

1 **Extreme site fidelity as an optimal strategy in an unpredictable**  
2 **and homogeneous environment**

3 Running Head: Gunnison sage-grouse site fidelity.

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23 **Abstract**

- 24 1. Animal site fidelity structures space-use, population demography, and ultimately gene  
25 flow. Understanding the adaptive selection for site fidelity patterns provides a  
26 mechanistic understanding to both spatial and population processes. This can be

27 achieved by linking space-use with environmental variability (spatial and temporal)  
28 and demographic parameters. However, rarely is the environmental context that  
29 drives the selection for site fidelity behavior fully considered.

- 30 2. We use ecological theory to understand whether the spatial and temporal variability  
31 in breeding site quality can explain the site fidelity behavior and demographic  
32 patterns of Gunnison sage-grouse (*Centrocercus minimus*). We examined female site  
33 fidelity patterns across multiple spatial scales: proximity of consecutive year nest  
34 locations, space-use overlap within and across the breeding and brooding season, and  
35 fidelity to a breeding patch. We also examined the spatial and temporal variability in  
36 nest, chick, juvenile, and adult survival.
- 37 3. We found Gunnison sage-grouse to be site faithful to their breeding patch, area of use  
38 within the patch, and generally to where they nest, suggesting an ‘Always Stay’ site  
39 fidelity strategy. This is an optimal evolutionary strategy when site quality is  
40 unpredictable. Further, we found limited spatial variability in survival within age  
41 groups, suggesting little demographic benefit to moving among patches. We suggest  
42 Gunnison sage-grouse site fidelity is driven by the unpredictability of predation in a  
43 relatively homogeneous environment, the lack of benefits and likely costs to moving  
44 across landscape patches and leaving known lek and breeding/brooding areas.
- 45 4. Space use and demography are commonly studied separately. More so, site fidelity  
46 patterns are rarely framed in the context of ecological theory, beyond questions  
47 related to the win-stay:lose-switch rule. To move beyond describing patterns and  
48 understand the adaptive selection driving species movements and their demographic  
49 consequences requires integrating movement, demography, and environmental  
50 variability in a synthetic framework.
- 51 5. Site fidelity theory provides a coherent framework to simultaneously investigate the  
52 spatial and population ecology of animal populations. Using it to frame ecological

53 questions will lead to a more mechanistic understanding of animal movement, spatial  
54 population structuring, and meta-population dynamics.

55 **Key-words:** animal movement; Gunnison sage-grouse; nest success; radio-telemetry; site  
56 fidelity theory; space-use; survival; win-stay:lose-switch.

## 57 **Introduction**

58 The spatial context of where and how species survive and reproduce is a fundamental  
59 component of their life history and ecology. A commonly observed behavior among animal  
60 species is the repeated use of distinct spatial areas in one or more seasons or stages of their  
61 life history (e.g., birds and mammals: Greenwood 1980; Lewis 1995; Hoover 2003, fishes:  
62 White & Brown 2013, amphibians: Sinsch 1991, crustaceans: Vannini & Cannicci 1995,  
63 molluscs: Lind 1989, reptiles: Broderick et al. 2007, insects: ?). The ubiquity of animals  
64 having fidelity to certain spatial areas suggests it is an evolutionary adaptive strategy in  
65 which individuals incur benefits from familiarity with their physical and social environment  
66 (Piper 2011). Site familiarity benefits and proximate causes of ‘site fidelity’ include efficient  
67 resource acquisition (Olsson et al. 2010), successful deterring of competitors (i.e., “resident  
68 advantage”; Jakobsson 1988), efficient movements and use of micro-environments (Vlasak  
69 2006), effective predator avoidance (Brown 2001), and decreased conflict with neighbors  
70 (Stamps 1987).

71 The evidence for fitness or demographic benefits of site fidelity has historically  
72 been limited (Piper 2011), but increasing (e.g., Lafontaine et al. 2017; Patrick &  
73 Weimerskirch 2017). Site fidelity is an emergent property of individual’s spatially  
74 restricting their movements to only certain areas. This restriction ultimately influences the  
75 population’s distribution and abundance and can structure meta-populations via  
76 immigration/emigration (Schmidt 2004; Matthiopoulos et al. 2005); lifetime space use  
77 patterns influence gene flow and thus evolutionary processes (Sugg 1996). Commonly, site

78 fidelity studies have focused on natal philopatry and breeding area fidelity because they  
79 have high fitness consequences (Schmidt et al. 2010). There has also been considerable  
80 focus on the evolutionary context and mechanisms driving natal dispersal (Mattysen 2012).  
81 However, it is increasingly appreciated that site fidelity, regardless of natal area, is an  
82 important process across time periods and activities outside the breeding season (Piper  
83 2011; Northrup et al. 2016; Patrick & Weimerskirch 2017) and may drive individual-based  
84 habitat associations for many years (McIntyre et al. 2017).

85           An individual's decision to remain faithful to its breeding area has often been  
86 linked to their past breeding experience (Hoover 2003; Schmidt 2004). This suggests  
87 individuals use their experiences to assess breeding site quality (Schmidt 2001). A simple  
88 decision rule that is widely supported across animal taxa (especially birds; Piper 2008) is  
89 that of the win-stay:lose-switch (WSLS) rule (Schmidt 2004): individuals return to a  
90 breeding site if they successfully produce young or switch breeding sites if they are  
91 unsuccessful. The type of information used in this decision is known as 'private  
92 information' (Schmidt et al. 2010). An alternative decision process is based on the  
93 perceived social information from neighboring individuals (Doligez et al. 2002; Piper 2011).  
94 Social information helps average over the stochasticity inherent in individual breeding  
95 success (as in the WSLS rule). The context of when private or social information may be  
96 advantageous, and more generally when site fidelity may be an evolutionary adaptive  
97 strategy, can be understood via the ecology of information theory (Schmidt et al. 2010).

98           The ecology of information theory frames breeding site fidelity decisions in terms  
99 of the spatial and temporal variability of the resources that affect breeding success (Switzer  
100 1997; Schmidt 2001; Schmidt et al. 2010; Table 1). Areas with high temporal variation  
101 provide little information (private or social) about breeding site quality, thus we expect  
102 breeding site decisions to be independent of past breeding experience (Schmidt et al. 2010).  
103 Furthermore, when there is low spatial variation in site quality within and among habitat  
104 patches (collection of possible breeding sites), regardless of temporal variability, we expect

105 an always-stay decision rule to be optimal when there are costs to moving (Switzer 1997).  
106 In contrast, if there is high spatial variation that is not temporally variable (thus  
107 predictable site quality), breeding experience provides valuable information about site  
108 quality and thus aids in the choice among available sites. In these environments, we should  
109 expect species to adopt a WSLs site fidelity strategy at either the site or habitat patch  
110 level (Schmidt et al. 2010). If site quality within a habitat patch varies more strongly than  
111 across patches, individuals benefit from being faithful at the site-level depending on their  
112 own breeding success (i.e., WSLs-Site, decision using private information). However, if site  
113 quality varies more among habitat patches than within a patch, individuals benefit by  
114 having high fidelity to the habitat patch. Thus, we should expect an individual to move  
115 among patches based on the breeding success of individuals within the patch (i.e.,  
116 WSLs-Patch, decision via social information).

117           Despite site fidelity and the WSLs rule being commonly examined in animal  
118 ecology, rarely are patterns evaluated in the context of theoretical expectations based on  
119 spatial and temporal variation in site quality. Even more so, we are unaware of site fidelity  
120 studies that consider the spatial constraints from a species' mating system, such as lekking.  
121 Lekking is a common mating system among birds and insects, in which males aggregate at  
122 distinct locations to display for females and obtain reproductive opportunities. The  
123 aggregation of both males and females have potential spatial constraints to where  
124 individuals subsequently nest, forage, incubate eggs, and brood chicks.

