

# Demographic declines over time and variable responses of breeding bird populations to human footprint in the Athabasca Oil Sands Region, Alberta, Canada

James F. Saracco<sup>1,\*</sup>, Peter Pyle<sup>1</sup>, Danielle R. Kaschube<sup>1</sup>, Monica Kohler<sup>2</sup>, Christine M. Godwin<sup>3</sup> and Kenneth R. Foster<sup>3</sup>

<sup>1</sup>The Institute for Bird Populations, Petaluma, California, USA

<sup>2</sup>Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, Alberta, Canada

<sup>3</sup>Owl Moon Environmental Inc., Fort McMurray, Alberta, Canada

\*Corresponding author: [jsaracco@birdpop.org](mailto:jsaracco@birdpop.org)

## ABSTRACT

Habitat loss and disturbance from industrial resource development may be contributing to declines in boreal bird populations. We applied hierarchical multi-species models to data from 31 bird species at 38 Monitoring Avian Productivity and Survivorship (MAPS) stations to assess 10-year (2011–2020) demographic trends and responses to energy sector disturbance (human footprint proportion) in the Athabasca oil sands region of Alberta, Canada. Adult captures, productivity, and residency probability all declined over the study period, and adult apparent survival probability also tended to decline. Consistent with the hypothesis that habitat loss may be driving declines, trends in adult captures, productivity, and survival were all more negative at stations with larger increases in disturbance over the study period. Species associated with early seral stages were more commonly captured at more disturbed stations, while species typical of mature forests were more commonly captured at less disturbed stations. Productivity was positively correlated with disturbance within 5-km of stations after controlling for disturbance within 1-km of stations, suggesting the importance of earlier successional habitat for post-fledging birds in the larger landscape. Adult apparent survival showed relatively little response to disturbance; stresses experienced beyond the breeding grounds likely play a larger role in influencing survival. Residency probability was negatively related to disturbance within 1-km scale of stations and could reflect processes affecting the ability of birds to establish or maintain territories in disturbed landscapes. We conclude that successional habitats that result from natural regeneration or restoration in disturbed areas, as well as decreased future footprint through recovery of mature forests and limiting of new disturbances, will both be important components of efforts to reverse population declines and maintain bird populations in the region.

**Keywords:** avian demography, boreal forest, capture–mark–recapture, human footprint, mist-netting, Monitoring Avian Productivity and Survivorship, resource development, population trend

## How to Cite

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## LAY SUMMARY

- Habitat loss and disturbance can affect the demography and trends of bird populations.
- We used avian monitoring data from 2011 to 2020 and anthropogenic disturbance data (human footprint) at two spatial scales (1-km and 5-km radius) from a network of bird-banding stations in the Athabasca oil sands region of Alberta, Canada, to assess trends in, and disturbance effects on, the abundance and demography of 31 breeding bird species.
- Abundance and demographic parameters declined, and trends in abundance, productivity, and adult apparent survival were all more negative at sites with increasing footprint; thus, decreasing future human footprint through habitat recovery in reclaimed industrial areas and limiting of new industrial disturbances will be critical for efforts to reverse bird population declines.
- Positive responses of an index of abundance (adult captures) and productivity of at least some species to disturbance at one or both spatial scales also suggest an important role for successional habitats that develop in the wake of disturbance as part of regional conservation efforts.

Déclin des populations au fil du temps et réponses variables des populations d'oiseaux nicheurs à l'empreinte humaine dans la région des sables bitumineux de l'Athabasca, en Alberta, au Canada

## RÉSUMÉ

La perte et les perturbations de l'habitat dues à l'exploitation industrielle des ressources pourraient contribuer au déclin des populations d'oiseaux boréaux. Nous avons appliqué des modèles hiérarchiques multi-espèces aux données provenant de 31 espèces d'oiseaux recueillies à 38 stations de suivi de la productivité et de la survie des oiseaux (*Monitoring Avian Productivity and Survivorship* ou MAPS) afin d'évaluer les

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tendances des populations sur 10 ans (2011–2020) et les réponses aux perturbations du secteur de l'énergie (proportion de l'empreinte humaine) dans la région des sables bitumineux de l'Athabasca en Alberta, au Canada. Les captures d'adultes, la productivité et la probabilité de résidence ont toutes diminué au cours de la période d'étude, et la probabilité de survie apparente des adultes a également eu tendance à diminuer. Conformément à l'hypothèse selon laquelle la perte d'habitat pourrait être à l'origine des déclin, les tendances dans les captures d'adultes, la productivité et la survie étaient toutes plus négatives aux stations où les perturbations avaient augmenté de façon plus importante au cours de la période d'étude. Les espèces associées aux premiers stades de succession étaient plus souvent capturées aux stations plus perturbées, alors que les espèces typiques des forêts matures étaient plus souvent capturées aux stations moins perturbées. La productivité était positivement corrélée avec la présence de perturbations dans un rayon de 5 km des stations après contrôle pour les perturbations dans un rayon de 1 km des stations, ce qui suggère que l'habitat des premiers stades de succession est important pour les oiseaux après leur envol à une échelle de paysage plus grande. La survie apparente des adultes a montré une réponse relativement faible aux perturbations; les stress subis en dehors des aires de reproduction jouent probablement un rôle plus important dans la survie. La probabilité de résidence était négativement liée aux perturbations dans un rayon de 1 km des stations et pourrait refléter les processus affectant la capacité des oiseaux à établir ou maintenir des territoires dans des paysages perturbés. Nous concluons que les habitats de succession qui sont le résultat de la régénération naturelle ou de la restauration dans les zones perturbées, de même que la diminution de l'empreinte future par le rétablissement des forêts matures et la limitation des nouvelles perturbations, seront des éléments importants des efforts visant à inverser le déclin des populations et à maintenir les populations d'oiseaux dans la région.

**Mots-clés:** démographie aviaire, forêt boréale, capture-marquage-recapture, empreinte humaine, filet japonais, Monitoring Avian Productivity and Survivorship, exploitation des ressources, tendance des populations.

## INTRODUCTION

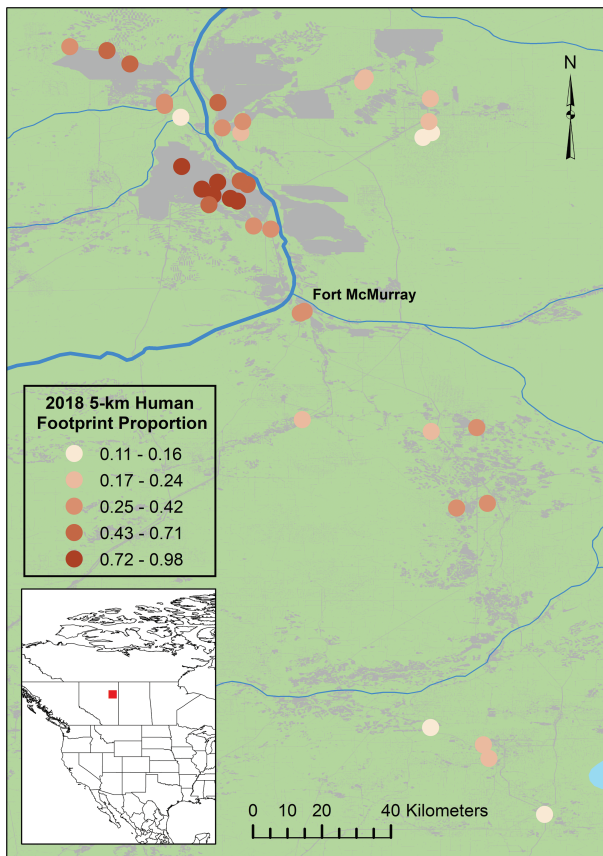
Bird populations in North America are declining (Rosenberg *et al.* 2019). Declines have been severe for many migratory bird species of the boreal region and may reflect loss or degradation of breeding or wintering habitats or stressors experienced along migration pathways (Hostetler *et al.* 2015, Wilson *et al.* 2018). Understanding the causes of declines is crucial for conserving biodiversity, given that boreal habitats harbor large proportions of populations of many bird species (Blancher and Wells 2005, Wells *et al.* 2011, Ruegg *et al.* 2020), some of which are of high conservation concern (Alberta Environment and Parks 2015, Environment and Climate Change Canada 2019).

Oil production in the Athabasca oil sands region of Alberta, Canada began in the 1960s and has rapidly expanded since the late 1990s (Heyes *et al.* 2018, Foster *et al.* 2019). This has resulted in the loss and alteration of habitats used by boreal breeding birds, and the recent surge in industry growth could be contributing to population declines (Wells *et al.* 2008, Mahon *et al.* 2016, 2019, Roberts *et al.* 2022). Although on a much smaller scale, regeneration of habitats on disturbed areas that no longer support energy production has also been progressing in recent decades, and larger scale industrial disturbances are legally required to be reclaimed to a state of equivalent land capability (Province of Alberta 2022). This reclamation process may take additional decades to complete (Hawkes and Gerwing 2019, Pyle *et al.* 2020) and may ultimately result in novel habitats and communities (Rooney *et al.* 2012, Audet *et al.* 2014). However, the transitional habitats established in the wake of disturbance can also be important for supporting a variety of wildlife, including birds (Foster *et al.* 2017, Hawkes and Gerwing 2019, Pyle *et al.* 2020).

