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Beyond overlap: considering habitat preference and fitness outcomes in the umbrella species concept

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Keywords

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Abstract

Umbrella species and other surrogate species approaches to conservation provide an appealing framework to extend the reach of conservation efforts beyond single species. For the umbrella species concept to be effective, populations of multiple species of concern must persist in areas protected on behalf of the umbrella species. Most assessments of the concept, however, focus exclusively on geographic overlap among umbrella and background species, and not measures that affect population persistence (e.g. habitat quality or fitness). We quantified the congruence between the habitat preferences and nesting success of a high-profile umbrella species (greater sage-grouse, *Centrocercus urophasianus*, hereafter 'sage-grouse'), and three sympatric species of declining songbirds (Brewer's sparrow *Spizella breweri*, sage thrasher *Oreoscoptes montanus* and vesper sparrow *Pooecetes gramineus*) in central Wyoming, USA during 2012–2013. We used machine-learning methods to create data-driven predictions of sage-grouse nest-site selection and nest survival probabilities by modeling field-collected sage-grouse data relative to habitat attributes. We then used field-collected songbird data to assess whether high-quality sites for songbirds aligned with those of sage-grouse. Nest sites selected by songbirds did not coincide with sage-grouse nesting preferences, with the exception that Brewer's sparrows preferred similar nest sites to sage-grouse in 2012. Moreover, the areas that produced higher rates of songbird nest survival were unrelated to those for sage-grouse. Our findings suggest that management actions at local scales that prioritize sage-grouse nesting habitat will not necessarily enhance the reproductive success of sagebrush-associated songbirds. Measures implemented to conserve sage-grouse and other purported umbrella species at broad spatial scales likely overlap the distribution of many species, however, broad-scale overlap may not translate to fine-scale conservation benefit beyond the umbrella species itself. The maintenance of microhabitat heterogeneity important for a diversity of species of concern will be critical for a more holistic application of the umbrella species concept.

Introduction

The overarching objective of conservation biology is the protection and continuity of entire biological communities and ecosystems (Soulé, 1985). Surrogate species conservation strategies have become popular in applied practice (Caro, 2003, 2010) and have been adopted in nationwide conservation efforts (e.g. U.S. Fish and Wildlife Service, 2015a). The umbrella species concept is one such

strategy, in which the protection of large areas required by one species (the umbrella species) is assumed to facilitate the protection of many other species (hereafter 'background species') with overlapping geographic distributions and habitat needs (Wilcox, 1984; Noss, 1990; Caro, 2003). Consideration of overlap in habitat quality among the umbrella and background species, however, has been lacking in assessments of the efficacy of umbrella species approaches to conservation. Given the extent of global habitat loss and

alteration (Newbold *et al.*, 2015), the remaining areas prioritized for the maintenance of suites of species ideally should optimize those that promote species' productivity and persistence, not just occupancy (Caro, 2010).

The inherent necessity to consider the viability of background species' populations was part of the original formulation of the umbrella species concept (Wilcox, 1984). Most recent applications, however, have focused on the overlap between the geographic ranges of multiple species, often using predictive species distribution models (Caro, 2003, 2010; Roberge & Angelstam, 2004). These measures of geographic overlap provide useful information regarding the potential function of an umbrella; however, such assessments say little about the ability to conserve background populations over the long term (Caro, 2003). Thus, rigorous assessments of the umbrella species concept require consideration of ecological information beyond overlap (e.g. abundance, habitat selection and productivity) for both the umbrella and purported background species (Caro, 2003; Roberge & Angelstam, 2004; Branton & Richardson, 2014; Carlisle & Chalfoun, 2020). Because evolved habitat preferences reflect important selective pressures (Martin, 1998; Chalfoun & Schmidt, 2012), background species that prefer similar habitats to the umbrella species and have higher productivity in those habitats will, presumably, fare the best under the umbrella.

Our objective was to quantify the habitat preferences and quality of a high-profile umbrella species, and determine whether they aligned with those of three sympatric background species of conservation concern. The greater sage-grouse (*Centrocercus urophasianus*, hereafter 'sage-grouse') is a ground-nesting bird found exclusively in the sagebrush-steppe ecosystem of western North America, and the sage-grouse is often considered an umbrella species for the conservation of sagebrush-associated wildlife species (Rich & Altman, 2001; Rowland *et al.*, 2006; Hanser & Knick, 2011; Gamo *et al.*, 2013; Copeland *et al.*, 2014). The sagebrush steppe ecosystem is one of the most imperiled in North America (Noss, LaRoe III, & Scott, 1995; Davies *et al.*, 2011), and many sagebrush-associated birds have garnered increased conservation attention in recent decades (Knick *et al.*, 2003). Sage-grouse have received the bulk of this attention and resources, in-part due to petitions to list the species under the U.S. Endangered Species Act (ESA; Knick *et al.*, 2003; Stiver, 2011; U.S. Fish and Wildlife Service, 2015b) and its Endangered species status in Canada (Government of Canada, 2021). Therefore, state-, provincial- and federal-level management for sage-grouse continues to be prioritized across their international range (U.S. Fish and Wildlife Service, 2013; State of Wyoming, 2019; Government of Canada, 2021).

We focused on three songbird species that co-occur with sage-grouse, also rely on sagebrush habitats, and have experienced population declines in recent decades (Rosenberg *et al.*, 2016) as focal background species: Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*) and vesper sparrow (*Pooecetes gramineus*). Brewer's sparrows and sage thrashers breed almost exclusively within sagebrush

steppe habitats of western North America and are considered sagebrush obligates; both nesting above ground level in the shrub layer (Reynolds, Rich, & Stephens, 1999; Rotenberry, Patten, & Preston, 1999). In contrast, Vesper sparrows breed in many open, grass-associated habitats (e.g. sagebrush steppe, prairie grasslands, montane meadows, etc.) across North America and nest exclusively on the ground (Jones & Cornely, 2002). Brewer's sparrows and sage thrashers are both species of conservation concern in North America (Knick *et al.*, 2003) and are listed as species of greatest conservation need in Wyoming (Wyoming Game and Fish Department, 2017), where our study took place. Since 1970, range-wide population sizes have declined by 35% for Brewer's sparrows and 44% for sage thrashers (Rosenberg *et al.*, 2016). Whereas vesper sparrows do not share the same level of conservation concern, their range-wide population declined by 30% during the same time period (Rosenberg *et al.*, 2016).

