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Research Paper

Avian response to plant community composition and structure in regenerating timber harvests protected by ungulate exclusion fencing

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ABSTRACT. Forests of eastern North America have been negatively impacted by excessive white-tailed deer browsing for decades. Previous studies have shown how deer-driven changes to forest structure, plant species composition, and microhabitat negatively impact forest birds. However, most experimental studies used relatively small plot sizes with few replications, limiting the transferability of findings to operational-scale timber harvests and landscape-scale management. We studied the influence of white-tailed deer browsing on breeding bird communities in ten pairs of operational-sized fenced and unfenced regeneration timber harvests in northcentral Pennsylvania. Based on a previous study that examined correlations between bird and deer abundance in Pennsylvania, we developed species-specific predictions about how density would vary between fenced and unfenced harvests. We predicted six species would show a negative response to deer and three would show a neutral response. Overall, diversity and composition of breeding bird communities did not differ between fenced and unfenced harvests. However, four species showed a negative response to deer, four showed a neutral response to deer, and one showed a positive response to deer. Thus, six of nine focal species aligned with our predictions: negative ($n = 4$) and neutral ($n = 2$). Densities of two remaining focal species were associated with vegetative features that also were consistent with our predictions. Our final focal species showed a strong positive association with unfenced harvests, contrary to our prediction. Our findings demonstrate that deer-induced impacts on vegetation in operational-scale timber harvests can have considerable influence on densities of some avian species. We conclude that the use of deer-exclusion fencing after timber harvests is an effective and sometimes necessary management tool to achieve maximum forestry and wildlife benefits.

Réponse des oiseaux à la composition et à la structure de la communauté végétale dans des parterres de coupe en régénération protégés par des clôtures d'exclusion des ongulés

RÉSUMÉ. Les forêts de l'Est de l'Amérique du Nord subissent l'impact négatif du broutage excessif des cerfs de Virginie depuis des décennies. Des études antérieures ont montré de quelle façon les changements apportés par le cerf à la structure de la forêt, à la composition des espèces végétales et au micro-habitat ont un impact négatif sur les oiseaux forestiers. Cependant, la plupart des études expérimentales ont utilisé des parcelles de taille relativement petite, avec peu de répétitions, limitant du coup la transférabilité des résultats à l'échelle opérationnelle de la récolte de bois et à la gestion à l'échelle du paysage. Nous avons étudié l'influence du broutage des cerfs de Virginie sur les communautés d'oiseaux nicheurs dans dix paires de parterres de coupe en régénération clôturés et non clôturés dans le centre-nord de la Pennsylvanie. Sur la base d'une étude précédente ayant examiné les corrélations entre l'abondance des oiseaux et des cerfs en Pennsylvanie, nous avons élaboré des prédictions spécifiques à chaque espèce quant à la variation de leur densité entre les parterres clôturés ou non clôturés. Nous avons prédit que six espèces présenteraient une réponse négative au cerf et trois une réponse neutre. Dans l'ensemble, la diversité et la composition des communautés d'oiseaux nicheurs n'ont pas différé entre les parterres clôturés ou non clôturés. Toutefois, quatre espèces ont montré une réponse négative au cerf, quatre ont eu une réponse neutre et une a réagi positivement au cerf. Ainsi, la réponse de six des neuf espèces focales correspondait à nos prédictions : négative ($n = 4$) et neutre ($n = 2$). Les densités de deux autres espèces focales étaient associées à des caractéristiques végétales qui correspondaient également à nos prédictions. La dernière espèce focale a montré une forte association positive avec les parterres non clôturés, contrairement à notre prédiction. Nos résultats indiquent que l'impact du cerf sur la végétation lors de récoltes forestières à l'échelle opérationnelle peut avoir une influence considérable sur les densités de certaines espèces aviaires. À notre avis, l'utilisation de clôtures d'exclusion des cerfs après la récolte de bois s'avère un outil de gestion efficace et parfois nécessaire pour qu'on obtienne le maximum d'avantages en matière de foresterie et de faune.

Key Words: *Browsing; forest management; herbivory; hierarchical distance modeling; ungulates; white-tailed deer*

INTRODUCTION

During the past half-century, 63.5% of all eastern forest bird species have declined in abundance (Rosenberg et al. 2019), emphasizing the need to understand how forest birds respond to habitat conditions. Forest birds rely on several vegetation features to forage, nest, and rear young (e.g., King et al. 2006, Raybuck et al. 2020), leading to intricate relationships among forest-bird communities and vegetation structure (James 1971, Cody 1981, Mills et al. 1991), plant species composition (Boves et al. 2013, Bellush et al. 2016), and insect prey availability (Robinson and Holmes 1982, Lynch and Whigham 1984, Bellush et al. 2016). Because of the clear relationship between forest birds and vegetation, herbivory has the potential to shape bird communities in complex ways (Rushing et al. 2020).

Browsing of seedlings and shoots by white-tailed deer (*Odocoileus virginianus*) reduces vegetative stem density, plant height, foliage density, and changes plant species composition (Gill and Beardall 2011). High deer densities can thus reduce the height of preferred forage species (Apsley and McCarthy 2004, Parker et al. 2020), such that the vegetation provides less than optimal habitat for forest birds (Baiser et al. 2008, Newson et al. 2012). Deer-induced changes in vegetation structure can negatively impact birds in a variety of ways (Fuller 2001), including reductions in the availability of invertebrate prey (Robinson and Holmes 1982, Allombert et al. 2005, Godfrey et al. 2018), reduced nest-site availability (Holway 1991, Hoover and Brittingham 1998, Schill and Yahner 2009), and increased nest predation (Martin and Roper 1988). Some avian functional groups (i.e., nesting and foraging) appear to be more sensitive than others to modification of vegetation by deer browsing (Holt et al. 2011, Chollet et al. 2016, Rushing et al. 2020). A common trend has emerged from past research on how deer impact forest birds, whereby species that nest and/or forage closer to the ground are affected more adversely than those that use the canopy for these activities (Holt et al. 2011, Chollet et al. 2016, Rushing et al. 2020).

The Mid-Atlantic region of the United States maintains the highest proportion of forest land (79%) with moderate or high browse impacts by white-tailed deer (McWilliams et al. 2018), suggesting that deer could play an important role in the dynamics of forest-bird populations in this region. For example, analyses of Breeding Bird Survey (BBS) and white-tailed deer abundance data collected over three decades revealed that avian species that nest and/or forage within the vegetation stratum accessible to deer (i.e., < 2 m) were more likely to decrease in abundance following increases in deer abundance than species that nest and/or forage higher in the canopy (i.e., > 2 m) (Rushing et al. 2020).

While previous research using BBS data is informative, field studies are warranted to test results and make more conclusive statements about deer impacts on forest birds (Rushing et al. 2020). We are aware of only a few studies that used paired deer exclusion and deer accessible plots to examine the effects of deer browsing on avian abundance (McShea and Rappole 2000, Holt et al. 2010, 2013). These studies provided insight into the effects of deer browsing on vegetation and avian communities, but used either small (≤ 0.63 ha) fenced and unfenced control plots (Holt et al. 2010, 2013) or lacked replication (< 5 replicates) and adjacency (≥ 1 km apart) (McShea and Rappole 2000). The small size of study plots may limit transferability of their findings to

larger operational-scale forest management. This limitation is particularly important because habitat management efforts for forest birds are usually performed at the stand level (i.e., Boves et al. 2013, Bakermans et al. 2015). Moreover, typical territory sizes of eastern forest passerines can range from 0.1 - 6 ha depending on the species (Billerman et al. 2020), thus studies that use small fenced and unfenced plots are unable to investigate bird community dynamics. Stand-level studies that use several adjacent paired fenced (deer excluded) and unfenced (deer accessible) operational-scale timber harvests are needed to elucidate dynamics more fully among deer, vegetation, and forest bird communities.