Bird populations may respond to habitat and disturbance at multiple spatial scales (Betts *et al.* 2014). For example, in the Athabasca oil sands region, the distribution and abundance of breeding birds has been correlated with anthropogenic disturbances at distances ranging from 0.15 to 6 km from survey points (Mahon *et al.* 2016, 2019). Avian productivity and age structure in this region has also been related to habitat structure, disturbance, or vegetation greenness at a relatively local scale (~0.25 km; Foster *et al.* 2017, Pyle *et al.* 2020). However, local-scale habitats may not always be representative of surrounding landscapes, and links between

demographic parameters and larger-scale landscape metrics may have consequences for bird population persistence (Lampila *et al.* 2005, Winiarski *et al.* 2017). A better understanding of avian demographic responses to disturbance at multiple scales would facilitate more effective management for species conservation in disturbed landscapes (Wells *et al.* 2011, Roy *et al.* 2019, Campbell *et al.* 2020).

Here, we assess recent trends in, and effects of human disturbance on, avian abundance and demography at a network of bird-banding stations operated in the Athabasca oil sands region, from 2011 to 2020, as part of the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante *et al.* 2004). Disturbance in this region is predominantly related to energy extraction (e.g., drilling, mining, transport, urbanization) but also includes some forest harvesting (Johnson and Miyanishi 2008, Jordaan 2012). We considered the effects of a cumulative “human footprint” proportion that encompassed all disturbance types, at two scales (1-km and 5-km radii from station centers). Disturbed areas within MAPS station boundaries largely consisted of regenerating vegetated areas of varying types and ages (Foster *et al.* 2017) with disturbances in the larger landscapes surrounding MAPS stations including both regenerating habitats as well as active industrial sites and infrastructure. We hypothesized that habitat disturbance would have an overall negative effect on avian demographic responses. However, we also expected that individual species would respond positively or negatively to disturbance depending on their habitat needs (Bayne *et al.* 2016, Mahon *et al.* 2016, 2019). For example, bird species typical of older mature forests may experience stronger negative effects due to habitat loss or degradation from all disturbance types, whereas species of earlier successional habitats may experience benefits from soft disturbances and/or recently reclaimed areas in landscapes otherwise dominated by more mature forested habitats. Therefore, we also estimated trends in population parameters to assess whether the direction of population and demographic trajectories were consistent across the assemblage of bird species (suggesting shared environmental drivers) or whether trends were more variable among species (suggesting variable responses to breeding habitat, non-breeding season factors, or life history traits). Finally, we assessed whether spatial variation in change in human footprint over the study period may have influenced spatial variation in demographic trends.



**FIGURE 1.** Distribution of 38 Monitoring Avian Productivity and Survivorship (MAPS) stations in the Athabasca Oil Sands Region, Alberta, Canada. Gray regions indicate human footprint disturbance and green regions represent natural land cover types based on 2018 data. MAPS stations are shaded by the proportion of human footprint disturbance within 5 km of station centers. Blue regions indicate water; the thicker blue line passing through Fort McMurray is the Athabasca River.

## METHODS

### Study Areas and Field Methods

We operated 38 MAPS stations according to standardized protocols (DeSante et al. 2004, 2020) for 2–10 years from 2011 to 2020 (Supplementary Material Table 1; Figure 1). Stations were sited to assess the effects of disturbance and reclamation on avian demographics in riparian, lowland, and upland terrestrial habitats in a boreal forest landscape that has undergone extensive development, largely stemming from oil and gas extraction activities (Foster et al. 2017). Each station was operated on single days spaced at ~10-day intervals between June 5 and August 7 (maximum of 6 days of operation per year for each station). On each day of station operation, 8–14 mist-nets were operated at fixed sites across ~8 ha of mostly riparian and proximal terrestrial habitats. Nets were opened for ~6 hr on each day of station operation, beginning at local sunrise. Effort (hours that each mist net was open) was recorded for all days of station operation. With few exceptions, each bird was banded with a uniquely numbered aluminum leg band, issued by the Canadian Wildlife Service. Birds were aged as either adults or birds that hatched in the given year (Pyle 1997), and band numbers of all recaptures were recorded (see Foster et al. 2017 for additional detail).

### Human Footprint Data

Global human footprint data (Venter et al. 2016, 2018) have been used to provide insights into avian demography and population dynamics at continental scales (Wilson et al. 2018). Here, we used locally derived human footprint data that were compiled more recently (2018) and at finer resolution (minimum pixel size = 0.8 ha) than were available from the global human footprint index (ABMI, 2017; <https://www.abmi.ca/home/data-analytics/da-top/da-product-overview/Human-Footprint-Products/HF-inventory.html>). From the 2018 footprint data, we summed the proportions of disturbed area over 20 disturbance classes, which included all cover types transformed from natural ecosystem cover to anthropogenically disturbed cover types, at 2 spatial scales: 1-km and 5-km radii surrounding station centers (Supplementary Material Table 1). Note that “anthropogenically disturbed” could include a variety of land cover types, including hard structures (e.g., roads or industrial infrastructure), early successional vegetation in cleared areas surrounding industrial infrastructure, and regenerating vegetation on sites in reclaimed areas or on smaller disturbed sites not requiring reclamation (e.g., linear disturbances). The 1-km and 5-km scales considered here are consistent with previous studies that have shown relationships between avian abundance and community structure response variables and habitat and disturbance covariates in the region (Mahon et al. 2016, 2019), as well as with documented scales of movement for breeding songbirds (Cooper and Marra 2020). Thus, we concluded that these 2 scales would be adequate to characterize potential bird responses to footprint. Footprint proportion values ranged from 0.05 to 1.00 at the 1-km scale (mean = 0.43) and from 0.10 to 0.98 at the 5-km scale (mean = 0.40; Figure 1). Disturbance classes included in the human footprint proportion were urban, industrial, and residential developments, well and mine sites, timber harvest blocks, human-created water sources (borrow pits, dugouts, sumps, canals, municipal water, and reservoirs), and linear features, such as seismic lines, pipelines, transmission lines, and vegetated roadsides (footprint proportions by disturbance class are provided in the data archive; see ABMI 2017 for additional detail on cover classification). Despite the large number of classes considered, about half of the cumulative human footprint proportion values were accounted for by just 2 classes, mine sites and other energy sector industrial developments, and the sum of these 2 classes was highly correlated with the sum of all 20 disturbance classes at both the 1-km ( $r = 0.94$ ;  $P < 0.001$ ;  $df = 36$ ) and 5-km ( $r = 0.98$ ;  $P < 0.001$ ;  $df = 36$ ) scales. Thus, bird responses reported here likely reflect responses to these 2 disturbance types at those scales.

In addition to the 2018 footprint data, we extracted 5-km radius footprint proportion values from an earlier compiled dataset representative of 2010, just before the start of our bird monitoring project, to assess changes in footprint over the study period and their potential impacts on bird populations. Footprint values were highly correlated between the 2010 and 2018 data sets ( $r = 0.98$ ;  $P < 0.001$ ;  $df = 36$ ). Overall, footprint increased across this time span (mean change in proportion = +0.07 and 36 of 38 stations showing increasing footprint); however, changes were highly variable among sites (range: −0.03 to 0.24). All footprint data were based on a NAD83/Alberta 10-TM (Forest) projection.

**TABLE 1.** Numbers of age-specific year-unique captures and adult capture–mark–recapture data from 2011 to 2020 for 31 species included in the multi-species demographic models. Age-specific capture data were included from all MAPS stations. Adult capture–recapture data were included from just stations that operated  $\geq 4$  year. Tree cover %, representing the average value for adult captures, is included as a coarse indicator of habitat use for each species and is represented as the color gradient in [Figures 2–5](#).

Species code	Common name	Scientific name	Tree cover %	Age-specific capture data			Adult capture–recapture data		
				No. stations	No. adults	No. juveniles	No. stations	No. individuals	No. recaptures
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	41.8	29	316	159	27	275	40
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>	39.1	37	1,487	217	35	1,402	134
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	38.4	31	689	321	30	681	28
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	36.4	32	754	128	30	691	84
CAJA	Canada Jay	<i>Perisoreus canadensis</i>	46.3	28	126	137	24	101	23
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	40.6	34	300	832	29	248	53
BOCH	Boreal Chickadee	<i>Poecile hudsonicus</i>	44.6	29	173	259	27	149	24
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	40.7	36	1,250	785	33	1,123	158
HETH	Hermit Thrush	<i>Catharus guttatus</i>	45.6	31	164	143	23	147	22
AMRO	American Robin	<i>Turdus migratorius</i>	39.7	36	656	179	34	591	79
TEWA	Tennessee Warbler	<i>Oreothlypis peregrina</i>	42.8	38	3,509	3,455	18	352	42
YEWA	Yellow Warbler	<i>Setophaga petechia</i>	35.4	23	403	267	33	711	107
MAWA	Magnolia Warbler	<i>Setophaga magnolia</i>	43.1	28	460	259	16	191	32
YRWA	Yellow-rumped Warbler	<i>Setophaga coronata</i>	47.1	30	410	172	24	375	29
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>	38.3	33	370	230	25	248	12
AMRE	American Redstart	<i>Setophaga ruticilla</i>	37.5	23	278	130	4	293	68
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>	39.0	37	774	441	16	289	79
NOWA	Northern Waterthrush	<i>Parkesia noveboracensis</i>	36.5	20	153	129	26	305	38
MOWA	Mourning Warbler	<i>Geothlypis philadelphia</i>	42.4	18	340	129	35	1,014	59
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	37.0	29	339	105	24	1,055	90
WIWA	Wilson's Warbler	<i>Cardellina pusilla</i>	45.2	26	250	184	15	134	18
CAWA	Canada Warbler	<i>Cardellina canadensis</i>	40.4	20	389	275	34	2,052	377
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	41.7	37	1,085	485	35	3,569	19
CCSP	Clay-colored Sparrow	<i>Spizella pallida</i>	21.6	25	1,266	976	20	339	67
SAVS	Savannah Sparrow	<i>Passerculus sandwichensis</i>	12.8	5	394	341	26	408	71
SOSP	Song Sparrow	<i>Melospiza melodia</i>	26.5	25	229	204	27	363	47
LISP	Lincoln's Sparrow	<i>Melospiza lincolnii</i>	37.7	37	838	842	29	337	34
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>	37.4	29	395	533	22	247	36



TABLE 1. Continued.

