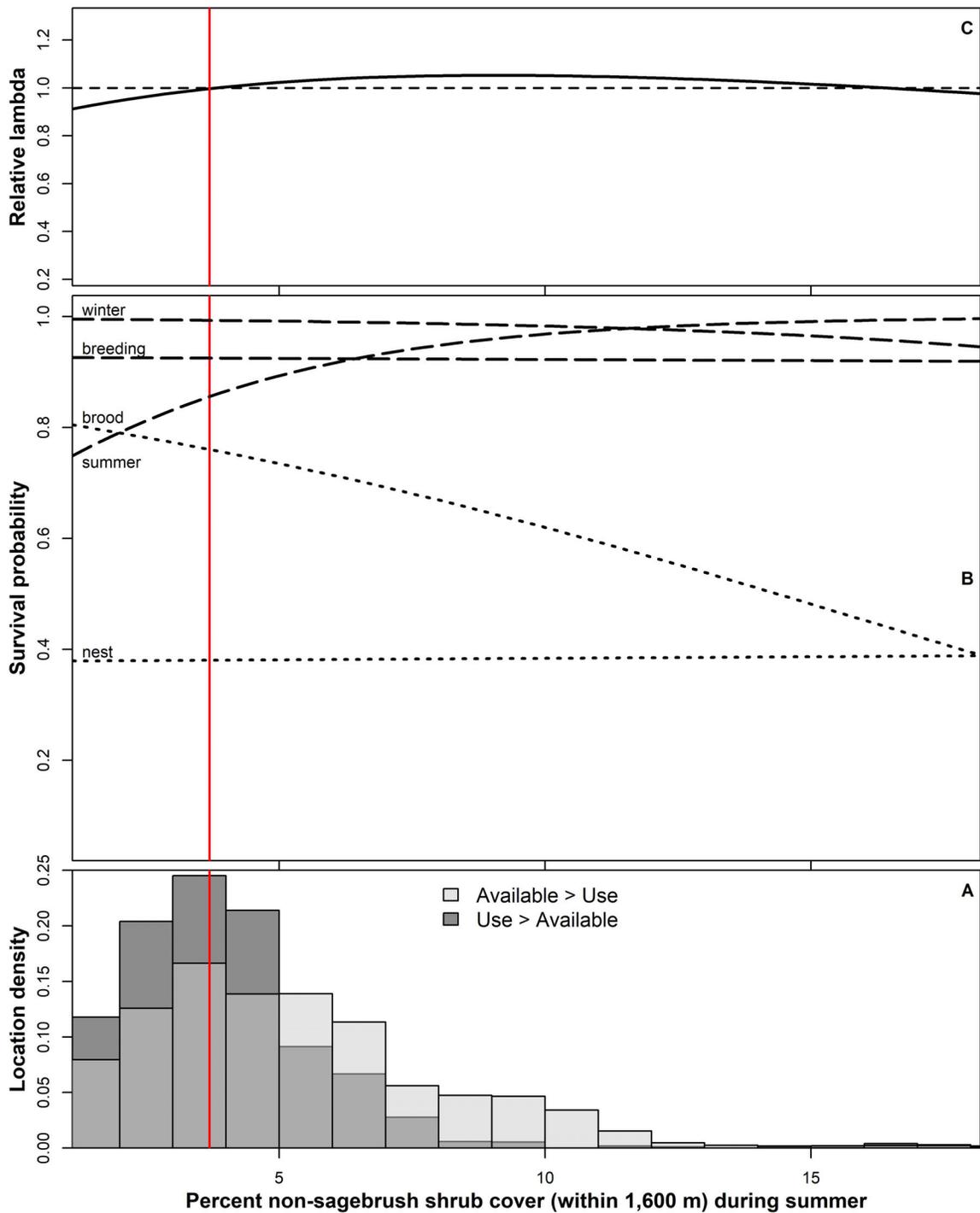


Fig. 3. Selection (A; available superimposed on use) by adult female greater sage-grouse relative to non-sagebrush shrub cover (%) during summer and effects of this summer habitat use on survival (B; dashed lines), fertilities (B; dotted lines), and relative fitness (C; dashed line represents population average) in Bighorn Basin, Montana and Wyoming, USA, 2011–2015. The x-axis limits represent the range of used habitat. The red vertical line is the median grouse-use location.