A recent study in Pennsylvania documented considerable differences in vegetation structure and plant community composition in pairs of adjacent fenced and unfenced timber harvests (Parker et al. 2020). In this paper, we studied breeding bird communities occupying the same series of timber harvests used by Parker et al. (2020). Our primary objective was to examine both community and species-specific responses of birds to vegetation structure and composition. Secondly, we wanted to further assess species-specific conclusions from Rushing et al. (2020), rather than guild-level links with deer abundance as previously described (Chollet and Martin 2013). We selected nine focal species that were common across our study sites (i.e., ≥ 45 detections/breeding season) that Rushing et al. (2020) found to be either negatively associated with or neutral to deer abundance. Specifically, we predicted that densities of Chestnut-sided Warbler (*Setophaga pensylvanica*), Black-and-white Warbler (*Mniotilta varia*), Gray Catbird (*Dumetella carolinensis*), Eastern Towhee (*Pipilo erythrophthalmus*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and Ovenbird (*Seiurus aurocapilla*) would be greater in fenced harvests and densities of Common Yellowthroat (*Geothlypistrichas trichas*), Field Sparrow (*Spizella pusilla*), and Red-eyed Vireo (*Vireo olivaceus*) would be equal between fenced and unfenced harvests.

METHODS

Study area

We studied forest birds in ten pairs of fenced and unfenced regenerating overstory removal timber harvests in Centre County in northcentral Pennsylvania (PA) (see Parker et al. 2020 for a more detailed description of the study area). An overstory removal harvest is part of an even-aged forest management strategy (i.e., shelterwood system) whereby nearly all canopy trees are removed from a stand to regenerate a forest (Brose et al. 2008). All harvests were on State Game Lands (SGL) managed by the Pennsylvania Game Commission (PGC): SGL 033 (7,100 ha), SGL 060 (3,540 ha), and SGL 100 (8,400 ha). All three of these SGLs were dominated by forest (88-94%), comprised of mostly dry-oak (*Quercus* spp.) heath, dry-oak mixed hardwood, and red maple (*Acer rubrum*) cover types. Each pair of fenced and unfenced sites were harvested at the same time by the same operators from 2009 - 2012. Immediately following harvest, fenced portions of the timber harvests were enclosed using 2-m tall woven-wire fencing specifically intended to exclude deer. Unfenced portions of the harvests were directly adjacent to the fenced portions and were completely accessible to deer. All regeneration was natural, and no supplemental plantings

occurred. Each pair of control (unfenced) and treatment (fenced) harvests had the same local landscape characteristics: thus, we utilized this unique management practice to assess our research objectives. Fences were not constructed explicitly for the purpose of our study. However, fenced portions were selected based on economies of scale with the intention to maximize the area of each harvest that was fenced given limited funding. Residual tree species composition and residual basal area (m^2/ha) for fenced (2.1 ± 0.58 ; mean \pm SE) and unfenced (3.3 ± 0.66) harvests were similar post-harvest. Fenced timber harvests ranged in size from 3.4 - 57.9 ha (18.8 ± 5.9 ha) and unfenced harvests ranged from 6.5 - 50 ha (20.2 ± 4.9 ha). Fencing was removed at two study sites in 2018, less than one year prior to our study. These fences were removed after foresters determined the woody regeneration had achieved heights beyond the reach of deer. We included both pairs in our study because the fencing had only recently been removed and had been in place for the first 9-10 years of stand initiation, and thus would still reveal potential differences in vegetation due to deer browsing (or lack thereof). Thus, there was some evidence of browsing in our fenced harvests, which was more thoroughly described in Parker et al. (2020). Estimated deer densities for our study area between 2009 and 2015 were 9.2-14.1 deer/ km^2 (Rushing et al. 2020). In addition to white-tailed deer, SGL 100 also supported a small population of free-ranging elk (*Cervus elaphus*).

Assessing breeding bird community

We conducted standard point count surveys to sample breeding bird communities within fenced and unfenced timber harvests (Ralph et al. 1995, Bibby et al. 2000). The number of points surveyed within a given timber harvest depended on its size and shape. We ensured that all point count locations were at least 250 m apart and ≥ 50 m from a harvest edge (if this was not possible, the survey was placed at the geometric center of the harvest). These criteria resulted in 28 fenced (range: 1-7) and 27 unfenced (range: 1-5) randomly placed survey locations. We visited each point twice to conduct avian surveys between 17 May and 7 June 2019 and 2020. Visits to the same location were separated by approximately 7 days (Huff et al. 2000). We completed all surveys between 15 minutes and 4 hours post-sunrise (Fuller and Langslow 1984, Lynch and Whigham 1984).

Each point count was conducted by a single observer ($n=4$), whereby some points were surveyed by the same observer and other times by a different observer. Observers waited one minute upon arriving at each point before initiating the survey to allow birds to settle down after potentially being disturbed (Bibby et al. 2000). We recorded date, start time, cloud cover (%), and wind level (Beaufort wind index) before starting each survey. Surveys were not conducted in unfavorable weather conditions, such as strong wind (> 4 on Beaufort wind index) or rain. During each 10-minute survey, we recorded the following for each individual detected: species, sex (if possible), detection type (visual, song, call, or other), distance from the observer when first detected (0-25 m, 25-50 m, 50-75 m, 75-100 m, > 100 m), and whether the individual was “in” or “out” of the harvest being surveyed. For example, if the observer was at a point count location 50 m from the edge and heard an individual > 50 m away in the direction of the edge, that individual was recorded as “out.” All flyover observations were also considered “out.” All point count locations were visited a third time in 2019 to conduct vegetation

surveys to characterize structure and woody species composition. Vegetation and site variables collected were: treatment (fenced or unfenced), cover variables ($n=6$), and horizontal and vertical vegetation density (for details see Parker et al. 2020).

Statistical analyses

We analyzed all data using program R version 3.5.3 (R Core Team 2019; RStudio Team 2019). Only singing males within the boundaries of the timber harvest being surveyed were included in our analyses. Additionally, detections > 100 m and individuals recorded as “out” were excluded from analyses. To compare community-level differences (i.e., not species-specific) between fenced and unfenced harvests, we ran a paired t-test comparing avian diversity, measured as effective species unit, which is the exponential of Shannon’s Diversity Index (Jost et al. 2006). Conversion of Shannon’s Diversity Index to effective number of species or the number of equally common species provides a more easily interpretable and comparable value (Jost et al. 2006). We calculated effective species unit for each point count location for both 2019 ($n=55$) and 2020 ($n=55$) and then averaged that value across points within each sample location (i.e., fenced and unfenced sites, $n=10$) to account for differences in number of points between pairs. We also examined community dissimilarity between fenced and unfenced harvests using the function *vegdist* in the package *vegan* in R to calculate Bray-Curtis Dissimilarity Index (Bray and Curtis 1957). The Bray-Curtis Dissimilarity Index provides a value for comparing compositional differences between two areas (Bray and Curtis 1957). A species was included in the analysis if it was detected during at least one visit.

