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Management of U.S. Agricultural Lands Differentially Affects Avian Habitat Connectivity

Justin P. Suraci, Tina G. Mozelewski, Caitlin E. Littlefield, Theresa Nogeire McRae, Ann Sorensen and Brett G. Dickson

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nuanced parameterization of agricultural lands based on field data for the target species, the results, and hence the management implications, can change [10].

Avian species range considerably in their capacity to use the agricultural landscape as primary or movement habitat. Agricultural intensification across North America has been a major driver of declines in farmland-associated bird species since the middle of the last century [3]. However, recent studies have noted the potential for supporting avian biodiversity on agricultural lands through wildlife-friendly farming practices and the promotion of functional connectivity across agricultural and mixed-use landscapes [11–13]. Identifying opportunities to support bird species habitat use and connectivity on agricultural lands is therefore an important conservation objective. Here, we examine the effects of agriculture on habitat suitability (as estimated by species encounter rates) and functional connectivity for three avian focal species that exemplify the complex effects of agriculture on species habitat use, movements, and populations: the Greater Sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse), the American Black Duck (*Anas rubripes*; hereafter, black duck), and the Bobolink (*Dolichonyx oryzivorus*).

These three focal species were selected due to their management relevance (all three are experiencing range contraction and/or population declines, see below) as well as to capture the diversity of agriculture-avian species interactions, which range from an avoidance of agricultural lands through occasional use to specialization during particular life history stages. The sage-grouse is experiencing ongoing loss of habitat due to the conversion of their required sagebrush (*Artemisia* spp.) habitat to agricultural and other land uses, habitat degradation from intensive grazing [14], and the spread of invasive annual grasses and conifer encroachment on western rangelands, which perpetuate rapid fire cycles and lead to the loss of sagebrush cover [15]. Despite grazing impacts, rangelands across the sage-grouse's extant range are thought to provide important movement habitat and are typically less strongly avoided than cultivated croplands [16]. The black duck, once the most common waterfowl species in Eastern North America, has experienced substantial declines since the mid-20th century [17]. The conversion of wetland habitat to agricultural and urban uses has been a major driver of declines for this and many wetland-dependent species [18]. However, in recent years, emerging evidence has shown that agricultural lands may provide important wintering and/or nesting habitat for black duck populations, with food availability in agricultural fields partially compensating for the loss of preferred wetland foraging habitat [17,19,20]. The Bobolink historically nested in native grasslands in the Northern U.S. and Southern Canada [21]. Bobolinks have also experienced substantial population declines (>70% decline since 1968) linked to agricultural intensification [3]. With the loss of native grasslands in North America, the majority of Bobolink breeding now occurs in pastures and grain fields [21], and major ongoing threats to Bobolink populations are linked to the intensity of agricultural management in these systems, i.e., the frequency and intensity of cutting, harvesting, and grazing [22].

The three focal species differ substantially in their life history and movement characteristics, and thus in their use of agricultural and other modified landscapes for connectivity. The sage-grouse is the least vagile of the three species, consisting of a mixture of resident and migrant populations that move relatively short distances (up to ~120 km) [16,23]. The relatively limited movement of sage-grouse, combined with the isolation of remnant habitat patches, has resulted in restricted gene flow between populations [14,24], which highlights the importance of maintaining and restoring connectivity across the sage-grouse range. For the present analysis, we examined sage-grouse habitat suitability and connectivity across the species' range during all seasons to quantify agricultural impacts on movements associated with migration as well as natal and breeding dispersal. The black duck exhibits intermediate movement capacity, with most populations undertaking seasonal migrations between the Southeastern U.S. and the Northeastern U.S. and Canada, with up to five stopovers during the migration [25,26]. Here, we examined the effects of agricultural land use on the suitability of and connectivity between potential black duck stopover sites during spring and fall migration, focusing our analyses on movements occurring between

migration start and end dates. The most vagile focal species is the Bobolink, a neotropical migrant that transits between breeding grounds in North America and wintering grounds in Central and South America, a migration that includes trans-oceanic non-stop flights of up to 3500 km [27]. Given their capacity for long-range movements, Bobolink migratory connectivity may be only minimally impacted by localized human land uses (e.g., agriculture). Bobolinks show high breeding site fidelity when returning from wintering grounds, but adults and especially fledglings may make exploratory movements within a breeding season to assess potential new breeding sites for the subsequent year. These within-breeding season movements—either natal dispersal outside a parent's territory or dispersal by breeding adults after a failed nesting attempt—are likely to be substantially shaped by local/regional landscape characteristics and, in particular, the intensity of agricultural management [4,28]. We therefore focused our Bobolink analysis on the effects of agricultural land uses on breeding season habitat suitability and connectivity during these exploratory movements.

For each focal species, we conducted U.S. range-wide analyses of both habitat suitability and connectivity. More so than our other focal species, the sage-grouse has been the subject of extensive conservation-focused research, including recent connectivity studies to inform sage-grouse management [29,30]. Here, we expand on this body of work by explicitly focusing on the effects of agricultural management on sage-grouse habitat and connectivity. To place our findings in the broader context of sage-grouse management-focused analyses, we quantitatively compare our connectivity results to those of existing models and discuss the complementarity of results across studies. For all focal species, we discuss the implications of our models for species habitat management in agricultural landscapes.

2. Methods

For each focal species, our basic workflow involved using detection data from eBird, the Cornell Lab of Ornithology's community science platform [31,32], to model habitat suitability via random forest models and then using the resulting habitat suitability surface as input to a circuit theory-based connectivity model. This workflow is outlined in Figure 1 and described in detail below.
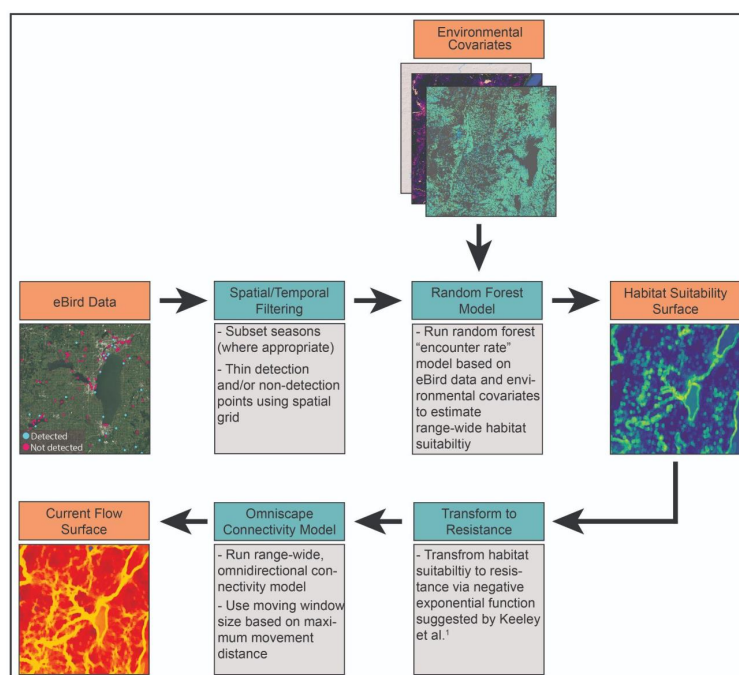

Figure 1. Analysis workflow, applied to each of the three focal species (Greater Sage-Grouse, American Black Duck, and Bobolink). Orange boxes denote data inputs and/or outputs. Blue boxes denote data processing or modeling steps. [1] Keeley et al. [33].