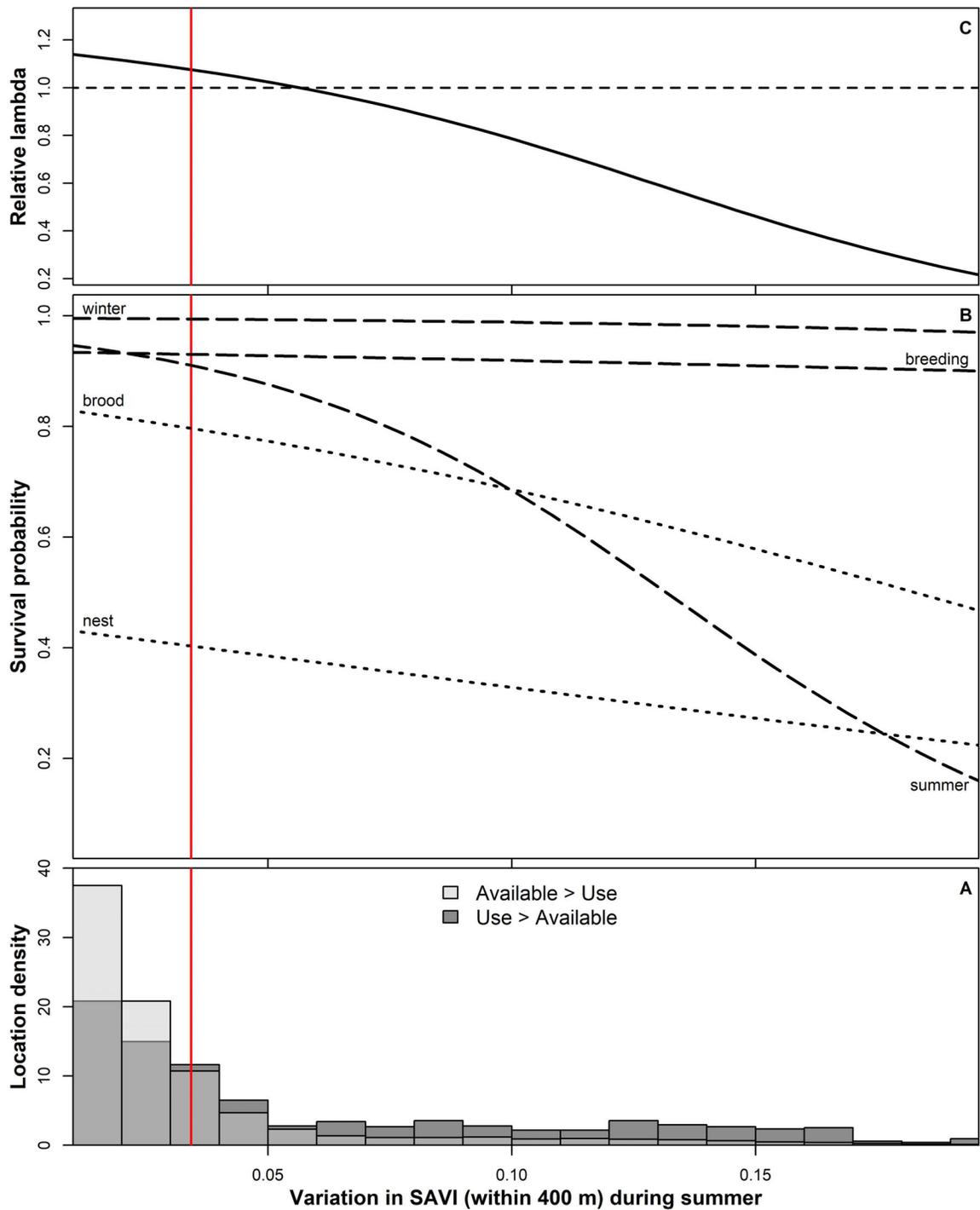


Fig. 4. Selection (A; available superimposed on use) by adult female greater sage-grouse relative to the variation (SD) in vegetation greenness (SAVI) during summer and effects of this summer habitat use on survival (B; dashed lines), fertilities (B; dotted lines), and relative fitness (C; dashed line represents population average) in Bighorn Basin, Montana and Wyoming, USA, 2011–2015. The x-axis limits represent the range of used habitat. The red vertical line is the median grouse-use location.

