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Methodology

A lidar-based openness index to aid conservation planning for grassland wildlife

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ABSTRACT. Visual openness is a key element in habitat selection for many animals of grasslands and other open habitats, especially birds. Obstructions to visual openness in the form of human infrastructure or inopportune woody vegetation growth can lead to habitat avoidance, and thus pose conservation challenges. Here we introduce a remotely sensed, lidar-based index of visual openness. Like previous indices of visual openness, ours is based on the vertical angle to the horizon; however, its calculation from remotely sensed data allows it to be easily mapped across the landscape. We illustrate its potential usage by calculating the index multiple ways within two large fields in central New Jersey, USA, and evaluating the effects of openness on habitat use by a grassland bird, the Grasshopper Sparrow (*Ammodramus savannarum*), within an occupancy modeling framework. We used the best performing model and digitally edited openness maps to project population responses under five hypothetical management scenarios of increased habitat openness. Occupancy modeling revealed that a version of the index calculated based on the maximum angle to the horizon best explained Grasshopper Sparrow occupancy patterns. Models also revealed that Grasshopper Sparrows showed a negative response to openness reductions caused by both powerlines and trees. Predictions based on the increased openness scenarios indicated that removal of tree lines and powerlines could increase patch-level occupancy of the sparrows in the affected fields by up to 15% and 9%, respectively. Where adequate data exist, this index has the potential to facilitate the study of openness-habitat use relationships in a variety of open-dwelling fauna and in a variety of habitats, from tundra to marshes to grasslands. Notably, it has promising potential for use in modeling habitat suitability and projecting potential impacts in response to anthropogenic changes in visual openness, such as wind farms, power infrastructure, or vegetation management.

Indice d'ouverture fondé sur le LiDAR et destiné à faciliter la planification de la conservation de la faune de prairies

RÉSUMÉ. L'ouverture visuelle est un élément clé dans la sélection de l'habitat pour de nombreux animaux de prairies et autres milieux ouverts, en particulier les oiseaux. Les obstructions de celle-ci, sous forme d'infrastructures humaines ou de croissance de la végétation ligneuse, peuvent conduire à l'évitement de l'habitat et poser ainsi des problèmes de conservation. Dans la présente étude, nous proposons un indice d'ouverture visuelle fondé sur la télédétection et le LiDAR. Comme d'autres indices d'ouverture visuelle, le nôtre est basé sur l'angle vertical par rapport à l'horizon; cependant, son calcul à partir de données de télédétection permet de le cartographier facilement dans le paysage. Nous illustrons son utilisation potentielle en calculant l'indice de plusieurs façons dans deux grands champs du centre du New Jersey, aux États-Unis, et en évaluant les effets de l'ouverture sur l'utilisation de l'habitat par un oiseau de prairies, le Bruant sauterelle (*Ammodramus savannarum*), dans un cadre de modélisation de la présence. Nous avons utilisé le modèle le plus performant et des cartes d'ouverture éditées numériquement pour projeter les réactions de la population sous cinq scénarios de gestion hypothétiques d'augmentation de l'ouverture de l'habitat. La modélisation de la présence a révélé qu'une version de l'indice calculée sur la base de l'angle maximal par rapport à l'horizon expliquait le mieux les profils de présence du Bruant sauterelle. Les modèles ont également révélé que les bruants réagissaient négativement aux réductions de l'ouverture causées par les lignes électriques et les arbres. Les prévisions basées sur les scénarios d'ouverture accrue ont indiqué que l'élimination de rangées d'arbres et de lignes électriques pourrait favoriser l'augmentation de la présence des bruants à l'échelle des îlots dans les champs étudiés de 15 % et de 9 %, respectivement. Lorsque les données adéquates existent, cet indice peut faciliter l'étude des relations entre l'ouverture et l'utilisation de l'habitat chez une variété de faune vivant en milieu ouvert et dans une diversité d'habitats, de la toundra aux marais en passant par les prairies. Il présente notamment un potentiel prometteur pour la modélisation de la qualité de l'habitat et la projection des impacts potentiels consécutifs aux changements anthropiques de l'ouverture visuelle, tels que les parcs éoliens, les infrastructures électriques ou la gestion de la végétation.

Key Words: *Ammodramus savannarum*; conservation planning; grassland birds; habitat suitability models; infrastructure; openness; wind energy

INTRODUCTION

Animals of open habitats such as grasslands, marshes, mudflats, tundra, and arid lands often have foraging, predator avoidance, and courtship strategies that rely on unobstructed views, or openness. Consequently, habitat changes that involve human infrastructure (Pruett et al. 2009), increased tree cover (Besnard and Secondi 2014, Fuhlendorf et al. 2017), or other visual obstructions (Renfrew and Ribic 2002, Attum 2007) can reduce habitat suitability (i.e., induce avoidance behaviors) and pose conservation challenges for open-country species. Here, we introduce a novel index of habitat openness based on remotely sensed lidar data and demonstrate its utility for conservation planning.

Openness, or the relative lack of visual obstruction, is an important predictive feature of habitat use for diverse taxa at a range of spatial scales (Burger 1977, Gerard and Loisel 1995, Renfrew et al. 2005, Attum 2007, Goodman 2009). In particular, birds of open habitats such as temperate grasslands and emergent marshes show preference for openness at scales from local nest sites (Burger 1977) to territory placement (Keyel et al. 2012, Marshall et al. 2020), with a lack of perches for predators and nest parasites frequently suggested as the underlying drivers (van der Vliet et al. 2008). Recent research has shown that visual openness, as measured by the mean or maximum angle to the horizon (e.g., the tops of nearby trees, landforms, or structures) from a given location, can explain patterns of occurrence for multiple species of grassland and tidal marsh birds better than area or edge distance measures (Keyel et al. 2012, 2013, Marshall et al. 2020). This may be on account of the fact that this metric more closely aligns with sensory perception mechanisms in birds than harder-to-perceive attributes such as distance or area (Renfrew and Ribic 2002, Keyel et al. 2012).

The management implications of a behavioral preference for openness are that human infrastructure installation (e.g., wind farms; Pruett et al. 2009), succession (Besnard and Secondi 2014, Fuhlendorf et al. 2017, Andersen and Steidl 2019), or even topography (Renfrew and Ribic 2002), can limit or reduce populations of fauna that use open habitats. Conversely, ecological restoration activities or planning decisions that consider openness have the potential to aid in conservation of these species (Pruett et al. 2009, Fuhlendorf et al. 2017, Lautenbach et al. 2020). The ability to map openness at scales from patches to landscapes could therefore provide a powerful conservation planning tool. Such tools, when coupled with field studies and analysis to better understand functional responses, would allow the exploration of predictions regarding existing habitat suitability (Guisan et al. 2013) and population responses to management scenarios. For example, wind energy and associated power transmission infrastructure are rapidly expanding globally, whereas studies have shown avoidance of such infrastructure by imperiled grassland species (e.g., the Lesser Prairie-Chicken, *Tympanuchus pallidicinctus*; Pruett et al. 2009).

