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

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Abstract

1. Animal site fidelity structures space use, population demography and ultimately gene flow. Understanding the adaptive selection for site fidelity patterns provides a mechanistic understanding to both spatial and population processes. This can be achieved by linking space use with environmental variability (spatial and temporal) and demographic parameters. However, rarely is the environmental context that drives the selection for site fidelity behaviour fully considered.

2. We use ecological theory to understand whether the spatial and temporal variability in breeding site quality can explain the site fidelity behaviour and demographic patterns of Gunnison sage-grouse (*Centrocercus minimus*). We examined female site fidelity patterns across multiple spatial scales: proximity of consecutive year nest locations, space-use overlap within and across the breeding and brooding seasons, and fidelity to a breeding patch. We also examined the spatial and temporal variability in nest, chick, juvenile and adult survival.

3. We found Gunnison sage-grouse to be site faithful to their breeding patch, area of use within the patch and generally where they nest, suggesting an "Always Stay" site fidelity strategy. This is an optimal evolutionary strategy when site quality is unpredictable. Further, we found limited spatial variability in survival within age groups, suggesting little demographic benefit to moving among patches. We suggest Gunnison sage-grouse site fidelity is driven by the unpredictability of predation in a relatively homogeneous environment, the lack of benefits and likely costs to moving across landscape patches and leaving known lek and breeding/brooding areas.

4. Space use and demography are commonly studied separately. More so, site fidelity patterns are rarely framed in the context of ecological theory, beyond questions related to the win-stay:lose-switch rule. To move beyond describing patterns and understand the adaptive selection driving species movements and

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their demographic consequences require integrating movement, demography and environmental variability in a synthetic framework.

5. Site fidelity theory provides a coherent framework to simultaneously investigate the spatial and population ecology of animal populations. Using it to frame ecological questions will lead to a more mechanistic understanding of animal movement, spatial population structuring and meta-population dynamics.

1 | INTRODUCTION

The spatial context of where and how species survive and reproduce is a fundamental component of their life history and ecology. A commonly observed behaviour among animal species is the repeated use of distinct spatial areas in one or more seasons or stages of their life history (e.g. birds and mammals: Greenwood, 1980; Hoover, 2003; Lewis, 1995, fishes: White & Brown, 2013, amphibians: Sinsch, 1991, crustaceans: Vannini & Cannicci, 1995, molluscs: Lind, 1989, reptiles: Broderick, Coyne, Fuller, Glen, & Godley, 2007 and insects: Switzer, 1997). The ubiquity of animals having fidelity to certain spatial areas suggests it is an evolutionary adaptive strategy in which individuals incur benefits from familiarity with their physical and social environment (Piper, 2011). Site familiarity benefits and proximate causes of "site fidelity" include efficient resource acquisition (Olsson & Brown, 2010), successful deterring of competitors (i.e. "resident advantage"; Jakobsson, 1988), efficient movements and use of microenvironments (Vlasak, 2006), effective predator avoidance (Brown, 2001) and decreased conflict with neighbours (Stamps, 1987).

The evidence for fitness or demographic benefits of site fidelity has historically been limited (Piper, 2011), but increasing (e.g. Lafontaine, Drapeau, Fortin, & St-Laurent, 2017; Patrick & Weimerskirch, 2017). Site fidelity is an emergent property of individual's spatially restricting their movements to only certain areas. This restriction ultimately influences the population's distribution and abundance and can structure meta-populations via immigration/emigration (Matthiopoulos, Harwood, & Thomas, 2005; Schmidt, 2004); lifetime space-use patterns influence gene flow and thus evolutionary processes (Sugg, Chesser, Dobson, & Hoogland, 1996). Commonly, site fidelity studies have focused on natal philopatry and breeding area fidelity because they have high fitness consequences (Schmidt, Dall, & Gils, 2010). There has also been considerable focus on the evolutionary context and mechanisms driving natal dispersal (Mathysen, 2012). However, it is increasingly appreciated that site fidelity, regardless of natal area, is an important process across time periods and activities outside the breeding season (Northrup, Anderson, & Wittemyer, 2016; Patrick & Weimerskirch, 2017; Piper, 2011) and may drive individual-based habitat associations for many years (McIntyre, Bester, Bornemann, Tosh, & Bruyn, 2017).

An individual's decision to remain faithful to its breeding area has often been linked to their past breeding experience (Hoover, 2003; Schmidt, 2004; Switzer, 1997). This suggests individuals use their experiences to assess breeding site quality (Schmidt, 2001). A simple decision rule that is widely supported across animal taxa (especially birds; Piper, Walcott, Mager, & Spilker, 2008) is that of the win-stay:lose-switch (WSLS) rule (Schmidt, 2004): individuals return to a breeding site if they successfully produce young or switch breeding sites if they are unsuccessful. The type of information used in this decision is known as "private information" (Schmidt et al., 2010). An alternative decision process is based on the perceived social information from neighbouring individuals (Doligez, Danchin, & Clobert, 2002; Piper, 2011). Social information helps average over the stochasticity inherent in individual breeding success (as in the WSLS rule). The context of when private or social information may be advantageous, and more generally when site fidelity may be an evolutionary adaptive strategy, can be understood via the ecology of information theory (Schmidt et al., 2010).