125           We used the Gunnison sage-grouse (*Centrocercus minimus*) to examine site  
126 fidelity behavior across multiple scales in the context of theoretical expectations based on  
127 the spatial and temporal variation in breeding site quality, and spatial constraints of their  
128 lek mating system. The Gunnison sage-grouse is a recently recognized species (Young et al.  
129 2000) occurring in the sagebrush (*Artemisia* spp.) habitats of southwestern Colorado and  
130 southeastern Utah, USA. The species was recently listed as federally threatened (USFWS  
131 2014). They are known to use different types of seasonal habitat throughout the annual

132 cycle, generally defined as the breeding (mating, nesting), brooding (rearing chicks), and  
133 winter seasons (Rice et al. 2017). We used a multi-year dataset (2004-2010) to examine site  
134 fidelity patterns and the influence of nest success across multiple scales: proximity of  
135 consecutive year nest locations, space-use overlap within the breeding season, and fidelity  
136 to a breeding patch. We also examined space-use fidelity within and across the brooding  
137 season, but without reliable measures of brood success, we did not link brooding area  
138 fidelity to demographic outcomes. Furthermore, we considered whether there are benefits  
139 to moving among breeding patches by examining the spatial and temporal variation in  
140 chick (< 30 days), juvenile (>30 days to 1 year), and yearling/adult (> 1 year) survival.  
141 Our objectives were to 1) characterize regional breeding patches and movement, 2) describe  
142 environmental spatial and temporal variability within and among breeding patches, 3)  
143 evaluate indirect evidence of spatial and temporal variability in breeding patch quality by  
144 examining seasonal range size, and 4) evaluate direct evidence by examining spatial and  
145 temporal variation in nest, chick, juvenile, and yearling/adult survival of Gunnison  
146 sage-grouse. These findings improved our understanding of the spatial demography of  
147 Gunnison sage-grouse and adaptive selection of these patterns.

148         We hypothesized Gunnison sage-grouse have high fidelity to a breeding patch,  
149 but not to specific nest sites within the patch (Fisher et al. 1993). Individuals are typically  
150 faithful to a lek or a lek complex (group of nearby leks; Connelly et al. 2011) and  
151 commonly nest within the same area as their lek (Gunnison sage-grouse: average of 2-4 km;  
152 Young et al. 2015). We did not expect Gunnison sage-grouse to be faithful to nest  
153 locations (Fisher et al. 1993).

## 154 **Materials and methods**

### 155 **Study Area**

156 We studied Gunnison sage-grouse (hereafter, sage-grouse) in the eastern portion of the  
157 Gunnison basin (Gunnison and Saguache counties, Colorado, USA). The basin comprise  
158 85-90% of the species' range, covered approximately 2,000 km<sup>2</sup>, and occurred between an  
159 elevation of 2,300 and 2,900 m. The study area was predominately sagebrush steppe,  
160 dominated by mountain big sagebrush (*Artemisia tridentate*) interspersed with rabbitbrush  
161 (*Chrysothamnus* spp.), antelope bitterbrush (*Purshia tridentata*), serviceberry  
162 (*Amelanchier* spp.), and mountain snowberry (*Symphoricarpos oreophilus*).

### 163 **Capture and Monitoring**

164 We captured sage-grouse from March to early May between 2004 and 2010 using  
165 spot-lighting techniques (Wakkinen et al. 1992; Giesen et al. 1982). We fit birds with a 17  
166 g necklace-style VHF radio-transmitter (model A4050 by Advanced Telemetry systems or  
167 model R12B by Holohil Systems, Ltd.) equipped with a 4-h mortality sensor. The  
168 transmitter was <2% of the weight of an average sage-grouse (female: 1270 g SD 90 g).  
169 Each radio-marked bird was relocated using hand-held antennas once every 1-3 days  
170 throughout the breeding (1 April - 15 July) and brooding seasons (16 July to 30  
171 September; Rice et al. 2017). Observers were trained to maximize the accuracy of azimuths  
172 while considering constraints, such as private property. Each relocation included recording  
173 multiple azimuths ( $\geq 2$ ) from known locations, typically within 30 minutes or less.  
174 Relocating individuals occurred throughout the day (0800-1700 hrs.). A female was  
175 determined to be nesting if found in the same location for more than 3 consecutive days.  
176 Visual observations of females on nests were avoided to minimize disturbance. After a  
177 female left the nest, the nest was located to assess the fate of the eggs (e.g., hatched,  
178 depredated, abandoned, or unknown) and a vegetation survey was conducted (Davis et al.

179 2015a). Sagebrush and grass cover and height surrounding the nest was surveyed using 30  
180 m transects, centered at the nest; vegetation cover and height was estimated at 5 m  
181 intervals along the transect. A Daubenmire frame (20 x 50 cm) was used to visually  
182 estimate the percent grass and forb cover.

## 183 **Breeding Patch and Environmental Variability**

184 We defined breeding patches based on *a priori* regional knowledge of breeding area  
185 affiliations separated by natural boundaries, including habitat and elevation (which covary  
186 with land-use patterns, such as agriculture and development; Fig. 1; see Appendix S1 in  
187 Supporting Information). Each patch consists of multiple leks. It is at this scale that we  
188 examined site fidelity within and among patches. The six breeding patches are South  
189 Parlin, North Parlin, Signal Mountain, Flat Top, Ohio Creek, and Chance Gulch (Fig. 1).

## 190 **Spatial and Temporal Variation in Breeding Site Quality**

191 Historical sage-grouse habitat consisted of large expanses of contiguous sagebrush, which  
192 are relatively stable ecosystems at the time scale of annual breeding site decision making.  
193 The dominant landscape scale disturbances were fire and herbivory from bison (*Bos bison*);  
194 fire rotation intervals were typically  $\geq 100$  years (Bukowski and Baker 2013) and grazing  
195 from large nomadic bison populations were likely highly temporally and spatially  
196 heterogeneous (Chambers et al. 2016). The relative temporal stability of these ecosystems  
197 would suggest annual correlation and thus predictability of site quality, at least at the scale  
198 relevant for selection processes of site fidelity via WSLs.

199 We considered environmental spatial variability within and among breeding  
200 patches by examining spatial patterns in nest site vegetation, annual precipitation, and  
201 soils. To understand whether there was greater variability in vegetation within or among  
202 patches, we fit a hierarchical Bayesian log-linear regression model to vegetation collected at  
203 nest sites. For each vegetation measure observed (shrub and grass cover and height;  $y_{i,s}$ ) at



204 nest  $i$  in breeding patch  $s$ , we estimated a mean ( $\mu_s$ ) and variance ( $\sigma_s^2$ ) for each breeding  
205 patch, where  $\log(y_{i,s}) \sim \text{Normal}(\mu_s, \sigma_s^2)$  and  $\mu_s$  are patch-level random effects  
206 ( $\mu_s \sim \text{Normal}(\mu_1, \tau^2)$ ). If  $\tau^2 > \sigma_s^2$ , there is more spatial variation across breeding patches  
207 than within patch  $s$ . We fit a similar model to investigate the variability in rainfall  
208 patterns (PRISM 30-Year Normals from 1981-2010; Resolution: 0.92 km x 0.72 km;  
209 PRISM 2017) at estimated sage-grouse locations (details provided below) within and across  
210 breeding patches. For each model, we used diffuse priors and fit the model using Markov  
211 Chain Monte Carlo (MCMC) methods. Last, we estimated the probability of sage-grouse  
212 locations belonging to a set of dominant soil moisture-temperature regimes using a  
213 multinomial log-linear model in the R package ‘nnet’. Soil data were compiled by Maestas  
214 et al. 2016 (Resolution: 0.01 km x 0.01 km). Variation in soil regimes provide indirect  
215 support to variation in dominant vegetation characteristics and their resistant/resilient  
216 properties (Chambers et al. 2016), and thus variation in breeding patch quality.