Species code	Common name	Scientific name	Tree cover %	Age-specific capture data			Adult capture–recapture data		
				No. stations	No. adults	No. juveniles	No. stations	No. individuals	No. recaptures
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>	41.8	37	2,314	1,518	34	731	43
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	50.7	19	150	280	19	128	28
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	38.5	23	165	47	22	154	12

### Tree Cover

To provide context for evaluating species responses in relation to overall habitat use, we extracted average 2011–2020 tree cover values for each station from the 0.25-km resolution Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Continuous Fields data product (MOD44B; DiMiceli et al. 2015) using the *mt\_batch\_subset* function in the MODISTools package (Tuck et al. 2014) in R (R Core Team 2021). We then averaged these station tree cover values across adult captures for each focal species to provide a coarse measure of the typical habitat association of the species with respect to percent tree cover. Note that tree cover values for individual stations were highly correlated with the human footprint data at the larger 1-km and 5-km radius scales; we consider it here primarily to represent a metric of more local habitat preference and to aid in visualization of demographic responses in the context of those preferences. Tree cover values ranged from 12.8 (Savannah Sparrow) to 50.7 (Dark-eyed Junco; see Table 1 for scientific names and values for all focal species).

### Statistical Analyses

We used hierarchical multi-species models to examine trends and demographic responses in an assemblage of 31 bird species to human footprint (Saracco et al. 2018, 2019). We considered 4 demographic responses: (1) number of adult captures (abundance index), (2) productivity (probability of a captured bird being a juvenile [i.e. aged as “hatching-year”] bird), (3) annual adult apparent survival probability, and (4) residency probability (probability of a newly marked adult bird being a resident in the local population). We included all species with  $\geq 100$  adult captures and  $\geq 10$  between-year recaptures (Table 1).

We modeled the number of adult captures of species  $i$ , station  $j$ , and year  $t$ , based on an overdispersed Poisson distribution,  $N_{i,j,t}^a \sim \text{Pois}(\lambda_{i,j,t})$  with the mean,  $\lambda_{i,j,t}$ , modeled as a log-linear function of spatial and temporal covariates and an overdispersion parameter,  $\varepsilon_{i,j,t}$ :

$$\log(\lambda_{i,j,t}) = \beta_{0[i]} + \beta_{1[i]} hf1_j + \beta_{2[i]} hf5r_j + \beta_{3[i]} (t - t^*) + \beta_{4[i]} (t - t^*) \Delta hf_j + \beta_{5[i]} \xi_{i,j,t} + \varepsilon_{i,j,t} \quad (1)$$

The  $\beta_{0-5[i]}$  represent species-varying intercepts and regression coefficients,  $hf1_j$  is the standardized (0 mean, 1 variance) 1-km human footprint proportion,  $hf5r_j$  is the standardized residuals from a beta regression of the 5-km human footprint proportion on the 1-km human footprint proportion (pseudo- $R^2 = 0.78$ ;  $P < 0.001$ ; estimated in R [R Core Team 2019] with the *betareg* package [Cribari-Neto and Zeileis 2010]), and  $\Delta hf_j$  is the change in 5-km footprint

proportion between 2010 and 2018. The  $\beta_{3[i]}$  term represents a log-linear trend effect and the  $t^* = 5$  to center the year covariate, and the  $\beta_{4[i]}$  represents an interaction effect between year and the change in 5-km footprint. The  $\xi_{i,j,t}$  is an effort covariate calculated as weighted mean station \* year effort across the six 10-day capture periods sampled each year with weights equal to the capture-period-specific capture rate of adult birds for the species across stations divided by the average weighted mean station \* year capture-period specific effort across years. Adult captures were positively related to the effort covariate ( $\hat{\mu}_{\beta_5} = 0.10$ ; 95% credible interval [CI]: 0.07, 0.14); this effect was consistent among species ( $\hat{\sigma}_{\beta_5} = 0.02$ ; 95% CI: 0.00, 0.06; mean estimates ranging from 0.10 to 0.11). We modeled the species intercepts and regression coefficients as  $\beta_{1-5[i]} \sim \text{Norm}(\mu_{\beta_{1-5}}, \sigma_{\beta_{1-5}}^2)$  with vague priors for hyperparameters,  $\mu_{\beta_{1-5}} \sim \text{Norm}(0, 1000)$  and  $\sigma_{\beta_{1-5}} \sim U(0, 100)$ . We modeled overdispersion as  $\varepsilon_{i,j,t} \sim \text{Norm}(0, \sigma^2)$  with  $\sigma \sim U(0, 100)$ .

We also considered a model that included an interaction between year and the 1-km human footprint,  $hf1_t$  as an alternative to the model that included the year \* footprint change interaction, to test the hypothesis that trend depended on 2018 human footprint values rather than footprint change, both for the adult captures model and for the productivity and Cormack–Jolly–Seber (CJS) models described below. However, coefficient estimates were close to zero (−0.02 to 0.01) with CIs broadly overlapping zero in all cases. Coefficients of all main effects were virtually identical between the two models; thus, we present only the results for the models with main effects and year \* footprint change effects described here.

We assessed productivity based on a binomial model of the number of juvenile captures,  $N_{i,j,t}^y \sim \text{Bin}(pY_{i,j,t}, N_{i,j,t}^{y+a})$ , where  $N_{i,j,t}^y$  is the number of juvenile captures,  $pY_{i,j,t}$  represents the probability of a captured bird being a juvenile bird, and  $N_{i,j,t}^{y+a}$  is the total number of juvenile and adult captures. As for adult captures, we defined a generalized linear mixed model for  $pY_{i,j,t}$  identical to Equation (1) with the exception that we used a logit-, rather than log-, link function for the response variable. In addition, the  $\xi_{i,j,t}$  covariate in the productivity model was the ratio of juvenile effort, calculated identically to the adult effort covariate in Equation (1) but for hatching-year birds, to adult effort. Thus, this covariate controlled for the proportion of effort in capture periods when juveniles were captured relative to effort in periods when adults were predominantly captured. As for the adult captures model, productivity was positively related to the effort covariate ( $\hat{\mu}_{\beta_5} = 0.04$ ; 95% CI: 0.00, 0.08), which was consistent among species with mean

estimates ranging from 0.03 to 0.06 ( $\hat{\sigma}_{\beta_5} = 0.03$ ; 95% CI: 0.00, 0.09). We expressed mean species-level productivity as the exponentiated intercepts from the model to provide estimates on a scale of number of juveniles per adult bird captured. We used prior distributions identical to those defined above for the adult captures model with exception to standard deviation hyperparameters, for which we used  $\sigma \sim U(0, 10)$ .

We modeled adult apparent survival,  $\phi_{i,j,t}$ , and residency,  $\pi_{i,j,t}$ , probabilities by applying a state-space version of a CJS model that accounts for transients to individual adult capture–recapture histories (Saracco *et al.* 2012). As with the productivity model, we allowed survival and residency to vary according to a logit-linear function of the human footprint covariates; however, we did not include effort or overdispersion parameters. The CJS model includes models for parameters describing the observation process, capture probability,  $p_{i,j,t}$ , and probability of recapturing a resident adult bird  $\geq 6$  days apart in the season it was banded (i.e. probability of predetermining a newly marked bird as a resident,  $\rho_{i,j,t}$  based on the assumption that multiple captures at least 6 days apart is an accurate indicator of residency; Saracco *et al.* 2012). For these parameters, we defined logit-linear models including random species-varying intercepts and zero-mean random species \* station effects with species-specific variances. For all CJS model intercept means, we defined priors for inverse-logit transformed values as  $U(0, 1)$ , rather than modeling these species means on a link-scale. Otherwise, vague prior distributions were defined as described above for the adult captures and productivity models.

