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RESEARCH ARTICLE

Congruence among multiple indices of habitat preference for species facing human-induced rapid environmental change: A case study using the Brewer's sparrow

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Abstract

1. Accurate evaluations of habitat preference are key to understanding optimal conditions for wildlife survival and reproduction. Habitat selection, however, usually is evaluated using a single index of preference, and congruence among multiple, relevant indices of preference is examined rarely.
2. We assessed the concordance between patterns of habitat preference using three different indices of breeding site preference in a migratory songbird. Specifically, we compared the chronology of territorial establishment, pair formation and reproductive initiation of the Brewer's sparrow (*Spizella breweri*) along a gradient of surface disturbance associated with natural gas development in Wyoming, USA during 2019.
3. We expected all three indices to demonstrate a preference for breeding sites with less surface disturbance, where reproductive success typically is higher. By contrast, all indices suggested suboptimal preference with respect to surface disturbance, with some discrepancy among them. The chronology of settlement and pairing did not vary across the disturbance gradient, whereas nest initiation tended to occur earlier at sites with more disturbance.
4. If the pattern of suboptimal selection of breeding sites that we identified is generalizable across other populations of migratory birds affected by energy development, the resultant lower fitness in those areas may exacerbate population declines.
5. Our results suggest that traditional, single-index approaches to the study of habitat selection, if chosen carefully, may provide adequate inference on habitat preferences. Different metrics, however, can lead to at least subtle differences in patterns of habitat selection. The simultaneous examination of multiple indices of preference across a diversity of systems would help clarify the contexts under which preference metrics can become decoupled.

KEYWORDS
Brewer's sparrow, energy development, habitat selection, human-induced rapid environmental change, sagebrush songbirds, sagebrush steppe, surface disturbance

1 | INTRODUCTION

Habitat choices are evolved behaviours that respond to important selective pressures (Jaenike & Holt, 1991; Martin, 1998), and help illuminate the conditions that organisms need to survive and reproduce. Habitat selection is therefore a seminal concept in ecology, and critical to accurately characterize for effective conservation and management (Morris, 2003). Complete and precise assessments of habitat preference are of particular importance during the current age of widespread and rapid habitat change, which has been labelled the Anthropocene (Crutzen, 2006). Despite their widespread use and importance, common methodologies employed to quantify habitat selection (e.g. use vs. availability analyses) may yield incomplete inference (Garshelis, 2000; Jones, 2001), in part because they rely on researchers to accurately define availability. Moreover, almost all studies of habitat selection rely upon singular indices of preference and an assumption that the chosen metric of preference can adequately describe the relationship between a focal population and the environmental conditions under study. Any index of preference, however, is limited inherently by the context in which it occurs. Preferences are constrained by factors such as individuals' imperfect knowledge of resources or conflicting benefits between habitat choices. Additionally, metrics of preference may be indirectly related to fitness outcomes such that the focal metric is merely correlated with the causal mechanism of habitat selection (Chalfoun & Schmidt, 2012). Evaluating the consistency between multiple, plausible metrics of preference may therefore generate more robust inference. Congruence among multiple indices of habitat preference, however, is assessed rarely.

Deciding where and when to breed comprises some of the most consequential choices an animal faces in its lifetime, as breeding sites influence whether animals are able to pair and produce offspring that survive (Caccamise, 1977; Hilden, 1965). Migratory animals in particular must make rapid and accurate evaluations of the immediate and future quality of potential breeding sites (Gendron, 1977; Hahn & Silverman, 2006). Because the earliest individuals to arrive on breeding grounds have the most options available, moreover, the first sites to be settled should provide robust inference on habitat preferences. Following settlement comes pairing and the initiation of reproduction. The chronology of habitat use within all three stages is generally expected to correspond, such that individuals (i.e. prospecting males, pairing females and mating pairs) will use higher before lower quality habitat within each stage (e.g. Lloyd & Martin, 2005). Each of these component stages may be inadequate on their own, however, to describe thoroughly the process of breeding site selection because of constraints imposed by preceding stages. For example, although suboptimal settlement in males could be mitigated to some degree by strong preference for high-quality sites by females, females can only choose from the distribution of resource options resulting from male territory choices. Thus, evaluations of habitat preference may be strengthened by assessing multiple indices of selection corresponding with different phases of the broader habitat selection process.