2.1. Focal Species Data

We obtained eBird data for each of our three focal species. eBird data were organized into "checklists," semi-structured surveys in which the observer records the observed species as well as variables associated with observation effort (e.g., distance traveled, number of observers). Datasets made available for use in research are subject to a rigorous pre-screening procedure (e.g., to remove false positives) and can be filtered to only include "complete" checklists, i.e., those in which the observer self-reports as having recorded all bird species detected [32]. By using only complete checklists, eBird data provide information on both the detections and non-detections of focal species, as non-detections are inferred from complete checklists in which the focal species is not observed [32]. Here, we used data from the November 2021 release of the eBird basic dataset (EBD), available at www.ebird.org/science/download-ebird-data-products (accessed on 5 January 2022). Following Strimas-Mackey et al. [34], we filtered the EBD to only include complete checklists and we reduced variation in sampling effort by only retaining checklists with $\leq$ ten observers, duration of $\leq$ 5 h, and a total travel distance of $\leq$ 5 km. We then created focal species datasets from the filtered EBD by retaining all checklists (both detections and non-detections) within each species' geographic range. We used range maps from the International Union for the Conservation of Nature (IUCN) for each of the three focal species [35–37], clipped to the borders of the conterminous U.S. Finally, we truncated each species-level dataset to only include data collected between 2014 and 2018 in an effort to align detection data with the year of our agricultural and other human land use intensity covariates (2016, see below). As noted above, for the sage-grouse, we modeled habitat suitability and connectivity across all seasons, and therefore retained all checklists between 2014 and 2018. Our black duck models focused on connectivity between stopover sites during annual migration. We therefore truncated our black duck dataset to include only detections and non-detections occurring between the minimum start date and maximum end date for both spring and fall migration (spring migration: 18 April to 28 June; fall migration: 5 October to 18 December [25]). To examine within-breeding season connectivity for Bobolink, we truncated our Bobolink dataset to only those checklists occurring between the beginning and end of the breeding season (1 May to 14 September [22,27]).

Community science data are known to be subject to several challenges, including spatial and temporal bias (e.g., tendencies for community members to conduct sampling close to home and/or only in favorable seasons [31,38,39]) and class imbalance (a tendency for non-detections to substantially outnumber detections, particularly for rare species [40]). To deal with these potential issues, we conducted spatial or spatiotemporal subsampling for each focal species [32,34]. Of the three focal species, sage-grouse had the most limited geographic range, as well as the smallest total number of checklists and the lowest percentage of detections relative to non-detections (0.3% of 321,034 checklists). Given the relatively limited amount of available information on where sage-grouses are present, we followed guidance in Robinson et al.'s work [40], retaining all checklists in which sage-grouse were detected and spatially subsampling non-detection checklists by randomly selecting a single non-detection checklist within each cell of a 10 × 10 km grid overlaid across the sage-grouse's geographic range. This resulted in a total of 1277 detection and 2782 non-detection checklists (nominal 31.5% detection rate). Both black duck and Bobolink have much larger geographic ranges and a substantially larger number of eBird checklists. We therefore performed spatiotemporal subsampling of all checklists for each species, randomly selecting one detection and one non-detection checklist for each year of the study (2014 to 2018) within each cell of a 20 × 20 km grid overlaid across each species' geographic range (note the larger grid cell size relative to sage-grouse to accommodate the much larger geographic ranges of black duck and Bobolink). This resulted in 7140 detection and 38,514 non-detection checklists for black duck (18.5% detection rate) and 11,335 detection and 46,663 non-detection checklists for Bobolink (24.3% detection rate). We prepared eBird datasets using the *auk* package [41] in R [42].

2.2. Model Covariates

For each focal species, we modeled habitat suitability as a function of several environmental and climatic covariates described in detail below (see also Table 1). Following the best practices for research with eBird data, we quantified all covariates within a 2.5 km radius of each checklist location, corresponding to the spatial precision of the species detection data (maximum travel distance for checklists included here = 5 km) and representing an ecologically relevant scale for many bird species [32,34]. Covariate values for each checklist location were calculated as either the mean value or percent cover within the specified radius and were derived by first calculating the focal mean (for continuous covariates) or focal sum (for binary covariates) at each pixel using circular kernels with a 2.5 km radius and then extracting these smoothed values for the pixel associated with each checklist location. To facilitate prediction from habitat suitability models, we also extracted smoothed values of all relevant covariates at all pixels within a 250 m × 250 m grid spanning each species' geographic range, buffered by the relevant movement distance for each species (see connectivity modeling section below for more on relevant movement distances).

To estimate the impacts of human modification, and in particular agricultural management intensity, on species habitat suitability and connectivity, we quantified mean human land use intensity, *L*, around each detection and non-detection location for each focal species. We used the *L* layers described in Suraci et al. [1] (see also [43]) which were derived based on a procedure originally developed by Theobald [44]. These *L* layers integrate multiple datasets to estimate the intensity of land use at each location (i.e., raster pixel) across the landscape for four categories of human modification: urbanization (including data on residential development and nighttime lights), transportation (including roads, railways, powerlines, and pipelines), energy (including oil and gas wells, coal mines, and utility-scale solar and wind installations), and agriculture. For agricultural land use intensity, we constructed a novel *L* layer that incorporates high-resolution (10 m) data on agricultural land cover/use circa 2016 developed for the American Farmland Trust's Farms Under Threat (FUT) analysis [45]. The FUT analysis integrated data from the 2016 National Land Cover Database (NLCD) [46], the US Department of Agriculture's Natural Resources Inventory [47], and several other US soil and land use databases (see [45] for details) to categorize all agricultural lands into one of four classes: *cropland* (areas used for the production of crops for harvest, including row crops and hayland), *pasture* (areas used primarily for growing introduced forage plants for livestock grazing), *rangeland* (areas composed primarily of native plants and/or non-cultivated introduced forage species used for livestock grazing or browsing), and *woodland* (natural or planted forest cover that is part of a functioning farm unit and no further than 160 m from cropland or pasture). As described in detail by Suraci et al. [1], the agricultural *L* layer incorporated novel estimates of agricultural management intensity on all cropland and pasture pixels based on variation in remotely sensed vegetation cover over five growing seasons (2014–2018). Variation in vegetation cover was estimated using a timeseries of normalized difference vegetation index (NDVI) values from NASA's MODIS system (MOD13Q1 products). Elsewhere, we have shown that our estimates of vegetation cover variation correlate strongly with other indicators of agricultural management intensity (e.g., fertilizer use, irrigation) and allow us to discriminate between pixels of the same agricultural cover type in terms of their potential impacts on wildlife movement [1]. *L* values for each land use category range between 0 and 1 and are based on underlying datasets quantifying human land use circa 2016. For the present analysis, we extracted values from each of the four *L* layers at each eBird checklist location, allowing us to consider, e.g., the effect of agricultural land use intensity on species habitat suitability separately from that of other land use categories.