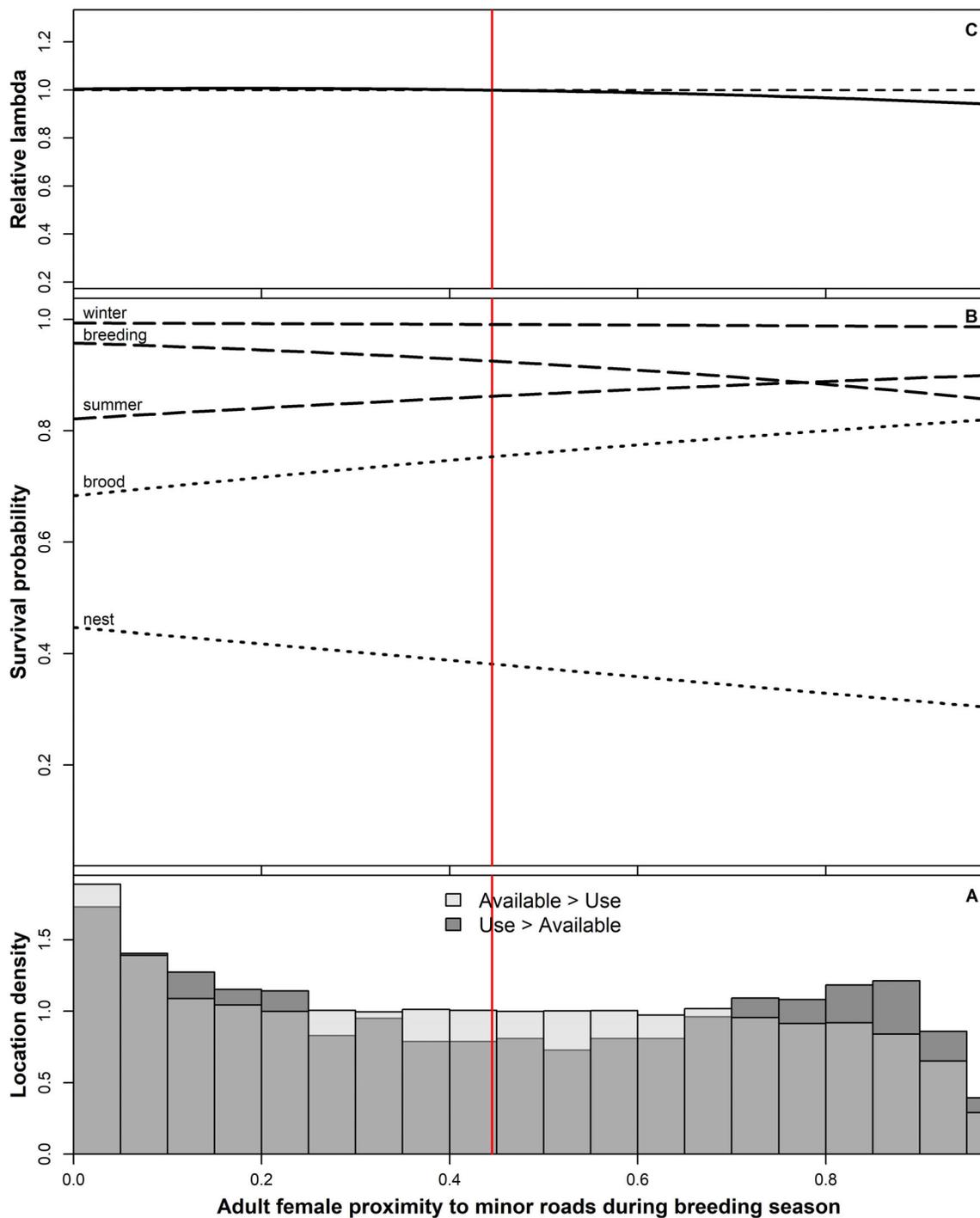


Fig. 5. Selection (A; available superimposed on use) by adult female greater sage-grouse relative to proximity (0–1 with larger numbers representing closer proximity) to minor roads during breeding season and effects of this breeding habitat use on survival (B; dashed lines), fertilities (B; dotted lines), and relative fitness (C; dashed line represents population average) in Bighorn Basin, Montana and Wyoming, USA, 2011–2015. The x-axis limits represent the range of used habitat. The red vertical line is the median grouse-use location.

perceptual traps for sage-grouse: non-sagebrush shrub cover for nesting, wetland and variability in heat load for brood rearing, variability in soil moisture and non-sagebrush shrub cover for summer survival, and non-irrigated agricultural disturbance for winter survival. Similarly, Aldridge and Boyce (2008) documented decreased sage-grouse brood selection for high grass cover even though more grass cover decreased chick mortality.

It is argued that maladaptive habitat selection should be associated with anthropogenic disturbance because it is a rapid landscape change and populations may not have had the necessary time to adapt (Battin 2004). Even though there are many examples of negative impacts from anthropogenic disturbance causing traps, there also are cases where environmental features appear to cause traps. Two examples include black-throated sparrows (*Amphispiza bilineata*) nesting more frequently in shrub communities where nest success was lower (Pidgeon et al. 2003) and lesser prairie chickens avoiding areas of low shrub density where nest success was no different than areas with high shrub density (Patten and Kelly 2010). Only 20% of the habitat characteristics where we documented an apparent maladaptive selection relationship were relative to anthropogenic disturbance. We documented negative influences on survival from anthropogenic disturbance; however, for most of these negative effects, grouse were responding adaptively by also avoiding these disturbances.