The ecology of information theory frames breeding site fidelity decisions in terms of the spatial and temporal variability of the resources that affect breeding success (Schmidt, 2001; Schmidt et al., 2010; Switzer, 1997; Table 1). Areas with high temporal variation provide little information (private or social) about breeding site quality, and thus, we expect breeding site decisions to be independent of past breeding experience (Schmidt et al., 2010). Furthermore, when there is low spatial variation in site quality within and among habitat patches (collection of possible breeding sites), regardless of temporal variability, we expect an always-stay decision rule to be optimal when there are costs to moving (Switzer, 1997). In contrast, if there is high spatial variation that is not temporally variable (thus predictable site quality), breeding experience provides valuable information about site quality and thus aids in the choice among available sites. In these environments, we should expect species to adopt a WSLS site fidelity strategy at either the site or habitat patch level (Schmidt et al., 2010). If site quality within a habitat patch varies more strongly than across patches, individuals benefit from being faithful at the site-level depending on their own breeding success (i.e. WSLS-Site, decision using private information). However, if site quality varies more among habitat patches than within a patch, individuals benefit by having high

TABLE 1 Theoretical optimal site fidelity predictions depending on temporal and spatial variability in site quality

Temporal variation	Spatial variation[a]	Information	Site fidelity prediction[b]
High	Site ≡ Patch	None	Always stay[c]
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 ≡ Patch	None	Always stay[c]
Low	Site > Patch	Private	Fidelity to Site (WSLS-Site)
Low	Patch > Site	Social	Fidelity to Patch (WSLS-Patch)

[a]Sites are locations within a patch.
[b]References: Schmidt (2001), Schmidt et al. (2010), Switzer (1993).
[c]Assuming there are costs to moving. Otherwise, individuals are expected to move following an ideal-free settlement strategy, thus indifferent to the site/patch or past experience (Schmidt, 2001).

fidelity to the habitat patch. Thus, we should expect an individual to move among patches based on the breeding success of individuals within the patch (i.e. WSLS-Patch, decision via social information).

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

We used the Gunnison sage-grouse (*Centrocercus minimus*) to examine site fidelity behaviour across multiple scales in the context of theoretical expectations based on the spatial and temporal variation in breeding site quality, and spatial constraints of their lek mating system. The Gunnison sage-grouse is a recently recognized species (Young, Braun, Oyler-McCance, Hupp, & Quinn, 2000) occurring in the sagebrush (*Artemisia* spp.) habitats of south-western Colorado and south-eastern Utah, USA. The species was recently listed as federally threatened (USFWS, 2014). They are known to use different types of seasonal habitat throughout the annual cycle, generally defined as the breeding (mating, nesting), brooding (rearing chicks) and winter seasons (Rice, Apa, & Wiechman, 2017). We used a multi-year dataset (2004–2010) to examine site fidelity patterns and the influence of nest success across multiple scales: proximity of consecutive year nest locations, space-use overlap within the breeding season and fidelity to a breeding patch. We also examined space-use fidelity within and across the brooding season, but without reliable measures of brood success, we did not link brooding area fidelity to demographic outcomes. Furthermore, we considered whether there are benefits to moving among breeding patches by examining the spatial and temporal variation in chick (<30 days), juvenile (>30 days to 1 year) and yearling/adult (>1 year) survival. Our objectives were to (a) characterize regional breeding patches and movement, (b)

describe environmental spatial and temporal variability within and among breeding patches, (c) evaluate indirect evidence of spatial and temporal variability in breeding patch quality by examining seasonal range size and (d) evaluate direct evidence by examining spatial and temporal variation in nest, chick, juvenile and yearling/adult survival of Gunnison sage-grouse. These findings improved our understanding of the spatial demography of Gunnison sage-grouse and adaptive selection of these patterns.

We hypothesized Gunnison sage-grouse have high fidelity to a breeding patch, but not to specific nest sites within the patch (Fischer, Apa, Wakkinen, Reese, & Connelly, 1993). Individuals are typically faithful to a lek or a lek complex (group of nearby leks; Connelly, Hagen, & Schroeder, 2011) and commonly nest within the same area as their lek (Gunnison sage-grouse: average of 2–4 km; Young et al., 2015). We did not expect Gunnison sage-grouse to be faithful to nest locations (Fischer et al., 1993).

2 | MATERIALS AND METHODS

2.1 | Study area

We studied Gunnison sage-grouse (hereafter, sage-grouse) in the eastern portion of the Gunnison basin (Gunnison and Saguache counties, Colorado, USA). The basin comprise 85%–90% of the species' range, covered approximately 2,000 km² and occurred between an elevation of 2,300 and 2,900 m. The study area was predominately sagebrush steppe, dominated by mountain big sagebrush (*Artemisia tridentate*) interspersed with rabbitbrush (*Chrysothamnus* spp.), antelope bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier* spp.) and mountain snowberry (*Symphoricarpos oreophilus*).

2.2 | Capture and monitoring

We captured sage-grouse from March to early May between 2004 and 2010 using spot-lighting techniques (Giesen, Schoenberg, & Braun, 1982; Wakkinen, Reese, Connelly, & Fischer, 1992). We fit

birds with a 17 g necklace-style VHF radiotransmitter (model A4050 by Advanced Telemetry systems or model R12B by Holohil Systems, Ltd.) equipped with a 4-hr mortality sensor. The transmitter was <2% of the weight of an average sage-grouse (female: 1,270 g SD 90 g). Each radio-marked bird was relocated using handheld antennas once every 1–3 days throughout the breeding (1 April–15 July) and brooding seasons (16 July–30 September; Rice et al., 2017). Observers were trained to maximize the accuracy of azimuths while considering constraints, such as private property. Each relocation included recording multiple azimuths (≥2) from known locations, typically within 30 min or less. Relocating individuals occurred throughout the day (0800–1700 hr.). A female was determined to be nesting if found in the same location for more than three consecutive days. Visual observations of females on nests were avoided to minimize disturbance. After a female left the nest, the nest was located to assess the fate of the eggs (e.g. hatched, depredated, abandoned or unknown) and a vegetation survey was conducted (Davis, Phillips, & Doherty, 2015a). Sagebrush and grass cover and height surrounding the nest were surveyed using 30-m transects, centred at the nest; vegetation cover and height were estimated at 5-m intervals along the transect. A Daubenmire frame (20 cm× 50 cm) was used to visually estimate the per cent grass and forb cover.