Knowledge of how species' occurrence or abundance vary with openness reduction caused by these features, e.g., via statistical modeling using new or existing field data, would allow quantitative predictions of the likely effects of introducing similar infrastructure elsewhere. Similarly, given that openness is a good predictor of abundance in the steeply declining Saltmarsh

Sparrow (*Ammospiza caudacuta*; Marshall et al. 2020), continuous maps of this measure could be used to prioritize marshes for restoration or management, e.g., the use of fire to remove woody vegetation (Kern and Shriver 2014). Using currently available methods, such investigations would require considerable field efforts in the form of manual openness measurements, e.g., site visits and dozens of clinometer readings, or the use of proxies such as distance to edge. Thus, a remotely sensed version of this index would greatly improve its utility.

Here we introduce a remotely sensed openness index calculated from a series of measured angles to the horizon and based on publicly available lidar data. We then demonstrate its use to evaluate the effects on within-field habitat usage (patch-level occupancy) by a forest edge-avoiding grassland bird, the Grasshopper Sparrow (*Ammodramus savannarum*). We hypothesized that local openness, as perceived by the birds, would be adequately captured by this index, and therefore we predicted higher occupancy with greater openness. We further demonstrate the conservation planning potential of the tool by evaluating the population implications of various hypothetical management scenarios that would increase openness within the fields.

METHODS

Study area

All fieldwork was performed within two former farm fields at Duke Farms, a 1108-ha preserve dedicated to sustainability, conservation, and education, in Hillsborough, New Jersey, USA. The fields, named Kaufman (77 ha) and Skeet Shoot (73 ha), were last in active agricultural production in 2001, and have been maintained as a grassland preserve (a mix of native and introduced grasses and forbs, mowed once every one or two years) since then. Kaufman is intersected by three tree lines, whereas Skeet Shoot has no tree lines, but has two rows of high-tension powerlines supported by five towers (~50 m tall) along its western edge (Fig. 1). The landscape immediately surrounding the preserve is primarily urban (> 70% residential or industrial cover within 8 km; Almendinger et al. 2020), and grassland bird habitat in the region consists mainly of 10–100 ha low-intensity hayfields and fallow fields, fragmented by tree lines, woodlots, and residential development.

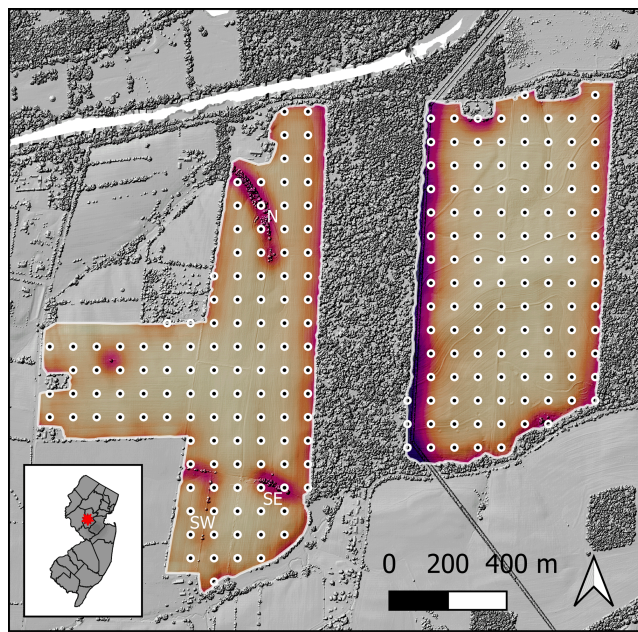
Openness indices

We obtained nine tiles (21 km²) of lidar data collected in 2018 from the State of New Jersey's Geographic Information Network website (<https://njgin.nj.gov/njgin/edata/elevation/>), encompassing Duke Farms and surrounding areas. Data were in point cloud format, with a sampling density of 5.4 points/m². We used the lidR package (R Core Team 2020, Roussel et al. 2020) to create two raster maps, a digital terrain model (DTM) and a digital surface model (DSM), from the classified lidar data at 1 m resolution. DTMs map the “bare earth” topography of the landscape, free from buildings or vegetation. DSMs map the highest-elevation lidar return, and therefore represent a three-dimensional model of the upper surfaces of vegetation and other features in the landscape (see Fig. 1). We wished to compute the openness index from approximately eye level to match previous work (Keyel et al. 2012). We therefore created a modified DTM by adding 1.61 m (eye level for author MCA) to each cell and then

created a final modified DSM for use in the openness analysis as follows: for each cell, we took the maximum value of corresponding cells in the two input raster maps, the modified DTM and the DSM. This had the effect that all cells with low vegetation (below eye height) in the final raster would be “hovering” at 1.61 m above the ground surface, and all horizon angles would be calculated from this uniform height. Before completing this final step, we first modified the DSM by replacing selected cells with zeros to digitally erase a tree line that was present during lidar data collection but was physically removed in April 2018 before bird sampling began. This had the effect of replacing those cells values with the 1.61 m base height. Finally, we used the same digital erasure technique to produce a second version of the final modified DSM without the high-tension powerlines present on the western edge of Skeet Shoot field. Although we used a base height of 1.61 m, the method can accommodate any base height equal or greater to the tallest herbaceous vegetation in a field.

We used the free program GRASS GIS (r.horizon function; GRASS Development Team 2020) to calculate and map openness based on the two final modified DSM versions, i.e., with and

Fig. 1. Survey points within the study fields Kaufman (left) and Skeet Shoot (right) at Duke Farms, Hillsborough, New Jersey, USA. The base map is a digital surface model showing the surface contours of fields, trees, and other features (visualized with “hill shading”). Colors represent the openness index with darker colors representing a higher maximum angle to the horizon (each cell represents a mean of all openness measurements within 40 m). The powerlines can be seen emerging from the northwest and southwest corners of Skeet Shoot field, and their effect on openness is visible as the darker colors along the western edge of the field. Tree lines in Kaufman field: SW – southwest tree line (shaped like an upside-down L); SE – southeast tree line; N – northern tree line. The inset map shows the project location within New Jersey.



without powerlines. The r.horizon function computes raster maps from a DSM with each 1 m² output cell representing the height in degrees to the highest point on the horizon for a given compass direction. We created 72 such maps, one for each 5-degree compass bearing interval, and used them to compute two versions of the openness index for comparison: the mean or maximum of the 72 horizon angle values for each cell; these are termed “mean-angle” and “maximum-angle” openness, respectively. Following Keyel et al. (2012), we then subtracted all values from 90 so that the final index increased with increasing levels of openness, ranging from 0 (completely closed in) to 90 or greater (completely open). To better match the spatial scale of our bird surveys, we then applied a circular moving average filter to the openness maps so that each cell value in the final maps represented an average of all openness values within a 40 m radius, rather than a single point. Data and code to reproduce these analyses, from raw lidar data through final raster maps, are available via Open Science Framework (<http://doi.org/10.17605/OSF.IO/VG5HU>).