The efficacy of surrogate species strategies also depends upon appropriate temporal frameworks. Sagebrush-associated songbirds are migratory and co-occur with sage-grouse only during the breeding season (Reynolds, Rich, & Stephens, 1999; Rotenberry, Patten, & Preston, 1999; Jones & Cornely, 2002). Furthermore, efforts to conserve sage-grouse commonly focus on protecting or enhancing sage-grouse breeding habitat (Connelly *et al.*, 2000; Doherty *et al.*, 2010a,b). The utility of the sage-grouse umbrella for the conservation of co-occurring songbirds therefore depends on concordance between their ecological requirements during the breeding season. If sage-grouse and songbird nesting requirements correspond, conservation actions undertaken to benefit sage-grouse will likely benefit both groups. Conversely, if the ecological requirements of sage-grouse and songbirds differ, additional management actions specific to declining songbirds may be warranted. Our objectives were therefore to assess the congruence between sage-grouse and songbirds in what areas had highest nest-site selection and nest survival.

Materials and methods

Study area

We conducted our study within a 2458-km² area in central Wyoming, USA (42°29'N, 107°49'W; Fig. 1) during 2012 and 2013. Central Wyoming is one of the last strongholds of intact landscapes dominated by sagebrush (Knick *et al.*, 2003), and nearly all (93.3%) of the study area was within the state-designated core population area of sage-grouse (State of Wyoming, 2011, 2019). Elevation in the study area ranged from 1775–2365 m (Gesch *et al.*, 2002). Mean annual temperature (from 1981 to 2010) ranged from 4.8 to 7.1°C, and mean annual precipitation from 21.4 to 32.6 cm (PRISM Climate Group, 2012). The area was predominantly sagebrush steppe, with overstory communities dominated by big sagebrush (*Artemisia tridentata*), with black sagebrush (*A. nova*), rabbitbrush (*Ericameria nauseosa*) and *Chrysothamnus viscidiflorus*) and greasewood



Figure 1 Greater sage-grouse nests and random points used to model nest-site selection and nest survival in central Wyoming, USA, 2012–2013. Areas of non-habitat (i.e. open water, riparian corridors, wetlands, montane forests and rocky outcroppings) that were masked from the study area prior to the analysis appear as hollow polygons.

(*Sarcobatus vermiculatus*) also present. Understory communities were dominated by bunchgrasses and forbs.

We established 20 songbird nest-searching plots within a broader sage-grouse monitoring area (see Smith, 2016; Smith *et al.*, 2019, 2023) where sage-grouse were already being captured and telemetered. Specifically, we established eight, 25-ha plots spanning a gradient of sage-grouse breeding population density (the five levels mapped by Doherty *et al.* (2010a, b) in 2012, and 12 additional, 24-ha plots in 2013. Plots were sited such that they maximized within-plot variability of sagebrush height and cover, allowing for a range of available nesting habitats (Chalfoun & Martin, 2007). Plots were 0.3–15.0 km from their nearest neighboring plot (Fig. 2). Additionally, all plots were >1.0 km from oil or gas wells and >0.1 km from medium or high-traffic roads (paved or unpaved) to control for the potential effects of human disturbance on study species (Gilbert & Chalfoun, 2011; Kirol *et al.*, 2015; Hethcoat & Chalfoun, 2015a). The distance from plots to the nearest sage-grouse capture location ranged from 1.3 to 12.6 km, and the distance from capture locations to where sage-grouse nested ranged from 0.4 to 15.3 km, suggesting that songbird nest-searching plots were sited within the likely nesting area of the sage-grouse individuals captured. Each plot was surveyed in 1 year of the study, 8 plots in 2012 and 12 plots in 2013.

We delineated the area to which spatial predictions of nest-site selection and nest survival would be made by selecting the 18, 12th-order watersheds (Wyoming Geospatial Hub, 2015) that encompassed a contiguous study area containing the songbird plots, and buffered the area by 3 km to correspond with the area where sage-grouse were being monitored (Smith, 2016; Pratt, Smith, & Beck, 2019; Smith *et al.*, 2023). Because our study species were all associated with sagebrush-steppe habitats, we removed areas of open water, riparian corridors, wetlands, montane forests and

rocky outcroppings from the study area polygon and masked these areas from consideration in our statistical models and predictions (Fig. 1).

Data collection

We located and monitored nests of sage-grouse and songbirds in 2012 and 2013 to assess nest-site selection and the survival of eggs or young in the nest (hereafter nest survival). Nests were monitored in adherence with protocols approved by the Wyoming Game and Fish Department (permit 33-801) and University of Wyoming (Institutional Animal Care and Use Committee protocols 03132011, 20140128JB0059, 20120518JC00200-01 and 20140425A C00096-01). We captured and radio-marked female sage-grouse near leks in spring (March–May) and at summer roosting locations (July–August) by spotlighting and hoop-netting individuals at night (Giesen, Schoenberg, & Braun, 1982; Wakkinen *et al.*, 1992). We attached a VHF (22 g, Model A4060; Advanced Telemetry Systems Incorporated, Isanti, MN, USA) or GPS (22 g PTT-100 Solar Argos/GPS PTT, Microwave Telemetry, Columbia, MD, USA) transmitter to each sage-grouse to locate the nest of marked individuals. Capture methods and locations are further described by Smith (2016), Pratt, Smith, & Beck (2019) and Smith *et al.* (2023). We recorded the location of each nest with a handheld GPS unit (Garmin GPSmap 62s, Garmin, Olathe, KS, USA; accuracy typically 2–10 m). We examined the nest contents (i.e. eggshells and eggshell membranes) after the sage-grouse left the nest location, and we considered a nest successful if at least one egg hatched (Rotella, Dinsmore, & Shaffer, 2004). See Smith (2016), Pratt, Smith, & Beck (2019) and Smith *et al.* (2023) for detailed descriptions of sage-grouse capture, telemetry and nest-monitoring methods.