For all species, we included topographic covariates in habitat suitability models, including mean elevation, slope, aspect, and ruggedness (an estimate of the variability in slope and aspect within a given neighborhood). All topographic variables were calculated using the ALOS World 3D Digital Surface Model (30 m resolution [48]). Ruggedness was estimated using the vector ruggedness metric (VRM) with a window size of 1 km [49]. For

each focal species, we also included one or more land cover covariates describing habitat types known to be important to that species. Sage-grouse are dependent on sagebrush habitat [23,50,51] and we therefore included the percent cover of sagebrush, using the LANDFIRE v2.0 Existing Vegetation Type (EVT) dataset (30 m resolution [52]) filtered to only those cover types with "sagebrush" in the EVT name. Black ducks are strongly associated with coastal and inland aquatic habitats for both nesting and foraging, including open water (lakes, ponds, rivers), wetlands, and tidal flats [17,19,20,53]. We used the 2016 NLCD to quantify the percent cover of open water (NLCD code 11), all wetlands (90, 95), and herbaceous wetlands (95), isolating the latter category because of the potential importance of herbaceous wetlands in providing emergent vegetation on which black ducks can forage [17]. We also quantified the percent cover of tidal flats circa 2015–2016 using the dataset developed by Murray et al. [54]. Bobolinks breed in grasslands and agricultural fields (pastures), and tend to avoid other cover types such as forested areas [21,22,55]. We used the NLCD to calculate percent cover of forests (NLCD codes 41–43) and shrublands (52). To develop a comprehensive estimate of grassland percent cover, we combined the footprints of the NLCD grassland and pasture/hay classes (71, 81) with that of pastures identified by the Farms Under Threat 2016 land cover layer [45].

Finally, we included one or more climate covariates for each focal species, with all climate covariates derived from NASA's Daymet v4 dataset [56]. For sage-grouse, we included mean daily snow water equivalent during winter months (1 November to 1 April), as snow cover can limit sage-grouse access to forage [23,57]. For sage-grouse and Bobolink, we included the mean daily minimum and maximum temperatures, and for all three species, we included mean daily precipitation. Because the majority of black duck detections occurred within the northern portion of their range, temperature covariates were largely confounded with latitude in model predictions, leading to predicted suitable habitat that was largely confined to northern areas and thus limiting our ability to analyze connectivity across the black duck's entire U.S. range. We therefore excluded temperature covariates from the black duck model and relied instead on land cover/use and precipitation, which is appropriate given their reliance on aquatic habitats. We calculated average daily minimum and maximum temperatures and average daily total precipitation across the entire year for sage-grouse. For black duck and Bobolink, we calculated means during the focal periods (i.e., spring/fall migration and breeding season, respectively). We extracted climate variables for the relevant periods between 2014 and 2018, corresponding to the timespans of the eBird detection datasets described above. Table 1 provides a summary of all covariates and the models in which they were used. All covariates were compiled, processed, and exported at 250 m resolution using Google Earth Engine (GEE) [58]; and the GEE Python API.

Table 1. Descriptions of the spatial covariates used in random forest models for each focal species.

Covariate Name	Source	Date	Native Resolution	Predictor Type	Sage-Grouse	Black Duck	Bobolink
Agricultural land use intensity	Suraci et al. 2023	2016	250 m	focal mean	x	x	x
Urban land use intensity	Suraci et al. 2023	2016	250 m	focal mean	x	x	x
Transportation land use intensity	Suraci et al. 2023	2016	250 m	focal mean	x	x	x
Energy land use intensity	Suraci et al. 2023	2016	250 m	focal mean	x	x	x
Elevation	ALOS Global DSM (AW3D) [1]	2021	30 m	focal mean	x	x	x
Slope	ALOS Global DSM (AW3D)	2021	30 m	focal mean	x	x	x
Aspect	ALOS Global DSM (AW3D)	2021	30 m	focal mean	x	x	x

Table 1. *Cont.*

Covariate Name	Source	Date	Native Resolution	Predictor Type	Sage-Grouse	Black Duck	Bobolink
Ruggedness	ALOS Global DSM (AW3D)	2021	30 m	focal mean	x	x	x
Sage brush	LANDFIRE v2.0: Existing Vegetation Type [2]	2016	30 m	percent cover	x		
Water	NLCD 2016 [3]	2016	30 m	percent cover		x	x
Herbaceous wetlands	NLCD 2016	2016	30 m	percent cover		x	
All wetlands	NLCD 2016	2016	30 m	percent cover		x	
Forest	NLCD 2016	2016	30 m	percent cover			x
Shrub	NLCD 2016	2016	30 m	percent cover			x
Grassland	NLCD 2016 & Farms Under Threat [4]	2016	30 m, 10 m	percent cover			x
Tidal flats	Murray et al. 2019	2014–2016	30 m	percent cover		x	
Snow-water equivalent	NASA Daymet V4 [5]	2014–2018	1 km	focal mean	x		
Maximum temperature	NASA Daymet V4	2014–2018	1 km	focal mean	x		x
Minimum temperature	NASA Daymet V4	2014–2018	1 km	focal mean	x		x
Precipitation	NASA Daymet V4	2014–2018	1 km	focal mean	x	x	x

[1] Takaku et al. [48]; [2] LANDFIRE [52]; [3] Dewitz et al. [46]; [4] CSP [45]; [5] Thornton et al. [56].

2.3. Random Forest Models of Habitat Suitability

We fit random forest (RF) models to detection/non-detection data for each species to predict the probability of encountering the species at a given location (i.e., "encounter rate") as a function of environmental and climatic covariates. RF models present several benefits for ecological classification and prediction problems, including high classification accuracy and the ability to deal with complex interactions and collinearity between covariates [59,60]. Following previous analyses [34,61–63], we considered encounter rate to be a proxy for habitat suitability and used a suite of model covariates (described below) to correct for potential variation in detection probability. The consideration of encounter rate as a proxy for habitat suitability is based on the assumption that encounter rates will be higher where species abundance/density is greater, and that density is positively associated with the suitability of the habitat. While this is a common assumption in the species distribution modeling literature [34,61–63], we acknowledge that encounter rate is an imperfect proxy for habitat suitability and could potentially vary between habitats in ways that are not strictly related to density if, for instance, a species is more cryptic in some habitats than in others.

Our process for fitting RF models to eBird data closely followed that described by Strimas-Mackey et al. [34]. For each species, we classified detection/non-detection data based on the spatial covariates described in Table 1 as well as a suite of covariates accounting for variation in detection probability between checklists [32]. These detection probability covariates included checklist year, Julian date, start time, duration, total distance traveled, and number of observers. Given that RF models have been shown to be robust to the inclusion of low-importance covariates [60], we fit a single model for each focal species, including all detection probability covariates and the environmental and climatic covariates shown in Table 1. Prior to model fitting, we randomly split each species' dataset into training (80% of checklists) and test sets (20% of checklists), using the training sets to fit RF models and the test sets to assess model accuracy. Using the *ranger* package [64] in R [42], we fit RF models to training data for each species using 500 trees and partitioning based on the Gini index [59]. To further reduce issues related to class imbalance, we used a balanced random forest approach in which, for each tree, an equal number of bootstrapped samples were selected from detections and non-detections [34]. We set the RF algorithm to predict probabilities rather than binary classification [65], which in this case provides an estimate of the encounter rate for the focal species at each checklist location. To validate our models,

we quantified their ability to predict withheld test data using five validation metrics: mean squared error, sensitivity, specificity, area under the receiver-operator characteristic curve (AUC), and the kappa statistic [66]. We used partial dependence plots [59], which show the marginal effect of a given covariate averaged across all other covariates, to visualize the relationship between individual covariates and species encounter rates.