2.3 | Breeding patch and environmental variability

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

2.4 | Spatial and temporal variation in breeding site quality

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

We considered environmental spatial variability within and among breeding patches by examining spatial patterns in nest site vegetation, annual precipitation and soils. To understand whether there was greater variability in vegetation within or among patches, we fit a hierarchical Bayesian loglinear regression model to vegetation

collected at nest sites. For each vegetation measure observed (shrub and grass cover and height; $y_{i,s}$) at nest i in breeding patch s, we estimated a mean (μ_s) and variance (σ_s^2) for each breeding patch, where $\log(y_{i,s}) \sim \text{Normal}(\mu_s, \sigma_s^2)$ and μ_s are patch-level random effects ($\mu_s \sim \text{Normal}(\mu_1, \tau^2)$). If $\tau^2 > \sigma_s^2$, there is more spatial variation across breeding patches than within patch s. We fit a similar model to investigate the variability in rainfall patterns (PRISM 30-Year Normals from 1981 to 2010; Resolution: 0.92 km × 0.72 km; PRISM Climate Group, 2017) at estimated sage-grouse locations (details provided below) within and across breeding patches. For each model, we used diffuse priors and fit the model using Markov Chain Monte Carlo (MCMC) methods. Last, we estimated the probability of sage-grouse locations belonging to a set of dominant soil moisture–temperature regimes using a multinomial loglinear model in the R package "nnet". Soil data were compiled by Maestas, Campbell, Chambers, Pellant, and Miller (2016) (resolution: 0.01 km × 0.01 km). Variation in soil regimes provide indirect support to variation in dominant vegetation characteristics and their resistant/resilient properties (Chambers et al., 2016), and thus variation in breeding patch quality.

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

2.5 | Spatial and temporal variation in nest success

To understand whether site and patch environmental variability translates into breeding area quality variability, we examined the spatial and temporal factors that are hypothesized to influence nest success (see Davis et al., 2015a). Specifically, we investigated nest site vegetation characteristics (shrub height, shrub cover, grass cover and grass height), breeding patch affiliation, temporal factors (e.g. year, timing of incubation initiation and nest age) and age of the nesting female (yearling or adult). We used a predictive modelling framework that optimizes within-sample predictive performance using cross-validation. Specifically, we fit the nest success data (1 = success, 0 = failure) using a logistic regression model with all standardized covariates that were optimized using the least absolute shrinkage and selection operator (LASSO; Tibshirani, 1996). We used five-fold cross-validation, evaluating shrinkage parameters using the average deviance (−2 × log-likelihood) of the left out data

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 to 2010 during the breeding and brooding seasons were assigned to a breeding area affiliation (top plot)
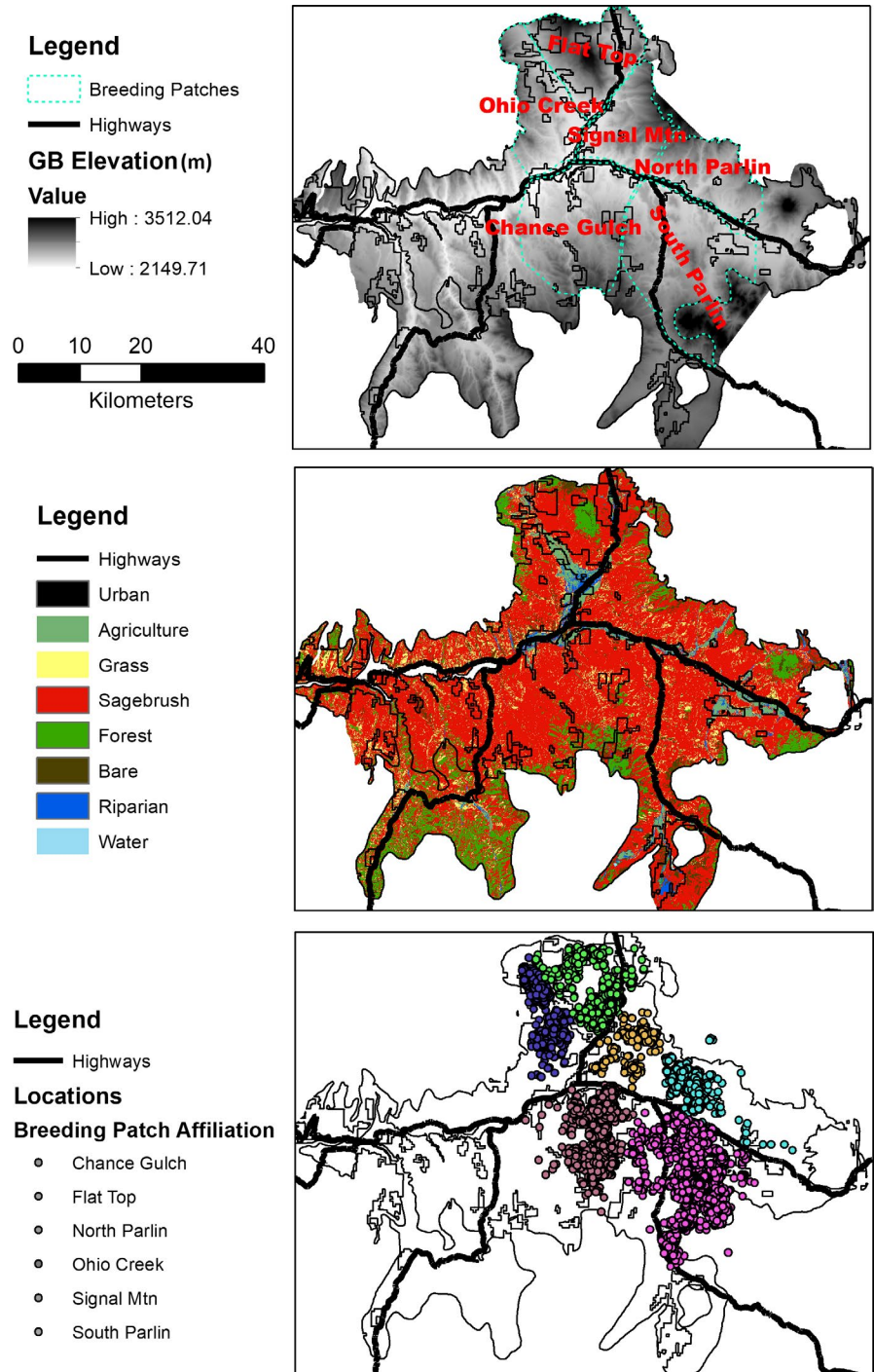
across all folds. LASSO regularizes model parameters, thereby accommodating numerical issues due to multicollinearity of covariates and providing variable selection by removing effects of covariates. The result is an optimal predictive model that is coherently interpretable in terms of important ecological effects (see Gerber, Kendall, Hooten, Dubovsky, & Drewien, 2015; Hooten & Hobbs, 2015). We used the same procedure to model nest success as a multinomial outcome to evaluate whether predation on nesting females or eggs drives nest failure and whether it varied spatially or temporally (0 = nest failed or was abandoned, 1 = nest failed due to the female