Bird surveys

We created an 80 m x 80 m grid of survey points within each field, retaining 238 points that covered nearly all grassland areas (Fig. 1) and that could be surveyed given available resources. Each point was visited four times in 2018, once each during the periods 1–20 May, 21 May–10 June, 11–30 June, and 1–20 July. During each visit, one of three observers stood at the point for five minutes, counting and recording the distance (calibrated using a laser rangefinder) of all grassland bird individuals detected within 125 m of the point. The observer would then travel to the next point and repeat, performing surveys at ~30 points per morning between 5:30 AM and 10:00 AM EDT. Survey effort at the points was divided among the three observers in a spatially dispersed manner to minimize bias. During each sample period, every other point in the two fields was surveyed by the primary observer (MCA), whereas the remainder of the points were surveyed by one of the two secondary observers (TA or CB). The order of point visits was alternated during each visit. For occupancy analyses, all individuals observed > 40 m from the survey point were discarded, thus preventing overlapping count circles among neighboring points. We did not conduct surveys when wind speeds exceeded three on the Beaufort scale (~5 m/s) or when precipitation was falling.

Occupancy analyses

We fit single season occupancy models in the R package umarked (function occu; Fiske and Chandler 2011) to evaluate how the probability of occupancy within habitat patches (40-m-radius plots) varied with the two versions of the openness index as calculated with and without powerlines. For these models, the detection and non-detection data collected during repeat visits to the survey points served as the response data with which to jointly evaluate detection probability (p), and true patch occupancy rates (ψ), i.e., the estimated true proportion of occupied patches after correction for imperfect detection (Kéry and Royle 2015). We evaluated models in an information theoretic framework based on Akaike Information Criterion for small sample sizes (AICc) and Akaike model weights (w); models within 2 AICc units were regarded as having similar performance (Burnham and Anderson 2002).

Table 1. Model selection results and model parameter estimates for models of Grasshopper Sparrow (*Ammodramus savannarum*) occupancy within small (40-m-radius) plots in two fields at Duke Farms, Hillsborough, New Jersey, USA.

Model [†]	k [‡]	Delta AICc [§]	AICc weight	Occupancy: Intercept (SE)	Occupancy: field slope (SE) [¶]	Occupancy: covariate slope (SE) [#]	Odds ratio (95% CI) [#]
<i>p</i> (obs) ψ (max w. wires)	6	0.00	0.26	-6.64 (1.42)	2.25 (0.47)	0.096 (0.023)	1.10 (1.05-1.15)
<i>p</i> (obs + date) ψ (max w. wires)	7	0.50	0.20	-6.66 (1.42)	2.26 (0.47)	0.096 (0.023)	1.10 (1.05-1.15)
<i>p</i> (obs + time) ψ (max w. wires)	7	1.20	0.14	-6.63 (1.41)	2.24 (0.47)	0.096 (0.023)	1.10 (1.05-1.15)
<i>p</i> (obs + date + time) ψ (max w. wires)	8	1.48	0.12	-6.65 (1.41)	2.26 (0.47)	0.096 (0.023)	1.10 (1.05-1.15)
<i>p</i> (obs) ψ (max wo. wires)	6	2.27	0.08	-8.29 (1.88)	1.89 (0.42)	0.123 (0.031)	1.13 (1.06-1.20)
<i>p</i> (obs + date) ψ (max wo. wires)	7	2.75	0.07	-8.31 (1.88)	1.90 (0.42)	0.124 (0.031)	1.13 (1.06-1.20)
<i>p</i> (obs + time) ψ (max wo. wires)	7	3.46	0.05	-8.28 (1.88)	1.88 (0.42)	0.123 (0.031)	1.13 (1.06-1.20)
<i>p</i> (obs + date + time) ψ (max wo. wires)	8	3.72	0.04	-8.31 (1.88)	1.89 (0.42)	0.124 (0.031)	1.13 (1.07-1.20)
<i>p</i> (obs) ψ (mean w. wires)	6	6.03	0.01	-14.29 (3.89)	2.28 (0.45)	0.202 (0.059)	1.22 (1.09-1.37)
<i>p</i> (obs + date) ψ (mean w. wires)	7	6.63	0.01	-14.24 (3.88)	2.28 (0.45)	0.201 (0.059)	1.22 (1.09-1.37)
<i>p</i> (obs + time) ψ (mean w. wires)	7	7.22	0.01	-14.27 (3.89)	2.27 (0.45)	0.202 (0.059)	1.22 (1.09-1.37)
<i>p</i> (obs + date + time) ψ (mean w. wires)	8	7.60	0.01	-14.20 (3.87)	2.28 (0.45)	0.200 (0.059)	1.22 (1.09-1.37)
<i>p</i> (obs) ψ (mean wo. wires)	6	12.51	0.00	-18.93 (6.27)	1.99 (0.41)	0.272 (0.095)	1.31 (1.09-1.58)
<i>p</i> (obs + date) ψ (mean wo. wires)	7	13.13	0.00	-18.67 (6.21)	2.00 (0.41)	0.268 (0.094)	1.31 (1.09-1.57)
<i>p</i> (obs + time) ψ (mean wo. wires)	7	13.69	0.00	-18.96 (6.27)	1.98 (0.41)	0.272 (0.094)	1.31 (1.09-1.58)
<i>p</i> (obs + date + time) ψ (mean wo. wires)	8	14.12	0.00	-18.90 (6.25)	1.99 (0.41)	0.271 (0.094)	1.31 (1.09-1.58)

[†]Covariates for detection probability (*p*) and occupancy (ψ) sub-models are shown in parentheses. For *p*, obs – observer; date – ordinal date; time – time of day. For ψ , covariates can be interpreted as follows: max – the version of the openness index computed based on the maximum angle to the horizon; mean – the version of the openness index computed based on the mean angle to the horizon; w. wires – openness calculated based on a digital surface model that included the powerlines in Skeet Shoot field; wo. wires – openness calculated based on a digital surface model from which the powerlines were digitally erased from Skeet Shoot field.

[‡]Number of model parameters.

[§]Akaike's Information Criterion adjusted for small sample sizes; difference from the minimum AICc value (742.89).

^{||}Intercept from the occupancy (ψ) sub-model.

[¶]Slope coefficient for field in the occupancy (ψ) sub-model: Skeet Shoot (1) or Kaufman (0).

[#]Slope coefficient and odds ratio are for the occupancy (ψ) sub-model covariate shown in the Model column.