Nest-Site Selection

RSF Value

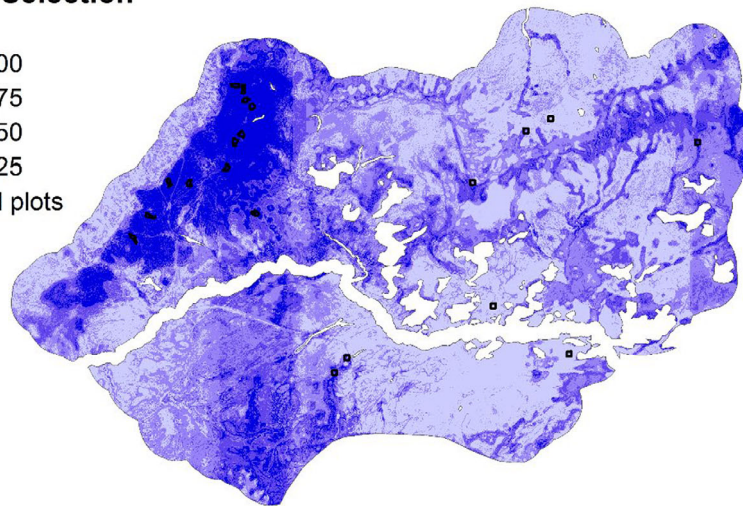
0.75 - 1.00

0.50 - 0.75

0.25 - 0.50

0.00 - 0.25

□ Songbird plots



Nest Survival

SPF Value

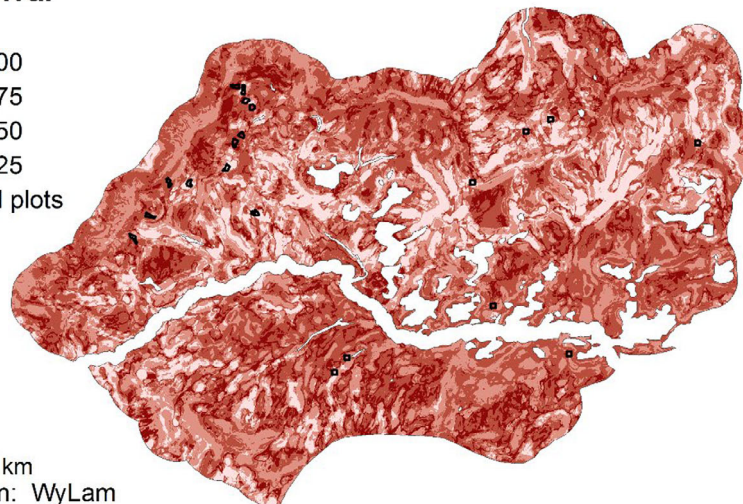
0.75 - 1.00

0.50 - 0.75

0.25 - 0.50

0.00 - 0.25

□ Songbird plots



10
N km
Projection: Wylam

Figure 2 Mapped model predictions of greater sage-grouse nest-site selection (top) and nest survival (bottom) in central Wyoming, USA, 2012–2013. Songbird nest-searching plots ($n = 20$) are also shown. Each map is a data-driven prediction created by modeling field-collected sage-grouse data as a function of variables describing habitat attributes using Random Forests. Areas of non-habitat (i.e. open water, riparian corridors, wetlands, montane forests and rocky outcroppings) that were masked from the study area prior to the analysis appear as white polygons.

We followed standard protocols (Martin & Geupel, 1993; Ralph *et al.*, 1993) to locate songbird nests within nest-searching plots between mid-May and mid-July by systematic searching every 2 days aided by observation of adult songbirds for signs of nesting activity. We standardized nest-searching effort among and within plots by ensuring that each plot was visited on a fixed schedule and that all portions of a plot were searched for a similar amount of time. On average, observers spent 75 person-hours searching for and monitoring songbird nests at each plot each year. We recorded the location of each nest with a handheld GPS unit, and monitored nests every 2–3 days until fledge or failure. A nest was considered successful if at least one nestling fledged from the nest (Rotella, Dinsmore, & Shaffer, 2004).

Nest success was determined by nest stage at previous check, examination of the nest remains and signs of parents feeding fledglings nearby (Martin & Geupel, 1993). We excluded from our sample any nests that were located >10 m outside plot boundaries.

Statistical analysis

Our analytical approach was to create a data-driven prediction of sage-grouse nest-site selection probability and a separate prediction of sage-grouse nest survival probability by modeling field-collected sage-grouse data as a function of variables describing habitat attributes. The field-collected songbird data could then be compared to sage-grouse

predictions to assess concordance between the umbrella and background species. Nest-site selection and nest survival analyses were conducted using Program R (R Core Team, 2017; version 3.3.3). We used the *ecoinfo* (Carlisle & Albeke, 2016; version 0.9.3), *raster* (Hijmans, 2015; version 2.5-8), *rgeos* (Bivand & Rundel, 2015; version 0.3-22), *rgdal* (Bivand, Keitt, & Rowlingson, 2015; version 1.2-5) and *sp* (Pebesma & Bivand, 2005; version 1.2-4) packages for spatial data handling and analyses. Random Forests models were fit and evaluated using the *randomForest* (Liaw & Wiener, 2002; version 4.6-12) and *rfUtilities* (Evans & Murphy, 2016; version 2.0-0) packages. We used the *snow* (Tierney *et al.*, 2013; version 0.4-2) and *snowfall* (Knaus, 2015; version 1.84-6.1) packages for parallel computing, and the *ggplot2* (Wickham, 2009; version 2.2.1), *ggthemes* (Arnold, 2017; version 3.4.0), *plyr* (Wickham, 2011; version 1.8.4) and *tidyr* (Wickham, 2016; version 0.6.1) packages for data management and plotting. We used ArcGIS (ESRI, 2014; version 10.2.2) to calculate geomorphometrics (Evans *et al.*, 2014; version 2.0-0) and create map figures.