We estimated density of each of our nine focal species with a hierarchical distance sampling model implemented using the *gdistsamp* function from the *unmarked* package (Fiske and Chandler 2011). The model implemented by this function is a modification of the distance sampling model proposed by Royle et al. (2004) and allows for multiple sampling occasions, between which the population is assumed to be closed. We fit the model using both visits to each point and summed the number of individuals detected for a given species into distance bins (0-25 m, 25-50 m, 50-75 m, 75-100 m). Detections > 100 m and individuals recorded as “out” were not included in these analyses. We used a two-part approach to assess a) density of each focal species between fenced and unfenced harvests and b) which vegetation or habitat variables showed the strongest relationship with the density of our focal bird species while accounting for imperfect detection (Kéry and Royle 2015). In order to use a static modeling framework for distance-based density estimates, we treated each point-year combination as a separate sample in our models ($n=110$) similar to the approach used by Fogg et al. (2014) and McNeil et al. (2020). We agree with Fogg et al. (2014) that this modeling approach better emphasizes strong associations between habitat conditions and the occupancy or density of avian species. We compared models based on AIC_c (Akaike’s Information Criterion adjusted for small sample size) values (Burnham and Anderson 2002).

When developing our models, we first established a model for detection probability before examining estimates of density or habitat and vegetation associations. We began by identifying the key function (hazard, exponential, or half normal) that best described the relationship between distance and detection probability of each species (Kéry and Royle 2015). We then ran

single covariate models that may describe additional variability in detection probability. Our detection probability covariates were ordinal date, time of day, wind, cloud cover (0-100%), precipitation (none, fog, mist, light rain, heavy rain, snow), and observer ($n=4$). For each species, all detection covariates that improved the detection model by $> 2.0 \Delta AIC_c$ when compared to the null (intercept-only) model were incorporated as detection covariates for models estimating density.

For each species, we ran two sets of models to examine factors influencing density because of the previously established relationship between deer-exclusion fencing and vegetation measurements at our study sites, whereby the use of fencing resulted in considerable differences in vegetation structure in regenerating timber harvests (Parker et al. 2020). For the first set of density models, we used only the site covariate “treatment” (fenced or unfenced) in our model to determine if there were substantial differences in the density of each focal species between treatment types. For the second set of density models, we examined the variation in the density of each focal species in relation to eight vegetation variables that could be directly influenced by deer herbivory (Table A1.1): *Rubus* spp. (hereafter *Rubus*) cover, forb cover, fern cover, grass cover, leaf litter cover, *Vaccinium* spp. (blueberry) and *Gaylussacia baccata* (huckleberry) cover, horizontal vegetation density, and vertical vegetation density. Because of sample size limitations and to avoid overparameterization in the models we fit single variable linear models (Burnham and Anderson 2002, McNeil et al. 2018, Rodríguez et al. 2019). We generated up to nine single-variable models - a null model followed by models containing one of the eight vegetation covariates. We also checked that each β 85% confidence interval did not overlap zero (Arnold 2010).

Prior to analysis, we found none of our vegetation variables were strongly correlated, $r < 0.45$ (Sokal and Rohlf 1969). For each species, we then tested each vegetation variable independently to determine if it influenced ($> 2 \Delta AIC_c$ from null model) avian density. Within this final model set, we used the highest-ranked model to predict the relationship between density of individual species and habitat variables. We ranked models according to ΔAIC_c and models $< 2.0 \Delta AIC_c$ of a top model were considered competing models (Burnham and Anderson 2002, McNeil et al. 2018). We determined a variable to be significant if it was $> 2 \Delta AIC_c$ from the null and if the β 85% confidence interval did not overlap zero (Arnold 2010). We used a goodness of fit test in the package *unmarked* to assess whether the highest-ranked model adequately fit the data for each species (Whitlock and Schluter 2009).

RESULTS

We recorded 3,578 individual detections representing 58 species across all sites (Table A2.1). Avian diversity (effective species unit) did not differ between fenced (9.2 ± 0.3) and unfenced (9.6 ± 0.6) harvests ($t = 0.8$, $df = 9$, $p = 0.4$), thus the number of equally common species did not differ. The Bray-Curtis Dissimilarity Index between fenced and unfenced harvests was 0.17, suggesting avian communities in fenced and unfenced harvests were similar.

Nine species met our criteria for inclusion in a two-part hierarchical distance modeling analysis (Fig. 1; Table 1) and had varying detection probabilities (Table A3.1). We found four species had greater densities (males/ha) in fenced harvests, one

had a greater density in unfenced harvests and densities of four species showed no difference between fenced and unfenced harvests (Fig. 1). Distance models revealed that Chestnut-sided Warblers (Table A4.1) had higher densities in fenced than unfenced harvests. The best-ranked vegetation model for Chestnut-sided Warbler density was horizontal vegetation density, which competed with *Rubus* cover and both showed a positive relationship with density (Table 1; Figs. 2a and 2b). Gray Catbird (Table A4.2) density was greater in fenced harvests and increased with greater amounts of *Rubus* cover and horizontal and vertical vegetation density (Table 1; Figs. 3a - 3c). Ovenbird (Table A4.3) density was greater in fenced harvests and increased with greater amounts of vertical vegetation density (Table 1; Fig. 4). Rose-breasted Grosbeak (Table A4.4) density was greater in fenced harvests and increased with greater amounts of horizontal vegetation density (Table 1; Fig. 5). Eastern Towhee (Table A4.5) density did not differ between fenced and unfenced harvests, but density decreased with greater amounts of forb cover (Table 1; Fig. 6). Black-and-white Warbler (Table A4.6), Common Yellowthroat (Table A4.7), and Red-eyed Vireo (Table A4.8) densities did not differ between fenced and unfenced harvests, and none of the vegetation features we measured showed a strong association with the densities for these three species. Lastly, Field Sparrow (Table A4.9) density was greater in unfenced harvests and increased with grass cover and decreased with vertical vegetation density (Table 1; Figs. 7a and 7b).

Fig. 1. Predicted beta estimates based on hierarchical distance models for the effect of treatment (fenced or unfenced) on density of each species in Pennsylvania during 2019 and 2020. The x-axis represents the beta estimate (β) for the effect of treatment (fenced or unfenced), whereby negative values indicate species were denser in fenced harvests and positive values indicate species were denser in unfenced harvests. Thick lines represent 85% confidence intervals and thin lines represent 95% confidence intervals. Species codes are as follows: Field Sparrow (FISP), Common Yellowthroat (COYE), Black-and-white Warbler (BAWW), Eastern Towhee (EATO), Red-eyed Vireo (REVI), Rose-breasted Grosbeak (RBGR), Ovenbird (OVEN), Chestnut-sided Warbler (CSWA), and Gray Catbird (GRCA). Species are color coded according to our predicted responses from Rushing et al. (2020) that used BBS data and deer population estimates in Pennsylvania. Species predicted to show a negative response to deer are dark grey and species predicted to show a neutral response to deer are light blue.