We found suggestive evidence that sage-grouse were avoiding major roads, a more intensive form of disturbance, which negatively affected nesting and adult breeding season survival. There have been multiple studies on impacts from oil and gas development, a type of high-intensity anthropogenic disturbance, on sage-grouse success. Brood survival was lower in proximity to more oil and gas development (Aldridge and Boyce 2007, Kirol et al. 2015). Holloran (2005) documented lower annual adult survival for grouse impacted by oil and gas development. Along with negative survival impacts, there is evidence that grouse avoid high-intensity disturbances. There is evidence relative to grouse avoiding oil and gas development and related high-intensity disturbance during nesting and brood rearing (Holloran 2005,

Aldridge and Boyce 2007, Kirol et al. 2015), and during winter (Doherty et al. 2008, Carpenter et al. 2010, Smith et al. 2014). It appears that most evidence suggests that sage-grouse react adaptively relative to high-intensity disturbances such as oil and gas development and that these activities will not likely result in ecological traps because of grouse avoidance of these features. This conclusion is also consistent with a previous analysis in this study area that showed both higher mortality risk and increased avoidance associated with active bentonite mining (Pratt and Beck 2019). The one case of an apparent maladaptive selection relationship relative to selecting a disturbance that decreased survival was breeding adults selecting for proximity to minor roads where they were more likely to die, an example of a possible ecological trap. Two-track roads could be attractive to sage-grouse females by facilitating movement while nesting and brood rearing, but they could likewise facilitate movement of predators, thereby increasing kill rates (Dickie et al. 2016). In contrast, Dinkins et al. (2014) observed higher adult survival with greater road density. Kirol et al. (2015) documented selection for minor roads for brood-rearing females, whereas Carpenter et al. (2010) documented avoidance of minor roads during winter. We also documented increased mortality of adults near minor roads during summer, but unlike the breeding season, during the summer season minor roads were avoided. After we accounted for overall fitness, adult females that were using areas closer to minor roads during the breeding season had below-average fitness, but this effect was likely not biologically significant (Fig. 5).