217           Measuring site quality is difficult due to the complexity of interacting  
218 environmental factors. Therefore, we examined variation in sage-grouse seasonal ranging  
219 across breeding patches as an indirect measure of patch quality. Intraspecific variation in  
220 range size can be understood in the context of optimal foraging theory, which predicts that  
221 animals will maximize energy intake while minimizing energetic expenditures, such as  
222 movement (Pyke et al. 1977; Northrup et al. 2016). Thus, individuals in areas of greater  
223 forage quality and quantity should use smaller areas. We examined seasonal range size by  
224 estimating the 95% isopleth of individuals’ utilization distribution within the breeding and  
225 brooding seasons (estimation details are described in the ‘Site Fidelity’ section). We  
226 quantify variation by estimating the semi-interquartile range ( $(Q_3 - Q_1)/2$ ) for each season  
227 and patch, as well as across patches. If the within patch semi-interquartile range was less  
228 than across patches, we considered there to be less variation within the patch.

## 229 **Spatial and temporal variation in nest success**

230 To understand whether site and patch environmental variability translates into breeding  
231 area quality variability, we examined the spatial and temporal factors that are  
232 hypothesized to influence nest success (see Davis et al. 2015a). Specifically, we investigated  
233 nest site vegetation characteristics (shrub height, shrub cover, grass cover, and grass  
234 height), breeding patch affiliation, temporal factors (e.g., year, timing of incubation  
235 initiation, and nest age), and age of the nesting female (yearling or adult). We used a  
236 predictive modeling framework that optimizes within-sample predictive performance using  
237 cross-validation. Specifically, we fit the nest success data (1 = success, 0 = failure) using a  
238 logistic regression model with all standardized covariates that was optimized using the  
239 least absolute shrinkage and selection operator (LASSO; Tibshirani 1996). We used 5-fold  
240 cross validation, evaluating shrinkage parameters using the average deviance ( $-2 \times$   
241 log-likelihood) of the left out data across all folds. LASSO regularizes model parameters,  
242 thereby accommodating numerical issues due to multicollinearity of covariates and  
243 providing variable selection by removing effects of covariates. The result is an optimal  
244 predictive model that is coherently interpretable in terms of important ecological effects  
245 (see Gerber et al. 2015; Hooten & Hobbs 2015). We used the same procedure to model nest  
246 success as a multinomial outcome to evaluate whether predation on nesting females or eggs  
247 drives nest failure and whether it varied spatially or temporally (0 = nest failed or was  
248 abandoned, 1 = nest failed due to the female or eggs being depredated, 2 = nest success).  
249 Predation could make quality nest site selection highly unpredictable and thus may affect  
250 female site fidelity. We conducted model fitting optimization and cross-validation for both  
251 analyses in the R package ‘glmnet’ (Friedman et al. 2010).

## 252 **Spatial and temporal variation in survival**

253 We further considered variation in breeding site quality by evaluating the spatial and  
254 temporal variation in chick, juvenile, and yearling/adult survival across breeding patches

255 by extending previous analyses of these populations (Davis et al. 2015b, 2016). We used  
256 the most parsimonious models of these analyses and include additional individual  
257 covariates indicating the breeding patch location of the individual. We evaluated temporal  
258 and spatial survival differences by comparing models using AIC, BIC, and likelihood ratio  
259 tests, and estimating the expected marginal differences between breeding patch coefficients  
260 (e.g.,  $\hat{\beta}_{\text{diff}} = \hat{\beta}_1 - \hat{\beta}_2$  with variance  $\text{Var}(\hat{\beta}_1) + \text{Var}(\hat{\beta}_2) - 2\text{Cov}(\hat{\beta}_1, \hat{\beta}_2)$ , where Cov is the  
261 covariance).

## 262 **Site Fidelity**

### 263 **Nest site fidelity**

264 We investigated nest site fidelity by examining whether individuals switch nesting locations  
265 among breeding patches and whether this occurred after nest failure in the previous year.  
266 We also estimated the Euclidean distance between consecutive year nesting locations and  
267 evaluated whether female sage-grouse are more likely to nest close to a previous nest  
268 location if they were successful in hatching eggs in the previous year. We analyzed data  
269 using a Bayesian log-linear regression model that included a single variable (NestSuccess)  
270 indicating whether the previous years nest was successful or not; priors on parameters were  
271 diffuse. We fit the model using MCMC and made inference based on posterior distributions.

272         If individuals showed fidelity to a successful nest location in the previous year,  
273 we assumed that there were demographic benefits, possibly due to site familiarity. To  
274 evaluate whether this was the case, we modeled whether nest success was different in the  
275 second year depending on whether an individual was successful or not in the first year. We  
276 analysed these data using a Bayesian logistic regression model with a single variable  
277 indicating whether the first year was successful or not (NestSuccessYear1).

278 **Breeding and brooding space-use and patch fidelity**

279 To understand whether female sage-grouse used the same breeding patches and sites across  
 280 years, we used telemetry data to simultaneously estimate animal locations along with  
 281 individual breeding and brooding season utilization distributions for each year. Breeding  
 282 utilization distributions correspond to activities after leaving the lek, during the nesting  
 283 period. We modeled the telemetry data using a recently developed Bayesian Azimuthal  
 284 Telemetry Model (ATM; Gerber et al. 2018) that properly accounts for spatial location  
 285 uncertainty within the utilization distributions. For each radio-tagged individual  
 286 ( $l = 1, \dots, L$ ) that is relocated on certain days ( $i = 1, \dots, N_l$ ) within each season/year, an  
 287 observer records a set of azimuths ( $\theta_{lij}; j = 1, \dots, J_{li}$ ) at known locations  $\mathbf{z}_{lij} \equiv (z_{1lij}, z_{2lij})'$   
 288 to estimate the sage-grouse's spatial location,  $\boldsymbol{\mu}_{li} \equiv (\mu_{1li}, \mu_{2li})'$ . We used the von Mises  
 289 distribution and a link function to relate the true animal location with the data,

$$\begin{aligned} \text{Observation Process: } \quad & \theta_{lij} \sim \text{von Mises}(\tilde{\theta}_{lij}, \kappa_{li}), \\ \text{Link Function: } \quad & \tilde{\theta}_{lij} = \tan^{-1} \left( \frac{\mu_{2li} - z_{2lij}}{\mu_{1li} - z_{1lij}} \right). \end{aligned} \tag{1}$$

290 The parameter  $\kappa$  is an estimate of azimuthal uncertainty, recognizing that the location of  
 291 each bird is not known exactly; simulations based on the sage-grouse data indicated good  
 292 statistical properties for estimating  $\kappa$  and thus coverage of the true animal location  
 293 (Gerber et al. 2018). We used the estimated spatial locations ( $\boldsymbol{\mu}_{li}$ ) along with a small  
 294 number of aerial and known locations, in a non-parametric kernel density estimator  
 295 (Hooten et al. 2017) to derive each individuals season/year utilization distribution. Aerial  
 296 locations were taken with a GPS during low-altitude flights that circled the bird's location.  
 297 We assumed these locations were not known exactly by treating them as multivariate  
 298 normal distributed, centered at the aerial location coordinates with a covariance matrix  
 299  $12.5^2 \mathbf{I}$ ; this allowed a maximum deviation from the GPS location of approximately 50 m.  
 300 For an individual that was relocated  $n$  times (a minimum of 10 locations) within a  
 301 season/year, we estimated their seasonal utilization distribution for the  $k^{\text{th}}$  MCMC

302 iteration using the 95% isopleth of the kernel function,

$$\hat{f}(\mathbf{c}) = \frac{\sum_{i=1}^n g((c_1 - \mu_{1i}^{(k)})/b_1)g((c_2 - \mu_{2i}^{(k)})/b_1)}{nb_1^2}, \quad (2)$$

303 evaluated at the locations  $\mathbf{c} \equiv (c_1, c_2)'$ , kernel function  $g(\cdot)$ , and bandwidth parameter  $b_1$ .