Habitat selection is applied frequently in assessments of wildlife response to human-induced rapid environmental change (hereafter HIREC; Martin et al., 2010; Mathisen, 1968; Sih et al., 2010). HIREC can corrupt the process of habitat selection via novel selective pressures and/or settlement cues to which animals are not adapted that result in reduced fitness (Hollander et al., 2011; Robertson & Hutto, 2006). Understanding whether and how populations may be able to persist in the face of HIREC through processes such as habitat selection can therefore facilitate informed conservation recommendations (Kristan, 2003; Wong & Candolin, 2014). Traditional, single-index approaches to understanding the effects of HIREC on habitat selection, however, may bias outcomes according to the specific context in which a chosen metric of preference occurs. Alternatively, habitat selection research based on multiple lines of evidence could confirm or temper conclusions drawn from single-index studies (Hale & Swearer, 2016).

One mechanism by which HIREC can decouple links between apparent and actual habitat quality is through the alteration of species interactions. Synanthropic species, for example, often capitalize on novel resources or disturbances associated with HIREC and become locally hyper-abundant (Chalfoun et al., 2002; Johnson et al., 2017; West et al., 2016). Altered species' abundance can in turn affect interactions such as predation or competition with important fitness consequences (Faeth et al., 2005). In North America's sagebrush steppe, habitat loss and disturbance associated with energy development have been linked to the increased abundance of rodent species that are the primary nest predators of declining sagebrush-obligate songbirds (Hethcoat & Chalfoun, 2015a, 2015b; Sanders & Chalfoun, 2018). Nest survival of sagebrush-obligate songbirds generally decreased with surface disturbance (Hethcoat & Chalfoun, 2015a). Given the fitness consequences associated with reproducing in proximity to energy development, sagebrush songbirds should make adaptive choices and favour areas with less energy development. Alternatively, adults may exhibit maladaptive breeding-site selection because of the relatively sudden and unprecedented increase in rates of nest predation. Thus, sagebrush songbirds provide a model system in which to compare and validate multiple indices of breeding sites preference in a migratory species relative to an ongoing source of HIREC worldwide.

We evaluated the breeding site selection of the Brewer's sparrow (*Spizella breweri breweri*) along a gradient of surface disturbance associated with natural gas development. The Brewer's sparrow is a declining (−0.9% range-wide annual decline, 1966–2019 [Sauer et al., 2017]; IUCN Least Concern [BirdLife International, 2018]) migratory songbird that breeds exclusively in the sagebrush steppe of interior western North America, an ecosystem that has experienced extensive habitat conversion and alteration range wide (Knick et al., 2003). Given the documented reductions in sagebrush songbird nest success associated with surface disturbance (Hethcoat & Chalfoun, 2015a), understanding whether or not songbirds select breeding sites optimally with respect to energy development will be crucial for risk assessments. Furthermore, single-index approaches may provide incomplete inference on the relationship between breeding site selection and HIREC.

We addressed two research questions: (1) do Brewer's sparrows select breeding sites optimally along the gradient of surface disturbance associated with energy development? and (2) how congruent are assessments across different indices of habitat preference? We assessed breeding habitat preference using three widely accepted indices, each representing a different temporal phase of the selection process: the chronology of (1) initial settlement, as represented by territorial establishment of breeding males, (2) mate selection, as represented by formation of breeding pairs, and (3) reproductive initiation, as represented by the initiation of first nests. Each of these indices are used to study the breeding site selection of wildlife, but simultaneous comparisons of selection patterns among multiple indices within the same system have been rare. We expected synchrony in habitat selection patterns among indices such that Brewer's sparrows would demonstrate a preference for sites surrounded by less surface disturbance regardless of the index under consideration, and would settle, pair and initiate nests later at sites with more disturbance.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was conducted within the Pinedale Anticline Project Area (PAPA), a natural gas field in Sublette County, Wyoming, USA on public lands administered by the Bureau of Land Management. Land cover at our study sites was dominated by big sagebrush (*Artemisia tridentata*). Although population trends for the Brewer's sparrow in Wyoming are stable or in moderate decline, energy development has been identified as a primary conservation challenge (Abernathy et al., 2017). We assessed Brewer's sparrow habitat preference at six historic, 25-ha research plots (Hethcoat & Chalfoun, 2015a, 2015b) during May to August of 2019. Plots were similar in terms of their vegetative structure and composition (Figure S1), but situated along a gradient of surface habitat disturbance associated with energy development (Figure 1). We quantified surface disturbance by calculating per cent (ha/km^2) of sagebrush habitat converted to energy development using a 1-km^2 buffer centred on each plot ($\bar{x}_{ha/km^2} = 17.8$, $\sigma = 15.9$ [5.0–41.2]). Surface disturbance associated with energy development consisted of roads, well pads, processing facilities and re-seeded ('reclaimed') areas. We hand-digitized surface disturbance using 2017 National Agricultural Imaging Program (USDA Geospatial Gateway [U.S. Department of Agriculture], 2017) rasters of our study area in ArcMap (Esri, 2011). We verified that 2017 imagery adequately depicted the contemporary state of our study area by cross-referencing surface disturbance with 2019 imagery available in the Sublette County GIS map server (Greenwood Mapping, Inc., 2020). Given the influence of shrub structure on food availability and nest predation risk for sagebrush songbirds (Chalfoun & Martin, 2007, 2009; Williams et al., 2011), we also confirmed that shrub height, cover and density did not vary systematically with surface disturbance (Appendix S1).