We used the validated RF models for each species and continuous rasters of spatial covariates to predict encounter rate across each species' geographic range (buffered by relevant movement distance, see below). We treated these predictions as spatially explicit estimates of habitat suitability, assuming that the probability of encountering a species will be higher in more suitable habitat [34,61–63]. Following Strimas-Mackey et al. [34], we accounted for detection probability in our habitat suitability surfaces by making predictions for a "standard" eBird checklist (travel distance = 1 km, duration = 1 h, number of observers = 1) in the year 2016 and setting the Julian date and checklist start times to those with the highest detection probability for each species (sage-grouse: 18 March (lekking season) at 05:02; black duck: 17 December (fall migration) at 05:05; Bobolink: 13 May at 05:05). Given that sage-grouse and black duck datasets spanned multiple seasons, we also developed comparison habitat suitability surfaces for these two species based on detection probability in other seasons of the year (sage-grouse: 15 July (post-breeding season); black duck: 19 March (spring migration)) to test model sensitivity to potential seasonal differences in detection probability. Habitat suitability surfaces ranged between 0 and 1 and were derived at 250 m resolution.

We quantified the effect of season and agricultural land use intensity (*L*) on predicted habitat suitability for each species by first sampling a large number of habitat suitability values at random locations distributed across each species' geographic range in the U.S. The total number of points sampled was proportional to the total area of each species' range, equaling approximately 5 random samples per 100 km^2 (sage-grouse: n = 105,608; black duck: n = 213,089; Bobolink: n = 236,833). For each species, we extracted the habitat suitability (i.e., encounter rate) value at each random point from the predicted habitat suitability surface based on the Julian date with highest detection probability. For the sage-grouse and black duck, we additionally extracted habitat suitability values from the comparison surfaces based on detection probability in other seasons of the year and compared these predicted values between the two seasons for each species via Pearson's correlation coefficient. For all species, we also extracted the agricultural *L* value at each random location and examined the relation between *L* and predicted habitat suitability by first grouping *L* into equally spaced bins (i.e., *L* = 0 (no agriculture), $0 < L \leq 0.25$, $0.25 < L \leq 0.5$, $0.5 < L \leq 0.75$, $0.75 < L \leq 1$) and calculating the median habitat suitability value in each bin.

2.4. Connectivity Modeling

We ran omnidirectional connectivity models for each focal species using the Omniscape algorithm [67,68], a circuit theory-based approach that models the movement of animals across the landscape as the flow of electrical current through a circuit [69,70]. In circuit theory-based models, current flow provides an estimate of the probability or intensity of the movement of organisms through each pixel on the landscape. Building from a circuit-theoretic approach, the Omniscape algorithm allows every pixel in a landscape raster to potentially serve as a source and/or target of movement, thus modeling current flow in all directions. Inputs for Omniscape models include a source strength surface, describing the predicted probability or intensity of movement from a given location, and a landscape resistance surface, which estimates the difficulty an animal experiences in moving through each pixel on the landscape. For each focal species, we used the habitat suitability surface to define source strength, thresholding the layer to only those pixels with habitat suitability greater than 0.2 to avoid treating the least suitable pixels as potential sources of animal

movement [67]. Following Keeley et al. [33], we used a negative exponential function to transform habitat suitability into landscape resistance, *R*, via

$$R = 100 - 99 * ((1 - \exp(-c * h))/(1 - \exp(-c)))$$

where *h* is the habitat suitability value at a given pixel and *c* is a constant that determines the degree of nonlinearity between *h* and *R*. Lower values of *c* produce linear or nearly linear relationships between *h* and *R*, while higher values of *c* produce increasingly non-linear relationships such that resistance declines more quickly with increasing values of habitat suitability. Following guidance from Keeley et al. [33], we chose a *c* value resulting in a moderately non-linear relationship between *h* and *R* (*c* = 8) to reflect the fact that many species are willing to move through otherwise relatively low suitability habitat, e.g., [71].

Omniscape employs a moving window approach in which each pixel in the source strength layer with a value greater than zero is iteratively treated as a target for electrical current. This target pixel is connected to all other non-zero pixels within the moving window radius, which serve as current sources. The moving window radius thus sets the maximum distance between movement start and end points. For each focal species, we determined the moving window size based on the animal's movement capacity and the seasonal/life history period over which analyses were run, referred to elsewhere in the text as the 'relevant movement distance'. Because our sage-grouse model addressed all seasons and movements, we treated the maximum observed movement distance in the literature (120 km) [16,23] as the relevant movement distance. This distance also captures recorded maxima for natal and breeding season dispersal [72,73]. For the black duck model, which focused on connectivity between migratory stopover sites, we considered the relevant movement distance to be 250 km, comparable to the average distance between stopover sites for all populations monitored by Coluccy et al. [25]. For the Bobolink model analyzing within-breeding season dispersal movements, we used the maximum observed distance between breeding sites (or natal site and first breeding site) for a single individual, which was approx. 10 km [4], as our relevant movement distance. Fajardo et al. [4] measured natal/breeding dispersal distances as the distance between sites used in consecutive breeding seasons (i.e., separated by migration to winter range and back). However, we assume here that these distances are a reasonable approximation of the distances Bobolinks will travel *within* a breeding season when undertaking exploratory movements to assess potential new breeding sites [28]. Connectivity models were run in the Omniscape.jl software package in Julia [68].

Following Suraci et al. [1], for each species, we compared current flow on agricultural lands with current flow on other land cover/land use types by extracting current flow values at each of the randomly sampled locations described above (sage-grouse: n = 105,608; black duck: n = 213,089; Bobolink: n = 236,833). We classified each random point as falling into one or more of the following categories: *cropland*, *pasture*, *rangeland*, *woodland*, or *all agriculture* (i.e., any one of the previous four categories), based on the FUT 2016 land cover layer described above [45]; *developed,* based on the 2016 NLCD [46] (NLCD classes 'developed—open space' and 'developed—low intensity', 'developed—medium intensity', and 'developed—high intensity'); *natural* land cover (all NLCD non-agricultural vegetation categories, i.e., cover classes 41–74 and 90–95); and *protected areas* (all public lands in the USGS Protected Areas of the US Database v2.1 [74] categorized as GAP status 1 or 2, i.e., permanently protected and managed for natural land cover). We also included a subset of natural land cover relevant to sage-grouse (and potentially other focal species): *sagebrush/shrub*, a combination of the LANDFIRE-based sagebrush layer (see above) and the NLCD "shrub/scrub" class. Agricultural, developed, and natural land categories were mutually exclusive, and we gave preference to FUT agricultural land cover classes where these overlapped with low density development or natural lands. This meant that areas in the Western U.S. classified as *rangeland* were excluded from the *sagebrush/shrub* category, with the latter therefore capturing areas with relatively low grazing pressure. Natural land cover classes were non-exclusive, with *sagebrush/shrub* being a subset of the broader *natural*

category and with an extensive overlap between *natural* and *protected areas*. Random point sampling and extraction were conducted in GEE.

2.5. Comparison with Existing Sage-Grouse Models

As noted in the Introduction, the sage-grouse has been the subject of extensive prior conservation-focused analysis, including recent connectivity studies [29,30]. We compared the results from our sage-grouse connectivity model with those of two existing circuit theory-based sage-grouse connectivity analyses to evaluate agreement between models. Crist et al. [29] used a network-based approach to examine connectivity between state-defined sage-grouse priority areas, basing landscape resistance on an existing range-wide model of sage-grouse habitat suitability. Row et al. [30] examined functional connectivity across five sage-grouse management zones (constituting the majority of the sage-grouse range), using a landscape genetic approach to estimate gene flow between sage-grouse lek groups. To quantify model agreement, we first thresholded the sage-grouse connectivity rasters from this analysis and from the two comparison studies to only those pixels in the top 25% of current flow values (i.e., high connectivity areas, HCAs). We then compared the spatial overlap between HCAs from our model with those of Crist et al. and Row et al. by calculating the percent of our top pixels overlapping with the top pixels of the comparison raster, and vice versa, clipping rasters so that the study extents matched. We conducted our complementarity analysis using the *raster* package [75] in R and via ArcGIS Pro (V3.0.0; Esri Inc., Redlands, California, USA, 2022).