or eggs being depredated, 2 = nest success). Predation could make quality nest site selection highly unpredictable and thus may affect female site fidelity. We conducted model fitting optimization and cross-validation for both analyses in the R package "glmnet" (Friedman, Hastie, & Tibshirani, 2010).

2.6 | Spatial and temporal variation in survival

We further considered variation in breeding site quality by evaluating the spatial and temporal variation in chick, juvenile and

yearling/adult survival across breeding patches by extending previous analyses of these populations (Davis, Phillips, & Doherty, 2015b, 2016). We used the most parsimonious models of these analyses and include additional individual covariates indicating the breeding patch location of the individual. We evaluated temporal and spatial survival differences by comparing models using AIC, BIC and likelihood ratio tests, and estimating the expected marginal differences between breeding patch coefficients (e.g. $\hat{\beta}_{diff} = \hat{\beta}_1 - \hat{\beta}_2$ 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 covariance).

2.7 | Site fidelity

2.7.1 | Nest site fidelity

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

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

2.7.2 | Breeding and brooding space-use and patch fidelity

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

$$\text{Observation Process:} \quad \theta_{lij} \sim \text{von Mises}(\tilde{\theta}_{lij}, \kappa_{li}),$$

$$\text{Link Function:} \quad \tilde{\theta}_{lij} = \tan^{-1}\left(\frac{\mu_{2li} - z_{2lij}}{\mu_{1li} - z_{1lij}}\right). \tag{1}$$

The parameter κ is an estimate of azimuthal uncertainty, recognizing that the location of each bird is not known exactly; simulations based on the sage-grouse data indicated good statistical properties for estimating κ and thus coverage of the true animal location (Gerber et al., 2018). We used the estimated spatial locations (μ_{li}) along with a small number of aerial and known locations, in a nonparametric kernel density estimator (Hooten, Johnson, McClintock, & Morales, 2017) to derive each individuals season/year utilization distribution. Aerial locations were taken with a GPS during low-altitude flights that circled the bird's location. We assumed these locations were not known exactly by treating them as multivariate normal distributed, centred at the aerial location coordinates with a covariance matrix $12.5^2\mathbf{I}$; this allowed a maximum deviation from the GPS location of approximately 50 m. For an individual that was relocated n times (a minimum of 10 locations) within a season/year, we estimated their seasonal utilization distribution for the kth MCMC iteration using the 95% isopleth of the kernel function,

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

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

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

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

where $0 \leq \text{BC} \leq 1$. BC will be approximately zero when there is no overlap and one when there is complete overlap. Therefore, a BC value of zero could indicate an individual used a different patch between years or the same patch, but different sites within a patch. To clarify how individuals' space use varies across and within breeding patches, we summarized results by BC value and breeding patch association for each UD comparison. Last, we investigated the proximity of individuals' space use by estimating the Euclidean distance between the highest UD densities being compared. We compared different sets of overlap in UDs to provide general and specific insights into site fidelity behaviour by comparing (a) among all UDs within and across seasons (breeding–breeding, brooding–brooding and breeding–brooding) for consecutive and non-consecutive years,

and (b) within breeding season by nest success. Since the number of spatial locations varied across individuals by season and year (10–54), we evaluated the consistency in our results by comparing inference from using all the location data and standardizing the number of locations to only 10 per individual by season and year.