2.2 | Settlement chronology

We used a spot mapping technique (Kendrick et al., 2015) to determine settlement and pairing patterns of Brewer's sparrows during visits to each of the six plots between 4 May and 17 June 2019. We surveyed one to three plots per day, and attempted to keep rates of visits even across plots throughout the study period, visiting each seven times, separated by an average of 6.73 days ($\sigma = 0.167$). We completed all visits during the peak of daily songbird activity (≤4 h after local sunrise time) and did not survey during inclement weather (rain, snow, freezing temperatures or wind ≤15 mph). We rotated observers between plots for each visit and walked systematic routes with random start locations and direction. For every singing male encountered during a survey, we recorded our own location using a handheld GPS, and the distance and direction to the focal bird using a laser range finder and a compass. Immediately following a survey, we used these data to determine actual locations of each singing male trigonometrically in ArcMap (Esri, 2011). We subsequently used this information to summarize the number of territorial males per plot visit. We recorded territorial behaviour (e.g. counter-singing, chasing) for each individual to assist in subsequent delineation of individuals.

2.3 | Pairing

We recorded information on the pairing status of male Brewer's sparrows during spot mapping visits via the unique vocalizations of paired versus unpaired individuals. Male Brewer's sparrows sing distinctly longer, more elaborate songs after successfully pairing (Walker, 2000; A. Chalfoun, unpublished data). Indeed, altered vocalization patterns and increased frequency of singing is a somewhat widespread strategy among passerines to reduce cuckoldry (Moller, 1991). We therefore believed this to be a reliable means of assessing pairing status. We also recorded behaviours such as copulation and nest-building to further assist in determining pairing status.

2.4 | Nest initiation

We measured the timing of the initiation (date first egg laid) of first nests within territories via systematic nest searching and monitoring. We searched plots for nests every other day, and located nests through a combination of behavioural observations of adults and