3. Results

Our results highlight the complex and contrasting relationships between agricultural land use intensity (*L*) and habitat suitability (estimated as encounter rate) for each species (Figure 1). For sage-grouse, median encounter rate values, based on predictions from an RF model using data across all seasons, were highest at relatively low, but non-zero, values of agricultural *L* (Figure 2a), corresponding to low-intervention agricultural areas such as private rangelands. Black duck migratory season encounter rates (Figure 2b) were typically lower at all levels of agricultural *L* compared to areas without agriculture (i.e., where *L* = 0), suggesting that agricultural lands provide relatively poor stopover habitat for black ducks. For Bobolink, median encounter rates during the breeding season were highest at intermediate-to-high levels of agricultural *L* (Figure 2c), reflecting this species' increasing dependence on cultivated landscapes for a nesting habitat.
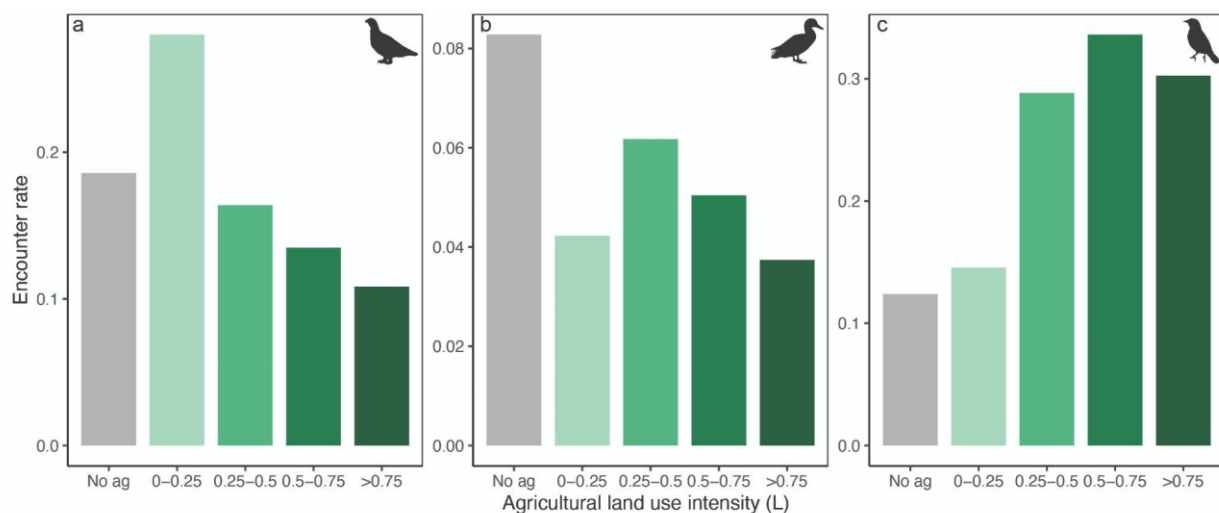

Figure 2. Median encounter rates for (**a**) Greater Sage-Grouse, (**b**) American Black Duck, and (**c**) Bobolink within bins of progressively increasing agricultural land use intensity (*L*). Median values are based on predictions from random forest models at thousands of random locations within each species' geographic range (see text for details).

For all species, however, raw detection/non-detection data were relatively sparse at higher levels of agricultural L (Figure S1), necessitating caution in interpreting results for the most intensely managed agricultural landscapes. Our validation procedure indicated that RF model predictive and discriminatory power was relatively strong for all species (Table 2), being particularly high for sage-grouse, which may reflect this species' relatively limited geographic range and strong association with sagebrush habitat [23,51]. Sage-grouse and black duck model predictions were relatively insensitive to differences in detection probability between seasons (Figure S2), with predicted encounter rate values from models based on different Julian dates being highly correlated (sage-grouse: detection probability based on 18 March vs. 15 July, Pearson's rho = 0.87; black duck: 17 December vs. 19 March, rho = 0.84).

Table 2. Validation metrics for each of the focal species random forest models.

	Mean Squared Error	Sensitivity	Specificity	AUC	Kappa
Sage grouse	0.076	0.75	0.967	0.944	0.744
Black duck	0.118	0.637	0.916	0.899	0.528
Bobolink	0.153	0.621	0.852	0.831	0.435

Maps of habitat suitability and connectivity across each species' geographic range (Figure 3) highlight potential target areas for management action to preserve high-quality habitat and connectivity within and among populations. Generally, year-round habitat suitability for sage-grouse, as well as areas of the highest predicted probability of movement (i.e., current flow) were concentrated in relatively flat, medium-to-high elevation (i.e., >1000 m) habitats with a high percent cover of sagebrush (Figure 3a,d). Habitat suitability and connectivity for migrating black ducks was strongly associated with water, being highest in coastal areas, along major river systems, and in the vicinity of the Great Lakes (Figure 3b,e). Bobolink breeding habitat suitability and connectivity was relatively diffused throughout the midwestern and northeastern regions of the U.S. (Figure 3c,f), reflecting this species' use of agricultural landscapes as a nesting habitat and a general avoidance of forested areas for breeding.

For sage-grouse, the median current flow value on rangelands was higher than that on most other land cover/land use types considered and comparable to median current flow on non-rangeland sagebrush/shrub habitat (Figure 4a). In contrast, cultivated croplands, which are typically characterized by substantially higher agricultural land use intensities than the other agricultural cover types [1], were predicted to support among the lowest levels of current flow for sage-grouse, compared to developed areas (Figure 4a). Our model had moderately high agreement with existing sage-grouse connectivity models, with high connectivity areas (HCAs, i.e., pixels with current flow values in the top quartile) predicted by our model capturing approximately 65% of HCAs identified by both Crist et al. [29] and Row et al. [30] (Table 3, Figure S3). HCAs identified by the two comparison models captured 47–52% of the HCAs identified by our model.

Table 3. Percent agreement between high connectivity areas (HCA, i.e., pixels with current flow values in the top quartile for a given model) predicted by our sage-grouse connectivity model (this study) and those predicted by two existing sage-grouse connectivity models (comparison models). Model agreement was calculated as both the percentage of HCA predicted by each comparison model falling within HCA predicted by this study and the percentage of this study's HCA falling within the HCA of each comparison model.