3 | RESULTS

3.1 | Capture and monitoring

A total of 94 female sage-grouse were relocated in at least two seasons with a minimum of 10 locations per season between 2004 and 2010 (see Appendix S2: Table A1). We observed a total of 23,869 azimuths across all individuals, which were used to estimate 6,057 locations of female sage-grouse. The number of azimuths observed per relocation varied, ranging from 2 to 12 (Appendix S1: Figure A1). Including aerial and known locations, we obtained a total of 6,608 sage-grouse locations. The number of locations for each individual observed in a season/year ranged from 10 to 54 with a median of 21.

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

3.2 | Spatial variation in breeding site quality

We found that vegetation characteristics were more variable within a breeding patch than across patches (Appendix S1: Figure A2). In contrast, we found considerably more variation in annual precipitation across patches than within (Appendix S1: Figure A3). We also found that sage-grouse locations dominantly occurred within frigid-ustic (cold-intermediate moisture) and cryic-udic (cool-moist) soils (Appendix S1: Figure A4). These soil regimes typify elevated productivity within shrub-steppe communities (Chambers et al., 2016). While the dominant soil types were generally similar across the breeding patches (Appendix S1: Figure A4), a model allowing the probabilities to vary across soil types (M_{soil}) had better predictive ability with the data (measured by AIC) than a model that considered them constant (M_{null}; $\Delta AIC_{M_{soil}} = 0$, $\Delta AIC_{M_{null}} = 15,069.57$).

We found noticeable variation in ranging area across breeding patches by season, suggesting patch-level variation in quality (Figure 2; Appendix S1: Figures A5 and A6). Variation in UD area across patches was generally greater in the breeding season than in the brooding season. Median patch-level ranging size in the breeding season was lowest at Ohio Creek and Flat Top (~2.9 km^2) and larger at Chance Gulch (5.60 km^2) and South Parlin (8.0 km^2). Signal Mountain UD areas were even larger at a median of 12.30 km^2 and largest at North Parlin with a median of 16.40 km^2. North Parlin was much more variable across breeding patches in the breeding season compared to within season, while the other patches were similar or less variable (Appendix S1: Figures A5 and A6). Based on optimal foraging theory, we would expect Ohio Creek and Flat Top to have a higher nest success, given the reduced energetic expenditure related to movement. Brooding season UD areas were smaller or equivalent in size to breeding season UD areas. Median UD areas were smallest at Flat Top (2.46 km^2), then Ohio Creek and South Parlin (~3.57 km^2), then Signal Mountain and Chance Gulch (~4.89 km^2), and were largest at North Parlin (9.61 km^2). Within-patch variation in the brooding season was greater than across patch variation only at North Parlin and Flat Top (Appendix S1: Figures A5 and A6).

3.3 | Spatial and temporal variation in nest success

We observed a total of 177 nests belonging to 120 individuals. We found no support for any covariates hypothesized to influence nest success and failure (Appendix S1: Figure A7). The optimal predictive model indicated a mean nest success of 0.446 ± 0.038 SE. We also found no support for any covariates hypothesized to influence nest failure, predation and nest success (Appendix S1: Figure A8). The optimal predictive model indicated a mean nest failure, predation and success of 0.070, 0.462 and 0.468, respectively.

3.4 | Spatial and temporal variation in survival

We found little evidence to suggest there was annual variation in chick, juvenile or adult/yearling survival; however, there was a fair amount of parametric uncertainty (Davis, Phillips, & Doherty, 2015b, 2016); Appendix S1: Tables A1–A3 and subsection "Spatial and temporal variation in survival"). We also found relatively minimal variation in survival of the different age groups by breeding patch (Appendix S1: Tables A1–A5 and Figure A9). Among all pairwise comparisons, we found chick survival was much higher (comparing maximum-likelihood estimates) at Ohio Creek than Signal Mtn. and North Parlin (Appendix S1: Table A4). In the juvenile survival analysis, we found North Parlin had higher survival than South Parlin. All other comparisons were not statistically significant; detecting differences that were not extreme was difficult due to high parameter uncertainty. Last, adult survival was generally similar among breeding patches (Appendix S1: Figure A9). However, we did find that Ohio Creek survival was marginally lower than North Parlin and Chance Gulch. Also, South Parlin survival was lower than North Parlin and Chance Gulch (Appendix S1: Table A4).
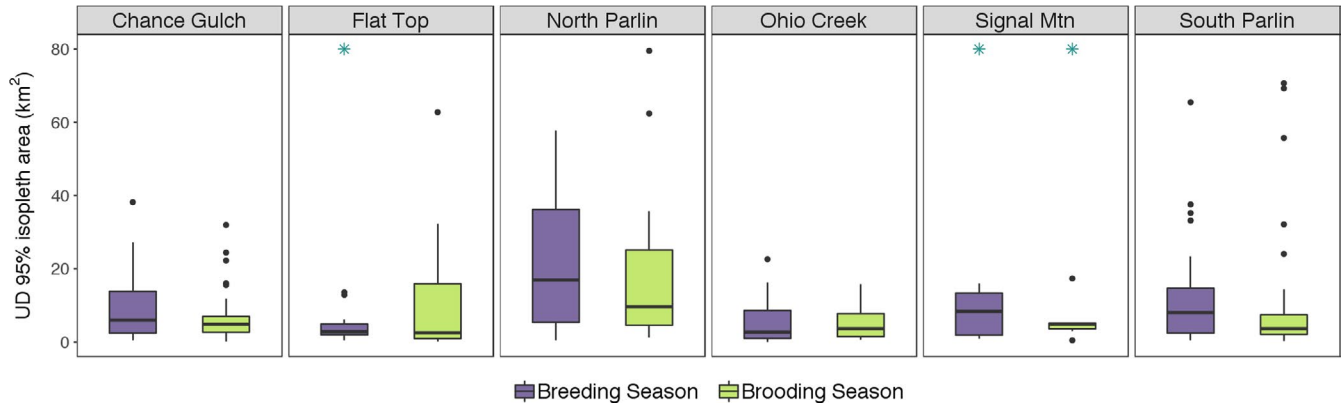
FIGURE 2 Summary plots of posterior median estimates of individual Gunnison sage-grouse' 95% utilization distribution area for the breeding and brooding seasons by breeding area patch. The symbol *indicates measurements beyond the maximum y-axis limit. Individual estimates along with 95% credible intervals can be found in Appendix S1: Figure A6