304 To measure breeding and brooding area site fidelity, we compared individuals'  
305 utilization probability distribution (UD) across seasons (breeding-breeding,  
306 brooding-brooding, breeding-brooding) and years. The UDs correspond to the post-lekking  
307 period. For each comparison, we measured site fidelity as a degree of overlap between UDs  
308 using the Bhattacharyya coefficient (Bhattacharyya 1943). For probability distributions  $p$   
309 and  $q$  over the same domain  $X$ , the Bhattacharyya coefficient is defined as,

$$\text{BC}(p, q) = \sum_{x \in X} \sqrt{p(x)q(x)}, \quad (3)$$

310 where  $0 \leq \text{BC} \leq 1$ . BC will be approximately zero when there is no overlap and one when  
311 there is complete overlap. Therefore, a BC value of zero could indicate an individual used a  
312 different patch between years or the same patch, but different sites within a patch. To  
313 clarify how individuals' space-use varies across and within breeding patches, we  
314 summarized results by BC value and breeding patch association for each UD comparison.  
315 Last, we investigated the proximity of individuals' space-use by estimating the Euclidean  
316 distance between the highest UD densities being compared. We compared different sets of  
317 overlap in UDs to provide general and specific insights into site fidelity behavior by  
318 comparing 1) among all UDs within and across seasons (breeding-breeding,  
319 brooding-brooding, and breeding-brooding) for consecutive and non-consecutive years, and  
320 2) within breeding season by nest success. Since the number of spatial locations varied  
321 across individuals by season and year (10 to 54), we evaluated the consistency in our  
322 results by comparing inference from using all the location data and standardizing the  
323 number of locations to only 10 per individual by season and year.

## 324 **Results**

### 325 **Capture and Monitoring**

326 A total of 94 female sage-grouse were relocated in at least two seasons with a minimum of  
327 10 locations per season between 2004 and 2010 (see Appendix S2 in Supporting  
328 Information Appendix 2, Table A1). We observed a total of 23,869 azimuths across all  
329 individuals, which were used to estimate 6,057 locations of female sage-grouse. The number  
330 of azimuths observed per relocation varied, ranging from 2 to 12 (Appendix 1, Fig. A1).  
331 Including aerial and known locations, we obtained a total of 6,608 sage-grouse locations.  
332 The number of locations for each individual observed in a season/year ranged from 10 to  
333 54 with a median of 21.

334         Each individual was observed from 2 to 11 seasons with a median of 3 seasons.  
335 The majority of individuals during the breeding season were only observed within a single  
336 breeding patch (81%). Fifteen individuals were observed in two patches and two were  
337 observed in three patches; these multi-patch observations were a small number of each  
338 individuals' location data (<5%), except for one individual that had 142 locations split  
339 between two patches. Individuals observed at multiple patches were not limited to only  
340 using adjacent patches. The majority of individuals during the brooding season (89%) were  
341 also only observed within a single patch; four individuals were only observed once at a  
342 second patch, while two individuals were observed at more than one patch, primarily in  
343 different years.

### 344 **Spatial variation in breeding site quality**

345 We found that vegetation characteristics were more variable within a breeding patch than  
346 across patches (Appendix 1, Fig. A2). In contrast, we found considerably more variation in  
347 annual precipitation across patches than within (Appendix 1, Fig. A3). We also found that  
348 sage-grouse locations dominantly occurred within frigid-ustic (cold-intermediate moisture)

349 and cryic-udic (cool-moist) soils (Appendix 1, Fig. A4). These soil regimes typify elevated  
350 productivity within shrub-steppe communities (Chambers et al. 2016). While the dominant  
351 soil types were generally similar across the breeding patches (Appendix 1, Fig. A4), a  
352 model allowing the probabilities to vary across soil types ( $M_{soil}$ ) had better predictive  
353 ability with the data (measured by AIC) than a model that considered them constant  
354 ( $M_{null}$ ;  $\Delta AIC_{M_{soil}} = 0$ ,  $\Delta AIC_{M_{null}} = 15069.57$ ).

355 We found noticeable variation in ranging area across breeding patches by season,  
356 suggesting patch-level variation in quality (Figs. 2, A5-A6). Variation in UD area across  
357 patches was generally greater in the breeding season than the brooding season. Median  
358 patch-level ranging size in the breeding season was lowest at Ohio Creek and Flat Top ( $\approx$   
359  $2.9 \text{ km}^2$ ) and larger at Chance Gulch ( $5.60 \text{ km}^2$ ) and South Parlin ( $8.0 \text{ km}^2$ ). Signal  
360 Mountain UD areas were even larger at a median of  $12.30 \text{ km}^2$  and largest at North Parlin  
361 with a median of  $16.40 \text{ km}^2$ . North Parlin was much more variable across breeding patches  
362 in the breeding season compared to within season, while the other patches were similar or  
363 less variable (Appendix 1, Figs. A5-A6). Based on optimal foraging theory, we would  
364 expect Ohio Creek and Flat Top to have a higher nest success, given the reduced energetic  
365 expenditure related to movement. Brooding season UD areas were smaller or equivalent in  
366 size to breeding season UD areas. Median UD areas were smallest at Flat Top ( $2.46 \text{ km}^2$ ),  
367 then Ohio Creek and South Parlin ( $\approx 3.57 \text{ km}^2$ ), then Signal Mountain and Chance Gulch  
368 ( $\approx 4.89 \text{ km}^2$ ), and were largest at North Parlin ( $9.61 \text{ km}^2$ ). Within patch variation in the  
369 brooding season was greater than across patch variation only at North Parlin and Flat Top  
370 (Appendix 1, Figs. A5-A6).

## 371 **Spatial and temporal variation in nest success**

372 We observed a total of 177 nests belonging to 120 individuals. We found no support for  
373 any covariates hypothesized to influence nest success and failure (Appendix 1, Fig. A7).  
374 The optimal predictive model indicated a mean nest success of  $0.446 \pm 0.038 \text{ SE}$ . We also

375 found no support for any covariates hypothesized to influence nest failure, predation, and  
376 nest success (Appendix 1, Fig. A8). The optimal predictive model indicated a mean nest  
377 failure, predation, and success of 0.070, 0.462, and 0.468, respectively.

## 378 **Spatial and temporal variation in survival**

379 We found little evidence to suggest there was annual variation in chick, juvenile, or  
380 adult/yearling survival, however, there was a fair amount of parametric uncertainty (Davis  
381 et al. 2015b, 2016; Appendix 1, Tables A1-A3 and subsection ‘Spatial and temporal  
382 variation in survival’). We also found relatively minimal variation in survival of the  
383 different age groups by breeding patch (Appendix 1, Tables A1-5; Fig. A9). Among all  
384 pairwise comparisons, we found chick survival was much higher (comparing maximum  
385 likelihood estimates) at Ohio Creek than Signal Mtn. and North Parlin (Appendix 1, Table  
386 A4). In the juvenile survival analysis, we found North Parlin had higher survival than  
387 South Parlin. All other comparisons were not statistically significant; detecting differences  
388 that were not extreme was difficult due to high parameter uncertainty. Last, adult survival  
389 was generally similar among breeding patches (Appendix 1, Fig. A9). However, we did find  
390 that Ohio Creek survival was marginally lower than North Parlin and Chance Gulch. Also,  
391 South Parlin survival was lower than North Parlin and Chance Gulch (Appendix 1, Table  
392 A4).

## 393 **Nest site fidelity**

394 Out of 43 individual sage-grouse with multiple years of nesting location data (consecutive  
395 years and not, range of 2-4 years per individual), only a single individual was observed to  
396 nest in more than one breeding patch. This individual was observed nesting in one patch in  
397 2005 and 2006 and a different patch in 2008 and 2010; in all years, this individual was  
398 successful at hatching chicks. Among 47 consecutive year nesting comparisons, (36 unique  
399 individuals) no birds were observed to switch breeding patch; 19 out of 47 were



400 unsuccessful in the previous year, but did not switch their patch. We found support for a  
401 negative effect ( $P(\beta_{\text{NestSuccess}} < 0) = 0.96$ ;  $E[\beta_{\text{NestSuccess}}] = -0.713, -1.45 \text{ to } 0.073$ , 95%  
402 credible interval) of nest success on the distance between consecutive year nest locations  
403 (Fig. 3). The median distance between nest locations when individuals were previously  
404 unsuccessful at hatching chicks was 357 m (209 - 598, 95% credible interval), which  
405 decreased when individuals were successful to 178 m (113 - 276, 95% credible interval).  
406 However, we found no improvement in nest success in the second year based on the first  
407 year nest success ( $P(\beta_{\text{NestSuccessYear1}} > 0) = 0.26$ ;  $E[\beta_{\text{NestSuccessYear1}}] = -0.404, -1.60 \text{ to } 0.790$ ,  
408 95% credible interval).