First, we evaluated 18 candidate detection probability models. These contained no covariates for the occupancy sub-model, but included models representing all possible combinations of observer, and linear and quadratic effects of ordinal date and time of day, as covariates for detection probability, as well as a null model with no covariates for *p*. We retained the top four models ($\Delta\text{AICc} < 2$) as base models on which to add the four occupancy sub-model covariates of interest individually to form the final model set. These four occupancy sub-models included the covariates mean-angle and maximum-angle openness, as calculated both with and without powerlines present. Thus, the final model set contained 16 models, or all pairwise combinations of four detection sub-models and four occupancy sub-models (see Table 1 for a list of the models). A binary variable indicating Skeet (1) or Kaufman (0) field was also included in each occupancy sub-model to allow for differences in occupancy levels by field. When evaluating the final model set, we reasoned that (1) if models containing a particular openness covariate consistently perform better based on AICc, it provides evidence that it better correlates with possible cues for openness in the birds; and (2) if models with openness computed with powerlines present consistently perform better than those without, it provides evidence that powerlines are affecting the sparrows' perception of openness.

Finally, for comparison to these angle-to-horizon measures, we separately evaluated a model containing the distance in meters to the nearest forest edge, a commonly used proxy for visual openness in the grassland bird literature (Fletcher and Koford 2003, Keyel et al. 2012, 2013). This variable was measured in a

geographic information system based on aerial photography. The model structure included the top-performing detection sub-model from the final model set, coupled with an occupancy sub-model including site plus the distance-to-edge covariate.

Addressing spatial autocorrelation

Although the 80-m distance between our points allowed full coverage of the fields, it also may have been close enough to result in spatial autocorrelation. High levels of spatial autocorrelation, if present in model residuals, can result in misleadingly small confidence intervals around point estimates such as slopes or model predictions. We tested for spatial autocorrelation in the residuals of the top-performing occupancy model using the correlog function within the ncf package in R (Bjornstad 2020). Finding evidence for spatial autocorrelation at 80-m point spacing (Moran's $I > 0.1$), we then refit the top model as a restricted spatial regression (RSR) occupancy model using the R package ubms (Kellner 2021; see Appendix 1 for further details). These models incorporate a spatial random effect based on a defined threshold distance and constrain this effect to allow unbiased inference on spatially autocorrelated covariates (Johnson et al. 2013). We evaluated 100 m and 150 m thresholds, corresponding to spatial groups including the nearest four or eight neighboring points, respectively (i.e., "rook" or "queen" adjacency). We then evaluated residuals from each model for spatial autocorrelation as above. We retained the RSR occupancy model with a 150 m threshold distance for use in prediction given that we found no evidence of spatial autocorrelation (see Appendix 1). This allowed us to predict the effects of various openness scenarios, with

Table 2. Summary statistics for two methods of calculating angle-to-horizon openness indices at 238 survey points within two fields at Duke Farms, Hillsborough, New Jersey, USA (Kaufman and Skeet Shoot, see Fig. 1).

Openness Metric	Management Scenario [†]	Kaufman		Skeet Shoot	
		Mean Openness (range)	% change from “No Action”	Mean Openness (range)	% change from “No Action”
Maximum-Angle Openness	No action	58.1 (36.2–66.6)	-	55.6 (12.9–66.1)	-
	SW tree line removed	58.6 (36.2–66.6)	0.9	55.6 (12.9–66.1)	-
	SE tree line removed	58.6 (36.2–66.6)	0.9	55.6 (12.9–66.1)	-
	N tree line removed	59.0 (36.4–66.6)	1.5	55.6 (12.9–66.1)	-
	All tree lines removed	60.1 (44.6–66.6)	3.4	55.6 (12.9–66.1)	-
Mean-Angle Openness	Powerlines removed	58.1 (36.2–66.6)	-	59.0 (28.5–66.5)	6.1
	No action	65.8 (53.6–70.9)	-	63.7 (35.7–67.5)	-
	SW tree line removed	66.0 (53.6–70.9)	0.3	63.8 (35.8–67.5)	-
	SE tree line removed	66.0 (53.6–70.9)	0.3	63.8 (35.8–67.5)	-
	N tree line removed	66.2 (57.4–70.9)	0.6	63.7 (35.7–67.5)	-
	All tree lines removed	66.5 (60.4–70.9)	1.1	63.8 (35.8–67.5)	-
	Powerlines removed	65.8 (53.6–70.9)	-	65.4 (51.6–67.6)	2.7

[†]The mean and range of openness values is shown for each of six management scenarios, as represented by surface elevation maps that were digitally edited to remove tree lines (Kaufman only) or powerlines (Skeet Shoot only).

associated uncertainty, while accounting for spatial non-independence among points.

Management scenarios

To evaluate the potential effects of five hypothetical management scenarios on Grasshopper Sparrow populations, we edited the final DSM raster to reflect each scenario and generated openness surfaces as described above. The scenarios included the removal of each of three tree lines within Kaufman field (scenarios 1–3), the removal of all three tree lines within Kaufman (scenario 4), and removal of the powerlines from Skeet Shoot (scenario 5; see Fig. 1). To evaluate the implications of each scenario, we generated predictions of occupancy probability for each 40-m-radius survey plot using the RSR occupancy model (Appendix 1) and the corresponding digitally edited openness map for covariate values. With this information, we estimated the total number of occupied plots within each field as the sum of predicted occupancy probabilities at each point (Kéry and Royle 2015), as well as the percent change in number of occupied plots in each scenario relative to the “no action” scenario.

RESULTS

Openness values across both fields averaged 64.8 (range: 35.7–70.9) at the 238 survey points using the mean-angle method and 56.9 using the maximum-angle method (range: 12.9–66.6). Mean openness was roughly similar in both fields, whereas Skeet Shoot had a wider range of values (Table 2). Digitally removing the powerlines increased average openness within Skeet Shoot field, the only field with powerlines, by 2.7–6.1%, whereas removing tree lines increased openness of Kaufman field, the only field with tree lines, by 1.1–3.4% (Table 2). Grasshopper Sparrows were detected at least once in 25 of 119 plots in Kaufman field, compared with 68 of 119 plots in Skeet Shoot.

The top-performing occupancy model contained an observer covariate in the detection sub-model, and the maximum-angle openness covariate (i.e., computed based on the maximum angle to the horizon) in the occupancy sub-model (Table 1). Occupancy

models that contained maximum-angle openness as a covariate performed substantially better than those based on mean-angle openness (sum of model weights = 0.96 vs. 0.04, respectively; Table 1). Parameter estimates for the relationship between occupancy and maximum-angle openness were very similar among the top four models, which were all within $2 \Delta AICc$ (all $\beta = 0.096$, 95% CI = 0.05, 0.14; Table 1). Among the maximum-angle openness models, those based on openness maps containing powerlines (i.e., the top four models in Table 1) performed substantially better than those without powerlines (sum of model weights = 0.76 vs. 0.24, respectively, when only the eight maximum-angle openness models are considered). Occupancy was also positively related to minimum distance to forest edge ($\beta = 0.0137$, 95% CI = 0.0058, 0.0217), but the model performed poorly when compared with maximum-angle openness models ($\Delta AICc = 3.3$, model weight = 0.05 when ranked with the model set in Table 1).