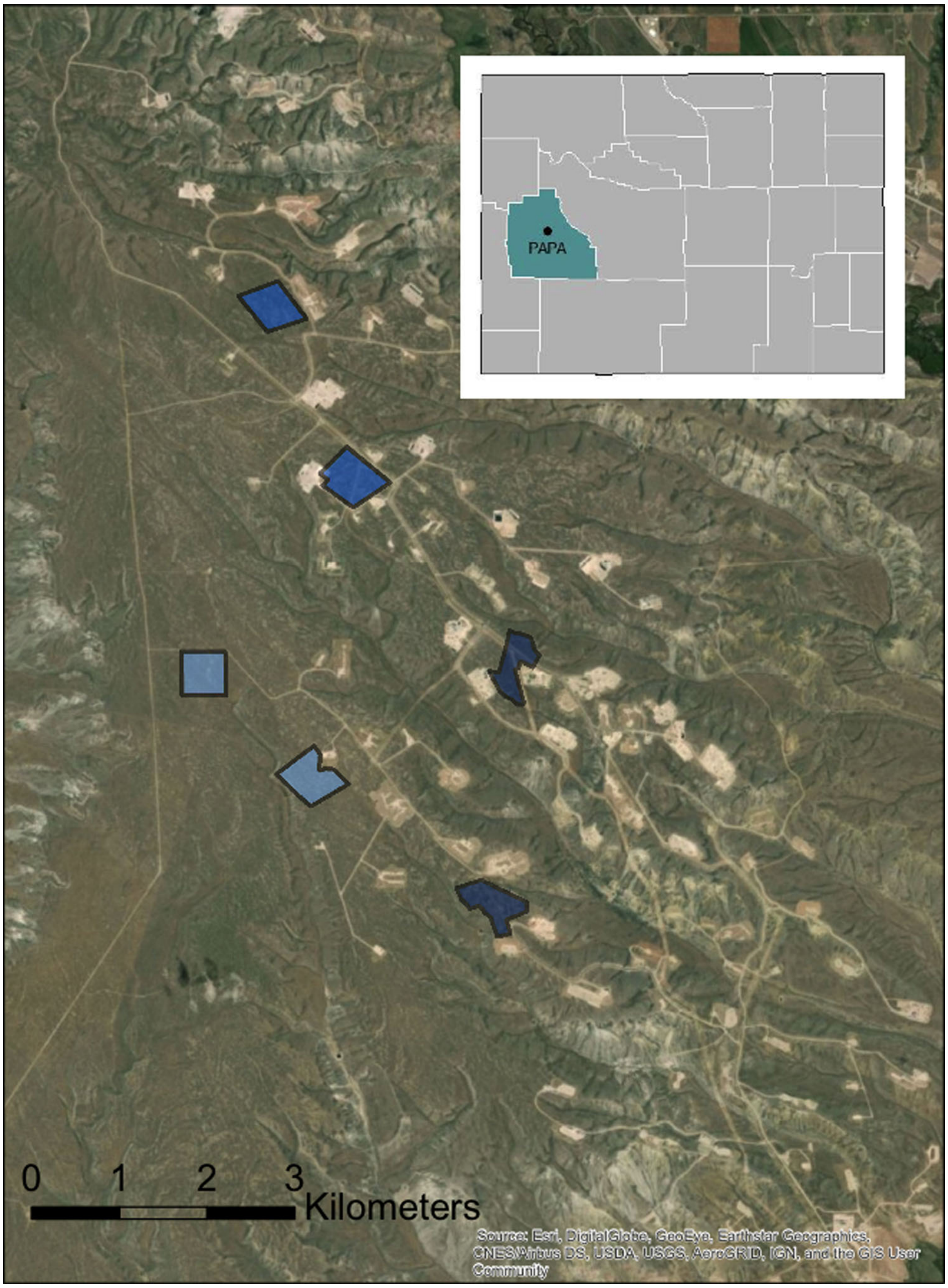

FIGURE 1 Study plots (~25 ha) used for the assessment of Brewer's sparrow (*Spizella breweri*) breeding site preferences within the Pinedale Anticline Production Area in Sublette County, Wyoming, USA during 2019. Polygons are shaded according to the amount of surrounding surface disturbance (ha/km^2), with darker shading indicating higher values.

systematic searching. We recorded the stage, number of eggs and young and adult activity when we initially found each nest and during each subsequent nest check (every 2–3 days). We recorded nest initiation as certain when the exact date that the first egg was laid was known (i.e. nests found during building or laying). For nests first located during the incubation or nestling stages, we estimated nest initiation dates by back-calculating based on average period lengths (10 days for incubation, and 8 days for nestling) using conventions detailed in Martin and Geupel (1993).

2.5 | Statistical analyses

Prior to analyses, we inspected each data set for outliers, homogeneity and zero-inflation, and evaluated potential co-linearity among covariates (Zurr et al., 2010). We used ranked candidate models using the Akaike information criterion corrected for small sample sizes (Burnham & Anderson, 2002). For all indices, we examined the directionality of preference via the relationship between the response variable in the model of a given index and either the amount of