## 409 **Breeding and brooding space-use and patch fidelity**

410 First, we found no changes in our inference to breeding and brooding space-use and patch  
411 fidelity between using all individuals' spatial locations and when standardizing the sample  
412 size (see Appendix 1). We found strong fidelity of individuals to their patch during both  
413 the breeding and brooding seasons (Appendix 1, Fig. A10;  $>0.91$  proportion of individuals  
414 used the same patch across all comparisons). Comparing consecutive year space-use in the  
415 breeding season, only a single individual (total of 46 comparisons) was observed to use two  
416 different patches. During the brooding season, only two individuals (total of 57  
417 comparisons) were observed to use different patches in consecutive years (one of these  
418 individuals was also observed in different patches during the breeding season). Comparing  
419 across consecutive and non-consecutive years also supports strong site fidelity to the patch;  
420 95% and 91% of all comparisons were within the same patch for the breeding and brooding  
421 season, respectively (73 and 90 total comparisons; Appendix 1, Fig. A10).

422 We found seasonal space-use overlap was variable, but consistently showed  
423 moderate overlap for all comparisons (Fig. 4; Appendix 1, Fig. A11). Notably, it was  
424 uncommon for an individual to use the same breeding patch (within or across seasons), but  
425 have no overlap in their space-use (i.e., BC value of 0). This was especially rare when

426 comparing within seasons. The median space-use overlap was highest within the breeding  
427 season, then the brooding season, then across these seasons (Fig. 4; Appendix 1, Fig. A11).  
428 The average Euclidean distance between UDs across all seasons and years was around 2 to  
429 3 km (Appendix 1, Fig. A12). The median Euclidean distance across breeding seasons was  
430 commonly between 0 and 1 km, but ranged up to 6 km, while the average distance across  
431 brooding seasons was commonly 0 to 2.5 km, but ranged up to 10 km. As such, most  
432 individuals use the same breeding patch for breeding and brooding across all years and  
433 generally use the same area within each season and somewhat across seasons.

434 We also found no indication that female sage-grouse move sites within the  
435 breeding season based on their previous nesting experience (Fig. 5; Appendix 1, Fig. A13).  
436 Across all comparisons, there was moderate spatial overlap regardless of nest success  
437 outcome. In fact, we found higher median overlap among consecutive years when a  
438 previous nest had failed. This result was also supported by a slightly lower median distance  
439 between UDs when a previous nest had failed (Appendix 1, Fig. A14). However, space-use  
440 overlap was moderate even when comparing across non-consecutive years by nest success,  
441 suggesting individuals simply use a similar area regardless of nesting outcome (Fig. 5). We  
442 also found moderate space-use overlap across brooding seasons and between  
443 breeding-brooding seasons (median BC values of  $\approx 0.45$ ; Figs. A15-A16). The median  
444 Euclidean distance between UDs across brooding season was 2 km, while between breeding  
445 to brooding seasons was slightly higher at 2.5 km (Figs. A17-A18).

## 446 Discussion

447 Rarely are site fidelity patterns framed in the context of relevant ecological theory, beyond  
448 questions related to the WSLs strategy. Site fidelity behavior and its influence on  
449 demography and movement can be understood in the context of environmental spatial and  
450 temporal variability (Schmidt et al. 2010). This allows a more mechanistic understanding  
451 of habitat selection across spatial scales (Lafontaine et al. 2017), as well as possible

452 metapopulation dynamics by recognizing the level of connectivity among habitat patches  
453 (Switzer 1997), which has important implications for population regulation (Matthiopoulos  
454 et al. 2005) and persistence (Schmidt 2004). More so, empirical studies framed by theory  
455 are essential to modifying the theory and its predictions based on new discoveries and  
456 previously unconsidered conditions and constraints.

457           In this study, we quantified female Gunnison sage-grouse site fidelity across  
458 multiple spatial scales, framing observations based on theorized drivers of spatial and  
459 temporal variability in breeding site quality. We found Gunnison sage-grouse to exhibit  
460 high site fidelity across spatial scales. Individuals were faithful to their breeding patch,  
461 area of use within their patch by season, and typically nested near their previous nesting  
462 location, using private information of their previous nest success outcome to decide the  
463 proximity (mean distance of 0.18 when successful and 0.36 km when unsuccessful).  
464 However, there was no support that this nest-level WSL rule is beneficial, as nesting  
465 closer to a previously successful nest did not improve the likelihood of success in the  
466 following year. However, we recognize that nest site selection may be based on variables  
467 that were not collected in this study, including brooding or fledgling success.

468           Despite the extreme site fidelity observed, we also found environmental variation  
469 across and within breeding patches, which suggests variation in site quality. Specifically, we  
470 found across patch variation in soil temperature-moisture regimes, precipitation, and  
471 generally the ranging size of UDs within the breeding season. We recognize that range size  
472 as a measure of site quality is a simplification of a complex behavioral movement process;  
473 we encourage future studies to focus on finer-scale movement as a means to better  
474 understand costs and benefits of movement. In terms of structural vegetation differences,  
475 we generally found more variability among sites within patches than across patches.  
476 However, despite these suggestive differences in site quality, we found no strong evidence of  
477 spatial (within or among patch) or temporal variation in nest success or chick, juvenile,  
478 and yearling/adult survival.

479 Without clear spatial variation in breeding site quality, there is no benefit to  
480 moving sites at any spatial scale. Our observations of nest site vegetation were all within  
481 optimal ranges according to habitat management guidelines for Gunnison sage-grouse  
482 (Davis et al. 2015a). Moreover, we found no evidence that nest failure due to the eggs or  
483 the female being depredated varied spatially or temporally. Nest failure due to predation  
484 was as likely as for the nest to be successful. It is believed that predation is the primary  
485 cause of mortality of all age classes of Gunnison sage-grouse (Young et al. 2015). This  
486 suggests that, while site quality may be predictable in terms of structural vegetation  
487 characteristics, it is unpredictable in terms of predation. Even when individuals were  
488 successful and subsequently nested in the following year closer to their previous nest (i.e.,  
489 following a WSLs strategy), there was no evidence of improved nest success. Individuals  
490 may simply be unable to cue in on sites to reduce nest predation, and thus live in a  
491 homogenous and unpredictable environment. Furthermore, we found weak spatial variation  
492 in survival of all age groups among patches, suggesting why sage-grouse may only rarely  
493 move patches.

494 Lekking birds are believed to have some of the highest levels of nest predation  
495 (Phillips 1990), and from experimental studies, there is strong evidence that predation  
496 pressure and predator hunting mode fundamentally affects prey movement and space-use  
497 (Miller et al. 2014). But also, breeding site fidelity strategy is known to depend on the  
498 specific cause of reproductive failure (Schmidt 2001). In considering the diverse predators  
499 of sage-grouse (includes birds of prey, corvids, and terrestrial mammals), which are  
500 typically wide-ranging generalists that likely take eggs and birds opportunistically (Hagen  
501 2011; Young et al. 2015; Conover & Roberts 2017), there may be nowhere to escape the  
502 possibility of predation. Therefore, in relatively homogenous habitat, in which individuals  
503 may be unable to avoid numerous opportunistic predators or assess breeding site quality in  
504 terms of predation pressure, the costs of movement may easily supersede any benefit,  
505 selecting individuals with extreme site fidelity. In fact, an always stay site fidelity strategy,

506 in which individuals do not use WSLs, is the evolutionary optimal strategy in  
507 unpredictable homogenous environments (Switzer 1997; Schmidt et al. 2010). Furthermore,  
508 minimizing movement, especially flying, is complementary with the behavioral and  
509 phenotypic selection for crypsis in sage-grouse. Despite being strong fliers, sage-grouse are  
510 mostly ground-dwelling, relying on camouflage until they are threatened and resort to  
511 flying (Young et al. 2015).