Habitat variables

We considered habitat attributes as predictor variables in our models that were potentially relevant to the ecology of sage-grouse (Aldridge & Boyce, 2007; Doherty *et al.*, 2008; Carpenter, Aldridge, & Boyce, 2010; Doherty, Naugle, & Walker, 2010; Kirol *et al.*, 2015) and sagebrush songbirds (Petersen & Best, 1985; Chalfoun & Martin, 2007), and that represented vegetation and geomorphology at several spatial scales (Table S1). We also included year as a predictor variable to accommodate any temporal changes in patterns of nest-site selection or survival. We included three remotely sensed vegetation layers (Homer *et al.*, 2012): an estimate of the percent canopy cover of sagebrush (*Artemisia* spp.), percent canopy cover of herbaceous plants and shrub height. In addition, we included reclassified versions of these vegetation datasets wherein each pixel was classified as either suitable or unsuitable based on established guidelines for breeding habitat of sage-grouse at arid sites (Connelly *et al.*, 2000). We included elevation as a predictor variable and calculated two geomorphometric measures at a 3×3 cell window from the digital elevation model (Gesch *et al.*, 2002): compound topographic index (CTI) and terrain ruggedness index (TRI). CTI is a steady-state wetness index, which served as a proxy for soil moisture and nutrient availability (Gessler *et al.*, 1995). TRI is a measure of the topographic heterogeneity ruggedness (Riley, DeGloria, & Elliot, 1999). Last, we included X and Y geographic coordinates as separate predictor variables to incorporate spatial structure into our statistical models (Evans *et al.*, 2011).

We included some variables at their native spatial resolution (30 and 10-m pixels for vegetation and geomorphometric datasets, respectively), and we summarized others using a moving-window analysis at three scales (Table S1). We calculated the mean and standard deviation within a 282-m radius (0.25 km²), 564-m radius (1 km²) and 1260-m radius (5 km²) focal circle around each pixel. We used

standard deviation (SD) as an estimate for habitat heterogeneity (Kastdalen *et al.*, 2003; Carpenter, Aldridge, & Boyce, 2010), and based radius sizes on previous research documenting relationships between landscape features and sage-grouse responses at multiple scales (Berry & Eng, 1985; Holloran & Anderson, 2005; Aldridge & Boyce, 2007; Doherty *et al.*, 2010a,b; Kirol *et al.*, 2015). Prior to model fitting, we used qr-matrix decomposition at a threshold of 0.06 to remove variables that exhibited multivariate redundancy (Murphy, Evans, & Storfer, 2010; Evans & Murphy, 2016). In sum, we carried forward 37 predictor variables; 24 that described vegetation, 11 that described geomorphometry, one that described spatial location and one that indicated the year the nest was used (Table S1).

Nest-site selection

We evaluated sage-grouse nest-site selection with a use-availability framework (Boyce *et al.*, 2002; Manly *et al.*, 2002; Johnson *et al.*, 2006), in which resource use was identified as nest locations of sage-grouse ($n = 127$) pooled across individuals to represent a population-level (type 1) design (Manly *et al.*, 2002; Thomas & Taylor, 2006). We compared nest locations to randomly sited pseudo-absence locations. For each year, we generated an equal ratio of pseudo-absence to nest locations, and we enforced a minimum distance rule to prevent the contamination of nest locations with pseudo-absence points and increase the range of environmental conditions sampled. We calculated the median distance between observed sage-grouse nests and their nearest neighboring nest each year, and enforced this as the minimum distance that pseudo-absence points could be from other pseudo-absence points for that year, or from nest points for that year (1242 m in 2012 and 1458 m in 2013).

We developed a resource selection function (RSF; *sensu* Manly *et al.*, 2002) to characterize sage-grouse nest-site selection using Random Forests, a non-parametric, machine-learning approach (Breiman, 2001a). Random Forests is well-suited for ecological modeling because it typically provides high classification accuracy, includes no parametric assumptions, can accommodate spatial structure within the data, and thrives on large numbers of predictor variables and interactions between them (Breiman, 2001a,b; Cutler *et al.*, 2007; Evans *et al.*, 2011). All Random Forests models consisted of 5001 trees, and we followed the Random Forests model selection methodology of Murphy, Evans, & Storfer (2010). We ran an initial model that included all predictor variables, and then used model improvement ratio (MIR) scores to develop 10 candidate models. Candidate models were nested subsets that included only variables with MIR scores above a given MIR threshold, and we considered the best-supported model to be the one in which the class error (i.e. maximum of the within-class classification errors) was the lowest. We evaluated model fit and stability of predictions using standard methods, namely OOB (out-of-bag) error, confusion matrices, cross-validation and an overall model significance test (detailed in Murphy, Evans, & Storfer, 2010; Evans *et al.*, 2011; Doherty *et al.*, 2016). To

diagnose overfitting, we employed a 10% data-withhold cross-validation with 1001 iterations. As a final validation procedure, we applied the overall model significance test of Murphy, Evans, & Storer (2010) and Evans *et al.* (2011), randomizing the input data and re-running the Random Forest model 1001 times to compare the model against a null expectation of performance. We used the highest-ranked RSF model to generate a spatially explicit prediction of the probability of nest-site selection across the study area. Because the highest-ranked RSF model only contained predictor variables at 30-m resolution, we predicted the RSF value for each 30-m pixel in the study area.

To assess whether the nest-site preferences of songbirds aligned with those of sage-grouse, we employed a randomization test based on a Monte Carlo resampling procedure (Manly & Navarro Alberto, 2020). We first calculated the mean RSF value at nest locations for each songbird species for each year. We then generated a null distribution of the mean RSF value for each species–year combination against which to test the observed statistic, wherein the null hypothesis was that songbirds sited their nests with no regard to the preferences of sage-grouse. The principal mechanism of the randomization test was to randomly resite each species' nests within the nest-searching plots (restricted to only those searched in that year) and recalculate the mean RSF value at these random nest locations. We implemented 1000 iterations of this procedure.