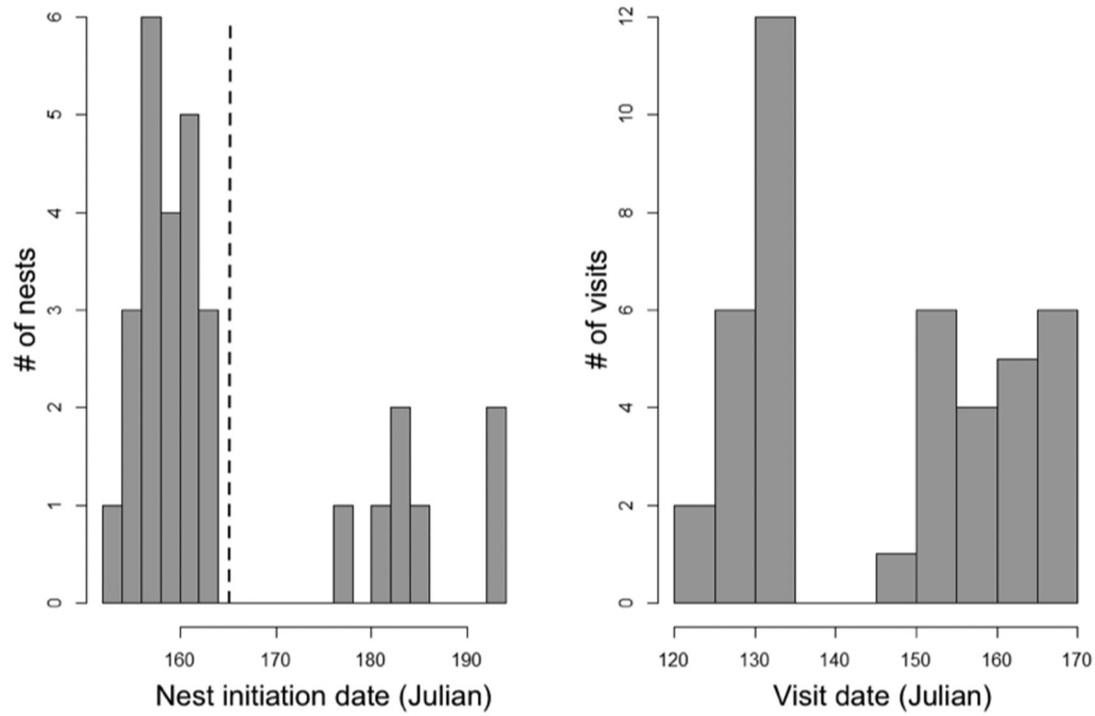

FIGURE 2 Temporal distributions of nest initiation data (left) and spot mapping visits (right) from six study plots located along a gradient of energy development at the Pinedale Anticline Production Area in Sublette County, Wyoming, USA during 2019. We delineated June 14 (dashed line, left panel) as the cut-off for Brewer's sparrow first nest initiation data because this corresponded with the end of that season's initial nesting peak. The continuity of spot mapping visits over time was disrupted by an extended spell of late winter weather (gap between Julian date 135 and 145, right panel) which greatly reduced Brewer's sparrow activity. We therefore made time a categorical variable when modelling settlement patterns.

surrounding surface disturbance (nest initiation) or an interaction between surface disturbance and time (settlement and pairing). We reasoned that optimal habitat preferences would consist of inverse relationships between each preference index and surface disturbance. Possible alternative responses included no preference (no relationship between the preference index and surface disturbance), and preferences that were more severely maladaptive, consisting of individuals favouring high-disturbance sites.

We assessed patterns of territorial settlement and pairing by evaluating the interaction between time (Julian date) and surface disturbance surrounding a given plot. Although we initially aimed to keep spot mapping visits continuous across all plots over time, an extended bout of late winter weather conditions (snow, freezing rain, below freezing temperatures) disrupted our sampling continuity (Figure 2). We therefore specified time as a categorical variable for our territorial settlement data through careful inspection of our data to ensure each time category had an approximately even sample size across disturbance classes (i.e. Period 1 = Julian dates 124–131, Period 2 = 132–135; Period 3 = 136–155; Period 4 = 156–168). Pair initiation did not occur prior to the sampling gap and we were therefore able to maintain time as a continuous variable in our pairing analysis.

We built global models for settlement and pairing analyses using generalized linear mixed models (GLMM) in lme4 (Bates et al., 2015) in the R software environment (R Core Team, 2018) that included random effects of plot and observer. For settlement, we first determined the optimal error distribution (Poisson vs. negative binomial) using the global model. We then compared the fit of the global model to time-only, disturbance-only and null models with the best-fitting error distribution from the previous step. We reasoned that strong support for the time-only and/or null models would indicate little or no preference for breeding sites relative to surface disturbance. Alternatively, support for the disturbance-only model would indicate sensitivity of Brewer's sparrow use of breeding sites relative to surface disturbance. However, we did not consider disturbance-only models to be indicative of habitat preference per se since they lacked a chronological component and our assessment of preference was based on relative differences in the timing of breeding behaviour across plots.

We modelled pairing patterns using proportional logistic regression in GLMM's with a binomial error distribution. Specifically, we modelled pairing as a series of trials with two outcomes, success (number of paired Brewer's sparrows on Julian date *i*) and failure (i.e. number of non-paired Brewer's sparrows on Julian date *i*). We compared the fit of a global model for pairing (i.e. with the interaction Julian date × surface disturbance and random effects of observer and plot) with time-only, disturbance-only and null models. Finally, we used a normal distribution and random effect of plot in linear mixed models of nest initiation, comparing a global model with a fixed effect of surface disturbance to a null model. We verified assumptions were met for models of each index of preference via examination of residual spread and quantile–quantile plots.