512           However, predation may not fully explain why Gunnison sage-grouse do not  
513 move among breeding patches. We might expect Gunnison sage-grouse to selectively move  
514 among patches in response to failed nesting due to nest predation because moving farther  
515 (across patches, rather than within) may be more likely to change predator communities  
516 and abundance, and thus predation pressure. Further, site fidelity to the patch may be  
517 partially a by-product of fidelity to a lek or lek complex. Fidelity to leks and lek proximity  
518 to nesting is well documented in sage-grouse populations (Connelly et al. 2011; Young et al.  
519 2015), including in this study population. However, we were unable to link space-use with  
520 specific lek locations, as we may not have observed all leks used by each individual. The  
521 selection pressure to nest within the general proximity to their lek and thus the costs of  
522 moving breeding patches is less clear. Patch-level variation may be irrelevant in site fidelity  
523 patterns and thus potential social information also irrelevant. Perhaps though, the diversity  
524 of ground and aerial predators in the sagebrush steppe has led to the selection against  
525 moving among patches to limit exposure to predation, and also because the ubiquity of  
526 opportunistic nest predators means that movements of any scale are irrelevant to altering  
527 nest predation pressure (as observed in this study). An additional factor that may explain  
528 the lack of long distance movements of Gunnison sage-grouse could be due to physiological  
529 constraints on grouse and generally all Galliformes. Galliformes are known to have flight  
530 muscles that are almost exclusively glycolytic muscle fibers, which limits flights to short  
531 bursts of activity before quickly fatiguing (Butler 2016). Therefore, to move long distances  
532 may require several short flight bursts, which are energetically costly and perhaps risky by

533 attracting the attention of predators. Last, we can not rule out that site fidelity may be at  
534 least partially due to a lack of density-dependent factors that when present would cause  
535 individuals to disperse rather than compete for limited resources (Harts et al. 2016).

## 536 **Consequences of site-fidelity**

537 Spatial segregation of subgroups by breeding patch affiliation within the eastern portion of  
538 the Gunnison basin suggests a high-level of spatial structuring. Over a seven year period,  
539 we observed few movements across breeding patches, suggesting that  
540 immigration-emigration processes have minimal influence on the meta-population dynamics  
541 among patches. Rather, within breeding patch dynamics in the breeding and brooding  
542 season are likely to drive changes in the abundance of this threatened bird. Theoretical  
543 results also suggest that high site fidelity of aggregated breeding species (e.g., lek or  
544 colonial breeders) can hinder population growth by reducing the colonization of unoccupied  
545 habitat, such that only a portion of the available habitat is occupied (Matthiopoulos et al.  
546 2005). We suggest habitat changes from anthropogenic and natural disturbances should be  
547 viewed in the context of the spatial scale of the breeding patches. Since all realistic  
548 landscape disturbances (i.e., fire and development) are smaller in spatial scale than the  
549 Gunnison Basin, it is arguable that the breeding patches afford a measure of population  
550 redundancy. Thus, environmental and anthropogenic change within one breeding patch is  
551 unlikely to affect birds associated with other breeding patches. However, the extent of  
552 movement among patches within the winter is still unknown. Further, we were not able to  
553 explicitly evaluate juvenile natal dispersal, which for many species occurs at higher rates  
554 than breeding dispersal (Harts et al. 2016).

## 555 **Conclusions**

556 Animal site fidelity is a commonly observed behavior that has important consequences to  
557 animal space-use and thus the spatial structuring of populations. Examining the spatial

558 and temporal variability of environmental and demographic outcomes contributed to the  
559 understanding of ecological processes likely driving Gunnison sage-grouse demography and  
560 site-fidelity patterns. Notably, their always-stay strategy suggests higher fitness outcomes  
561 by minimizing movements and capitalizing on site familiarity benefits in an environment  
562 where nest predation is ubiquitous, breeding/brooding habitat is generally suitable,  
563 demographic benefits to moving are minimal, and moving may incur higher predation risk.  
564 Given the extreme site fidelity observed in this study, future population and habitat  
565 management could be framed in the context of these spatial affiliations.

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## 706 **Supplementary Material**

707 Appendix 1: Additional study details and results tables and figures.

708 Appendix 2: Data summary table of the number of locations and azimuths of Gunnison  
709 sage-grouse by year and season.

## 710 **Acknowledgments**

711 Any use of trade, firm, or product names is for descriptive purposes only and does not  
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## 718 **Data Accessibility**

719 Data are archived at Dryad (DOI pending review). Location data are not publicly available  
720 due to concerns of providing detailed spatial information on a federally threatened species.  
721 Data requests can be made at Colorado Parks and Wildlife with Dr. James Gammonley,  
722 [jim.gammonley@state.co.us](mailto:jim.gammonley@state.co.us).

## 723 **Author Contributions**

- 724 • BDG, MBH, CPP, MBR, JHG, ADA, and AJD conceived the ideas and contributed  
725 to critical editing of previous drafts and gave final approval for publication.
- 726 • BDG, MBH, CPP designed the statistical framework and fit the data.
- 727 • BDG led the writing of the manuscript.

Table 1: Theoretical optimal site fidelity predictions depending on temporal and spatial variability in site quality.

Temporal Variation	Spatial Variation <sup>1</sup>	Information	Site Fidelity Prediction <sup>2</sup>
High	Site $\equiv$ Patch	None	Always Stay <sup>3</sup>
High	Site $>$ Patch	None	No Fidelity - move among sites, rather than patches, regardless of breeding success
High	Patch $>$ Site	None	No Fidelity - move among patches, rather than sites, regardless of breeding success
Low	Site $\equiv$ Patch	None	Always Stay <sup>3</sup>
Low	Site $>$ Patch	Private	Fidelity to Site (WSLS-Site)
Low	Patch $>$ Site	Social	Fidelity to Patch (WSLS-Patch)

31 728 <sup>1</sup>Sites are locations within a patch.

729 <sup>2</sup>References: Switzer 1993, Schmidt et al. 2001, Schmidt et al. 2010.

730 <sup>3</sup>Assuming there are costs to moving. Otherwise, individuals are expected to move following an ideal-free settlement strategy,  
731 thus indifferent to the site/patch or past experience (Schmidt 2001).