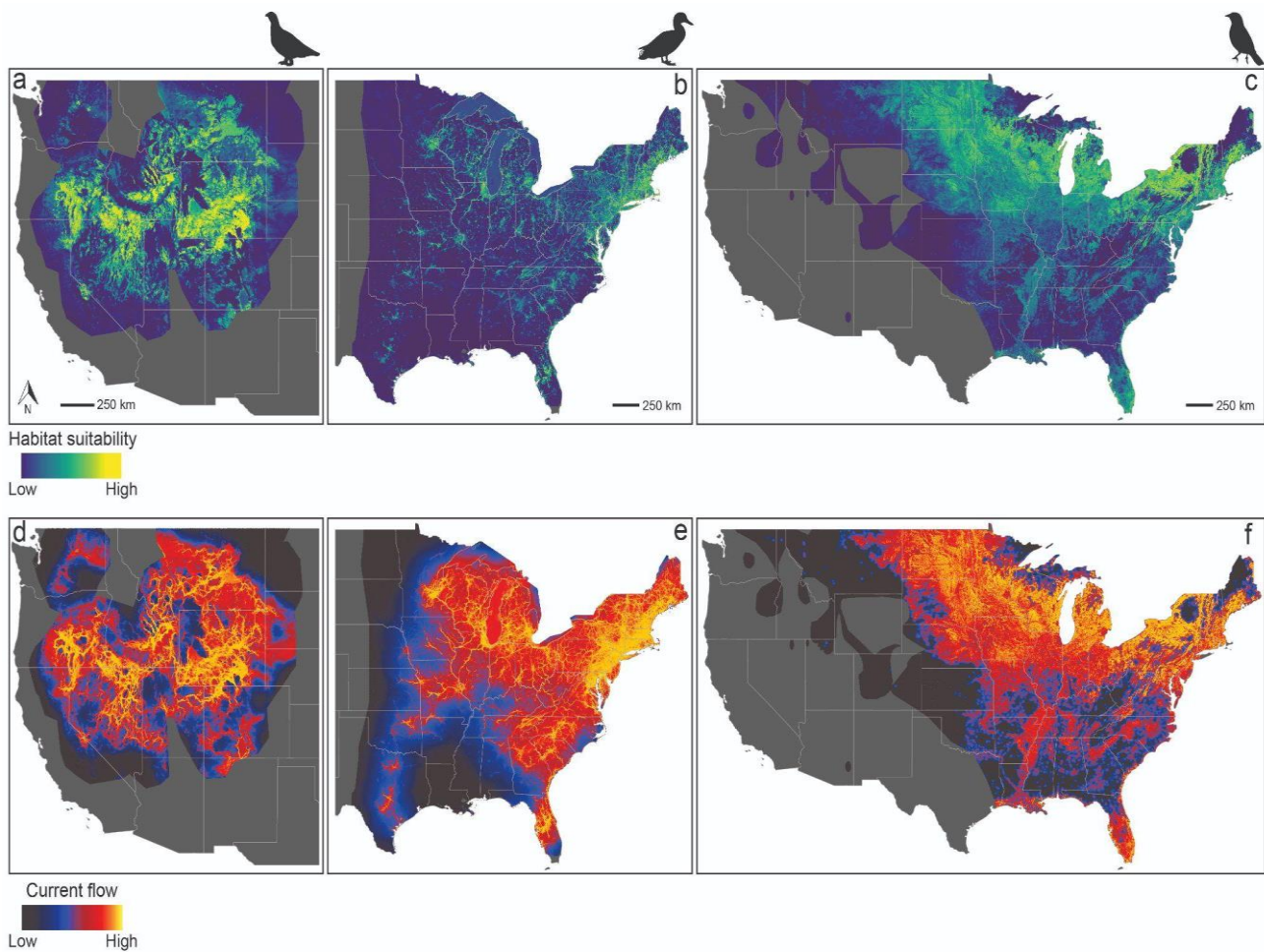| Comparison Model	Comparison Model HCA within This Study's HCA	This Study's HCA within Comparison Model HCA
Crist et al. 2017	64.6%	47.1%
Row et al. 2018	65.5%	52.4%

Figure 3. Habitat suitability (as predicted from random forest models) and the predicted probability of movement (i.e., current flow, as predicted from circuit theory-based connectivity models) for Greater Sage-Grouse in all seasons (**a**,**d**), American Black Duck during spring and fall migrations (**b**,**e**), and Bobolink during the breeding season (**c**,**f**). Model results are shown across each species' geographic range in the U.S. (based on IUCN range maps, see text for details).

Current flow for migrating black ducks tended to be lowest on agricultural lands relative to more developed or natural land cover/land use types (Figure 4b), though woodlands—patches of remnant forest cover associated with a functioning farm unit where management intensity is typically low—were predicted to provide some support for black duck movement, as indicated by median current flow values. For Bobolink, croplands exhibited among the highest median current flow values of any land cover/land use type (Figure 4c), emphasizing the importance of cultivated landscapes for this species during the breeding season. Our model predicted very low current flow values for Bobolink on natural land cover types and within protected areas (Figure 4c), likely reflecting this species' avoidance of forested habitats.

Current flow was high on developed lands for both black ducks and Bobolinks (Figure 4b,c), suggesting substantial potential for movement through suburban and urban landscapes. High predicted movement through developed areas (and correspondingly high predicted habitat suitability, Figure 3b,c) could stem in part from the tendency of community scientists to collect data in or near the cities in which they live. However, comparing detection/non-detection data for black ducks and Bobolinks suggests that encounter rates for these species are indeed higher in more developed areas; the distribution of urban land use intensities (*L*) at locations where birds were detected was shifted toward higher

urban *L* values relative to non-detection locations (Figure 5) despite both detection and non-detection checklists having the same potential for spatial bias toward urban areas.
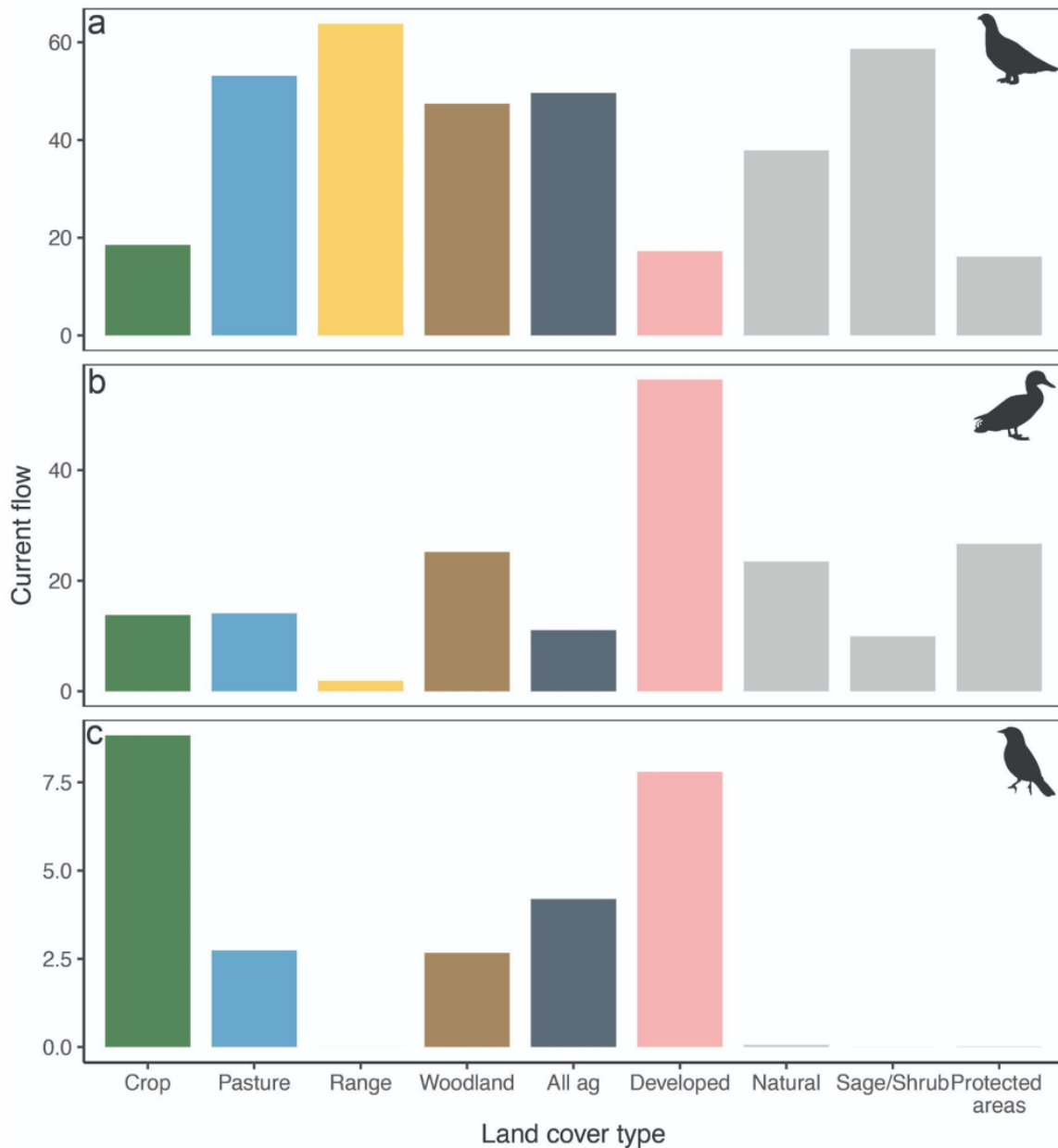