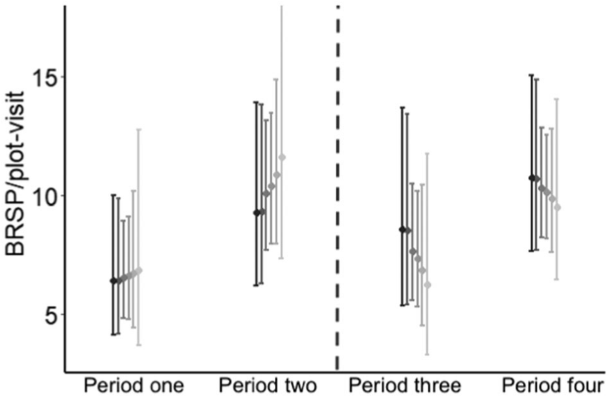

FIGURE 3 Settlement chronology of Brewer's sparrows in relation to natural gas development within the Pinedale Anticline Production Area in Sublette County, Wyoming, USA, during 2019. Model-predicted estimates of density (and 95% confidence intervals) in each survey period are displayed across a gradient ($N = 6$ study plots) of per cent surface disturbance (ha/km^2) associated with development, with darker colours representing less and lighter colours representing more surface disturbance. Date ranges for each survey period were period one: May 4–May 11; period two: May 12–May 15; period three: May 16–June 4; and period four: June 5–17. The dashed line indicates the gap in sampling caused by a prolonged period of inclement weather.

TABLE 1 Candidate models used to evaluate the habitat selection of Brewer's sparrows across a gradient of surface disturbance associated with natural gas development within the Pinedale Anticline Production Area in Wyoming, USA during 2019

Model structure	*k*	Model type	ΔAIC_c
Settlement			
~Time Period	6	Poisson GLMM	0.00
~Null	3	Poisson GLMM	1.23
~Disturbance	4	Poisson GLMM	3.76
~Disturbance × Time Period	10	Poisson GLMM	12.40
Pairing			
~Julian date	4	Binomial GLMM	0.00
~Disturbance × Julian date	6	Binomial GLMM	4.91
~Null	3	Binomial GLMM	50.26
~Disturbance	4	Binomial GLMM	52.43
First Nest Initiation			
~Null	3	LMM	0.00
~Disturbance	4	LMM	0.15

Note: We compared patterns of habitat selection across three different metrics of preference: The chronology of territorial settlement, pairing and nest initiation. All settlement and pairing models included random effects of observer and plot ID, whereas nest initiation models included a random effect of plot only. Time was characterized as a continuous variable (Julian date) for pairing and categorically by grouped Julian dates for settlement. ΔAIC_c is the difference in Akaike information criterion values corrected for small sample size between the best fitting model and the model listed. Top models are listed in bold.

3 | RESULTS

3.1 | Settlement chronology

A Poisson distribution fit our settlement data better than a negative binomial distribution (ΔAIC_c = 2.45) and was therefore used in all subsequent models. Brewer's sparrow counts fell into four temporally distinct units such that May 4–11 corresponded with period one, May 12–15 period two, May 16–June 4 period three, and June 5–17 period four (Figure 3). The settlement of Brewer's sparrows was unrelated to surface disturbance. Although the time-only model was competitive, we considered the null model for settlement to provide the best fit for our data given the largely uninformative additional parameters appearing in the time-only model (Arnold, 2010; Table 1). Finally, in the global model for settlement, the focal interaction between surface disturbance and time did not significantly influence the density of territorial males (Figure 3).

3.2 | Pairing

We first detected pairing on 1 June, after which the proportion of paired Brewer's sparrows increased rapidly at all plots (Figure 4). A peak in pairing status was followed by an abrupt drop off in counts of paired males, which we attributed to a reduction in the display rate of paired males as they began to attend to nests. The time-only model unequivocally provided the best fit for our pairing data, and disturbance had no effect on pairing in any of the models we tested (Table 1). The probability of pairing at all sites increased significantly during the period sampled ($\beta = 0.15$, $p < 0.001$).

3.3 | Nest initiation

We located and monitored 47 Brewer's sparrow nests across all plots and used a subset of the 22 earliest nests for our investigation of the initiation chronology of first nests. We inspected histograms of nest initiation dates for Brewer's sparrows to determine our cut-off for the initial nesting peak (Figure 2), and used nests with initiation dates ranging from June 1 to June 13. Seven nests had certain dates of nest initiation and 15 were back calculated. Nest initiation occurred significantly earlier at sites with more surface disturbance according to the model which included surface disturbance as a fixed effect ($\beta = -0.115$, $p = 0.005$; Figure 5). However, this surface disturbance model held little advantage in fit over the null model of nest initiation (Table 1).