Nest survival

We evaluated sage-grouse nest survival by comparing successful nests ($n = 63$) to failed nests ($n = 64$). We calculated a separate survival probability function (SPF; *sensu* Kirolo *et al.*, 2015) for sage-grouse nest survival using Random Forests and the same model selection procedure detailed for the RSF. The highest-ranked SPF model contained predictor variables at both 10 and 30-m resolution, so, we converted the 30-m datasets to 10-m resolution using the nearest neighbor method before using the highest-ranked SPF model to generate a spatially explicit prediction of the probability of nest survival for each 10-m pixel in the study area.

We used the logistic-exposure method (Shaffer, 2004) to assess whether songbird nest survival was higher where sage-grouse nest survival was predicted to be higher. Because songbird nests that fail early in the nesting cycle are less likely to be discovered by observers, apparent nest survival (proportion of observed nests that survive to fledged young) can overestimate actual nest survival (Mayfield, 1975; Shaffer, 2004; Johnson, 2007). The logistic-exposure method is a generalized linear model that corrects for this bias and estimates daily nest-survival rates in a regression framework (Shaffer, 2004). We used an information theoretic approach to compare the weight of evidence supporting each of three candidate models for each species (Burnham & Anderson, 2002). The candidate models were nested, with the most complex model including the SPF value at the nest site, the year and an interaction between SPF and year. The simplest model included only SPF as a predictor variable, and the

intermediate model included SPF and year. We determined the relative performance of each candidate model by calculating model weights (Anderson, 2008), and we evaluated evidence of one model over another based on second-order Akaike's Information Criterion (AICc; Akaike, 1974; Burnham & Anderson, 2002) or by comparing model weights (Burnham & Anderson, 2002). We screened for uninformative model parameters by comparing ΔAICc and log-likelihood values within model sets after model fitting (Burnham & Anderson, 2002; Anderson, 2008; Arnold, 2010).

Results

Nest-site selection

We located and monitored 127 sage-grouse and 407 songbird nests over the course of our study (Table 1). The highest-ranked RSF model (Table S2) predicted sage-grouse nest-site selection as a function of four predictor variables: X coordinate, sagebrush cover, mean binary sagebrush cover within 1-km² window and mean shrub height within 0.25-km² window. Predictor variables are listed in order of importance as ranked in Random Forests (Figure S1). The non-parametric nature of Random Forests precludes a single directionality being assigned to each effect, but in general terms, sites with highest probability of sage-grouse nest site selection had higher sagebrush cover, intermediate shrub height and were in the western portion of the study area (Figure S2).

The RSF model correctly classified 78.7% of sage-grouse nest sites and 74.0% of available locations, for an overall error rate of 23.6% from the internal OOB hold-out procedure (Table S5, Figure S3). The independent cross-validation yielded similar results, with a mean error rate of 23.7% and the overall model significance test resulted in $P < 0.001$, indicating model stability and lack of over-fitting. All documented sage-grouse nests had RSF values >0.65 , and 16.1% of the study area had RSF values greater than or equal to this value (Fig. 2).

The mean value of the sage-grouse RSF at songbird nest sites varied by species and were consistently higher in 2013 than in 2012 (Table 2). The mean RSF value at Brewer's sparrow nests in 2012 was 0.10 units higher (95% CI = 0.05–0.15) than the null expectation built under the assumption of random nest siting, suggesting that Brewer's sparrows preferred similar nesting habitats to those of sage-grouse in 2012 (Fig. 3). For all other species–year combinations, the mean RSF value at nest sites was within the range

Table 1 Sample sizes of nests for greater sage-grouse and three species of sagebrush-associated songbirds nesting in central Wyoming, USA, 2012–2013

Species	2012	2013	Total
Greater sage-grouse	53	74	127
Brewer's sparrow	99	170	269
Sage thrasher	21	63	84
Vesper sparrow	7	47	54

Table 2 Mean values of a resource selection function for greater sage-grouse (RSF) and survival probability function for greater sage-grouse (SPF) at nests of three species of sagebrush-associated songbirds nesting in central Wyoming, USA, 2012–2013. The RSF is a relative measure of nest-site preference, and the SPF is a measure of the probability of a nest surviving to produce young

Species	RSF			SPF		
	2012	2013	Overall	2012	2013	Overall
Brewer's sparrow	0.51	0.93	0.78	0.36	0.52	0.46
Sage thrasher	0.49	0.91	0.81	0.48	0.51	0.48
Vesper sparrow	0.37	0.92	0.85	0.37	0.49	0.47

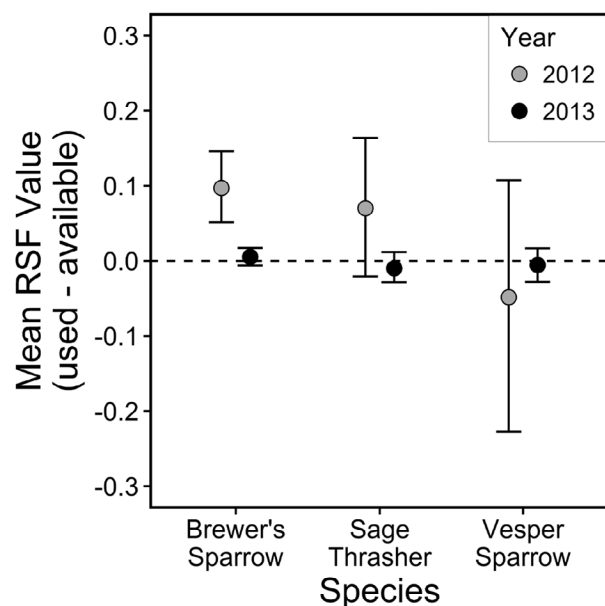


Figure 3 Nest-site selection patterns of three songbird species relative to the nesting habitat preferred by greater sage-grouse in central Wyoming, USA, 2012–2013. Selection scores >0 indicate selection for the habitat sage-grouse prefer, and scores <0 indicate avoidance of the habitat sage-grouse prefer. Error bars indicate 95% CIs from the Monte Carlo procedure.

of the null expectation, indicating there was no evidence that songbirds shared the nest-site preferences of sage-grouse (Fig. 3).