We implemented models with JAGS (Plummer 2003) in R (R Core Team 2021) via the *jagsUI* package (Kellner 2021). Posterior inferences were based on running 4 Markov chain Monte Carlo simulations (Gilks *et al.* 1996) of 100,000 iterations following an adaptive phase of 20,000 iterations, burn-in phase of 20,000 iterations, and thinning chains by 10 (total iterations kept = 32,000). For adult capture rate and productivity models, we assessed goodness-of-fit based on Bayesian  $P$ -values, which enumerate the frequencies of differences in chi-square ( $\chi^2$ ) statistics between observed data and data generated at each MCMC iteration (Kéry and Royle 2016). Results of both models suggested adequate fit ( $P = 0.27$  for the adult captures model, and  $P = 0.71$  for the productivity model). We report all parameter estimates as posterior distribution means with 95% CIs and consider effect estimates with 95% CIs not overlapping zero to be statistically significant.

## RESULTS

Mean station-scale estimates of avian response variables based on the midpoint year (2015) and average disturbance values for each of the 31 species included in the analyses are reported in Table 2. The number of adults captured/station/year where a bird was encountered as a breeding species averaged 1.18 [0.85, 1.16] and varied from 0.36 for Dark-eyed Junco to 9.31 for Tennessee Warbler. Productivity at these stations averaged 0.57 [0.42, 0.75] and ranged from 0.12 for Alder Flycatcher to 2.71 for Black-capped Chickadee. Adult annual apparent survival probability across species averaged 0.43 [0.37, 0.48] and ranged from 0.17 for Tennessee Warbler to 0.60 for Canada Jay. Residency probability averaged 0.55 [0.48, 0.62] and ranged from <0.4 for Alder Flycatcher, Least Flycatcher, and Wilson's Warbler to 0.73 for Black-capped Chickadee.

## Adult Captures

We found little evidence of an overall effect of human footprint on the mean adult abundance index for the 31 bird species at either the 1-km ( $\hat{\mu}_{\beta_1} = 0.04$  [0.16, 0.23]) or 5-km ( $\hat{\mu}_{\beta_2} = 0.02$  [0.07, 0.11]) footprint scales (Figure 2A and B). Nevertheless, there was high variation among species in responses to footprint ( $\hat{\sigma}_{\beta_1} = 0.52$  [0.39, 0.70];  $\hat{\sigma}_{\beta_2} = 0.23$  [0.17, 0.31]). Seven species (23%) showed significant negative, and 11 species (35%) showed significant positive, adult abundance-footprint relationships at the 1-km scale; and 5 species (16%) showed significant negative, and 8 species (26%) showed significant positive, relationships between adult abundance and the 5-km human footprint residuals (Figure 2D and E). Four species had significant negative relationships with footprint at both scales (Canada Warbler, Mourning Warbler, Magnolia Warbler, and Yellow-rumped Warbler), while one species had contrasting relationships between scales (Least Flycatcher: positive at 1-km and negative at 5-km radii). As expected, adult captures of species more frequently captured at stations with greater tree cover tended to be more negatively affected by footprint than species that were more commonly encountered at earlier successional stations with less tree cover, particularly at the 1-km scale.

The average species adult abundance index declined over the study period ( $\hat{\mu}_{\beta_3} = 0.04$  [0.07, 0.01]); however, here too there was high variation among species ( $\hat{\sigma}_{\beta_3} = 0.08$  [0.06, 0.11]; Figure 2C). We found significant negative trends for 11 species that tended to be associated with more forested habitats; while 2 other species associated with earlier successional habitats, showed significant positive trends (Clay-colored Sparrow and Alder Flycatcher; Figure 2F).

## Productivity

We found little evidence of a relationship between average species productivity and human footprint at the 1-km scale ( $\hat{\mu}_{\beta_1} = 0.00$  [0.08, 0.09]; Figure 3A). However, there was high variation among species ( $\hat{\sigma}_{\beta_1} = 0.19$  [0.12, 0.28]): 3 species showed significant negative relationships (White-throated Sparrow, Swamp Sparrow, Least Flycatcher) and 2 species showed significant positive relationships (Tennessee Warbler, Yellow-rumped Warbler) at that scale (Figure 3D). In contrast, we found an overall positive relationship between productivity and human footprint at the 5-km scale after accounting for footprint at the 1-km scale ( $\hat{\mu}_{\beta_2} = 0.11$  [0.04, 0.19]; Figure 3B). This effect was highly variable among species ( $\hat{\sigma}_{\beta_2} = 0.17$  [0.11, 0.25]). Six species (19%) had positive effects with 95% CIs not overlapping zero, but only one had a negative effect with 95% CIs not overlapping zero (Hermit Thrush; Figure 3E).

There was a relatively consistent decline in productivity across species ( $\hat{\mu}_{\beta_3} = -0.07$  [-0.09, -0.05]) across years (Figure 3C), with species mean estimates ranging from -0.04 to -0.11 ( $\hat{\sigma}_{\beta_3} = 0.03$  [0.00, 0.06]; Figure 3F). There was no apparent association between productivity trends or responses to disturbance and tree cover associations of adult captures.

## Adult Apparent Survival Probability

Adult apparent survival probability tended to be positively associated with human footprint ( $\hat{\mu}_{\beta_1} = 0.06$  [-0.03, 0.14] and  $\hat{\mu}_{\beta_2} = 0.04$  [-0.03, 0.12]; Figure 4A and B). Although there was some variation among species ( $\hat{\sigma}_{\beta_1} = 0.06$  [0.00, 0.19] and  $\hat{\sigma}_{\beta_2} = 0.06$  [0.00, 0.16]), all species coefficients for footprint effects had 95%

**TABLE 2.** Mean (95% CIs) estimates of avian response variables for 31 bird species captured at 38 MAPS stations from 2011 to 2020 in the Athabasca oil sands region based on posterior distributions of back-transformed intercepts from multi-species demographic models. Scientific names are presented in Table 1.

Common name	Adult abundance index (birds/station)	Productivity index (juveniles/adult)	Adult apparent survival probability	Residency probability
Yellow-bellied Sapsucker	1.00 (0.81, 1.22)	0.37 (0.28, 0.48)	0.31 (0.22, 0.4)	0.66 (0.52, 0.82)
Alder Flycatcher	3.37 (2.90, 3.89)	0.12 (0.10, 0.14)	0.49 (0.42, 0.57)	0.35 (0.29, 0.42)
Least Flycatcher	1.31 (1.09, 1.57)	0.55 (0.44, 0.68)	0.27 (0.16, 0.39)	0.39 (0.26, 0.56)
Red-eyed Vireo	1.93 (1.63, 2.26)	0.13 (0.10, 0.17)	0.54 (0.45, 0.63)	0.60 (0.46, 0.77)
Canada Jay	0.37 (0.28, 0.47)	1.16 (0.83, 1.57)	0.60 (0.47, 0.73)	0.67 (0.49, 0.86)
Black-capped Chickadee	0.78 (0.65, 0.94)	2.71 (2.22, 3.28)	0.56 (0.47, 0.67)	0.73 (0.58, 0.87)
Boreal Chickadee	0.47 (0.37, 0.58)	1.54 (1.17, 1.98)	0.43 (0.30, 0.56)	0.63 (0.46, 0.82)
Swainson's Thrush	3.38 (2.91, 3.90)	0.51 (0.43, 0.59)	0.56 (0.50, 0.63)	0.47 (0.38, 0.58)
Hermit Thrush	0.45 (0.35, 0.56)	0.88 (0.65, 1.16)	0.42 (0.29, 0.57)	0.51 (0.33, 0.71)
American Robin	1.60 (1.36, 1.87)	0.19 (0.15, 0.24)	0.46 (0.37, 0.54)	0.67 (0.53, 0.84)
Tennessee Warbler	9.31 (8.16, 10.58)	0.73 (0.64, 0.82)	0.17 (0.06, 0.34)	0.51 (0.33, 0.72)
Yellow Warbler	0.88 (0.70, 1.10)	0.64 (0.48, 0.85)	0.44 (0.35, 0.54)	0.53 (0.41, 0.67)
Magnolia Warbler	1.14 (0.91, 1.39)	0.57 (0.44, 0.73)	0.46 (0.37, 0.55)	0.53 (0.42, 0.65)
Yellow-rumped Warbler	0.93 (0.76, 1.12)	0.40 (0.31, 0.51)	0.38 (0.28, 0.49)	0.57 (0.42, 0.74)
Black-and-white Warbler	0.95 (0.79, 1.14)	0.55 (0.43, 0.68)	0.44 (0.32, 0.57)	0.52 (0.34, 0.72)
American Redstart	0.66 (0.51, 0.82)	0.42 (0.30, 0.58)	0.49 (0.37, 0.61)	0.58 (0.39, 0.78)
Ovenbird	1.88 (1.61, 2.19)	0.51 (0.43, 0.61)	0.30 (0.21, 0.41)	0.47 (0.32, 0.64)
Northern Waterthrush	0.58 (0.44, 0.73)	0.75 (0.53, 1.02)	0.56 (0.44, 0.69)	0.55 (0.38, 0.74)
Mourning Warbler	1.40 (1.07, 1.79)	0.37 (0.27, 0.49)	0.57 (0.48, 0.66)	0.55 (0.44, 0.68)
Common Yellowthroat	0.83 (0.67, 1.00)	0.25 (0.18, 0.34)	0.42 (0.29, 0.55)	0.63 (0.47, 0.80)
Wilson's Warbler	0.69 (0.55, 0.86)	0.72 (0.54, 0.93)	0.35 (0.21, 0.51)	0.34 (0.21, 0.52)
Canada Warbler	1.36 (1.09, 1.68)	0.76 (0.59, 0.95)	0.44 (0.33, 0.55)	0.46 (0.32, 0.62)
Chipping Sparrow	2.74 (2.36, 3.17)	0.25 (0.21, 0.30)	0.40 (0.31, 0.51)	0.54 (0.40, 0.69)
Clay-colored Sparrow	0.89 (0.68, 1.13)	0.67 (0.49, 0.89)	0.38 (0.28, 0.49)	0.57 (0.44, 0.71)
Savannah Sparrow	3.82 (0.88, 11.66)	0.49 (0.22, 0.94)	0.46 (0.35, 0.58)	0.65 (0.49, 0.81)
Song Sparrow	0.39 (0.29, 0.51)	0.99 (0.69, 1.37)	0.35 (0.24, 0.47)	0.58 (0.44, 0.74)
Lincoln's Sparrow	1.80 (1.53, 2.09)	1.02 (0.86, 1.20)	0.41 (0.34, 0.49)	0.61 (0.52, 0.72)
Swamp Sparrow	0.98 (0.79, 1.19)	1.44 (1.14, 1.80)	0.31 (0.20, 0.43)	0.59 (0.48, 0.73)
White-throated Sparrow	6.89 (6.00, 7.88)	0.52 (0.45, 0.59)	0.41 (0.37, 0.45)	0.68 (0.62, 0.75)
Dark-eyed Junco	0.36 (0.24, 0.50)	2.35 (1.64, 3.31)	0.52 (0.37, 0.67)	0.54 (0.37, 0.73)
Rose-breasted Grosbeak	0.55 (0.43, 0.69)	0.25 (0.16, 0.36)	0.49 (0.34, 0.65)	0.48 (0.28, 0.71)