4 | DISCUSSION

Habitat selection is vital to understanding the conditions that animals need to survive and reproduce, a task of particular urgency given the myriad ways in which anthropogenic environmental change is altering

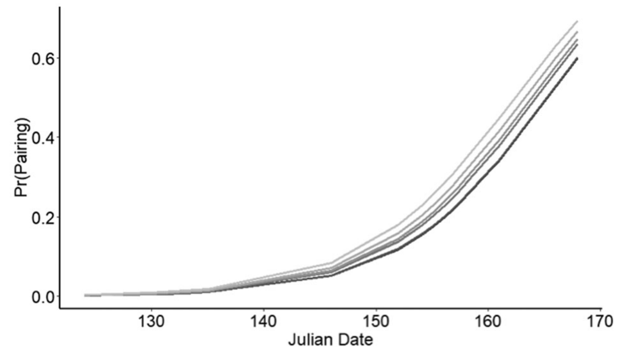

FIGURE 4 Pairing chronology of Brewer's sparrows in relation to natural gas development within the Pinedale Anticline Production Area in Sublette County, Wyoming, USA, during 2019. Model-predicted estimates of the probability that a given male Brewer's sparrow encountered during a survey was paired are shown for a gradient of per cent surface disturbance (ha/km^2) associated with development surrounding six, 25-ha study plots. Surface disturbance density surrounding plots ranged from 0.5 ha/km^2 (darkest coloured line) to 41.2 ha/km^2 (lightest coloured line).

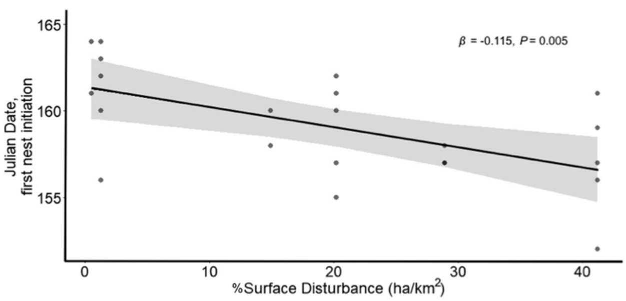

FIGURE 5 Julian date of first nest initiations for Brewer's sparrows in relation to natural gas development within the Pinedale Anticline Production Area in Sublette County, Wyoming, USA, during 2019. Model-predicted estimates of nest initiation dates across a gradient of surface disturbance associated with natural gas development are represented by the black line. Note that this surface disturbance model held no advantage in fit over the null model for nest initiation.

those conditions. Yet, conventional approaches to the study of habitat selection usually draw inference from singular indices of preference, and congruence among multiple indices rarely is evaluated simultaneously within the same system. We found general agreement among three indices of preference that suggested a pattern of suboptimal habitat selection along a disturbance gradient for a migratory songbird, although with unequal severity across indices. Although a preference for sites with higher fitness outcomes would be predicted under an optimal preference scenario, two of the three indices we assessed suggested no preference across sites, whereas the third suggested some level of preference for sites associated with poorer fitness outcomes. Specifically, territorial settlement and pairing of Brewer's sparrows were invariant with respect to surface disturbance associated with natural gas development, which is known to depress nest success (Hethcoat & Chalfoun, 2015a, 2015b), whereas pairs tended to initiate nests earlier at sites with more surrounding surface disturbance.

Brewer's sparrows in our study therefore appeared unable to assess and preferentially breed in areas that tend to confer higher nesting success. Habitat choices are informed by a set of proximate cues, which animals use to indirectly and directly assess the favourability of circumstances at a given place and time for a given activity (Emmering & Schmidt, 2011; Williams & Nichols, 1984). In our study system, surface disturbance associated with energy development increases the risk of nest predation (Hethcoat & Chalfoun, 2015a), which is the primary source of nest failure. The risk of nest predation is associated with the abundance of primary nest predators (Hethcoat & Chalfoun, 2015b; Sanders & Chalfoun, 2019). The singly most influential predator, however, the deer mouse (*Peromyscus maniculatus*), which was responsible for >50% of Brewer's sparrow nest depredations during 2011–2018 (Hethcoat & Chalfoun, 2015b; A.D. Chalfoun, unpublished data), forages nocturnally. Predation risk may therefore be difficult for parent birds, with limited night-time activity and vision, to assess and track with accuracy (Slay et al., 2012). The nocturnal vigilance of nesting Brewer's sparrows has not been examined explicitly, though one parent tends to spend most of the night attending the nest (A. D. Chalfoun, personal observation), which likely limits the ability of parents to obtain information on rodent distribution and activity in the area.