Nest survival

Overall, 49.6% of sage-grouse nests succeeded in hatching young, with nest success slightly higher in 2013 than in 2012 (Table S3). The highest-ranked SPF model (Table S4) predicted sage-grouse nest survival as a function of four predictor variables: SD of CTI within 1-km² window, mean sagebrush cover within 0.25-km² window, SD of TRI within 5-km² window and mean TRI within 1-km² window. Predictor variables are listed in order of importance as ranked in Random Forests (Figure S1). Although no clear directionality is evident in the habitat-survival relationships, the general

pattern was that sites with highest probability of sage-grouse nest survival had higher sagebrush cover, intermediate heterogeneity in wetness and intermediate values of both ruggedness and heterogeneity in ruggedness (Figure S4).

The SPF model correctly classified 68.3% of successful sage-grouse nests and 62.5% of failed sage-grouse nests, for an overall error rate of 34.7% from the internal OOB hold-out procedure (Table S6, Figure S3). The independent cross-validation yielded similar results, with a mean error rate of 38.3% and the overall model significance test resulted in $P < 0.001$, indicating model stability and lack of over-fitting. All documented sage-grouse nests that hatched had SPF values >0.66, and 21.9% of the study area had SPF values greater than or equal to this value (Fig. 2).

We monitored the survival of 407 songbird nests for a combined total of 5578 nest-days. Nest survival was generally higher for songbirds than sage-grouse (Table S3). Mean values of the sage-grouse SPF at songbird nests varied by species and were consistently higher in 2013 than 2012 (Table 2). The top-ranked model for Brewer's sparrows and vesper sparrows was Survival ~ SPF + Year (Table S7, Table S9). The top-ranked model for Sage Thrashers was Survival ~ SPF (Table S8). For all species, the model weight of the top-ranked model was ≥ 0.58 , and the second-ranked model was within 2 AICc units. However, in all cases, the second-ranked model differed from the top-ranked model only in the addition of an uninformative parameter (Anderson, 2008; Arnold, 2010), so we chose to base inference on the top-ranked model for each species.

Nest survival of all songbird species was unrelated to sage-grouse nest survival as predicted using the SPF (Fig. 4). The point estimate and 95% CI for the SPF odds ratio was 1.48 (0.51–4.25) for Brewer's sparrow, 0.87 (0.13–5.70) for sage thrasher and 2.60 (0.22–35.39) for vesper sparrow (Fig. 4), with all CIs containing 1.00 indicating no conclusive direction of effect. When controlling for SPF, survival was higher in 2013 than in 2012 for both Brewer's sparrows (odds ratio = 3.00, 95% CI for odds ratio = 1.80–5.13; Fig. 4, Table S3) and vesper sparrows (odds ratio = 4.53, 95% CI for odds ratio = 1.32–14.33; Fig. 4, Table S3).

Discussion

Surrogate species strategies often are lauded for providing a conceptual and logistical shortcut to achieving conservation goals, given limited resources (Caro, 2010). Across the sagebrush biome of North America, areas of suitable breeding season habitat for sage-grouse have been prioritized for conservation efforts (U.S. Fish and Wildlife Service, 2013; Chambers *et al.*, 2017; Government of Canada, 2021), and the habitat needs of sage-grouse are often assumed to serve as a proxy for the needs of other sagebrush-associated species (Chambers *et al.*, 2017). The extent to which this assumption is valid, however, necessitates empirical evaluation and is critical for the management and conservation of many other species of concern in the sagebrush biome. Most examinations to date of the efficacy of sage-grouse as an