In contrast to the negative effects from disturbance, non-irrigated agricultural disturbance provided possible survival benefits for the winter and breeding seasons. We have no clear understanding of how agricultural disturbances could provide survival benefits except to speculate that sage-grouse predators were avoiding these same disturbances or that predators experienced increased mortality in these areas. The agricultural variables in our analysis do not represent large-scale conversion of sagebrush to agriculture, which clearly has a negative effect on sage-grouse populations (Swenson et al. 1987, Smith et al. 2016). In general, anthropogenic

disturbances can create scenarios of perceptual traps because animals can perceive anthropogenic activity as a predation risk and avoid habitat that only has the appearance of greater risk of mortality (Frid and Dill 2002).

Animals cannot directly observe the fitness consequences of their selection decisions but can only observe the physical characteristics of their environment. The potential for mismatch between the environmental cue and the fitness outcome increases the more indirect the cue is (e.g., deciding where to forage based on current food abundance vs. vegetation structure around a nest at hatching based on vegetation structure at nest initiation; Schlaepfer et al. 2002, Kristan 2003). This could partially explain why we observed an apparent maladaptive relationship between selection and success for nesting. An alternative explanation is secondary fitness benefits that make it worth using risky habitat. This was suggested by Smith et al. (2018), who reported brood-rearing female sage-grouse in central Wyoming selected riskier habitats with more open herbaceous cover for foraging chicks, whereas broodless females selected less risky, more concealed habitat. In addition, Aldridge and Boyce (2008) reported brood-rearing female sage-grouse in southern Alberta may have selected riskier areas with less grass cover to maximize foraging opportunities. This was similarly suggested by Gibson et al. (2016a) in that nest-site selection by female sage-grouse may be a function of her selecting brood-rearing habitat and not necessarily for nest survival. For example, a female could be constrained to poorer quality nesting habitat because it is all that is available within proximity to brood habitat. She chooses to avoid using less risky nesting habitat for the greater chance of survival of her future brood. The initial steps of our research documented an apparent disconnect between habitat selection and success, but this does not directly represent a disconnect with fitness because these areas could be providing alternative benefits. Therefore, we calculated the relative fitness metric to document any carry-over effects on other vital rates that cumulatively determine fitness. The argument of secondary fitness benefits did not coincide with our observations of a possible perceptual trap relative to nesting habitat. Females who nested in areas with more non-

sagebrush cover (within 400 m) not only were more likely to have successful nests but were also more likely to have successful broods (Fig. 2). In our study area, low values (<2.5%) of non-sagebrush shrub cover, which were associated with below-average fitness but highly selected for, represented the typical sage-grouse nesting habitat of expansive monotypic stands of sagebrush (Connelly et al. 2011). Moderate values (between 2.5% and 10.5%), which were associated with above-average fitness but not selected for, represented edge habitat. High values (>10.5%) of non-sagebrush shrub cover were not used. We speculate that we observed lower nest survival in typical sage-grouse nesting habitat because predators in these areas, such as the common raven (*Corvus corax*; Bui et al. 2010), are specialists actively searching for sage-grouse nests possibly unlike those in edge habitat.