Figure 4. Median current flow values on agricultural lands (cropland, pasture, rangeland, woodland, and all agricultural categories combined ('all ag')) for each focal species, as compared to median current flow in developed areas and landscapes characterized by more natural land cover (i.e., all natural lands ('natural'), areas characterized by sagebrush or other shrub cover that do not overlap with identified rangelands ('sage/shrub'), and lands within USGS GAP 1 and GAP 2 protected areas). Recall that 'woodland' in this context refers to natural or planted tree cover associated with a functioning farm unit. Median current flow values are shown for (**a**) Greater sage-grouse, (**b**) American Black Duck, and (**c**) Bobolink. Note that, given differences between connectivity model inputs, current flow values are not comparable across species and should only be interpreted here in terms of relative differences between different land cover/use types.
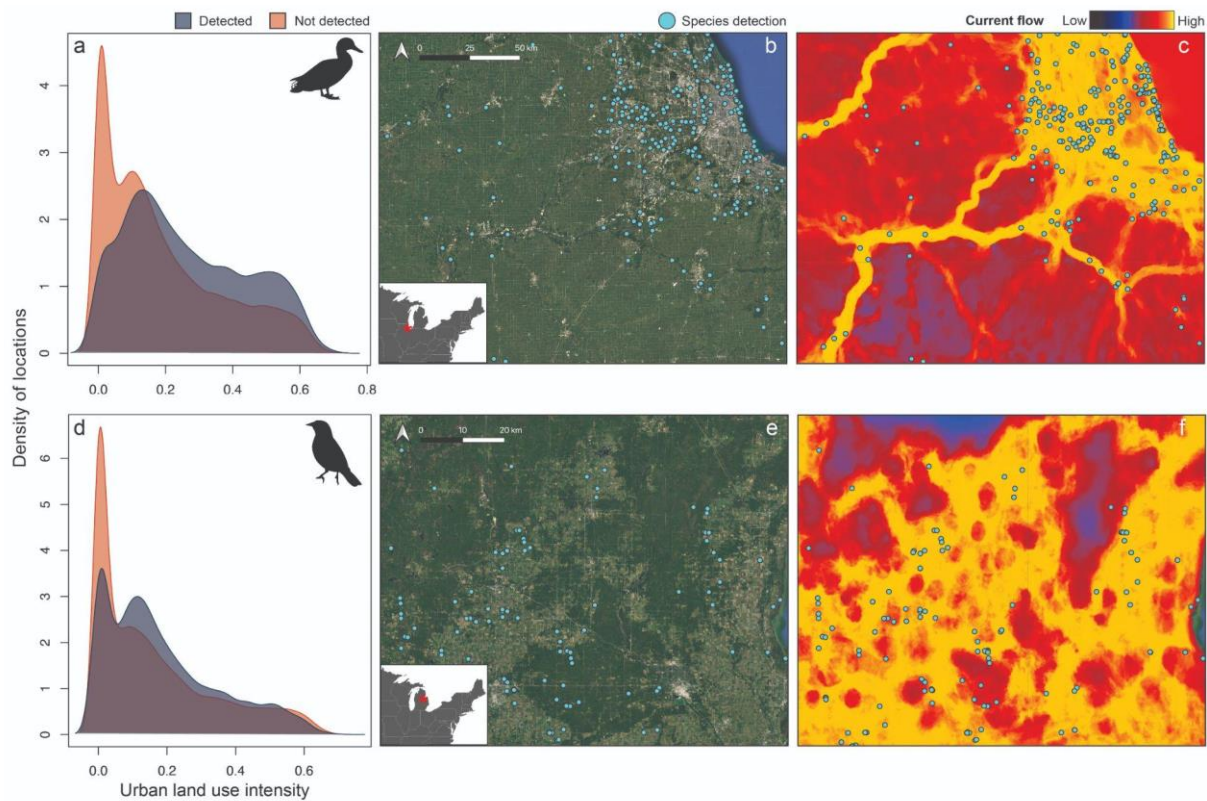
Figure 5. Use of developed habitats by American Black Duck (black duck; top row) and Bobolink (bottom row). Kernel density plots (**a**,**d**) show the distribution of urban land use intensity values at locations where each species was detected (blue) and not detected (orange). Satellite imagery (**b**,**e**) and corresponding connectivity surfaces (**c**,**f**) show species' locations and predicted movement potential (current flow) across development gradients in two example landscapes.

4. Discussion

Given that agriculture covers approximately 50% of land area in the lower 48 states [1], understanding the complex effects of agriculture on avian species movement and habitat use will be critical to maintaining connectivity, and therefore population persistence, for many species. This work highlights the complexity of agriculture–wildlife interactions, with species varying substantially in the potential for agricultural lands to provide habitat and/or movement pathways. Our results suggest that agricultural landscapes can in some cases provide valuable movement habitat for sage-grouse and Bobolinks, depending on the type and intensity of agriculture practiced, while providing limited value for migratory black ducks. For all three species, the capacity for agricultural lands to contribute to species persistence likely depends heavily on management practices (e.g., grazing intensity, mowing, or harvest frequency). Here, we offer key considerations for preserving or enhancing the capacity of agricultural lands to support avian habitat and connectivity and identify federal conservation incentive programs that can support wildlife-friendly management.

For sage-grouse, our connectivity model predicted that private rangelands support among the highest current flow values of any of the land cover types considered. This result confirms previous findings that private lands (particularly ranchlands) in the Western U.S. play an important role in supporting sage-grouse movement [16], providing critical pathways through areas of increased disturbance such as energy development [76]. Previous work has highlighted negative associations between sage-grouse and agricultural lands [77,78], and indeed our results indicate that cultivated croplands supported only low levels of current flow compared to developed areas, while overall habitat suitability declined quickly as agricultural management intensity (*L*) increases beyond relatively low values. However, by distinguishing between agricultural land uses and management

intensities, we found that less intensively managed agricultural landscapes (rangelands, and to a lesser extent pasture and remnant tree cover on farms, i.e., "woodlands") can potentially support sage-grouse movement.