3.5 | Nest site fidelity

Out of 43 individual sage-grouse with multiple years of nesting location data (consecutive years and not, range of 2–4 years per individual), only a single individual was observed to nest in more than one breeding patch. This individual was observed nesting in one patch in 2005 and 2006 and a different patch in 2008 and 2010; in all years, this individual was successful at hatching chicks. Among 47 consecutive year nesting comparisons, (36 unique individuals) no birds were observed to switch breeding patch; 19 out of 47 were unsuccessful in the previous year, but did not switch their patch. We found support for a negative effect ($P(\beta_{NestSuccess} < 0) = 0.96$; $E[\beta_{NestSuccces}] = -0.713$, -1.45 to 0.073, 95% credible interval) of nest success on the distance between consecutive year nest locations (Figure 3). The median distance between nest locations when individuals were previously unsuccessful at hatching chicks was 357 m (209–598, 95% credible interval), which decreased when individuals were successful to 178 m (113–276, 95% credible interval). However, we found no improvement in nest success in the second year based on the first-year nest success ($P(\beta_{NestSuccessYear1} > 0) = 0.26$; $E[\beta_{NestSuccessYear1}] = -0.404$, -1.60 to 0.790, 95% credible interval).

3.6 | Breeding and brooding space-use and patch fidelity

First, we found no changes in our inference to breeding and brooding space-use and patch fidelity between using all individuals' spatial locations and when standardizing the sample size (see Appendix S1). We found strong fidelity of individuals to their patch during both the breeding and brooding seasons (Appendix S1: Figure A10; >0.91 proportion of individuals used the same patch across all comparisons). Comparing consecutive year space use in the breeding season, only a single individual (total of 46 comparisons) was observed to use two different patches. During the brooding season, only two individuals (total of 57 comparisons) were observed to use different patches in consecutive years (one of these individuals was also observed in different patches during

the breeding season). Comparing across consecutive and non-consecutive years also supports strong site fidelity to the patch; 95% and 91% of all comparisons were within the same patch for the breeding and brooding season, respectively (73 and 90 total comparisons; Appendix S1: Figure A10).

We found seasonal space-use overlap was variable, but consistently showed moderate overlap for all comparisons (Figure 4; Appendix S1: Figure A11). Notably, it was uncommon for an individual to use the same breeding patch (within or across seasons), but have no overlap in their space use (i.e. BC value of 0). This was especially rare when comparing within seasons. The median space-use overlap was highest within the breeding season, then the brooding season, then across these seasons (Figure 4; Appendix S1: Figure A11). The average Euclidean distance between UDs across all seasons and years was around 2–3 km (Appendix S1: Figure A12). The median Euclidean distance across breeding seasons was commonly between 0 and 1 km, but ranged up to 6 km, while the average distance across brooding seasons was commonly 0–2.5 km, but ranged up to 10 km. As such, most individuals use the same breeding patch for breeding and brooding across all years and generally use the same area within each season and somewhat across seasons.