CIs overlapping zero (Figure 4D and E). Adult apparent survival probability tended to decline over the study period ( $\hat{\mu}_{\beta_3} = -0.03$  [−0.08, 0.02]; Figure 4C). Twenty-three species (74%) had mean survival trend estimates < 0; however, as for the footprint effects, 95% CIs on mean trend estimates for all species overlapped zero (Figure 4F).

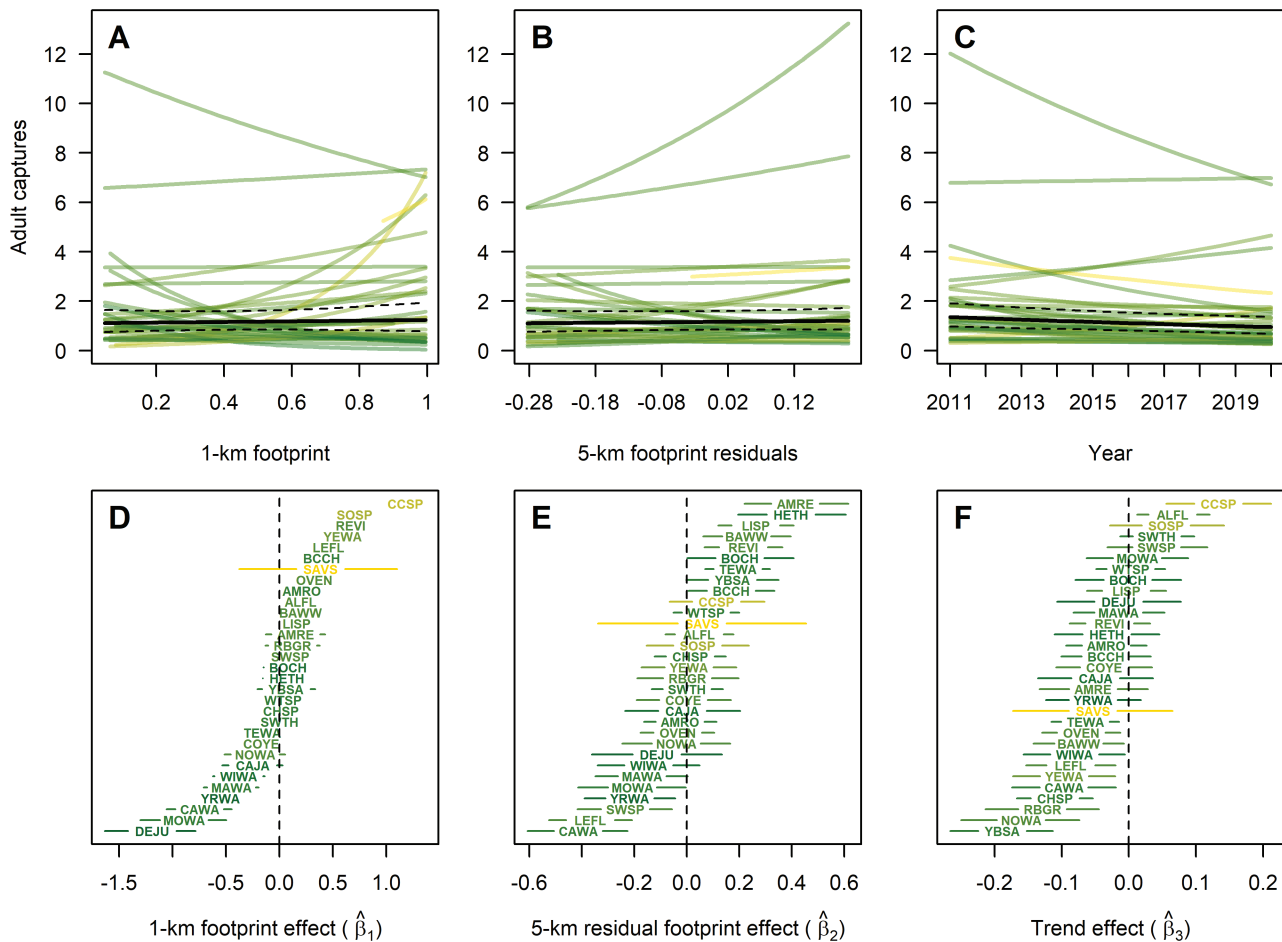
### Residency Probability

Residency probability was negatively associated with human footprint at the 1-km scale ( $\hat{\mu}_{\beta_1} = -0.16$  [−0.33, −0.01];  $\hat{\sigma}_{\beta_1} = 0.10$  [0.00, 0.28]; Figure 5A). Thus, newly marked birds were more likely to be transients in habitats that were more disturbed at this scale. All species mean effect estimates for the 1-km footprint covariate were negative and several had 95% CIs < 0 (Alder Flycatcher, Swainson's Thrush, Lincoln's Sparrow; Figure 4D). We found little evidence of an effect of a 5-km footprint, after accounting for the 1-km footprint, on mean species residency probability ( $\hat{\mu}_{\beta_2} = -0.05$  [−0.17, 0.07];  $\hat{\sigma}_{\beta_2} = 0.17$  [0.02, 0.34]; Figure 5B) or individual species residency probabilities (Figure 5E). Mean species residency probability declined over the study period ( $\hat{\mu}_{\beta_3} = -0.05$

[−0.09, −0.01]). Although variable ( $\hat{\sigma}_{\beta_3} = 0.05$  [0.01, 0.10]), mean species trend estimates were negative for all species, and 95% CIs were < 0 for 3 species (Yellow Warbler, Ovenbird, Chipping Sparrow; Figure 5C and F).

### Trend Dependence on Change in Footprint

Trends in adult captures were more negative at stations with larger increases in 5-km radius human footprint proportion over the study period ( $\hat{\mu}_{\beta_4} = -0.03$  [−0.04, −0.01]; Figure 6A), with mean estimates for all species effect ranging from −0.02 to −0.04 ( $\hat{\sigma}_{\beta_4} = 0.01$  [0.00, 0.04]). Productivity showed a very similar pattern in average trends ( $\hat{\mu}_{\beta_4} = -0.02$  [−0.04, −0.00]; Figure 6B), again with relatively little variation among species with mean estimates for all species ranging from −0.01 to −0.03 ( $\hat{\sigma}_{\beta_4} = 0.02$  [0.00, 0.04]). Average adult apparent survival trend also tended to be more negative at sites with greater footprint increases ( $\hat{\mu}_{\beta_4} = -0.03$  [−0.07, 0.01]; Figure 6C), although the year × footprint change effect was more variable among species for the survival model ( $\hat{\sigma}_{\beta_4} = 0.05$  [0.00, 0.11]), ranging from  $\hat{\beta}_4 = -0.06$  (−0.14, −0.01) for White-throated Sparrow to  $\hat{\beta}_4 = 0.02$  (−0.07, 0.18) for



**FIGURE 2.** Predicted responses (A–C) and effect sizes (D–F) for a multi-species hierarchical model of adult captures per station and year varying as a log-linear function of the human footprint proportion at 1-km radius (A, D), the human footprint proportion at 5-km radius after accounting for correlation between 1-km and 5-km footprints (B, E), and year (i.e. trend across the 10-year [2011–2020] period; C, F). Solid black lines in A–C represent medians of the mean species responses; dashed lines delineate 95% credible intervals. Individual species responses in A–C are represented with lines indicating the median posterior prediction. Species codes in D–F (see Table 1) show positions of median effect sizes and error bars indicate 95% credible intervals. Shading spans a canopy-cover gradient whereby species most frequently caught at stations with relatively low tree cover are lighter and species most frequently caught at sites with greater tree cover are darker. Vertical dashed lines at 0.0 in D–F are added for reference.