Refitting the top-performing model using restricted spatial regression yielded a slightly steeper slope for the openness–occupancy relationship ($\beta = 0.134$) with a wider 95% CI (0.070, 0.212; Table 3, Fig. 2). This slope indicates that the odds a habitat patch is occupied increases by 14% for each unit increase in the maximum-angle openness index (odds ratio = 1.14, 95% CI: 1.07, 1.24), and doubles with every 5 unit increase (i.e., using the equation $\text{fold increase} = e^{(\beta \times \text{openness})}$). Detection probability based on this model ranged from 25% (95% CI = 14%, 40%) to 33% (24%, 44%) depending on the observer (Table 3).

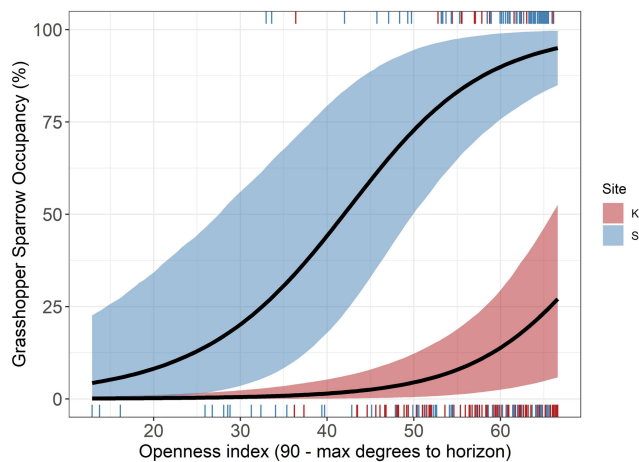
The three management scenarios involving digital removal of the southwestern, southeastern, and northern tree lines within Kaufman field resulted in predicted increases in patch occupancy of 5.0% (95% CI = 2.9%, 7.1%), 3.9% (2.5%, 5.3%), and 6.0% (4.1%, 7.3%), respectively (Fig. 3). When all tree lines were removed, there was a predicted increase of 15.1% (9.6%, 20.4%). When the powerlines within Skeet Shoot field were digitally removed, there was a predicted increase of 9.0% (95% CI = 4.6%, 11.0%).

Table 3. Parameter estimates and associated uncertainty for a restricted spatial regression (RSR) model (threshold = 150 m; see Appendix 1) describing Grasshopper Sparrow (*Ammodramus savannarum*) detection and occupancy probability at Duke Farms, Hillsborough, New Jersey, USA.

	Parameter [†]	Estimate (logit scale)	95% Credible Intervals
Occupancy sub-model	Intercept	-9.997	-15.145, -6.008
	Site	4.384	2.479, 7.323
	Max-angle Openness	0.134	0.070, 0.212
	RSR [tau]	0.017	0.003, 0.053
Detection sub-model	Intercept	-1.113	-1.789, -0.441
	Observer2	0.403	-0.310, 1.118
	Observer3	0.409	-0.386, 1.215

[†] Site was a binary variable representing Kaufman (0) and Skeet Shoot (1) fields; max-angle openness is the lidar-based openness index based on maximum angle to the horizon; RSR [tau] is a precision term for the spatial random effect with smaller values representing greater variability.

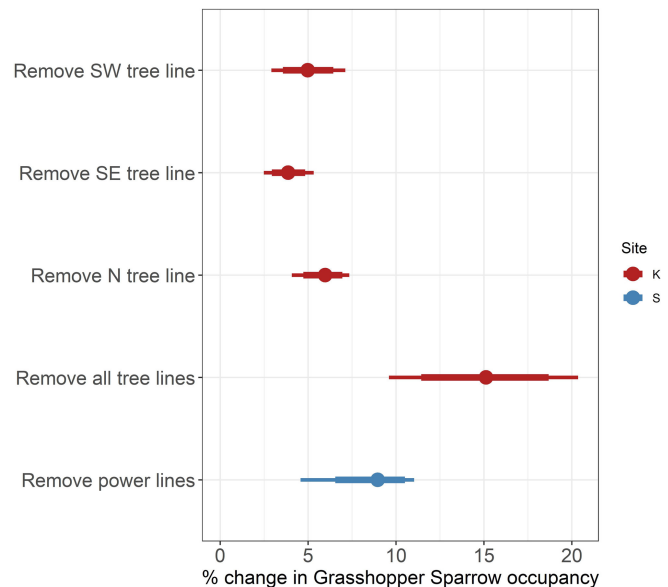
Fig. 2. Probability of Grasshopper Sparrow (*Ammodramus savannarum*) patch occupancy (40-m circular plots) versus the maximum-angle openness index in two fields (K – Kaufman; S – Skeet Shoot) at Duke Farms, Hillsborough, New Jersey, USA. Detection and non-detection data by survey point are shown at the top and bottom plot margins, respectively. Predicted occupancy (lines) and 95% credible intervals (shading) are based on the fixed effects from a restricted spatial regression occupancy model described in the Methods and in Appendix 1.



DISCUSSION

Visual openness can be a powerful predictor of the behavior and ecology of fauna that use open habitats (Renfrew et al. 2005, Attum 2007, Marshall et al. 2020). As a result, accurate and low-cost measurements of this attribute have great potential to inform management and conservation decisions. Our work introduces an index based on a remotely sensed angle to the horizon, permitting the mapping and quantification of openness across potentially large spatial scales, yet also at a fine enough spatial resolution to adequately predict patch-level occupancy patterns. With this approach, we extend the potential of similar indices (Keyel et al. 2012, 2013, Marshall et al. 2020) that would require labor-intensive fieldwork, including travel and many manual clinometer

Fig. 3. Predicted percent change in patch occupancy of Grasshopper Sparrows (*Ammodramus savannarum*) under five openness management scenarios within two fields (K – Kaufman; S – Skeet Shoot) at Duke Farms, Hillsborough, New Jersey, USA. Tree lines only occurred in Kaufman, while powerlines only occurred in Skeet Shoot (see Fig. 1 for tree and powerline locations). Thicker and thinner portions of the error bars represent 80% and 95% credible intervals, respectively, based on a restricted spatial regression occupancy model described in the Methods and in Appendix 1.



readings, to achieve similar results. We compared two versions of our index (mean-angle and maximum-angle) by evaluating their predictive performance for the within-field distribution of a grassland bird, the Grasshopper Sparrow. We then demonstrated how such models can be coupled with digitally edited openness maps to predict responses to plausible management scenarios.

The distinctive ecological attributes of open habitats have led to evolutionary specialization in animals in the form of anti-predator and courtship behaviors (Gerard and Loisel 1995, Muir and Colwell 2010), morphology and physiology (Goodman 2009),

and habitat selection at a range of spatial scales (Burger 1977, van der Vliet et al. 2008). A preference for visually open locations, or, conversely, the avoidance of visual obstructions, has been documented in diverse vertebrate taxa and is thought to be adaptive in each case on account of the association of such visual obstructions with perches or other cover for predators (Attum 2007, Goodman 2009, Keyel et al. 2012). In birds, various measures of visual openness have been shown to correlate with territory placement, though not with reproductive success, in numerous species in North America and Europe (Fletcher and Koford 2003, van der Vliet et al. 2008, Keyel et al. 2013, Marshall et al. 2020). However, correlation is not necessarily causation, and other mechanisms besides active avoidance of visual obstructions have been suggested as potentially confounding (or synergistic) drivers of local distribution in these grassland species. These drivers may include differing vegetation characteristics (Renfrew et al. 2005), avoidance of roads and other non-grassland ecotones (e.g., croplands; Fletcher and Koford 2003, Renfrew et al. 2005), locations of active predator territories (van der Vliet et al. 2008), or longer-term processes such as lower survival or reproduction in less-open areas.