We also found no indication that female sage-grouse move sites within the breeding season based on their previous nesting experience (Figure 5; Appendix S1: Figure A13). Across all comparisons, there was moderate spatial overlap regardless of nest success outcome. In fact, we found higher median overlap among consecutive years when a previous nest had failed. This result was also supported by a slightly lower median distance between UDs when a previous nest had failed (Appendix S1: Figure A14). However, space-use overlap was moderate even when comparing across non-consecutive years by nest success, suggesting individuals simply use a similar area regardless of nesting outcome (Figure 5). We also found moderate space-use overlap across brooding seasons and between breeding–brooding seasons (median BC values of ~0.45; Appendix S1: Figures A15 and A16). The median Euclidean distance between UDs across brooding season was 2 km, while between breeding-to-brooding seasons was slightly higher at 2.5 km (Appendix S1: Figures A17 and A18).
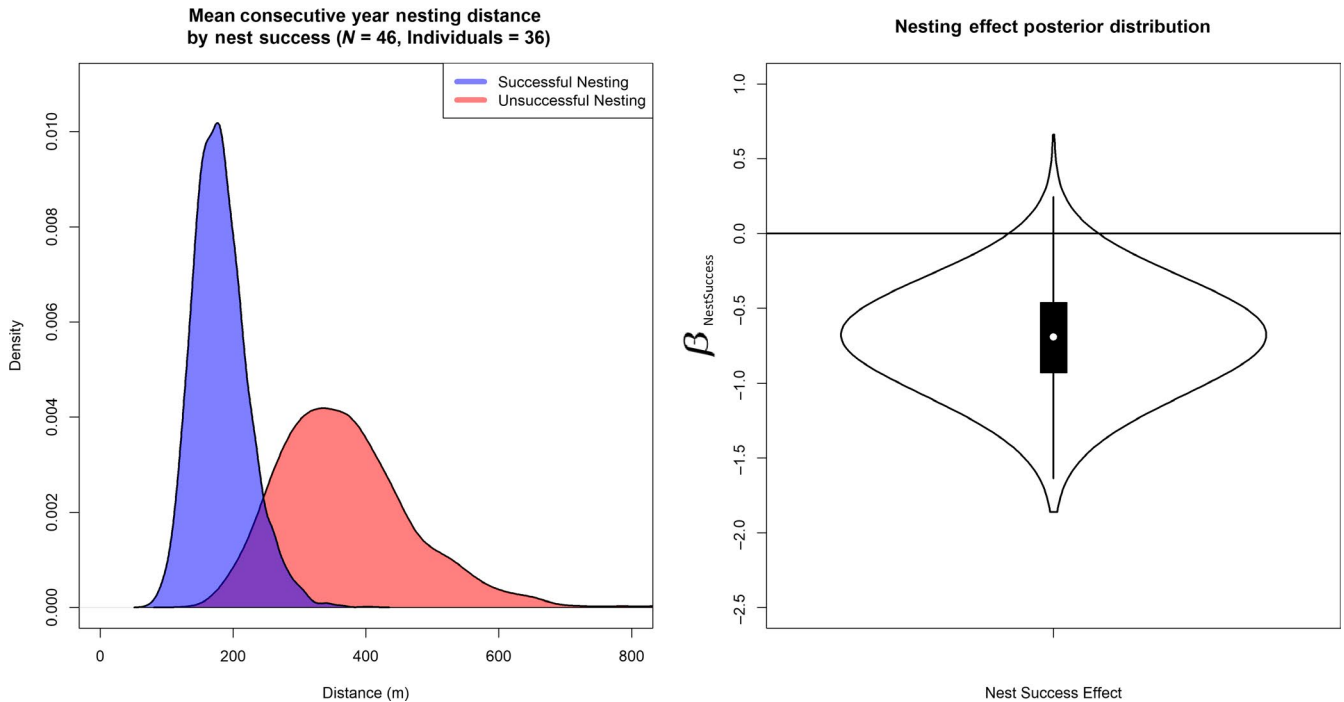
FIGURE 3 Posterior distributions of mean distance (left plot) and nest success effect (on the log-scale; right plot) between consecutive year nest locations of Gunnison sage-grouse

4 | DISCUSSION

Rarely are site fidelity patterns framed in the context of relevant ecological theory, beyond questions related to the WSLS strategy. Site fidelity behaviour and its influence on demography and movement can be understood in the context of environmental spatial and temporal variability (Schmidt et al., 2010). This allows a more mechanistic understanding of habitat selection across spatial scales (Lafontaine et al., 2017), as well as possible meta-population dynamics by recognizing the level of connectivity among habitat patches (Switzer, 1997), which has important implications for population regulation (Matthiopoulos et al., 2005) and persistence (Schmidt, 2004). More so, empirical studies framed by theory

are essential to modifying the theory and its predictions based on new discoveries and previously unconsidered conditions and constraints.

In this study, we quantified female Gunnison sage-grouse site fidelity across multiple spatial scales, framing observations based on theorized drivers of spatial and temporal variability in breeding site quality. We found Gunnison sage-grouse to exhibit high site fidelity across spatial scales. Individuals were faithful to their breeding patch, area of use within their patch by season, and typically nested near their previous nesting location, using private information of their previous nest success outcome to decide the proximity (mean distance of 0.18 when successful and 0.36 km when unsuccessful). However, there was no support that this nest-level WSLS rule is beneficial, as

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 S1: Figure A11
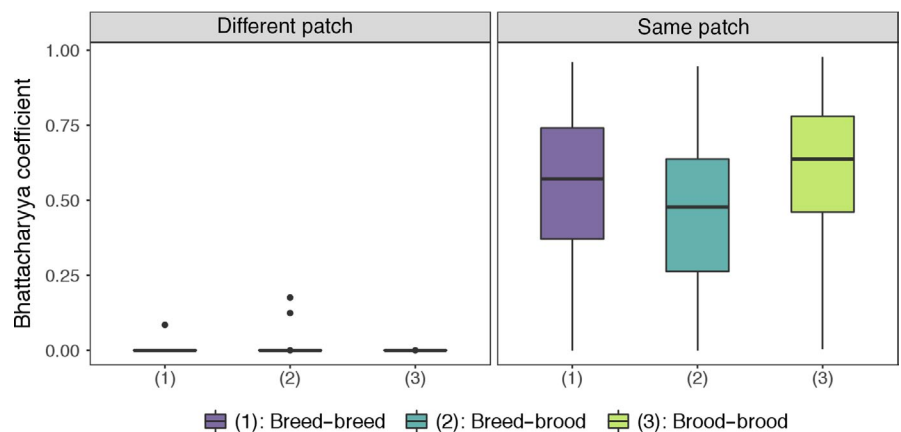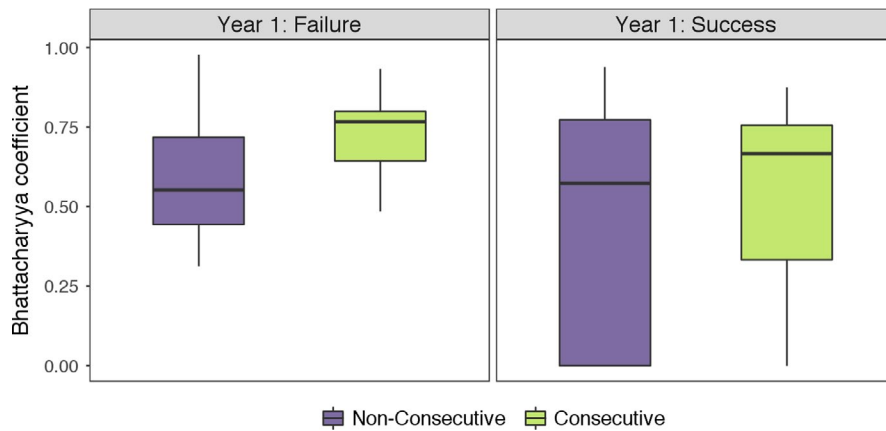
FIGURE 5 Summary plots of the posterior median Bhattacharyya coefficient estimates of space-use overlap across breeding seasons by nesting success for consecutive and non-consecutive years. Individual estimates and associated 95% credible intervals can be found in Appendix S1: Figure A13