Mourning Warbler. We found little evidence that residency probability trends varied with footprint change ( $\hat{\mu}_{\beta_4} = 0.00$  [–0.03, 0.04]; Figure 6D) with all individual species having 95% CIs overlapping zero and ranging from  $\hat{\beta}_4 = -0.02$  (–0.12, 0.03) for Least Flycatcher to  $\hat{\beta}_4 = 0.03$  (–0.03, 0.12) for Swainson’s Thrush ( $\hat{\sigma}_{\beta_4} = 0.03$  [0.00, 0.08]).

## DISCUSSION

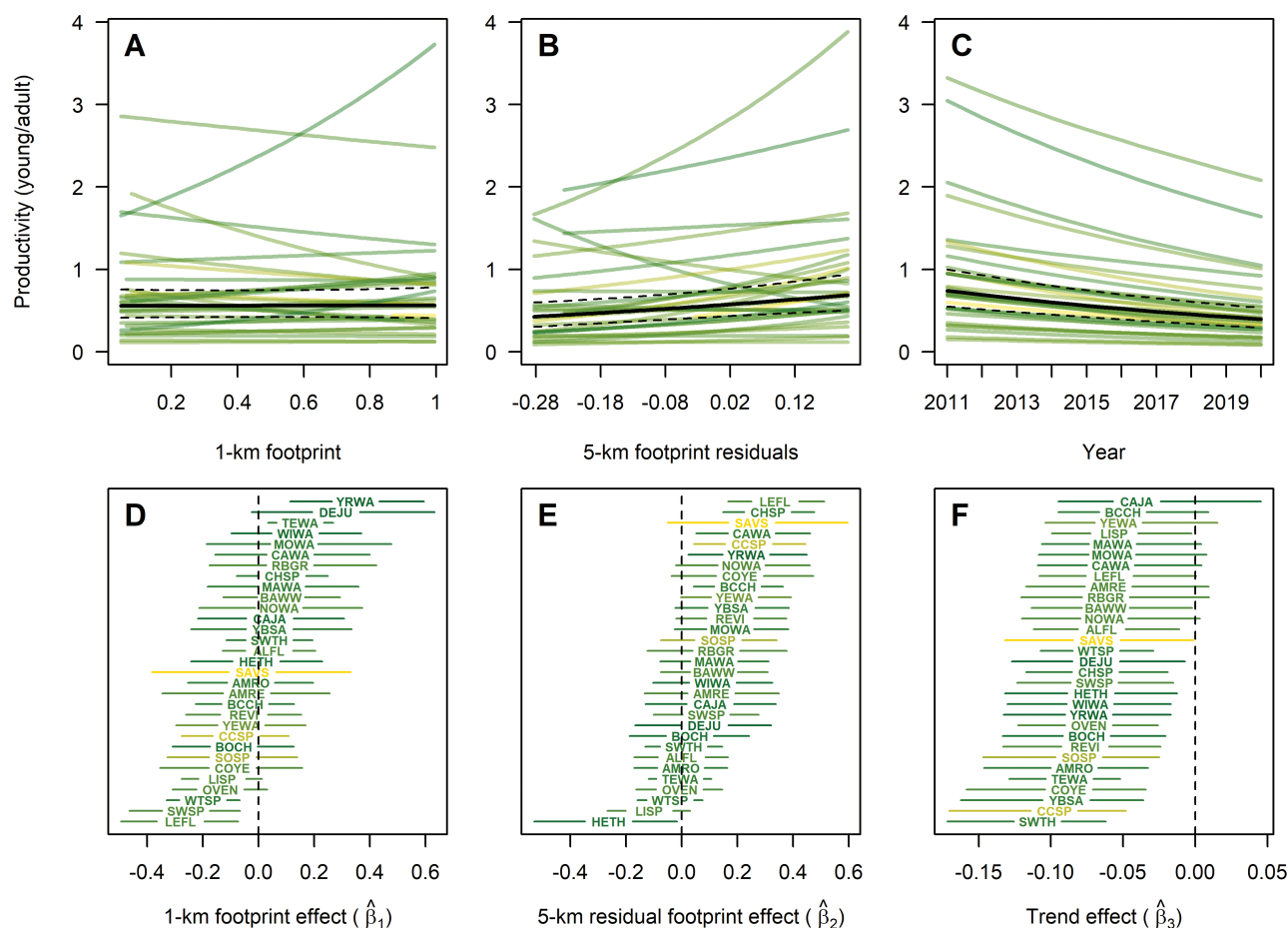
Support for the hypothesis of negative effects of landscape scale disturbance on demographic parameters of the 31 bird species included in our analyses was mixed. This result is consistent with those of previous work that showed a variety of responses among species and demographic parameters to habitat and disturbance at local scales (Bayne *et al.* 2016, Foster *et al.* 2017, Mahon *et al.* 2019, Pyle *et al.* 2020). Our multi-species approach and test of responses to an overall disturbance metric do not capture individual species responses to specific habitat characteristics, such as types of fragmentation or disturbance (e.g., linear features; Bayne *et al.* 2016), or the specific spatial scales relevant to individual species and

how they perceive their habitats (Betts *et al.* 2014, Mahon *et al.* 2016, 2019); rather, our results highlight a variety of community-level and individual species-level responses habitat disturbances related to oil sands resource development in northeastern Alberta.

Of particular interest was the tendency for declines in abundance and demographic rates over time. These declines could reflect, in part, increasing human footprint across the region (ABMI 2017). Indeed, we found footprint increases between 2010 and 2018 at 36 of our 38 study sites, and our demographic models suggested trends in abundance, productivity, and survival were all more negative at sites with larger increases in footprint. The consistency of demographic responses to footprint changes among species, despite variation among species responses to overall footprint, suggests the importance of landcover type and age. For example, footprint increases between 2010 and 2018 would be expected to largely represent new industrial development, and thus loss of habitat for all species, while preexisting footprint included regenerating habitat on previously disturbed and reclaimed sites.

While our observed changes in footprint proportion were consistent with demographic declines, other related factors