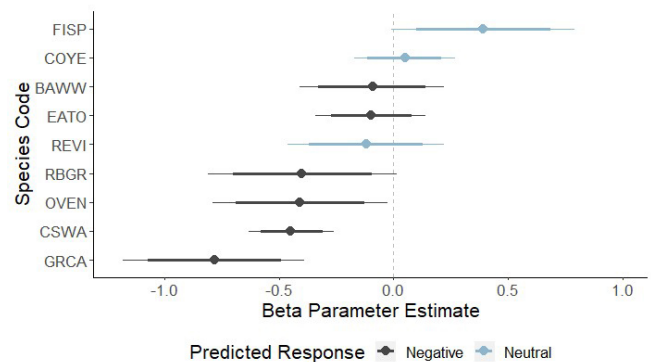


Table 1. Hierarchical distance modeling results for nine focal forest bird species detected in fenced and unfenced regenerating timber harvests in Pennsylvania in 2019 and 2020. Here we show β estimate, standard error (SE), lower and upper 85% confidence intervals for the treatment (fenced or unfenced) model and for each highest ranked or competing vegetation model for each species. We also report each \hat{c} value to assess model overdispersion. The top variable for predicting density represents our highest ranked model $> 2 \Delta$ AICc from the null and is followed by competing models. All models included detection probability (p) with associated detection covariates. Models included density (λ) with any influential covariates (Table A1.1). Black-and-white Warbler, Common Yellowthroat, and Red-eyed Vireo had the null model as their highest ranked model. Predicted response is based off Rushing et al. 2020.

Common Name	Highest ranked model and competing model(s) [†]	β Estimate	SE	Lower 85% CI	Upper 85% CI	\hat{c} value	Predicted response to deer (Rushing et al. 2020)
Gray Catbird [‡]	$p(\text{obs}), \lambda(\text{treatment})$	-0.780	0.203	-1.072	-0.489	0.90	Negative
	$p(\text{obs}), \lambda(\text{horzveg})^{\dagger}$	0.284	0.106	0.131	0.437	0.92	
	$p(\text{obs}), \lambda(\text{rubus})$	0.254	0.089	0.125	0.383	0.95	
Chestnut-sided Warbler [‡]	$p(\text{obs}), \lambda(\text{vertveg})$	0.239	0.101	0.094	0.384	0.95	Negative
	$p(\cdot), \lambda(\text{treatment})$	-0.445	0.094	-0.581	-0.309	0.82	
	$p(\cdot), \lambda(\text{horzveg})^{\dagger}$	0.115	0.055	0.037	0.194	0.85	
Ovenbird [‡]	$p(\cdot), \lambda(\text{rubus})$	0.087	0.05	0.015	0.159	0.91	Negative
	$p(\text{cloud}), \lambda(\text{treatment})$	-0.408	0.196	-0.689	-0.126	0.89	
	$p(\text{cloud}), \lambda(\text{vertveg})$	0.430	0.102	0.284	0.577	0.86	
Rose-breasted Grosbeak [‡]	$p(\cdot), \lambda(\text{treatment})$	-0.398	0.210	-0.700	-0.096	0.90	Negative
	$p(\cdot), \lambda(\text{horzveg})$	0.460	0.119	0.289	0.632	0.92	
Red-eyed Vireo [‡]	$p(\cdot), \lambda(\text{treatment})$	-0.121	0.173	-0.370	0.128	0.82	Neutral
	$p(\cdot), \lambda(\cdot)$	-	-	-	-	-	
Eastern Towhee	$p(\cdot), \lambda(\text{treatment})$	-0.097	0.123	-0.274	0.081	0.91	Negative
	$p(\cdot), \lambda(\text{forb})$	-0.176	0.063	-0.267	-0.085	0.89	
Black-and-white Warbler	$p(\cdot), \lambda(\text{treatment})$	-0.093	0.162	-0.327	0.140	0.83	Negative
	$p(\cdot), \lambda(\cdot)$	-	-	-	-	-	
Common Yellowthroat [‡]	$p(\text{wind}), \lambda(\text{treatment})$	0.047	0.112	-0.114	0.207	0.87	Neutral
	$p(\text{wind}), \lambda(\cdot)$	-	-	-	-	-	
Field Sparrow	$p(\cdot), \lambda(\text{treatment})$	0.393	0.204	0.099	0.687	0.84	Neutral
	$p(\cdot), \lambda(\text{grass})$	0.229	0.085	0.106	0.351	0.82	

[†] Highest ranked vegetation model

[‡] Species results aligned with Rushing et al. 2020

[§] Detection covariates: Ordinal date (“date”), time of day (“time”), wind using the Beaufort wind index (“wind”; scale of 0-5), cloud cover (“cloud”; 0-100%), precipitation (“precip”; none, fog, mist, light rain, heavy rain, snow), and observer (“obs”; n = 4)

Fig. 2. Chestnut-sided Warbler density (males/ha) as a function of the best supported hierarchical distance model (A) and a competing model (B). Horizontal vegetation density (A) and *Rubus* cover (B) were positively associated with Chestnut-sided Warbler density in fenced and unfenced timber harvests in Pennsylvania in 2019 and 2020. The solid line represents density estimates and the dashed lines represent 95% confidence intervals.

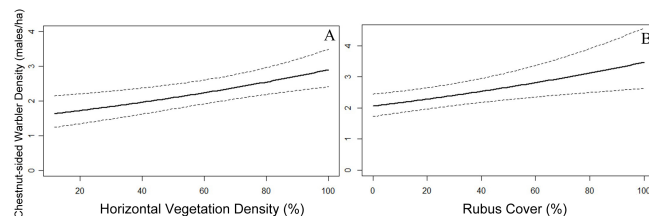
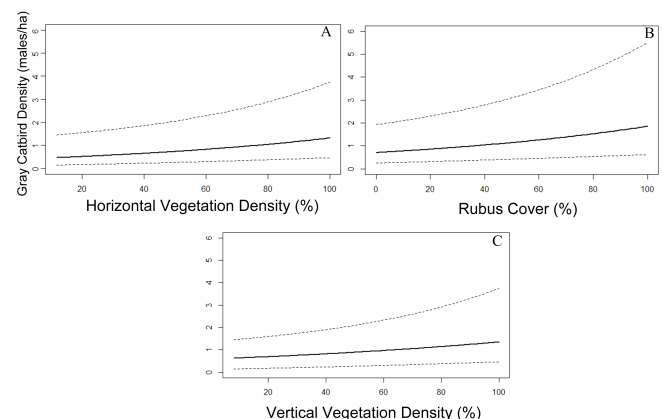


Fig. 3. Gray Catbird density (males/ha) as a function of the best supported hierarchical distance model (A) and competing models (B) and (C). Horizontal vegetation density (A), *Rubus* cover (B), and vertical vegetation density (C) were positively associated with Gray Catbird density in fenced and unfenced timber harvests in Pennsylvania in 2019 and 2020. The solid line represents density estimates and the dashed lines represent 95% confidence intervals.



DISCUSSION

Our findings, derived from field observations combined with results from statewide BBS trends in Rushing et al. (2020), reveal that browsing by white-tailed deer has varying effects on breeding birds using regenerating timber harvests in Pennsylvania. Despite several species-level differences, avian diversity (i.e., effective

Fig. 4. Ovenbird density (males/ha) as a function of the best supported hierarchical distance model. Vertical vegetation density was positively associated with Ovenbird density in fenced and unfenced timber harvests in Pennsylvania in 2019 and 2020. The solid line represents density estimates, and the dashed lines represent 95% confidence intervals.