Our results revealed an association between visual openness and Grasshopper Sparrow occupancy, but, like other studies, our findings are correlational. Confidently establishing causation, and indeed disentangling the effects of multiple correlated predictors, may ultimately require a controlled, experimental approach. Thus, the occupancy–openness relationship we observed, and especially the predicted changes under various management scenarios, may be better viewed as testable hypotheses than as ecological certainty. However, in smaller scale management situations such as our study site (Duke Farms) or similar wildlife refuges, this is likely to be the best source of evidence available. At such scales, this information can form the start of the cycle of adaptive management: planning, performing management actions, measuring impacts, adjusting the plan, and repeating (Moir and Block 2001). Given the relative ease with which our openness index can be calculated, we envision it facilitating an expansion of such evidence-generating processes for a variety of open-dwelling species and ecosystems, in varied forms ranging from controlled experiments to broader-scale observational studies to smaller-scale adaptive management efforts.

Although we evaluated our lidar-based openness index for a single species at a high-resolution spatial scale, it is illuminating to consider its potential broader utility in other contexts. One potential conservation issue to which it may be applied is the rapid expansion of wind energy on grassland birds in the Great Plains in North America and in other visually open biomes globally. Wind turbines and associated infrastructure have been shown to displace, i.e., reduce abundance or occurrence, at least eight grassland bird species, extending to distances of 100 m and beyond (Pruett et al. 2009, Shaffer and Buhl 2016). Displacement has thus far been evaluated using distance-based metrics. However, indices based on angle to the horizon (e.g., Keyel et al. 2012; this study) may be more appropriate because they are sensitive to the height of visual obstructions. For example, two turbines of different heights, both at 100 m away, would have differing effects on angle-based openness measures, but not on distance-based measures. Modeling the relationship between

openness and abundance or occupancy via field studies at wind farms with various turbine heights could allow predictive modeling of the potential effects on grassland birds where wind turbines are being considered for erection. Thus, a mapped openness index, edited to reflect proposed scenarios, can contribute to ongoing efforts to optimally site wind turbines to avoid biodiversity and conservation conflicts or to offset such effects (Fargione et al. 2012, Shaffer et al. 2019).

Our index could also prove useful for assessing the impacts of other, more common, visual obstructions within grasslands, including woody vegetation and built infrastructure such as the powerlines evaluated in our study. Disruption of fire and grazing patterns, and the subsequent encroachment of small trees and shrubs, has become a key conservation issue for birds and other inhabitants of North American grassland ecosystems, from the Northern Great Plains (e.g., cedar; Fuhlendorf et al. 2017, Symstad and Leis 2017) to the semiarid grasslands of the southwest (e.g., mesquite; Andersen and Steidl 2019). Smaller, cultural grasslands of Europe and in eastern North America, such as our study fields, are also subject to grassland bird population limitation by reduced openness, including by tree lines (O’Leary and Nyberg 2000, Besnard and Secondi 2014) and ecological succession (Lautenbach et al. 2020). Powerlines and other human-built visual obstructions can similarly result in population reductions in grassland birds due to habitat avoidance (van der Vliet et al. 2008, Pruett et al. 2009), and knowledge of their potential impacts can therefore inform siting decisions. Our case study illustrates the potential of mapping and modeling openness to provide quantitative information in support of restoration and development decisions on a local scale. For example, increasing visual openness by removing the three internal tree lines within Kaufman field was predicted to increase the area occupied by Grasshopper Sparrows by 15%. Similarly, an increase of 9% was predicted from the removal of powerlines within Skeet Shoot field. Such increases are not guaranteed on account of the lack of certainty regarding causality, but they represent clear testable hypotheses with great power to inform adaptive management efforts.

Expanding predictive modeling of species occurrence or abundance to larger spatial extents is also possible by using mapped openness as a covariate in regional-scale species distribution models (Guisan et al. 2013). The extent to which openness measures based on digital surface elevation data can improve existing species distribution models for grassland birds (e.g., Thogmartin et al. 2006) is an open research question that will determine its utility for large-scale conservation planning efforts such as gap analyses. Scaling up our technique of digitally editing openness maps may also prove useful. For Grasshopper Sparrows, we used this digital editing technique to reflect hypothetical management scenarios and to predict their effects on occupancy at the field level. Coupling similarly edited openness maps at a much larger spatial scale with species distribution models could be used to predict the outcomes of landscape-level initiatives to increase openness. For example, such efforts could aid planning of landscape-scale prescribed fire initiatives in prairie (Fuhlendorf et al. 2017, Andersen and Steidl 2019) or emergent tidal marsh ecosystems (Kern and Shriver 2014, Marshall et al. 2020, Skipwith 2020) where a lack of openness has been shown to negatively correlate with bird populations.

Data availability may pose the greatest potential barrier to the widespread adoption of our lidar-based openness index in the near term, specifically, spatial gaps in coverage and lack of consistency in spatial resolution. However, in the United States, spatial coverage of lidar point cloud data has increased rapidly in recent decades and it is now available for a majority of eastern and midwestern states, including much of the prairie, as well as complete coverage of coastal areas (<http://www.nationalmap.gov>, <http://www.coast.noaa.gov/inventory>). Although these data were primarily collected for other purposes, including elevation mapping and disaster planning, they have found diverse ecological applications in both open and forested habitats (Davies and Asner 2014, Correll et al. 2019). The increasing spatial coverage of lidar data in North America may someday approach that of some European countries, such as Switzerland, that already have nationwide lidar data available at a uniform spatial resolution (Wüest et al. 2020).

The temporal resolution of surface elevation data is an equally important consideration contributing to its usefulness in the measurement and mapping of openness. In our case study, lidar data were available from the exact year of our field effort (2018), but even still, our digital surface model required minor editing (the removal of one tree line) to match on-the-ground conditions. In our case, only one additional lidar data set was available, from 2008, and it produced a roughly similar digital surface model to that produced from the 2018 data with only minimal editing (M. C. Allen, *unpublished data*). Ultimately, the validity of using temporally mismatched lidar and field data to model openness effects will depend on the degree of change in the intervening period, which could be assessed by inspecting aerial photography or conducting field visits. It is also possible to address temporal gaps by collecting custom lidar or photogrammetric surface elevation data with unmanned aircraft systems (Correll et al. 2019, Iglhaut et al. 2019, Bankert et al. 2021). Finally, contemporaneous surface elevation and field population data likely already exist in many locations and could be retrospectively analyzed to study population responses to openness. Notably, the Konza Prairie Long Term Ecological Research site, as part of the National Ecological Observatory Network (NEON), performs regular grassland bird population monitoring and has at least four consecutive years of lidar data available (<http://www.neonscience.org/data>). With more applications for lidar and other forms of surface elevation data being developed every year (ecological and otherwise; Davies and Asner 2014, Iglhaut et al. 2019), the temporal resolution of data collection seems likely to increase in parallel with ongoing increases in spatial extent.