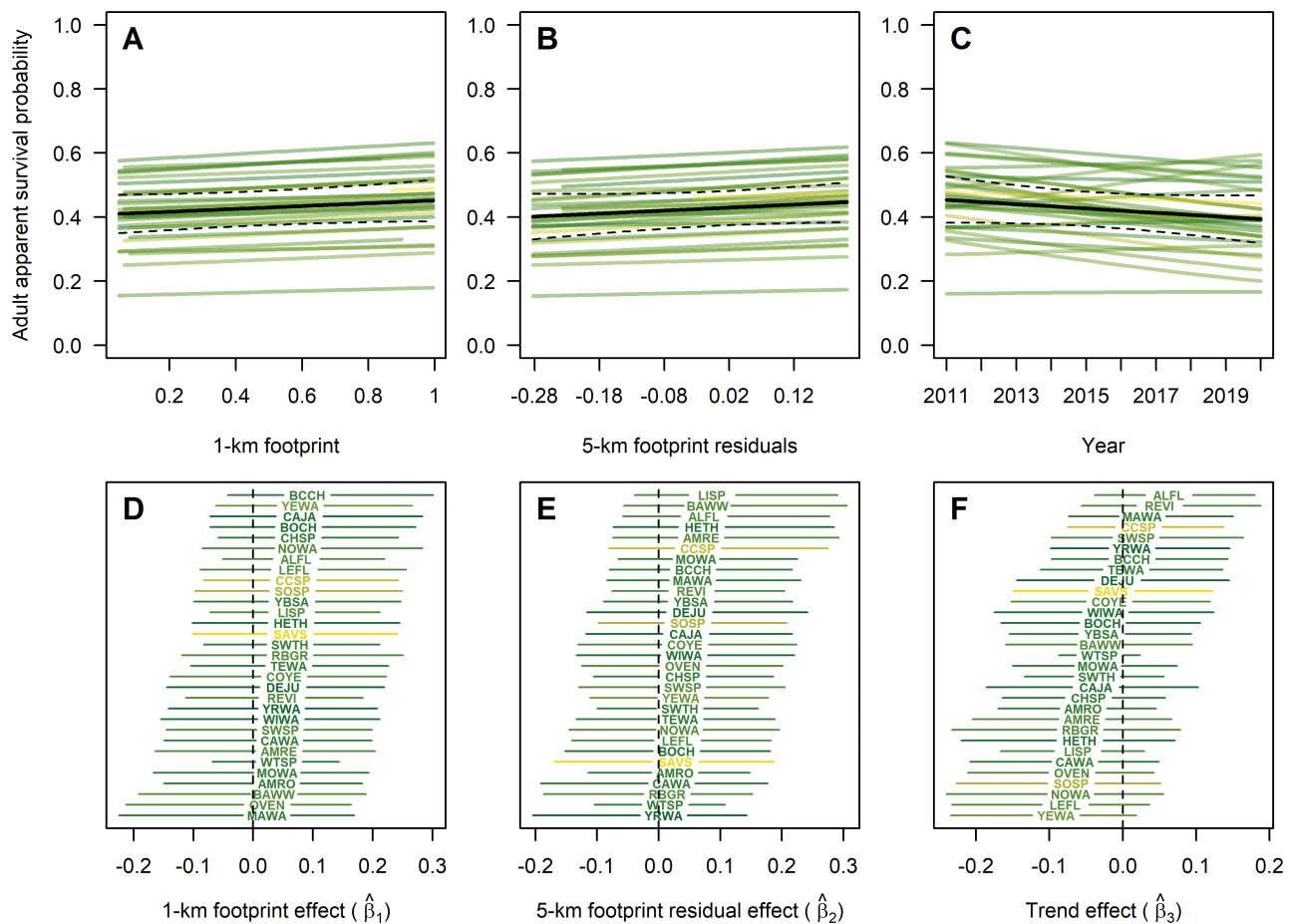


**FIGURE 3.** Predicted productivity (ratio of young to adult birds; **A–C**) and effect sizes (**D–F**) from a multi-species hierarchical model whereby the probability of a captured bird is a young (hatching-year) bird varies as a logit-linear function of the human footprint proportion at 1-km radius (**A, D**), the human footprint proportion at 5-km radius after accounting for correlation between 1-km and 5-km footprints (**B, E**), and year (i.e. trend across the 10-year [2011–2020] period; **C, F**). See [Figure 2](#) for additional detail.

may also have contributed to declines. For example, contaminants entering the food chain through air or water sources (e.g., [Kraus 2019](#), [Chibwe et al. 2021](#)) can be distributed across large spatial scales ([Brook et al. 2019](#)) and can affect diet, growth, physiology, and demographic rates of birds ([Hallinger et al. 2011](#), [Cruz-Martinez et al. 2015](#), [Ma et al. 2018](#), [Hebert 2019](#)). However, [Godwin et al. \(2019\)](#) found little indication that proximity to a contaminant source affected productivity or nestling growth of Tree Swallows (*Tachycineta bicolor*) in our study region, and population-level impacts of contaminants in this system otherwise remain largely unknown ([Roberts et al. 2022](#)). Finally, other unmodeled factors undoubtedly influenced dynamics and trajectories of populations. For example, heavy rain and flooding were observed across the region in 2013, wildfire impacted several monitoring stations in 2016, and vegetation succession on reclaimed portions of study areas all likely contributed to variation in demography and population sizes ([Foster et al. 2017](#)). Parsing the relative roles of these various contributors is beyond the scope of the present study. Future populations will be shaped by these and other drivers related to climate and landcover change ([Stralberg et al. 2015](#)); thus, understanding how these factors act independently and in combination to affect population trajectories should be a priority for future research.

We found little effect of footprint on the average adult abundance index of the assemblage of 31 species at either the 1-km or 5-km scales. While abundance indices derived from mist-net samples can reflect underlying patterns of relative abundance ([Dunn and Ralph 2004](#)), differences in habitat structure or disturbance and nuances of net placement in relation to habitat may also affect availability for capture ([Remsen, and Good 1996](#)) or numbers of transient individuals ([Silkey et al. 1999](#)). We selected net sites in a manner intended to minimize inter- and intra-station differences in net capture efficacy ([DeSante et al. 2004](#)). Therefore, we suggest that patterns in our abundance index largely mirrored underlying patterns of abundance, rather than patterns of capture probability.

Species showing the strongest positive responses of adult captures to footprint included those more frequently captured at stations with less tree cover and that favor open and younger deciduous habitats and forest openings (e.g., Alder Flycatcher, Clay-colored Sparrow, Song Sparrow, Yellow Warbler; [Schieck and Song 2011](#)). However, Red-eyed Vireo and Ovenbird (species associated with older deciduous and mixed forest types; [Schieck and Song 2011](#)) also showed positive adult capture responses to disturbance, consistent with the findings of [Mahon et al. \(2019\)](#). Nevertheless, these species may be less abundant near specific disturbance types such as seismic lines, pipelines, and well pads ([Bayne et al.](#)



**FIGURE 4.** Predicted adult apparent survival probability (**A–C**) and effect sizes (**D–F**) from a multi-species hierarchical model whereby survival probability varies as a logit-linear function of the human footprint proportion at 1-km radius (**A**, **D**), the human footprint proportion at 5-km radius after accounting for correlation between 1-km and 5-km footprints (**B**, **E**), and year (i.e. trend across the 10-year [2011–2020] period; **C**, **F**). See Figure 2 for additional detail.

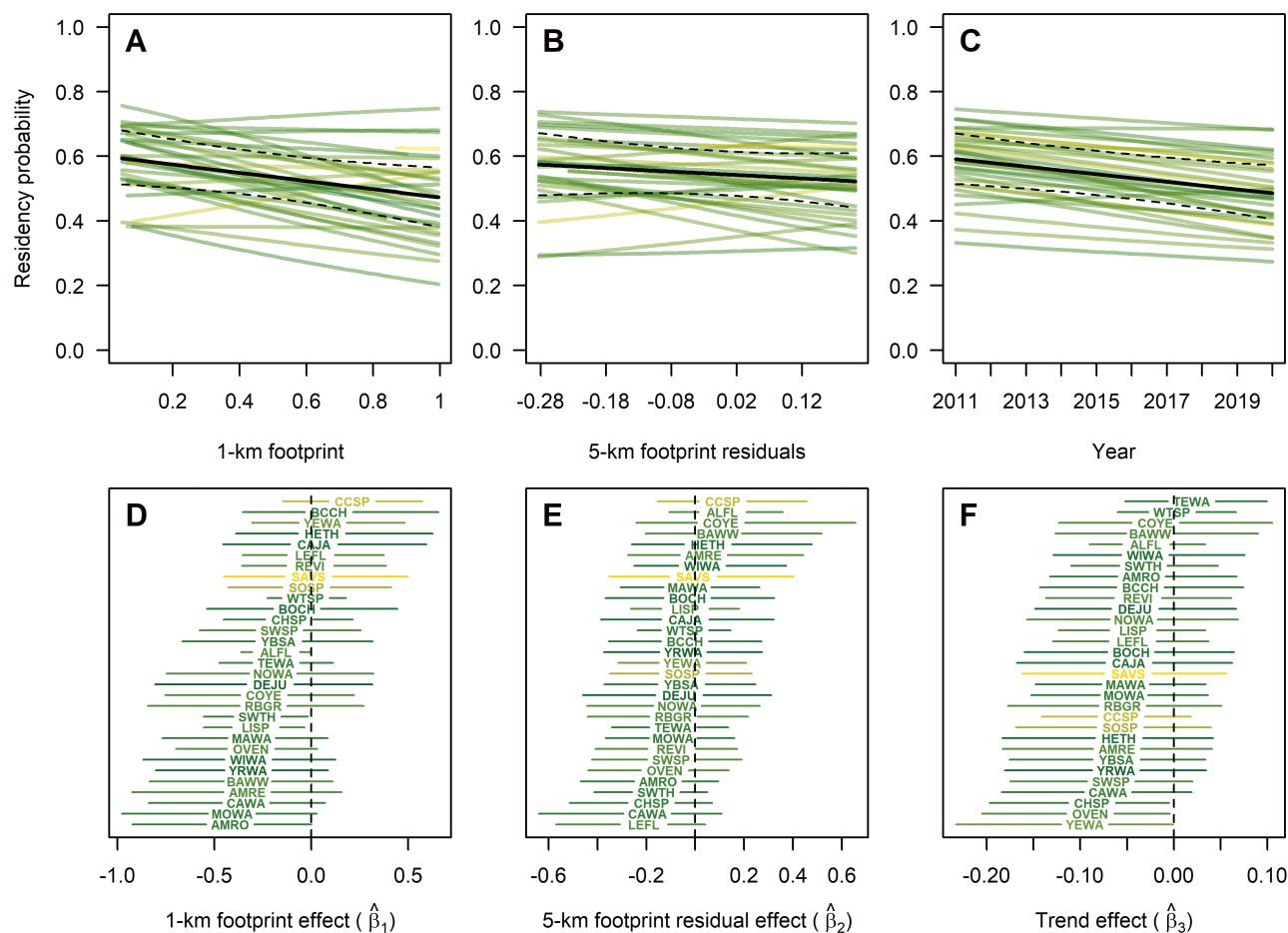
2016). Adult captures of Canada Warbler, a species of conservation concern in Canada (Alberta Environment and Parks 2015, Environment and Climate Change Canada 2019), showed consistent negative responses to human footprint and strong decline in captures over the study period. This finding is consistent with results reported by Wilson *et al.* (2018), which relied in part on data included here, though that study found that declines likely also reflected low survival and recruitment correlated with habitat loss on wintering grounds.