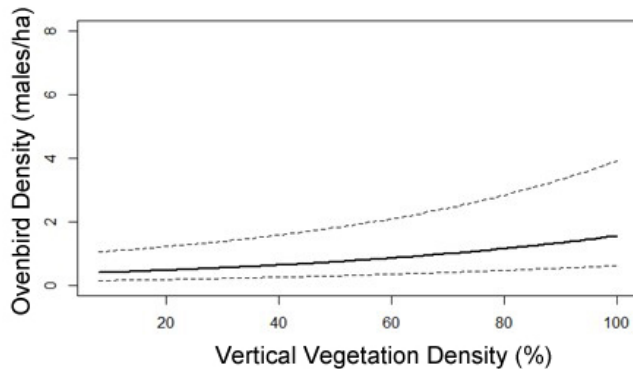
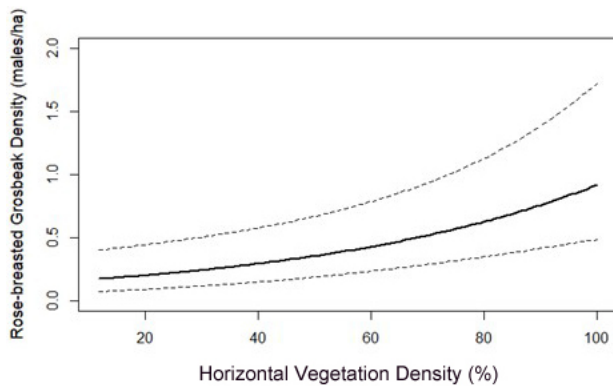


Fig. 5. Rose-breasted Grosbeak density (males/ha) as a function of the best supported hierarchical distance model. Rose-breasted Grosbeak density was positively associated with horizontal vegetation density in fenced and unfenced timber harvests in Pennsylvania in 2019 and 2020. The solid line represents density estimates, and the dashed lines represent 95% confidence intervals.



species unit) and community composition (i.e., Bray-Curtis Dissimilarity) did not differ between our fenced and unfenced harvests. A study in Virginia also reported species-level differences between fenced and unfenced harvests, but no difference in species diversity (McShea and Rappole 2000). We caution against using only avian species diversity and community composition (i.e., presence/absence) to assess deer impacts on avian populations, as those measures lack reliable correlations with density of individual species and vegetation characteristics.

Although our focal species results reveal some inconsistencies with results from Rushing et al. (2020), the overall effect of deer herbivory on vegetation (Parker et al. 2020) and focal species

Fig. 6. Eastern Towhee density (males/ha) as a function of the best supported hierarchical distance model. Forb cover was negatively associated with Eastern Towhee density in fenced and unfenced timber harvests in Pennsylvania in 2019 and 2020. The solid line represents density estimates and the dashed lines represent 95% confidence intervals.

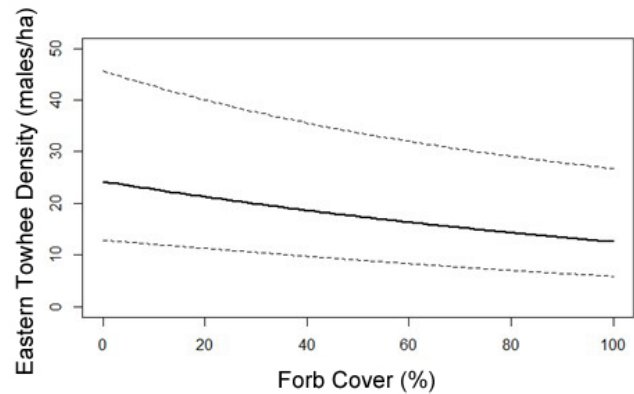
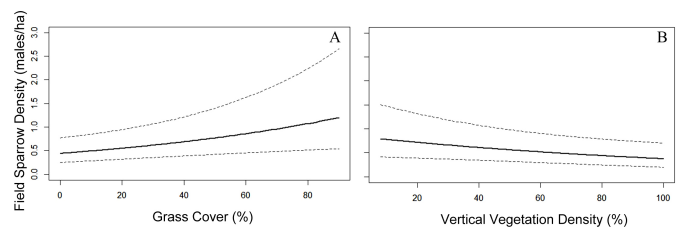


Fig. 7. Field Sparrow density (males/ha) as a function of the best supported hierarchical distance model (A) and a competing model (B). Grass cover (A) was positively associated with Field Sparrow density and vertical vegetation density (B) was negatively associated with Field Sparrow density in fenced and unfenced timber harvests in Pennsylvania in 2019 and 2020. The solid line represents density estimates, and the dashed lines represent 95% confidence intervals.



densities across our study sites is clear. In fact, density estimates for six of nine focal species followed our initial predictions. Differences between predicted and observed results likely stem from variance in lag times. The effects of deer over-browsing on avian communities are not immediate, and thus the temporal impacts are non-linear. For example, there can be substantial lags between deer impacts on vegetation and subsequent avian response (Chollet et al. 2015, Rushing et al. 2020). Our findings are associated with 7-11 year-old regenerating harvests, whereas Rushing et al. (2020) used a 4-year time lag in their analyses. In other words, the predicted and observed avian communities were at different ecological points on their temporal trajectories. Nonetheless, the overall consistency of our results with those of Rushing et al. (2020) on direction of measured effects of deer (i.e., negative or neutral) provides compelling evidence that deer-driven changes to vegetation in regenerating forests affect the densities of several avian species.

Consistent with our predictions, four of six species we expected to be negatively impacted by deer and had higher densities in fenced harvests (Chestnut-sided Warbler, Gray Catbird, Ovenbird, and Rose-breasted Grosbeak). Chestnut-sided Warblers and Gray Catbirds are known to respond positively to forest management that results in regenerating understories (e.g., timber harvesting) (Yahner 2003, Tozer et al. 2010, Chizinski et al. 2011, Smith et al. 2020). Both species were positively associated with horizontal vegetation density and *Rubus* cover, and Gray Catbird abundance was also positively associated with vertical vegetation density. A concurrent study that examined vegetation composition and structure in these same study sites found *Rubus* cover and horizontal and vertical vegetation density to be greater in fenced harvests (Parker et al. 2020), likely providing optimal nesting habitat for Chestnut-sided Warblers and Gray Catbirds (Hunter et al. 2001, Schlossberg and King 2009).

Ovenbird and Rose-breasted Grosbeak densities were also positively associated with vertical vegetation density (Ovenbird), and horizontal vegetation density (Rose-breasted Grosbeak). Research elsewhere reported that Ovenbird abundance increased as fenced plots advanced from herbaceous to woody dominated understories (McShea and Rappole 2000). Similarly, past studies found Rose-breasted Grosbeaks selected areas with more sapling cover, which was greater in our fenced harvests, and lower basal area (Smith et al. 2007). Moreover, Richmond et al. (2012) reported that Rose-breasted Grosbeak exhibited the highest densities in stands 16-20 years post-harvest. Thus, it is reasonable to expect that as our harvests continue to age and fenced areas achieve greater woody vegetation density, both Ovenbird and Rose-breasted Grosbeak densities will continue to diverge between fenced and unfenced harvests.

We predicted Black-and-white Warbler and Eastern Towhee densities would be negatively impacted by deer herbivory, however, we found that the presence of fencing had no effect on their densities. While this result contrasts with our original hypothesis, our observations can be attributed to the habitat generalist behaviors employed by both species, (Greenlaw 2020, Kricher 2020) whereby they are known to occur in a wide range of forest habitat conditions. Given the discrepancy in time lags described earlier, it is also reasonable to suggest that a species like Eastern Towhee would have shown a positive association with our fenced harvests in years more immediately following disturbance when vegetation structure inside fences would have been closer to optimal.