We note that extensive research effort has been devoted to the conservation of sage-grouse and the broader sagebrush ecosystem, including a recently released, multi-institutional sagebrush conservation design plan [79] and several prior models of sage-grouse connectivity, e.g., [16,29,30]. Our intention is for the present analysis to complement these efforts by differentiating between agricultural classes and management intensities, thereby highlighting potential targets for sage-grouse conservation on these working lands. This complementarity is illustrated by our quantitative comparison with the sage-grouse connectivity models developed by Crist et al. [29] and Row et al. [30]. This comparison showed that our model captures the majority (~65%) of high connectivity habitat identified by the two existing models while also highlighting additional areas of potential importance on agricultural landscapes. The two previous models, which were conducted at coarser spatial resolutions, tended to identify large, contiguous patches of high connectivity separated by large expanses of lower connectivity lands. Our model provides a higher resolution look at sage-grouse connectivity, capturing substantial proportions of the high connectivity patches identified by Crist et al. and Row et al. while also identifying potentially important movement pathways between these larger patches that in many cases pass through rangeland habitat (see Figure S3 for a visual comparison of high connectivity areas identified by each model). It is also worth noting that, when parameterizing our connectivity model, we employed a relatively large maximum movement distance (120 km as the maximum distance between two potentially connected pixels on the landscape) in an effort to capture not only typical sage-grouse movement patterns, but also the potential for rare long-distance movements [16,23]. As such, our model highlights areas of potential connectivity between populations, which may be relevant to maintaining or increasing gene flow. Conservation incentives that preserve relatively intact rangelands (e.g., the USDA's Agricultural Conservation Easements Program (ACEP)) and programs that support the maintenance of native vegetation on cultivated landscapes (e.g., USDA's Conservation Reserve Program (CRP)) will be critical to sage-grouse conservation and can help to reduce conflicts with residential and energy development [80]. Our maps of sage-grouse habitat suitability and functional connectivity across working landscapes can be used to identify where on private lands such conservation-focused programs are likely to be most effective.

Our analysis suggests that, of the three focal species considered here, migrating black ducks were the most sensitive to agriculture, exhibiting low habitat suitability and low predicted connectivity during the migratory season on agricultural land cover types across the range of management intensities. The low predicted movement of black ducks on agricultural lands likely stems from this species' dependence on wetlands, coastal areas, and other aquatic habitats as migratory stopover sites [81,82]. Preventing further conversion of aquatic habitats to agriculture or other uses will therefore be critical to ensuring the preservation of important stopover habitat for black ducks. While our results suggest limited potential for agricultural lands to support black duck connectivity during migration, previous work indicates a role for croplands and pastures in providing foraging opportunities for ducks during other times of the year (e.g., overwinter) [19,20]. Federal incentive programs can play an important role in protecting and restoring wetlands on or near working farms to support migratory habitat (e.g., through the USDA's CRP or Farmable Wetlands programs), as well as incentivizing wildlife-friendly farming practices that support black duck use of agricultural areas (e.g., through the USDA's Environmental Quality Incentives Program (EQIP) and Conservation Stewardship Program (CSP)). The Working Lands for Wildlife program (administered by the USDA's Natural Resources Conservation Service) can also supply landowners with financial and technical assistance to restore and protect wetland habitat on working lands and make wildlife-friendly improvements to croplands and pastures. Importantly, however, conflict can arise when waterfowl usage of agricultural areas results in crop damage [83]. Compensatory payments to farmers in several European

countries have been effective in reducing such conflicts [84] and could be considered as a conservation strategy on working lands in the U.S.

With the loss of native grasslands, grain fields and pastures are increasingly important as breeding habitat for Bobolink [21,55]. Our models reflected this dependence on agriculture, with breeding season habitat suitability predicted to be relatively high in areas of moderate to high agricultural management intensity, and croplands exhibiting the highest median current flow value of any of the land cover types considered. However, despite the high breeding season movement potential through managed agricultural landscapes, Bobolink breeding success can nonetheless be substantially negatively impacted by intensive management regimes that involve frequent harvest or mowing [22], which may disturb or destroy nesting habitat multiple times during the breeding season [85]. Mismatches between Bobolink reproductive timing and the harvest or mowing cycles of the agricultural fields they depend on is only predicted to increase under changing climate conditions. McGowan et al. [86] found that, while haying dates in Vermont advanced by approximately ten days between 2002 and 2019, Bobolink nest initiation dates remained relatively constant. The importance of agricultural lands throughout the Eastern and Midwestern U.S. for Bobolink breeding season movements and the threats to breeding success posed by intensive management regimes highlight the critical importance of incentivizing "land sharing" conservation approaches (i.e., practices that maintain or enhance the capacity of farms to support biodiversity through wildlife-friendly farming practices) [7,87] on grain and pasture fields to ensure the persistence of Bobolink and other grassland bird species. The federal government can play a role in supporting such wildlife-friendly practices through programs such as the USDA's CSP or EQIP programs, and other funding mechanisms that compensate farmers to adjust harvest timing to account for grassland bird nesting cycles.

Our models predicted relatively high current flow through developed areas for both black ducks and Bobolinks. For black ducks, the fact that many urban areas are situated along coastal or inland waterways may explain this apparent preference for urbanized landscapes as stopover habitat and thus high values of predicted current flow near urbanized areas (see Figure 5b,c). Detection data suggested that Bobolinks are less likely to be found in the most highly developed landscapes but are often detected in suburban areas and parks (Figure 5e). This was reflected in our Bobolink connectivity results, with current flow tending to be high in moderately developed and agricultural landscapes, but lower in heavily urbanized environments (Figure 5f). For both species, detection data indicated that, while individuals are rarely detected in the most heavily developed environments (e.g., urban cores), they do use locations adjacent to these developed areas (urban green spaces and waterways in the case of black ducks [88] and suburban and exurban open spaces for Bobolinks [89]). It is also worth noting that, to avoid potential errors associated with eBird count data, we treated each eBird checklist on which one or more individuals of a given species were detected as one species detection event, and it therefore remains possible that the detection events of black ducks or Bobolinks in urban areas tended to involve fewer individuals than detection events in other habitat types. However, we expect that this is unlikely to substantially influence our connectivity results given that these species do at least occasionally move through developed landscapes.

Agricultural lands play a critical role in facilitating movement, foraging, and other important processes for many avian species, but require thoughtful management and strong partnerships with landowners to balance the potential benefits to wildlife with landowner livelihoods and the necessity of maintaining a sustainable food supply. As noted above, government conservation incentive programs can be a key component of such management, and the effectiveness of these programs has been demonstrated by prior research. For example, changes to grazing regimes and the planting of perennial vegetation as part of CRP-funded conservation and restoration programs have been shown to increase grassland bird densities [90] and support year-round habitat for sage-grouse [14]. Similarly, the Working Lands for Wildlife program has helped producers conserve more than eight million acres of sage-grouse habitat. However, the substantial land area devoted

to agriculture and limits on government spending for conservation programs necessitate strategic approaches to allocating conservation resources. Our range-wide analyses of habitat suitability and connectivity for three bird species impacted by agricultural land uses can help to inform where government incentive programs are most critically needed across the U.S. and are likely to be the most effective in conserving or restoring habitat for these species.

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