nesting closer to a previously successful nest did not improve the likelihood of success in the following year. However, we recognize that nest site selection may be based on variables that were not collected in this study, including brooding or fledgling success.

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

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

Lekking birds are believed to have some of the highest levels of nest predation (Phillips, 1990), and from experimental studies, there

is strong evidence that predation pressure and predator hunting mode fundamentally affects prey movement and space use (Miller, Ament, & Schmitz, 2014). But also, breeding site fidelity strategy is known to depend on the specific cause of reproductive failure (Schmidt, 2001). In considering the diverse predators of sage-grouse (includes birds of prey, corvids and terrestrial mammals), which are typically wide-ranging generalists that likely take eggs and birds opportunistically (Conover & Roberts, 2017; Hagen, 2011; Young et al., 2015), there may be nowhere to escape the possibility of predation. Therefore, in relatively homogenous habitat, in which individuals may be unable to avoid numerous opportunistic predators or assess breeding site quality in terms of predation pressure, the costs of movement may easily supersede any benefit, selecting individuals with extreme site fidelity. In fact, an always stay-site fidelity strategy, in which individuals do not use WSLS, is the evolutionary optimal strategy in unpredictable homogenous environments (Schmidt et al., 2010; Switzer, 1997). Furthermore, minimizing movement, especially flying, is complementary with the behavioural and phenotypic selection for crypsis in sage-grouse. Despite being strong fliers, sage-grouse are mostly ground-dwelling, relying on camouflage until they are threatened and resort to flying (Young et al., 2015).

However, predation may not fully explain why Gunnison sage-grouse do not move among breeding patches. We might expect Gunnison sage-grouse to selectively move among patches in response to failed nesting due to nest predation because moving farther (across patches, rather than within) may be more likely to change predator communities and abundance, and thus predation pressure. Further, site fidelity to the patch may be partially a by-product of fidelity to a lek or lek complex. Fidelity to leks and lek proximity to nesting is well documented in sage-grouse populations (Connelly et al., 2011; Young et al., 2015), including in this study population. However, we were unable to link space-use with specific lek locations, as we may not have observed all leks used by each individual. The selection pressure to nest within the general proximity to their lek and thus the costs of moving breeding patches is less clear. Patch-level variation may be irrelevant in site fidelity patterns and thus potential social information also irrelevant. Perhaps though, the diversity of ground and aerial predators in the sagebrush steppe has led to the selection against moving among patches to limit exposure

to predation, and also because the ubiquity of opportunistic nest predators means that movements of any scale are irrelevant to altering nest predation pressure (as observed in this study). An additional factor that may explain the lack of long distance movements of Gunnison sage-grouse could be due to physiological constraints on grouse and generally all Galliformes. Galliformes are known to have flight muscles that are almost exclusively glycolytic muscle fibres, which limits flights to short bursts of activity before quickly fatiguing (Butler, 2016). Therefore, to move long distances may require several short flight bursts, which are energetically costly and perhaps risky by attracting the attention of predators. Last, we cannot rule out that site fidelity may be at least partially due to a lack of density-dependent factors that when present would cause individuals to disperse rather than compete for limited resources (Harts, Jaatinen, & Kokko, 2016).

4.1 | Consequences of site fidelity

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

5 | CONCLUSIONS

Animal site fidelity is a commonly observed behaviour that has important consequences to animal space use and thus the spatial structuring of populations. Examining the spatial and temporal variability of environmental and demographic outcomes contributed to the understanding of ecological processes likely driving Gunnison sage-grouse demography and site fidelity patterns. Notably, their always-stay strategy suggests higher fitness outcomes by minimizing

movements and capitalizing on site familiarity benefits in an environment where nest predation is ubiquitous, breeding/brooding habitat is generally suitable, demographic benefits to moving are minimal, and moving may incur higher predation risk. Given the extreme site fidelity observed in this study, future population and habitat management could be framed in the context of these spatial affiliations.

AUTHORS' CONTRIBUTIONS

B.D.G., M.B.H., C.P.P., M.B.R., J.H.G., A.D.A., and A.J.D. conceived the ideas and contributed to critical editing of previous drafts and gave final approval for publication; B.D.G., M.B.H. and C.P.P. designed the statistical framework and fit the data; B.D.G. led the writing of the manuscript.

DATA AVAILABILITY STATEMENT

Data are archived at the Dryad Digital Repository: https://doi.org/10.5061/dryad.7c834db (Gerber et al., 2019). Location data are not publicly available due to concerns of providing detailed spatial information on a federally threatened species. Data requests can be made at Colorado Parks and Wildlife with Dr. James Gammonley, jim.gammonley@state.co.us.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.