We expected that Field Sparrow, Common Yellowthroat, and Red-eyed Vireo would have equal densities in fenced and unfenced harvests and our results support this prediction for the latter two species. Common Yellowthroats use a variety of vegetation communities for nesting habitat, such as thickets, old fields, and regenerating forests up to 10 years post-harvest (Thompson and DeGraaf 2001, Schlossberg and King 2009, Guzy and Ritchison 2020). This species has previously shown a positive relationship with low statured shrubs (Yahner 1986, Schlossberg et al. 2010) and a negative relationship with density of overstory trees and basal area (Yahner 1986). Red-eyed Vireo is a woodland generalist species and nests from the understory to midstory and forages primarily in the canopy and subcanopy (McWilliams and Brauning 2000; Cimprich et al. 2020). Shrub density, canopy

cover, and basal area did not differ between our fenced and unfenced harvests (Parker et al. 2020), likely explaining why Common Yellowthroat and Red-eyed Vireo densities did not differ between the two treatment types.

We also predicted Field Sparrow would be a “deer-neutral” species, however, we found its density was considerably greater in unfenced harvests. This species nests in old fields and young regenerating timber harvests (Yahner 1986, Thompson and DeGraaf 2001, Keller et al. 2003) and is understood to have a positive association with grass cover (Pennington and Blair 2011) and negative association with tree density (Reidy et al. 2014). Our unfenced harvests had shorter woody stems, more herbaceous cover, and similar amounts of residual canopy trees relative to fenced harvests (Parker et al. 2020). As such, it appears that deer browsing in our unfenced sites impeded forest succession and maintained vegetation conditions favorable to Field Sparrows, while forest succession in our fenced harvests had started to advance beyond optimal conditions for Field Sparrows. As our harvests continue to age, deer herbivory will likely prolong the amount of time unfenced harvests retain early successional conditions needed by this species, and densities will likely become more disparate between fenced and unfenced harvests.

Although numerous studies, including ours, have documented negative impacts of excessive deer browsing on forest-bird communities (deCalesta 1994, McShea and Rappole 2000, Baiser et al. 2008), it is important to recognize that eastern forests evolved with deer and their herbivory serves an important ecological role. Our fenced harvests were entering the stem exclusion stage (i.e., closed canopy of dense saplings) at the time of this study, thus forest succession was starting to limit the heterogeneous structure that is typical of young, regenerating stands. Moderate browsing by deer, which is determined by the interplay between deer densities and forage availability in local landscapes, (Royo et al. 2017, McWilliams et al. 2018) is likely to slow forest succession and maintain young forest conditions (i.e., a mosaic of herbaceous plants, shrubs, and saplings) that are favorable for some bird species. Moderate browsing could benefit species like Field Sparrow, Eastern Towhee, and Common Yellowthroat due to maintenance of favorable nesting conditions (Thompson and DeGraaf 2001, Bakermans et al. 2015). Moreover, moderate browsing by deer promotes understory complexity in forests post-disturbance (i.e., fire, windthrow) by reducing abundance of highly palatable, fast-growing species (Royo et al. 2010). When browsing is completely removed and the canopy is opened because of disturbance, understories can become dominated by fast-growing woody species (e.g., *Rubus* spp. and *Prunus pensylvanica*) and lack forbs, shrubs, and ferns, thus reducing the overall diversity of the site (Royo et al. 2010, DiTommaso et al. 2014, Faison et al. 2016). We encourage managers to carefully consider the timing of fence removal to optimize a balance between successful stand regeneration and the benefits that deer browsing can impart on forest biodiversity.

Vegetation features affected by the presence of fencing appeared to influence densities of several avian species we monitored. However, we recognize that some of our species showed only modest effects. Although deer exclusion fencing is a costly forest management practice, its use results in tall, dense vegetation and increased heights of regenerating tree species, which is desirable

for timber production (Parker et al. 2020) and formation of quality habitat for several songbird species. While not a focus of our study, the tall and dense vegetation conditions inside deer fences may also be attractive to many songbird species because foliage density is highly predictive of prey density (Marshall and Cooper 2004). Songbirds have been shown to select areas with high prey availability (Bellush et al. 2016), which can be affected by deer herbivory (Chips et al. 2015, Roberson et al. 2016). Moreover, the dense vegetation associated with fenced timber harvests likely also serves as important post-fledging habitat for many forest birds known to seek out such conditions to rear their young (King et al. 2006, Raybuck et al. 2020, Fiss et al. 2021).

To our knowledge, no research has assessed bird communities immediately following harvest and up to 10+ years post-harvest in multiple pairs of fenced and unfenced timber harvests. Such research might show how vegetation and bird communities diverge and change over time in fenced versus unfenced harvests. One limitation of our study was that we did not examine reproductive success (i.e., nest success and/or fledgling survival). Thus, future studies that compare prey availability, nesting success, and post-fledging habitat use and survival within fenced and unfenced timber harvests could elucidate new ecological patterns. Researchers should continue to periodically monitor avian communities in fenced/unfenced harvests as they advance through the stem exclusion, pole, and mature forest stages. It is reasonable to conclude from our findings, and those from Parker et al. (2020), that forests subjected to excessive browsing by white-tailed deer likely have reduced carrying capacity (i.e., territory densities) and annual recruitment rates for many avian species. This underscores the need to mitigate excessive deer browsing as part of efforts to recover avian populations.

Responses to this article can be read online at:
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Appendix 1

Table A1.1. Site covariate names and descriptions for the vegetation variables used in our hierarchical distance modeling analysis. All vegetation data was collected in northcentral Pennsylvania in 2019.

Site Covariate Name	Average \pm SEM		Description
	Fenced	Unfenced	
Rubus	0.36 \pm 0.08	0.05 \pm 0.03	<i>Rubus</i> spp. cover
Forb	0.37 \pm 0.07	0.55 \pm 0.04	Forb cover
Fern	0.48 \pm 0.07	0.56 \pm 0.07	Fern cover
Grass	0.04 \pm 0.02	0.23 \pm 0.05	Grass cover
Litter	0.96 \pm 0.02	0.96 \pm 0.01	Leaf litter cover
Vacc	0.27 \pm 0.06	0.38 \pm 0.09	<i>Vaccinium</i> spp. and <i>Gaylussacia</i> spp. cover
Horzveg	0.76 \pm 0.06	0.54 \pm 0.06	Horizontal vegetation density
Vertveg	0.71 \pm 0.05	0.42 \pm 0.09	Vertical vegetation density

Appendix 2

Table A2.1. Number of detections for each avian species observed within fenced and unfenced timber harvests in Pennsylvania in 2019 and 2020. We used the sum of detections between our two visits at a given survey location to quantify total number of detections for each species.