We used multiple indices to describe habitat preferences relative to a form of human-induced rapid environmental change, thereby providing thorough and well-rounded evidence for maladaptive habitat choice compared with traditional, single-index approaches (Hale & Swearer, 2016). Habitat selection is used frequently in conservation and management planning, and accurate conclusions regarding animal–habitat relationships are critical for timely and effective management decisions and optimizing limited conservation resources (Garshelis, 2000). By evaluating multiple indices of breeding site preference, we were able to demonstrate that Brewer's sparrows consistently made maladaptive habitat choices with respect to surface disturbance associated with energy development throughout the breeding site selection process. Moreover, the variation in severity of suboptimal preference among our indices suggests that single-index approaches may provide incomplete or imprecise characterizations of habitat selection. We suggest that several, plausible indices of habitat preference may lead to more rigorous evaluations of habitat selection, and strengthen conclusions on wildlife–habitat relationships used in conservation planning.

If the pattern of suboptimal breeding site selection we identified for Brewer's sparrows is generalizable to other ecosystems affected by energy development, there may be cumulative consequences for the population trajectories of sensitive species. Indeed, energy development, specifically oil and natural gas, has emerged as a primary conservation challenge not only in sagebrush steppe (Knick et al., 2011) but a host of terrestrial ecosystems (Bernath-Plaisted & Koper, 2016; Chalfoun, 2021; Northrup & Wittemeyer, 2012). Construction of roads, well pads and pipelines for oil and natural gas development has contributed to both the direct loss and fragmentation of habitat (Butt et al., 2013; Copeland et al., 2011; Finn & Knick, 2011).

Whether areas with more energy development represent population sinks (Kristan., 2003; Pärt et al., 2007), however, remains unclear. In our system, nesting failures (Hethcoat & Chalfoun, 2015a, 2015b) could be counterbalanced by other fitness components such as post-fledging survival, and/or the dispersal dynamics between our study populations and those in surrounding regions (Pulliam, 1988). The examination of multiple indices of reproductive fitness and dispersal parameters in relation to energy development and other forms of human-induced habitat changes would therefore comprise a fruitful line of future inquiry (Maresh Nelson et al., 2020; Streby et al., 2014).

Although our findings suggest a lack of adaptive choice in relation to surface disturbance, the limited temporal span of our study precludes assessment of the generality of our results. Limited temporal scale can certainly constrain conclusions from the study of habitat selection (Schooley, 1994), as animal behaviour can be context dependent and vary in response to ambient environmental conditions (Szaro et al., 1990). We therefore encourage continued study of the breeding site preferences of Brewer's sparrows and other species to determine the viability of our results in a broader temporal context.

Furthermore, habitat choices occur across multiple, nested spatial scales, in response to different selective pressures that can vary by scale (Chalfoun & Martin, 2007; Reidy et al., 2017). Brewer's sparrows may therefore cue in on surface disturbance at smaller spatial scales than the 25-ha scale at which we studied. Different choices, moreover, can be subject to unique cues and constraints, and the general scale of influence we used may not have been equally relevant across the contexts in which each of our indices of preference takes place. Thus, differences in scale sensitivity between indices may partially explain the variation in severity of preference we observed between settlement and pairing versus nest initiation. Selecting biologically relevant scales of inference, such as individual breeding territories for example, may provide more informative conclusions on what role, if any, surface disturbance might play in songbird habitat choices.

5 | CONCLUSIONS

Wildlife decisions, such as habitat choices, are context-dependent events. Our study demonstrates the value of using multiple, relevant indices of habitat preference to increase the confidence in conclusions drawn from investigations of habitat selection. We used multiple indices of habitat preference to evaluate the response of a declining songbird to HIREC during the breeding period, and identified consistent signals of suboptimal habitat choice. The identification of such mismatches between contemporary habitat choices and habitat quality is critical given the extent of habitat change worldwide. Identifying where potentially maladaptive wildlife habitat choices are occurring, for example, may warrant additional management scrutiny. Carefully selecting the most appropriate indices of habitat preference, and the inclusion of multiple indices of preference when feasible, will yield more thorough and precise understanding of habitat selection in a changing world.

AUTHOR CONTRIBUTIONS

Anna D. Chalfoun initiated the research question. Anna D. Chalfoun and Max Carlin developed the methodology and wrote the manuscript. Max Carlin collected and analysed data.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.w3r2280sd (Carlin & Chalfoun, 2022).

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PEER REVIEW

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SUPPORTING INFORMATION

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

Figure S1. Variation in shrub structure metrics among six study plots at the Pinedale Anticline Production Area (PAPA), Sublette County, Wyoming. Measurements of shrub height (top), shrub cover (middle), and shrub density (bottom) from previous research at our study sites (Hethcoat and Chalfoun 2015b) were used to ensure that microhabitat did not vary systematically with surface disturbance.

Supplementry Information

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