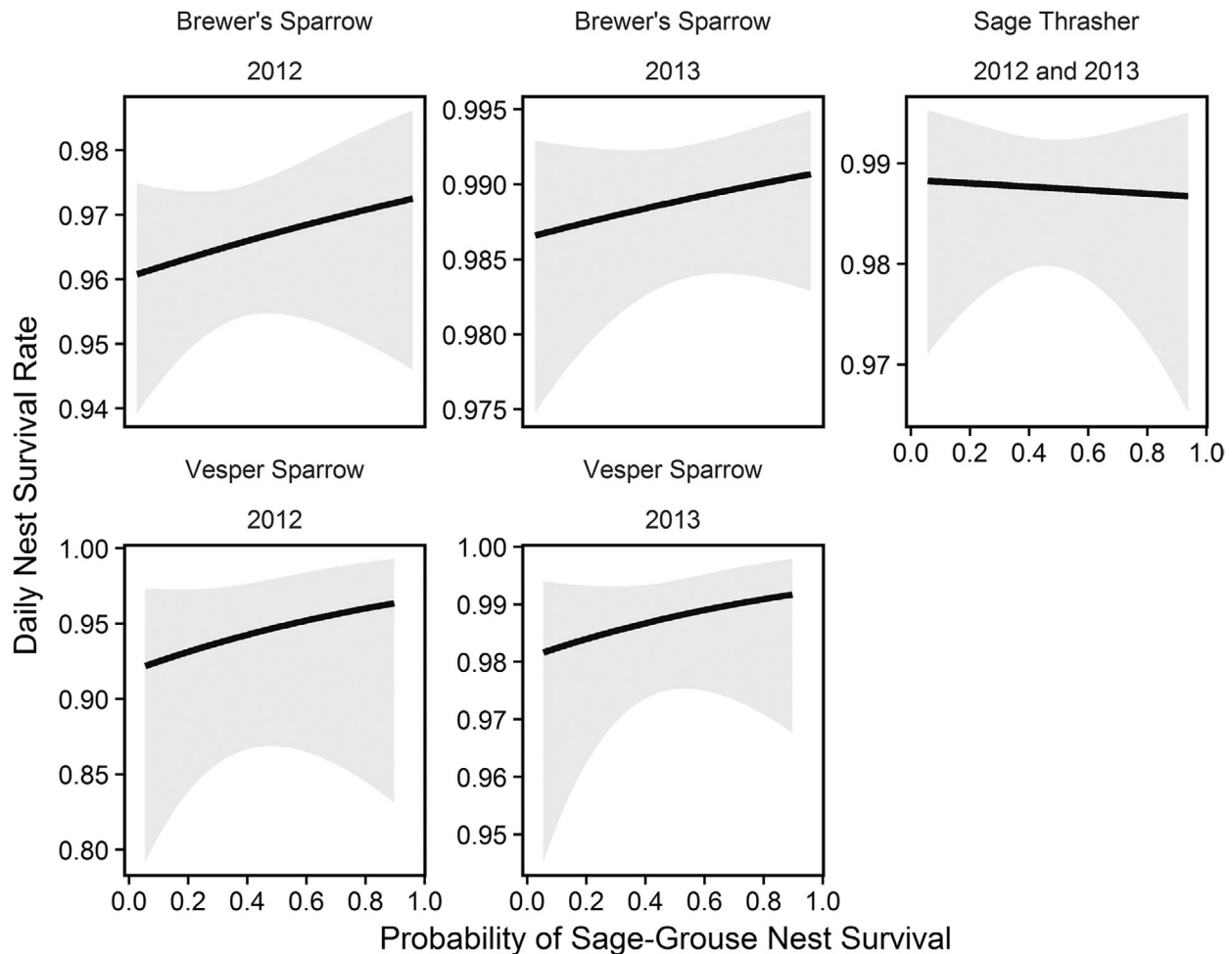


Figure 4 Nest survival of three songbird species relative to model-predicted nest-survival rates for greater sage-grouse in central Wyoming, USA, 2012–2013. Shaded regions indicate 95% CIs.

umbrella, moreover, have not considered overlap in preferred habitats or fitness outcomes. We evaluated the patterns of nest-site selection and habitat features associated with the nest survival of sage-grouse and three species of declining sagebrush-associated songbirds, and found limited concordance. Brewer's sparrows selected similar nesting habitats to those of sage-grouse during the first year of study only, and the habitat attributes associated with nesting success differed between sage-grouse and all three songbird species. Our study was limited to examining only direct relationships between nest-site selection and nest-site selection, or nest survival and nest survival; cross-relationships between selection and survival (e.g. songbirds selecting nesting habitats that produce higher nest success for sage-grouse) could exist, but a test of cross-relationships was beyond the scope of this study.

One plausible explanation for the lack of similarity between higher quality nesting habitat for sage-grouse and sagebrush songbirds was variation in nest predator assemblages. Nest predation is the primary source of nest failure

for both sage-grouse (Schroeder & Baydack, 2001) and sagebrush songbirds (Chalfoun & Martin, 2007; Hethcoat & Chalfoun, 2015a); however, their documented nest predator assemblages differ substantially. Most evaluations of the primary nest predators of sage-grouse invoke common ravens (*Corvus corax*) and mammalian mesocarnivores (Coates & Delehanty, 2010; Dinkins *et al.*, 2016; Conover & Roberts, 2016); whereas, the primary nest predators of sagebrush songbirds are rodents (Hethcoat & Chalfoun, 2015b) and snakes, if prevalent (Rotenberry & Wiens, 1989; Chalfoun & Martin, 2007). The microhabitats that most affect nest predation risk likely vary by nest predator species; so, by extension, variation in primary nest predators should result in variation in the attributes of safer nest sites across avian species.

The incongruence of sage-grouse and sagebrush songbird habitat preferences and quality that we document herein, however, does not necessarily negate the value of the sage-grouse as an umbrella at broader spatial scales (e.g. Rowland *et al.*, 2006; Gamo *et al.*, 2013; Carlisle *et al.*, 2018b), and

others have documented some congruence between nest-site characteristics selected by sage-grouse and Brewer's sparrows elsewhere (Barlow *et al.*, 2020). The study of ecology typically is organized hierarchically in terms of spatial scale (Allen & Hoekstra, 1992; Molles Jr., 2005), and ecological relationships often vary across scales (Wiens, 1989; Levin, 1992; Chalfoun & Martin, 2007; du Toit, 2010). Therefore, the seeming paradox that sage-grouse conservation benefits background species when viewed through a broad-scale lens, all while not benefitting background species when viewed through a fine-scale lens, is an entirely plausible outcome. Our results challenge some of the historic assumptions about surrogate species strategies, such as that of nestedness (*sensu* Patterson, 1987), wherein the area requirements, and by extension the habitat suitability of background species, are assumed to be nested subsets of those of the umbrella species (Lindenmayer *et al.*, 2002). Moreover, our findings question the premise that surrogate relationships are maintained across spatial scales (Lindenmayer *et al.*, 2002).

At the relatively fine spatial scale of our study (songbird nest-searching plots totaling 4.9 km²), we found little evidence that management actions that prioritize the conservation of sage-grouse nesting habitat would be beneficial to sagebrush-associated songbirds. Our results largely contrast with previous assessments (Rich, Wisdom, & Saab, 2005; Rowland *et al.*, 2006; Hanser & Knick, 2011; Donnelly *et al.*, 2017; Carlisle *et al.*, 2018b) that were conducted at broader spatial scales (e.g. across single or multiple ecoregions) and using coarser measures of concordance (e.g. overlap in predicted distributions or areas of high abundance), and with one assessment at fine spatial scales (Barlow *et al.*, 2020). Given that the habitat preferences of sage-grouse and sagebrush-associated songbirds are scale dependent (Chalfoun & Martin, 2007; Connelly, Rinkes, & Braun, 2011; Hanser & Knick, 2011), the lack of concordance between the habitat preference and productivity of these species may not be surprising. We caution that the assumption that habitat needs of background species are subsumed within the umbrella species' needs at all spatial scales invokes long-established misconceptions inherent in the interpretation of information across spatial scales (e.g. ecological fallacy and the modifiable aerial unit problem; Robinson, 1950; Openshaw, 1984).