Common Name	Scientific Name	Number of detections	
		2019	2020
Alder Flycatcher	<i>Empidonax alnorum</i>	4	9
American Crow†	<i>Corvus brachyrhynchos</i>	2	6
American Goldfinch	<i>Spinus tristis</i>	30	35
American Redstart	<i>Setophaga ruticilla</i>	33	22
American Robin	<i>Turdus migratorius</i>	24	17
Baltimore Oriole	<i>Icterus galbula</i>	5	3
Black-and-white-Warbler	<i>Mniotilta varia</i>	107	106
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	4	0
Black-capped Chickadee	<i>Poecile atricapillus</i>	12	14
Brown-headed Cowbird	<i>Molothrus ater</i>	21	19
Blue-headed Vireo	<i>Vireo solitarius</i>	0	3
Blackburnian Warbler	<i>Setophaga fusca</i>	1	1
Blue Jay	<i>Cyanocitta cristata</i>	16	17
Brown Thrasher	<i>Toxostoma rufum</i>	1	2
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	1	2
Black-throated Green Warbler	<i>Setophaga virens</i>	0	17
Blue-winged Warbler	<i>Vermivora cyanoptera</i>	1	0
Cedar Waxwing	<i>Bombycilla cedrorum</i>	32	27
Chipping Sparrow	<i>Spizella passerine</i>	2	2
Common Raven†	<i>Corvus corax</i>	2	1
Common Yellowthroat	<i>Geothlypis trichas</i>	214	235
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	362	358
Downy Woodpecker	<i>Picoides pubescens</i>	0	1
Eastern Bluebird	<i>Sialia sialis</i>	1	2
Eastern Phoebe	<i>Sayornis phoebe</i>	0	1
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	237	226
Eastern Wood Pewee	<i>Contopus virens</i>	4	3
Field Sparrow	<i>Spizella pusilla</i>	90	76
Great-crested Flycatcher	<i>Ouriarchus crinitus</i>	4	1
Gray Catbird	<i>Dumetella carolinensis</i>	95	152
Golden-winged Warbler	<i>Vermivora chrysoptera</i>	13	5
Hairy Woodpecker	<i>Leuconotopicus villosus</i>	3	0
House Wren	<i>Troglodytes aedon</i>	1	0
Indigo Bunting	<i>Passerina cyanea</i>	32	16
Least Flycatcher	<i>Empidonax minimus</i>	4	12
Magnolia Warbler	<i>Setophaga magnolia</i>	2	0
Mourning Dove	<i>Geothlypis Philadelphia</i>	18	15

Nashville Warbler	<i>Leiothlypis ruficapilla</i>	5	6
Northern Flicker	<i>Colaptes auratus</i>	11	13
Norther Parula	<i>Setophaga Americana</i>	0	1
Ovenbird	<i>Seiurus aurocapilla</i>	63	92
Pileated Woodpecker	<i>Dryocopus pileatus</i>	1	1
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	54	95
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	5	3
Red-eyed Vireo	<i>Vireo olivaceus</i>	100	72
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	1	0
Ruffed Grouse†	<i>Bonasa umbellus</i>	7	7
Scarlet Tanager	<i>Piranga olivacea</i>	35	34
Song Sparrow	<i>Melospiza melodia</i>	36	26
Tennessee Warbler	<i>Leiothlypis peregrina</i>	0	1
Tree Swallow	<i>Tachycineta bicolor</i>	1	0
Veery	<i>Catharus fuscescens</i>	33	33
White-breasted Nuthatch	<i>Sitta carolinensis</i>	3	10
Wild Turkey†	<i>Meleagris gallopavo</i>	4	0
Wood Thrush	<i>Hylocichla mustelina</i>	11	23
White-throated Sparrow	<i>Zonotrichia albicollis</i>	0	1
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	1	3
Yellow Warbler	<i>Setophaga petechia</i>	1	1

† Species that were not used in our diversity analysis

Appendix 3

Table A3.1. Detection probability for each focal species in 2019 and 2020 for our hierarchical distance modeling analysis. We calculated average, minimum (100 m from observer), and maximum (0 m from observer) detection probability for each species. Note: Field Sparrow detection did not differ because more individuals were detected at the furthest distance bins (50-75m and 75-100m).

Common Name	Average	Minimum (100m)	Maximum (0m)
Chestnut-sided Warbler	0.68	0.4	1.0
Common Yellowthroat	0.71	0.4	1.0
Gray Catbird	0.44	0.0	1.0
Black-and-white Warbler	0.77	0.4	1.0
Eastern Towhee	0.80	0.5	1.0
Red-eyed Vireo	0.54	0.2	1.0
Rose-breasted Grosbeak	0.84	0.6	1.0
Field Sparrow	1.0	1.0	1.0
Ovenbird	0.77	0.4	1.0

1 **Appendix 4**

2
 3 Hierarchical distance modeling results for detection (top) and density (bottom) for Chestnut-
 4 sided Warbler (Table A4.1), Gray Catbird (Table A4.2), Ovenbird (Table A4.3), Rose-breasted
 5 Grosbeak (Table A4.4), Eastern Towhee (Table A4.5), Black-and-white Warbler (Table A4.6),
 6 Common Yellowthroat (Table A4.7), Field Sparrow (Table A4.8), and Red-eyed Vireo (Table
 7 A4.9). The top variable for predicting density represents our highest ranked model $> 2 \Delta AIC_c$
 8 from the null (.). All models included detection probability (p) with associated detection
 9 covariates: Ordinal date (“date”), time of day (“time”), wind using the Beaufort wind index
 10 (“wind”; scale of 0-5), cloud cover (“cloud”; 0-100%), precipitation (“precip”; none, fog, mist,
 11 light rain, heavy rain, snow), and observer (“obs”; n = 4). Models included density (λ) with any
 12 influential covariates (See appendix 1 for list of covariates). Also shown are the number of
 13 model parameters (k), model weight (w), and Δ Akaike’s Information Criterion adjusted for
 14 small sample size (ΔAIC_c).
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16 Table A4.1

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Chestnut-sided Warbler detection models – Hierarchical Distance			
Model	k	ΔAIC_c	w
<i>p</i> (.)	4	0.00	0.27
<i>p</i> (obs)	7	0.26	0.24
<i>p</i> (cloud)	5	1.63	0.12
<i>p</i> (date)	5	1.89	0.10
<i>p</i> (wind)	5	2.04	0.10
<i>p</i> (time)	5	2.10	0.09
<i>p</i> (precip)	6	2.47	0.08

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Chestnut-sided Warbler models – Hierarchical Distance			
Model	k	ΔAIC_c	w
<i>p</i> (.), λ (horzveg)	5	0.00	0.64
<i>p</i> (.), λ (rubus)	5	1.53	0.30
<i>p</i> (.), λ (grass)	5	6.20	0.03
<i>p</i> (.), λ (vertveg)	5	8.21	0.01
<i>p</i> (.), λ (.)	4	8.79	0.01
<i>p</i> (.), λ (forb)	5	8.87	0.01
<i>p</i> (.), λ (fern)	5	10.49	0.00
<i>p</i> (.), λ (litter)	5	10.77	0.00
<i>p</i> (.), λ (vacc)	5	10.95	0.00

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Table A4.2

Gray Catbird detection models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{obs})$	6	0.00	0.99
$p(\cdot)$	3	11.77	0.00
$p(\text{cloud})$	4	12.80	0.00
$p(\text{wind})$	4	13.05	0.00
$p(\text{date})$	4	13.78	0.00
$p(\text{time})$	4	13.84	0.00
$p(\text{precip})$	5	13.85	0.00

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Gray Catbird models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{obs}), \lambda(\text{horzveg})$	7	0.00	0.30
$p(\text{obs}), \lambda(\text{rubus})$	7	0.06	0.30
$p(\text{obs}), \lambda(\text{vertveg})$	7	1.89	0.12
$p(\text{obs}), \lambda(\text{fern})$	7	2.07	0.11
$p(\text{obs}), \lambda(\text{forb})$	7	2.50	0.09
$p(\text{obs}), \lambda(\text{grass})$	7	4.47	0.03
$p(\text{obs}), \lambda(\text{vacc})$	7	4.93	0.03
$p(\text{obs}), \lambda(\cdot)$	6	5.30	0.02
$p(\text{obs}), \lambda(\text{litter})$	7	7.14	0.01