We found no consistent response of productivity to human footprint proportion at the 1-km scale. Nevertheless, our hypothesis of negative footprint effects on productivity was supported for several species at that scale and could reflect loss or degradation of preferred nesting habitat (Hethcoat and Chalfoun 2015), although other correlated factors, such as noise associated with industrial activities, could also play a role (Williams *et al.* 2021). Only 2 species showed significant positive productivity responses to disturbance at the 1-km scale (Tennessee Warbler and Yellow-rumped Warbler). These positive responses suggest that regenerating vegetation in reclaimed or post-fire sites could provide cover for nest sites or food resources for post-fledging birds. We generally found little correspondence between adult capture responses of individual species to footprint and their productivity responses to footprint, which highlights the value of considering demographic (i.e. vital rate,

or population change parameters), as well as abundance responses, to better elucidate patterns of habitat quality (Johnson 2007, Skaggs *et al.* 2020). For example, we found that Dark-eyed Junco and Yellow-rumped Warbler were among the species whose adult abundance index values were most negatively affected by footprint; however, productivity of these 2 species tended to be higher in more disturbed landscapes, suggesting that the few individuals that nested there were productive (particularly at the 1-km scale). In contrast, other species showed the opposite pattern—positive responses of adults to footprint, but lower productivity in those landscapes (e.g., Ovenbird, Least Flycatcher), suggesting that these landscapes may represent an ecological trap for at least some species (Van Horne 1983).

At the 5-km scale, after accounting for footprint correlation between the 1-km and 5-km scales, we found an overall positive relationship between productivity and disturbance. This could reflect age-specific patterns of movement and the relative importance of early successional habitat for post-breeding birds (Marshall *et al.* 2003, Chandler *et al.* 2012), particularly for juveniles (Anders *et al.* 1998, Perneluzi *et al.* 2014). Thus, restoration of habitat in disturbed areas may contribute to population sustainability for some species, even in cases where breeding use may be limited.

We found little effect of disturbance at the 1- and 5-km distances from our banding stations on adult apparent survival



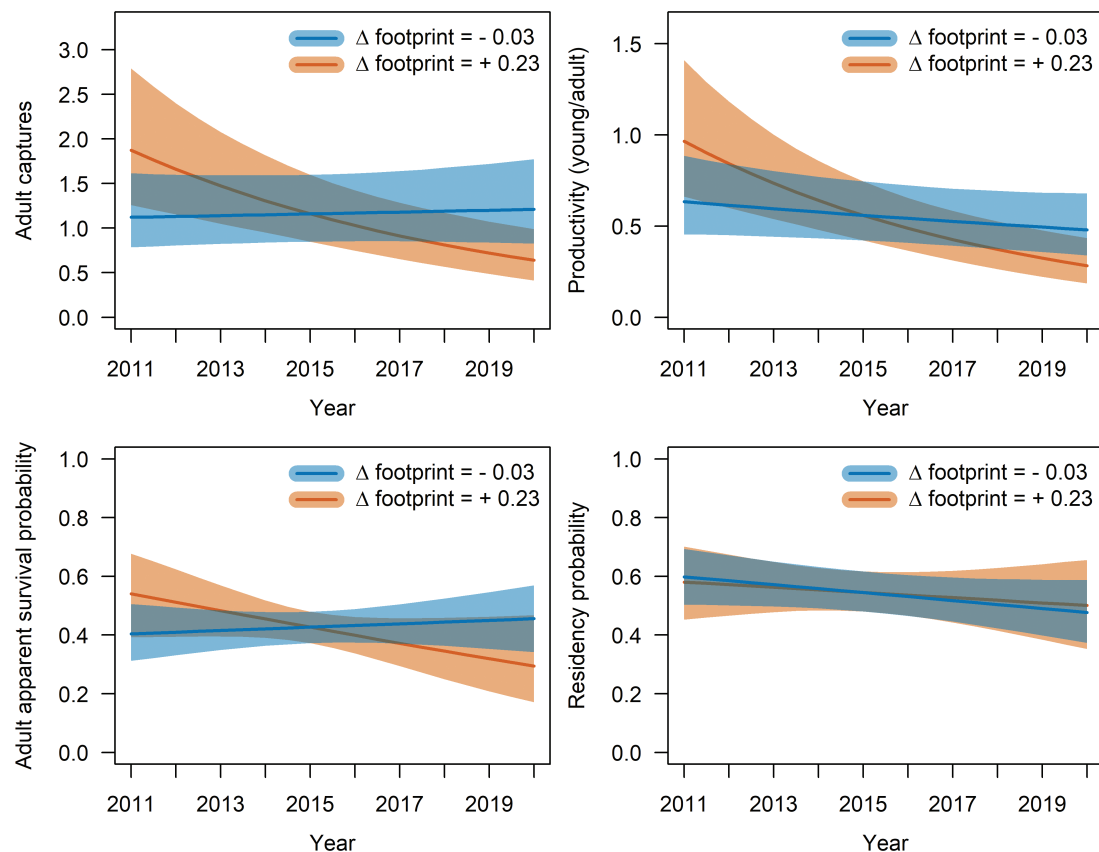
**FIGURE 5.** Predicted residency probability (probability of a newly marked individual being a resident; **A–C**) and effect sizes (**D–F**) from a multi-species hierarchical model whereby residency probability varies as a logit-linear function of the human footprint proportion at 1-km radius (**A**, **D**), the human footprint proportion at 5-km radius after accounting for correlation between 1-km and 5-km footprints (**B**, **E**), and year (i.e. trend across the 10-year [2011–2020] period; **C**, **F**). See Figure 2 for additional detail.

probability and only weak evidence of a decline in survival over the study period. The relative lack of signal in the survival response to local disturbance could reflect the influence of non-breeding ground effects in driving this vital rate; for example, as described for Canada Warbler by Wilson et al. (2018). Assessment of the influence of survival rates and trends inclusive of wintering ground habitat change will require greater detail on the connectivity of populations and habitats across the annual cycle as well as detailed habitat and disturbance mapping information for the wintering ranges, information that is currently lacking for most species in our study.

We found a negative relationship between residency probability and disturbance within 1 km of MAPS stations. Residency may be lower in more disturbed areas due to yearling adult birds unable to establish territories (Pyle et al. 2020) or to territorial males that abandon territories due to inability to attract mates (Bayne and Hobson 2001). Particular disturbance types may also contribute to low residency rates for some species. For example, seismic lines may hinder territory establishment or defense in Ovenbirds (Lankau et al. 2013). It is worth noting, however, that because our residency metric only applies to newly marked birds, it does not measure true residency probability in the population. For example, some variation in our residency probability metric among stations may simply reflect differences in the proportions of

individuals already marked resulting from variation in capture probabilities among stations or how long the station has been operated (Hines et al. 2003). Given that the bird species considered here are relatively short-lived and that capture probabilities were relatively low (mean ~ 0.30), we do not feel that such effects substantially biased our inferences about human footprint covariate effects or trends in residency. We suggest that additional work via model development and deployment of other field techniques (e.g., radio-telemetry; Lankau et al. 2013, Kornegay et al. 2018) would be useful for better understanding spatial and temporal variation in true residency.

Despite our finding of overall declines related to disturbance or increases in disturbance, we also found that a broad array of species showed positive responses to footprint for at least one response variable or spatial scale. These positive responses likely reflect the early successional habitats that were included in our cumulative footprint metric and suggest that, while minimizing future disturbance should clearly remain a conservation priority, particularly for some species of concern (e.g., Canada Warbler), regenerating habitats on disturbed sites can also benefit bird populations. Nevertheless, we acknowledge that complex industrial landscapes such as this include multiple stressors that may act at unique temporal or spatial scales and will impact individual species



**FIGURE 6.** Trends in adult captures (A), productivity (B), and adult apparent survival probability (C) were more negative at sites that had an increasing 5-km radius human footprint proportion over the study period compared to sites with stable or declining footprint proportion. In contrast, residency probability trends (D) showed little evidence of dependence on footprint proportion. Predicted mean species relationships (median  $\pm$  95% CI) are shown for human footprint proportion change values representing the site with the greatest decline in footprint proportion (blue) compared to the site with the greatest observed increase in footprint proportion (orange).

differently. Thus, development of effective management strategies for individual species and energy sector disturbance types will benefit from an additional study aimed at understanding how various disturbance and habitat types, as well as various pathways to habitat recovery, affect bird populations. For example, while the main contributors to our human footprint proportion were larger disturbance types subject to reclamation requirements, others (e.g., seismic lines) are not and may regenerate more slowly than reclaimed sites or sites disturbed by forest fire (Barber *et al.* 2021) and so may have longer lasting impacts on bird populations. Finally, understanding the potential role that non-breeding habitats play in contributing to population trends must also be considered in conservation efforts for migratory species.

## Supplementary material

Supplementary material is available at *Ornithological Applications* online.

## Acknowledgments

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## Ethics statement

All birds were captured and banded following protocols and permits issued by the Canadian Wildlife Service Bird Banding Office (Master Permit 10858) and Alberta Environment and Parks.

## Author contributions

K.R.F., C.M.G., P.P., and D.R.K. conceived the program; K.R.F. and C.M.G. managed and executed the field program; J.F.S., P.P., D.R.K., M.K., K.R.F., and C.M.G. wrote the paper; J.F.S. and D.R.K. analyzed the data.

## Data availability

Analyses reported in this article can be reproduced using the data provided by Saracco *et al.* (2022).



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