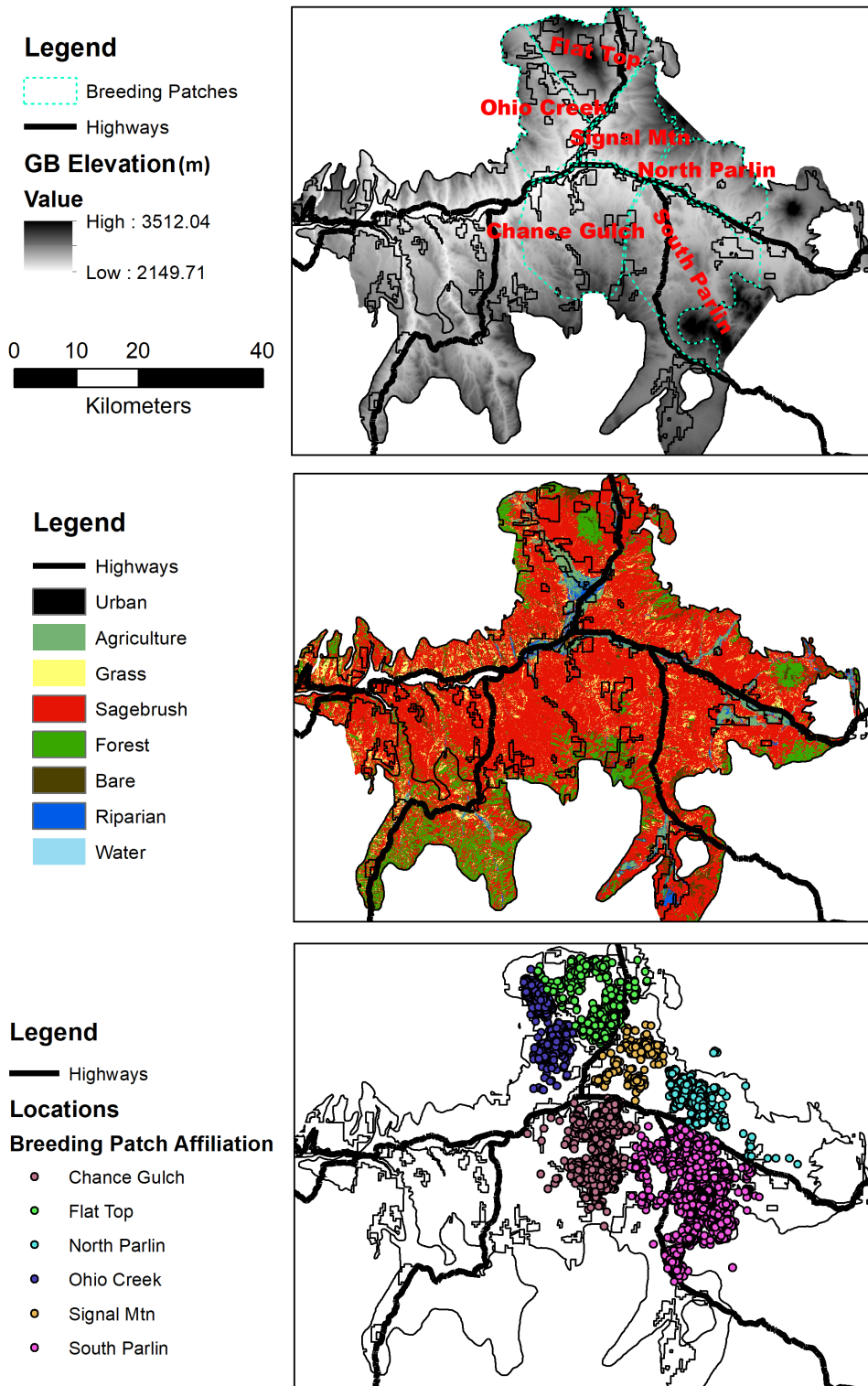
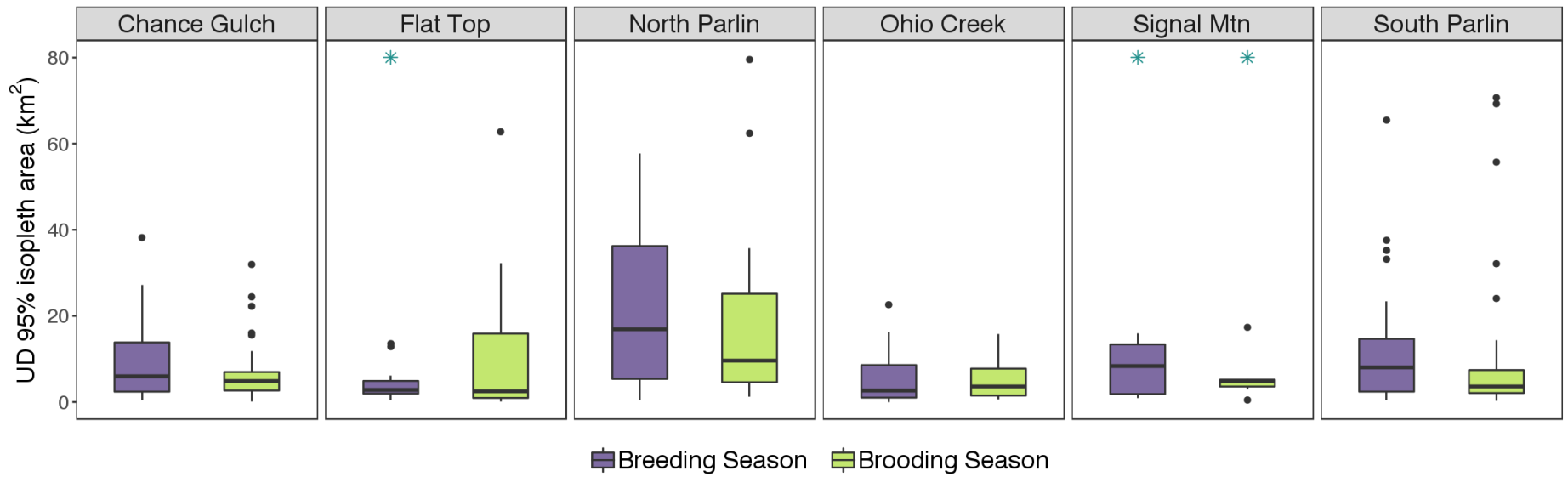


Figure 1: Elevation (top plot) and vegetation (middle plot) classification throughout the Gunnison sage-grouse critical habitat in the Gunnison basin of Colorado, USA. Point estimate locations (bottom plot) for all individuals tracked from 2004-2010 during the breeding and brooding seasons were assigned to a breeding area affiliation (top plot).





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Figure 2: Summary plots of posterior median estimates of individual Gunnison sage-grouse' 95% utilization distribution area for the breeding and brooding seasons by breeding area patch. The symbol \* indicates measurements beyond the maximum y-axis limit. Individual estimates along with 95% credible intervals can be found in Appendix 1, Fig. A6.