We expected secondary fitness benefits to be a likely explanation for the apparent maladaptive association between selection and survival we observed during the summer season. During summer, adults were selecting for more variability in vegetation greenness, which represents a selection for irrigated fields close to sagebrush or other sharp transitions between mesic sites and dry upland sites, but these areas were associated with higher mortality which makes it an example of a possible ecological trap. These areas provide better forage during the hot, dry summer and could help sage-grouse recover from the physically demanding breeding season (Fischer et al. 1996, Connelly et al. 2011). Therefore, these higher-quality forage areas could provide fitness benefits that are worth the increased mortality risk. However, grouse using these areas were associated with lower nest and brood success and slightly lower winter and breeding survival (Fig. 4). In our study area, lower values (0.01–0.055) for variability in vegetation greenness, which were associated with higher fitness and used by sage-grouse, represented moderate to high-elevation sagebrush. Higher values (>0.055), which were associated with below-average fitness and selected for, represented the edge of irrigated hayfields at lower elevations. In our study area, grouse that used lower elevation hayfields travelled shorter distances to access this habitat from their nesting and brood-rearing

areas that also occurred at lower elevations (Pratt, *unpublished data*). In contrast, grouse that used higher elevation mountain sagebrush communities travelled greater distances and nested and reared broods at both lower and higher elevations. There is evidence that sage-grouse can have lower nest and brood success at lower elevations (Gibson et al. 2016b, Cutting et al. 2019) possibly because of increased selection of these same habitats by predators (Coates et al. 2016). These observations are consistent with ours in that the grouse that are being attracted to low-elevation irrigated hayfields are already associated with lower nest and brood success. Even though this variable represents vegetation, it is still dependent on land use practices. Human activity could be causing an ecological trap by creating conditions attractive to sage-grouse but where they will ultimately be less successful. Predator communities could be different between low-elevation irrigated fields and high-elevation sagebrush, and grouse appeared more concentrated in the irrigated fields. Another possible explanation is the likely increased risk of West Nile virus associated with irrigated fields (Naugle et al. 2005). One of our GPS-equipped sage-grouse mortalities tested positive for West Nile and it was located in an irrigated field. Recovering carcass remains quickly after mortalities occurred was not an objective of our research, and this was the only carcass we tested. There has been recent interest in restoring riparian-type mesic habitat for sage-grouse during summer. Even though this type of habitat was not common in our study area, our results suggest that survival of sage-grouse should be monitored relative to the use of such restoration projects that are striving to increase the amount of green vegetation (Robertson et al. 2013).

Robertson and Hutto (2006) argue that you cannot prove existence of an ecological trap without proving actual preference for the habitat, which is not possible through a use vs. availability study such as ours. Regardless if we documented actual ecological and perceptual traps, in the practical sense, as it relates to conservation, it appears that there are possible disconnects between selection and success. In addition, we argue that ecological and perceptual traps are practically indistinguishable when using a habitat use vs. availability study without knowing

the actual thought process made by the animal. Whether an animal selects, or avoids, a habitat characteristic is two sides of the same coin (or variable). For example, do sage-grouse select for the presence of sagebrush or do they avoid the absence of sagebrush? However, when it comes to conservation, a biologist will have to speculate and experiment because addressing ecological traps requires removing the attractant while a perceptual trap requires removing the deterrent (Robertson et al. 2013). For example, the attractive cue for aquatic insects that lay eggs on man-made structures instead of on water was identified as reflected polarized light, and then, it was determined how to reduce this deleterious attractant (Kriska et al. 1998, Horvath et al. 2010).

We acknowledge that while our analysis identified associations between sage-grouse and landscape characteristics, our results do not necessarily represent cause and effect relationships. We emphasize that we do not believe that our findings equivocally show that sage-grouse are driven by maladaptive habitat selection of the identified habitat characteristics because we were not able to account for every possible secondary fitness benefit that grouse could be gaining from riskier areas. We believe that a primary benefit from our study is that we have identified areas that warrant further investigation. We especially believe that summer habitat use relative to irrigated hayfields warrants further investigation. Research questions should address the possible mechanisms explaining apparent maladaptive selection, or what are the secondary fitness benefits that grouse are gaining from selecting risky areas. Other secondary fitness benefits we did not account for include increased nest initiation, clutch size, egg hatchability, number of chicks fledged, and juvenile survival (Taylor et al. 2012).

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