Our index, and the demonstration of its potential uses, fits within the broader category of ecological scenario evaluation and prediction, a key step in the process of assessing alternative courses of action in support of biodiversity and ecosystem targets (Guisan et al. 2013, Nicholson et al. 2019). Lidar and photogrammetric surface elevation data are already being used to support distribution modeling of plant species (Wüest et al. 2020) and for modeling relationships between animal habitat use and forest structure (Davies and Asner 2014, Iglhaut et al. 2019). Extending this to grassland fauna with respect to well-studied behavioral preferences for openness introduces new research possibilities. For example, the index could also easily be applied to other open habitats, such as savannah, tundra, mudflat, open ocean, or arid lands, where the role of openness in animal habitat

selection and conservation has been less fully explored than in temperate grasslands or marshes (Keyel et al. 2013, Marshall et al. 2020). Although challenges associated with data availability will impede its use in some locations, we expect this limitation to diminish over time. Ultimately, a remotely sensed tool that allows ready measurement of openness at a variety of spatial scales represents an advance that permits the asking of new questions for fauna of open habitats, ranging from the behavior of individuals to the ecology and conservation of populations.

Responses to this article can be read online at:
<https://www.ace-eco.org/issues/responses.php/2078>

Author Contributions:

MCA, TA, and CB performed data acquisition and curation; MCA performed data analysis and wrote the original draft; all authors contributed substantively to reviewing and editing the final manuscript.

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LITERATURE CITED

- Almendinger, T., M. Van Clef, J. F. Kelly, M. C. Allen, and C. Barreca. 2020. Restoring forests in central New Jersey through effective deer management. *Ecological Restoration* 38 (4):246-256. <https://doi.org/10.3368/er.38.4.246>
- Andersen, E. M., and R. J. Steidl. 2019. Woody plant encroachment restructures bird communities in semiarid grasslands. *Biological Conservation* 240:108276. <https://doi.org/10.1016/j.biocon.2019.108276>
- Attum, O. 2007. Can landscape use be among the factors that potentially make some ungulates species more difficult to conserve? *Journal of Arid Environments* 69(3):410-419. <https://doi.org/10.1016/j.jaridenv.2006.10.013>
- Bankert, A. R., E. H. Strasser, C. G. Burch, and M. D. Correll. 2021. An open-source approach to characterizing Chihuahuan Desert vegetation communities using object-based image analysis. *Journal of Arid Environments* 188:104383. <https://doi.org/10.1016/j.jaridenv.2020.104383>
- Besnard, A. G., and J. Secondi. 2014. Hedgerows diminish the value of meadows for grassland birds: potential conflicts for agri-environment schemes. *Agriculture, Ecosystems & Environment* 189:21-27. <https://doi.org/10.1016/j.agee.2014.03.014>
- Bjornstad, O. N. 2020. ncf: Spatial covariance functions. R package version 1.2-9. [online] URL: <https://CRAN.R-project.org/package=ncf>
- Burger, J. 1977. Role of visibility in nesting behavior of Larus gulls. *Journal of Comparative and Physiological Psychology* 91 (6):1347-1358. <https://doi.org/10.1037/h0077405>

- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Correll, M. D., C. S. Elphick, W. Hantson, B. B. Cline, E. L. Tymkiw, W. G. Shriver, and B. J. Olsen. 2019. A multi-scale comparison of elevation measurement methods in northeastern tidal marshes of the United States. *Wetlands* 39:633-643. <https://doi.org/10.1007/s13157-018-1110-x>
- Davies, A. B., and G. P. Asner. 2014. Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology & Evolution* 29(12):681-691. <https://doi.org/10.1016/j.tree.2014.10.005>
- Fargione, J., J. Kiesecker, M. J. Slaats, and S. Olm. 2012. Wind and wildlife in the Northern Great Plains: identifying low-impact areas for wind development. *PLoS One* 7(7):e41468. <https://doi.org/10.1371/journal.pone.0041468>
- Fiske, I., and R. Chandler. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43(10):1-23. <https://doi.org/10.18637/jss.v043.i10>
- Fletcher Jr, R. J., and R. R. Koford. 2003. Spatial responses of bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. *Auk* 120(3):799-810. <https://doi.org/10.1093/auk/120.3.799>
- Fuhlendorf, S. D., T. J. Hovick, R. D. Elmore, A. M. Tanner, D. M. Engle, and C. A. Davis. 2017. A hierarchical perspective to woody plant encroachment for conservation of Prairie-Chickens. *Rangeland Ecology and Management* 70(1):9-14. <https://doi.org/10.1016/j.rama.2016.08.010>
- Gerard, J., and P. Loisel. 1995. Spontaneous emergence of a relationship between habitat openness and mean group size and its possible evolutionary consequences in large herbivores. *Journal of Theoretical Biology* 176(4):511-522. <https://doi.org/10.1006/jtbi.1995.0217>
- Goodman, B. A. 2009. Nowhere to run: the role of habitat openness and refuge use in defining patterns of morphological and performance evolution in tropical lizards. *Journal of Evolutionary Biology* 22(7):1535-1544. <https://doi.org/10.1111/j.1420-9101.2009.01766.x>
- GRASS Development Team. 2020. Geographic Resources Analysis Support System (GRASS) Software. Version 7.8. Open Source Geospatial Foundation. [online] URL: <http://grass.osgeo.org>
- Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. Tulloch, T. J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, T. G. Martin, J. R. Rhodes, R. Maggini, S. A. Setterfield, J. Elith, M. W. Schwartz, B. A. Wintle, O. Broennimann, M. Austin, S. Ferrier, M. R. Kearney, H. P. Possingham, and Y. M. Buckley. 2013. Predicting species distributions for conservation decisions. *Ecology Letters* 16(12):1424-1435. <https://doi.org/10.1111/ele.12189>
- Iglhaut, J., C. Cabo, S. Puliti, L. Piermattei, J. O'Connor, and J. Rosette. 2019. Structure from motion photogrammetry in forestry: a review. *Current Forestry Reports* 5(3):155-168. <https://doi.org/10.1007/s40725-019-00094-3>
- Johnson, D. S., P. B. Conn, M. B. Hooten, J. C. Ray, and B. A. Pond. 2013. Spatial occupancy models for large data sets. *Ecology* 94:801-808. <https://doi.org/10.1890/12-0564.1>
- Kellner, K. 2021. ubms: Unmarked Bayesian models with Stan. R package version 1.0.2.9007. [online] URL: <https://kenkellner.com/ubms/>
- Kern, R. A., and W. G. Shriver. 2014. Sea level rise and prescribed fire management: implications for seaside Sparrow population viability. *Biological Conservation* 173:24-31. <https://doi.org/10.1016/j.biocon.2014.03.007>
- Kéry, M., and J. A. Royle. 2015. Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS. Volume 1: prelude and static models. Academic, London, UK.
- Keyel, A. C., C. M. Bauer, C. R. Lattin, L. M. Romero, and J. M. Reed. 2012. Testing the role of patch openness as a causal mechanism for apparent area sensitivity in a grassland specialist. *Oecologia* 169:407-418. <https://doi.org/10.1007/s00442-011-2213-8>
- Keyel, A. C., A. M. Strong, N. G. Perlut, and J. M. Reed. 2013. Evaluating the roles of visual openness and edge effects on nest-site selection and reproductive success in grassland birds. *Auk* 130(1):161-170. <https://doi.org/10.1525/auk.2012.12039>
- Lautenbach, J. M., N. Stricker, M. Ervin, A. Hershner, R. Harris, and C. Smith. 2020. Woody vegetation removal benefits grassland birds on reclaimed surface mines. *Journal of Fish and Wildlife Management* 11(1):89-98. <https://doi.org/10.3996/062019-JFWM-053>
- Marshall, H., E. J. Blomberg, V. Watson, M. Conway, J. B. Cohen, M. D. Correll, C. S. Elphick, T. P. Hodgman, A. R. Kocek, A. I. Kovach, W. G. Shriver, W. A. Wiest, and B. J. Olsen. 2020. Habitat openness and edge avoidance predict Saltmarsh Sparrow abundance better than habitat area. *Condor* 122(3):duaa019. <https://doi.org/10.1093/condor/duaa019>
- Moir, W. H., and W. M. Block. 2001. Adaptive management on public lands in the United States: commitment or rhetoric? *Environmental Management* 28:141-148. <https://doi.org/10.1007/s002670010213>
- Muir, J. J., and M. A. Colwell. 2010. Snowy Plovers select open habitats for courtship scrapes and nests. *Condor* 112(3):507-510. <https://doi.org/10.1525/cond.2010.090196>
- Nicholson, E., E. A. Fulton, T. M. Brooks, R. Blanchard, P. Leadley, J. P. Metzger, K. Mokany, S. Stevenson, B. A. Wintle, S. N. C. Woolley, M. Barnes, J. E. M. Watson, and S. Ferrier. 2019. Scenarios and models to support global conservation targets. *Trends in Ecology and Evolution* 34(1):57-68. <https://doi.org/10.1016/j.tree.2018.10.006>
- O'Leary, C. H., and D. W. Nyberg. 2000. Treelines between fields reduce the density of grassland birds. *Natural Areas Journal* 20(3):243-249. [online] URL: <https://www.researchgate.net/publication/288358147>
- Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009. Avoidance behavior by Prairie Grouse: implications for development of wind energy. *Conservation Biology* 23(5):1253-1259. <https://doi.org/10.1111/j.1523-1739.2009.01254.x>