Identifying and addressing conservation challenges at the appropriate spatial scale is a ubiquitous dilemma in conservation biology (du Toit, 2010). Areas perceived to be of high value to sage-grouse are prioritized for conservation at both regional and local scales (Doherty, Naugle, & Walker, 2010; Doherty *et al.*, 2011, 2016). Our work suggests that local-scale prioritizations of sage-grouse nesting habitat would likely omit areas of high value to nesting sagebrush songbirds. The inverse of this may be more troubling because the loss or fragmentation of areas perceived to be of low value to sage-grouse is not only tolerated, but often facilitated by policy. For example, habitat loss and fragmentation threaten sage-grouse populations range wide (Connelly *et al.*, 2011a,b). Energy development is a widespread form of habitat loss in large portions of the sage-grouse range (Naugle *et al.*, 2011), and a growing number

of studies document the negative effects of energy development (particularly oil and gas) on sage-grouse (reviewed in Naugle *et al.*, 2011). As such, the U.S. Bureau of Land Management (BLM) has recommended that areas of lower value to sage-grouse be prioritized for oil and gas leasing and development (U.S. Bureau of Land Management, 2016). Energy development also negatively influences the abundance and nest success of sagebrush-associated songbirds (Gilbert & Chalfoun, 2011; Hethcoat & Chalfoun, 2015a,b); however, because our results demonstrate little congruence between higher value nesting habitat of songbirds and sage-grouse, many current management regimes could run contrary to what is best for sagebrush-associated songbirds. Indeed, management actions intended to improve sage-grouse habitats at relatively fine spatial scales have been shown to have negative impacts on some non-target species (Norvell, Edwards, & Howe, 2014; Carlisle *et al.*, 2018a).

With respect to another high-profile surrogate species (the northern spotted owl, *Strix occidentalis caurina*), Simberloff (1998:249) cautioned that 'there is no inherent reason why the fact that this bird is threatened and of special interest would mean that its fate reflects those of other species.' The same may apply to the greater sage-grouse. We acknowledge that the conservation of biodiversity is limited by available resources and often necessitates action in spite of uncertainty or incomplete information (Soulé, 1985; Rich & Altman, 2001). Our study, however, corroborates a growing body of evidence revealing holes in the sage-grouse umbrella, and that the umbrella often collapses at finer spatial scales (Hanser & Knick, 2011; Carlisle *et al.*, 2018a,b; Dinkins & Beck, 2019; Timmer, Aldridge, & Fernández-Giménez, 2019; Carlisle & Chalfoun, 2020).

Some argue that surrogate strategies such as umbrella species have attained important success in shifting conservation focus from single-species approaches (e.g. those embodied in traditional wildlife management; Krausman, 2002) to more holistic, ecosystem-level approaches (Simberloff, 1998). However, no one species can completely represent another in terms of ecological requirements (Rich & Altman, 2001), and we reassert that the simplifying assumptions inherent in surrogate species strategies are tenuous until founded upon rigorous scientific testing (Simberloff, 1998; Lindenmayer *et al.*, 2002; Seddon & Leech, 2008). We expect that studies such as ours that transcend distributional overlap and examine habitat preferences and productivity at finer spatial scales will be critical in terms of improving understanding of the contexts under which surrogate species management may be most appropriate.

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Author contributions

All authors conceived the ideas and designed methodology; JC and KS collected the data; JC analyzed the data; JC and AC led the writing of the paper; all authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest

The authors declare no conflicts of interest.

Data availability statement

Data and associated analysis scripts are available in a public GitHub repository: https://github.com/jcarlis3/Data_Carlisle2023_ACV.

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Supporting information

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

Table S1. Candidate predictor variables used to model nest-site selection and nest survival of greater sage-grouse in central Wyoming, USA, 2012–2013.

Table S2. Model selection results for Random Forests RSF model classifying greater sage-grouse nests and available points in central Wyoming, USA, 2012–2013.

Table S3. Average probability of nest success (and 95% CI) for greater sage-grouse and three species of sagebrush-associated songbirds nesting in central Wyoming, USA, 2012–2013.

Table S4. Model selection results for Random Forests SPF model classifying greater sage-grouse nest survival in central Wyoming, USA, 2012–2013.

Table S5. Confusion matrix for final RSF model fit to greater sage-grouse nest-site data from central Wyoming, USA, 2012–2013.

Table S6. Confusion matrix for final SPF model fit to greater sage-grouse nest-survival data from central Wyoming, USA, 2012–2013.

Table S7. Model-selection results for logistic-exposure models describing the daily nest-survival rate of Brewer's sparrows in central Wyoming, USA, 2012–2013 relative to model-predicted nest-survival rates for greater sage-grouse.

Table S8. Model-selection results for logistic-exposure models describing the daily nest-survival rate of sage thrashers in central Wyoming, USA, 2012–2013 relative to model-predicted nest-survival rates for greater sage-grouse.

Table S9. Model-selection results for logistic-exposure models describing the daily nest-survival rate of vesper sparrows in central Wyoming, USA, 2012–2013 relative to model-predicted nest-survival rates for greater sage-grouse.

Figure S1. Variable importance rankings for the final RSF (left) and SPF (right) models fit to greater sage-grouse data from central Wyoming, USA, 2012–2013.

Figure S2. The influence of each predictor variable in the final RSF model fit to greater sage-grouse data from central Wyoming, USA, 2012–2013.

Figure S3. Convergence of bootstrap error rates across 5001 random forest trees for RSF (left) and SPF (right) models fit to greater sage-grouse data from central Wyoming, USA, 2012–2013.

Figure S4. The influence of each predictor variable in the final SPF model fit to greater sage-grouse data from central Wyoming, USA, 2012–2013.