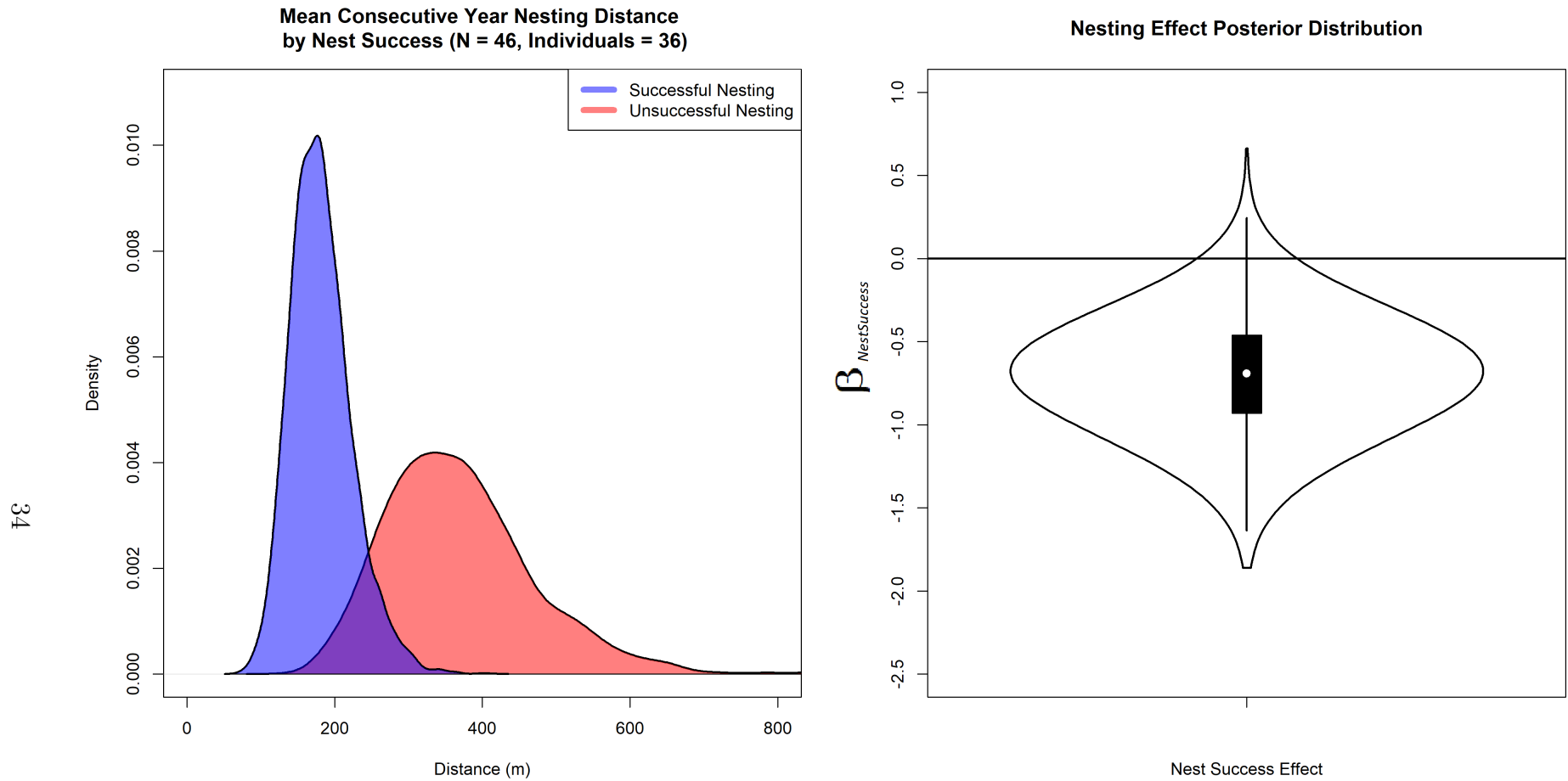


Figure 3: Posterior distributions of mean distance (left plot) and nest success effect (on the log-scale; right plot) between consecutive year nest locations of Gunnison sage-grouse.

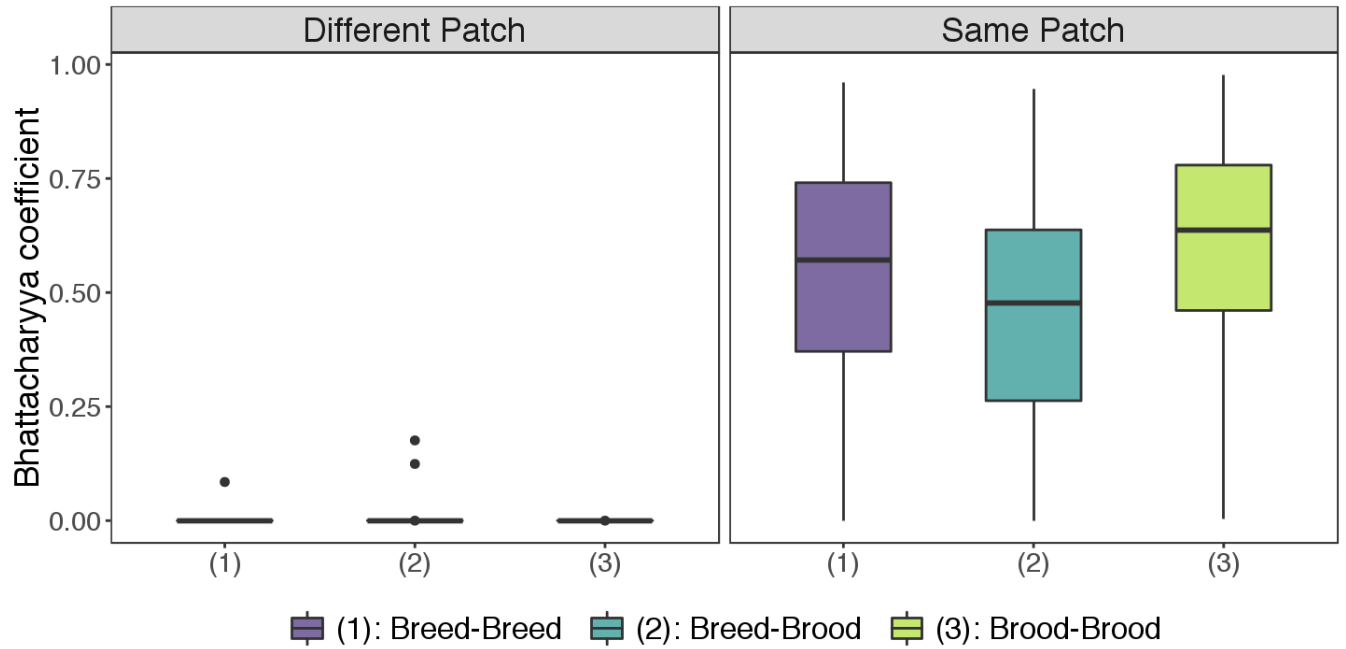


Figure 4: Summary plots of the posterior median space-use overlap (Bhattacharyya Coefficient) among all comparisons (consecutive and non-consecutive years) within individual sage-grouse by season and whether the utilization distribution occurred in the same breeding patch or different breeding patches. Individual estimates and associated 95% credible intervals can be found in Appendix 1, Fig. A11.

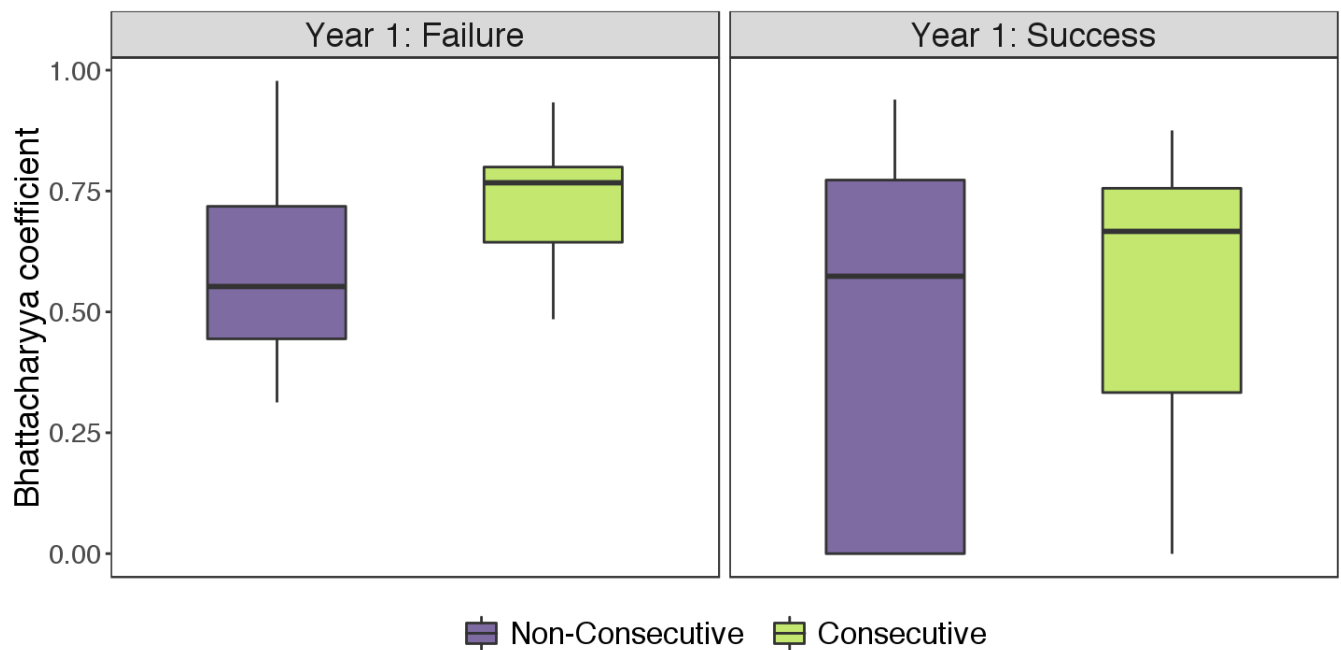


Figure 5: Summary plots of the posterior median Bhattacharyya coefficient estimates of space-use overlap across breeding seasons by nesting success for consecutive and non-consecutive years. Individual estimates and associated 95% credible intervals can be found in Appendix 1, Figure A13.