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [online] URL: <https://www.r-project.org/>

Renfrew, R. B., and C. A. Ribic. 2002. Influence of topography on density of grassland passerines in pastures. *American Midland Naturalist* 147(2):315-325. [https://doi.org/10.1674/0003-0031\(2002\)147\[0315:IOTODO\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2002)147[0315:IOTODO]2.0.CO;2)

Renfrew, R. B., C. A. Ribic, and J. L. Nack. 2005. Edge avoidance by nesting grassland birds: a futile strategy in a fragmented landscape. *Auk* 122(2):618-636. <https://doi.org/10.1093/auk/122.2.618>

Roussel, J. R., D. Auty, N. C. Coops, P. Tompalski, T. R. Goodbody, A. S. Meador, J. Bourdon, and A. Achim. 2020. lidR: An R package for analysis of Airborne Laser Scanning (ALS) data. *Remote Sensing of Environment* 251:112061. <https://doi.org/10.1016/j.rse.2020.112061>

Shaffer, J. A., and D. A. Buhl. 2016. Effects of wind-energy facilities on breeding grassland bird distributions. *Conservation Biology* 30:59-71. <https://doi.org/10.1111/cobi.12569>

Shaffer, J. A., C. R. Loesch, and D. A. Buhl. 2019. Estimating offsets for avian displacement effects of anthropogenic impacts. *Ecological Applications* 29(8):e01983. <https://doi.org/10.1002/eap.1983>

Symstad, A. J., and S. A. Leis. 2017. Woody encroachment in northern great plains grasslands: perceptions, actions, and needs. *Natural Areas Journal* 37(1):118-127. <https://doi.org/10.3375/043.037.0114>

Skipwith, A. 2020. Endangered and threatened wildlife and plants: threatened species status for eastern Black Rail with a section 4(d) rule. Federal Register 85:63764-63803. Fish and Wildlife Service, Charleston, South Carolina, USA. [online] URL: <https://www.federalregister.gov/documents/2020/10/08/2020-19661/endangered-and-threatened-wildlife-and-plants-threatened-species-status-for-eastern-black-rail-with>

Thogmartin, W. E., M. G. Knutson, and J. R. Sauer. 2006. Predicting regional abundance of rare grassland birds with a hierarchical spatial count model. *Condor* 108(1):25-46. <https://doi.org/10.1093/condor/108.1.25>

van der Vliet, R. E., E. Schuller, and M. J. Wassen. 2008. Avian predators in a meadow landscape: consequences of their occurrence for breeding open-area birds. *Journal of Avian Biology* 39(5):523-529. <https://doi.org/10.1111/j.0908-8857.2008.04310.x>

Wüest, R. O., A. Bergamini, K. Bollmann, and A. Baltensweiler. 2020. LiDAR data as a proxy for light availability improve distribution modelling of woody species. *Forest Ecology and Management* 456:117644. <https://doi.org/10.1016/j.foreco.2019.117644>



APPENDIX 1. Plot of spatial autocorrelation (Moran's I) in residuals of the top-performing occupancy model (Table 1). The model was fit using the R package *ubms* (Kellner 2021) with no spatial component (top graph); with restricted spatial regression (RSR; Johnson et al. 2013) and a 100 m threshold (middle graph); and with RSR and a 150 m threshold (bottom graph). Covariates for the occupancy sub-model included site and maximum-angle openness, while covariates for the detection sub-model included only observer. Models were run with 3 chains of 7500 warmup and sampling iterations each. Model convergence was assessed based on the Gelman-Rubin statistic ($R_{hat} < 1.1$). Points in the figures show Moran's I calculated for model residuals among points within 100 m distance bins. Numbers below the points show the sample sizes of point pairs. All distance bins of the 150-m-threshold model had Moran's I values of < 0.1 with $P > 0.05$. The top two graphs show evidence of spatial autocorrelation among points, including a pattern of high (> 0.1) Moran's I values among nearby points, and decreasing values with increasing lag distances.