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Table A4.3

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Ovenbird detection models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{cloud})$	4	0.00	0.46
$p(\text{precip})$	5	1.89	0.18
$p(\cdot)$	3	2.49	0.13
$p(\text{date})$	4	3.16	0.10
$p(\text{wind})$	4	4.60	0.05
$p(\text{time})$	4	4.64	0.05
$p(\text{obs})$	6	5.21	0.03

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Ovenbird models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{cloud}), \lambda(\text{vertveg})$	5	0.00	1.00
$p(\text{cloud}), \lambda(\text{grass})$	5	16.49	0.00
$p(\text{cloud}), \lambda(\text{fern})$	5	16.72	0.00
$p(\text{cloud}), \lambda(\cdot)$	4	16.84	0.00
$p(\text{cloud}), \lambda(\text{horzveg})$	5	17.34	0.00
$p(\text{cloud}), \lambda(\text{vacc})$	5	18.75	0.00
$p(\text{cloud}), \lambda(\text{rubus})$	5	18.77	0.00
$p(\text{cloud}), \lambda(\text{forb})$	5	18.99	0.00
$p(\text{cloud}), \lambda(\text{litter})$	5	19.01	0.00

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Table A4.4

Rose-breasted Grosbeak detection models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{wind})$	4	0.00	0.46
$p(\cdot)$	3	1.64	0.20
$p(\text{time})$	4	2.80	0.11
$p(\text{date})$	4	3.53	0.08
$p(\text{cloud})$	4	3.76	0.07
$p(\text{precip})$	5	4.94	0.04
$p(\text{obs})$	6	5.57	0.03

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Rose-breasted Grosbeak models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\cdot), \lambda(\text{horzveg})$	4	0.00	0.78
$p(\cdot), \lambda(\text{vertveg})$	4	2.58	0.22
$p(\cdot), \lambda(\text{rubus})$	4	12.48	0.00
$p(\cdot), \lambda(\text{grass})$	4	12.73	0.00
$p(\cdot), \lambda(\text{litter})$	4	14.58	0.00
$p(\cdot), \lambda(\cdot)$	3	14.65	0.00
$p(\cdot), \lambda(\text{fern})$	4	15.90	0.00
$p(\cdot), \lambda(\text{vacc})$	4	16.76	0.00
$p(\cdot), \lambda(\text{forb})$	4	16.79	0.00

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Table A4.5

Eastern Towhee detection models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{wind})$	5	0.00	0.34
$p(\cdot)$	4	1.24	0.18
$p(\text{obs})$	7	2.04	0.12
$p(\text{cloud})$	5	2.04	0.12
$p(\text{time})$	5	2.11	0.12
$p(\text{date})$	5	3.33	0.06
$p(\text{precip})$	6	3.55	0.06

Eastern Towhee models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\cdot), \lambda(\text{forb})$	5	0.00	0.69
$p(\cdot), \lambda(\text{litter})$	5	2.73	0.18
$p(\cdot), \lambda(\cdot)$	4	5.72	0.04
$p(\cdot), \lambda(\text{fern})$	5	7.18	0.02
$p(\cdot), \lambda(\text{vacc})$	5	7.27	0.02
$p(\cdot), \lambda(\text{horzveg})$	5	7.66	0.01
$p(\cdot), \lambda(\text{vertveg})$	5	7.75	0.01
$p(\cdot), \lambda(\text{rubus})$	5	7.76	0.01
$p(\cdot), \lambda(\text{grass})$	5	7.79	0.01

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Table A4.6

Black-and-white Warbler detection models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\cdot)$	4	0.00	0.33
$p(\text{cloud})$	5	1.06	0.19
$p(\text{time})$	5	1.69	0.14
$p(\text{date})$	5	1.75	0.14
$p(\text{wind})$	5	1.77	0.14
$p(\text{precip})$	6	3.80	0.05
$p(\text{obs})$	7	5.96	0.02

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Black-and-white Warbler models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\cdot), \lambda(\cdot)$	4	0.00	0.26
$p(\cdot), \lambda(\text{litter})$	5	1.89	0.10
$p(\cdot), \lambda(\text{forb})$	5	2.04	0.10
$p(\cdot), \lambda(\text{vertveg})$	5	2.04	0.09
$p(\cdot), \lambda(\text{horzveg})$	5	2.13	0.09
$p(\cdot), \lambda(\text{grass})$	5	2.16	0.09
$p(\cdot), \lambda(\text{rubus})$	5	2.18	0.09
$p(\cdot), \lambda(\text{fern})$	5	2.18	0.09
$p(\cdot), \lambda(\text{vacc})$	5	2.19	0.09

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Table A4.7

Common Yellowthroat detection models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{wind})$	5	0.00	0.63
$p(\cdot)$	4	3.02	0.14
$p(\text{cloud})$	5	3.14	0.13
$p(\text{time})$	5	5.05	0.05
$p(\text{date})$	5	5.21	0.05
$p(\text{obs})$	7	21.72	0.00
$p(\text{precip})$	6	44.12	0.00

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Common Yellowthroat models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{wind}), \lambda(\cdot)$	5	0.00	0.19
$p(\text{wind}), \lambda(\text{litter})$	6	0.12	0.18
$p(\text{wind}), \lambda(\text{vertveg})$	6	0.99	0.12
$p(\text{wind}), \lambda(\text{grass})$	6	1.12	0.11
$p(\text{wind}), \lambda(\text{fern})$	6	1.37	0.10
$p(\text{wind}), \lambda(\text{rubus})$	6	1.43	0.09
$p(\text{wind}), \lambda(\text{vacc})$	6	1.68	0.08
$p(\text{wind}), \lambda(\text{horzveg})$	6	1.74	0.08
$p(\text{wind}), \lambda(\text{forb})$	6	2.22	0.06

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Table A4.8

Red-eyed Vireo detection models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{obs})$	6	0.00	0.88
$p(\text{date})$	4	4.08	0.11
$p(\cdot)$	3	10.89	0.00
$p(\text{wind})$	4	12.38	0.00
$p(\text{precip})$	5	12.59	0.00
$p(\text{cloud})$	4	12.80	0.00
$p(\text{time})$	4	12.91	0.00

Red-eyed Vireo models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\text{obs}), \lambda(\text{vertveg})$	8	0.00	0.37
$p(\text{obs}), \lambda(\cdot)$	7	1.75	0.15
$p(\text{obs}), \lambda(\text{grass})$	8	2.47	0.11
$p(\text{obs}), \lambda(\text{rubus})$	8	2.93	0.09
$p(\text{obs}), \lambda(\text{vacc})$	8	3.32	0.07
$p(\text{obs}), \lambda(\text{forb})$	8	3.64	0.06
$p(\text{obs}), \lambda(\text{horzveg})$	8	3.87	0.05
$p(\text{obs}), \lambda(\text{fern})$	8	3.90	0.05
$p(\text{obs}), \lambda(\text{litter})$	8	4.02	0.05

Table A4.9

Field Sparrow detection models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\cdot)$	3	0.00	0.34
$p(\text{time})$	4	0.96	0.21
$p(\text{wind})$	4	1.61	0.15
$p(\text{date})$	4	2.16	0.12
$p(\text{cloud})$	4	2.16	0.12
$p(\text{precip})$	5	4.16	0.04
$p(\text{obs})$	6	6.32	0.01

Field Sparrow models – Hierarchical Distance			
Model	k	ΔAIC_c	w
$p(\cdot), \lambda(\text{grass})$	4	0.00	0.44
$p(\cdot), \lambda(\text{vertveg})$	4	0.93	0.28
$p(\cdot), \lambda(\text{horzveg})$	4	3.55	0.08
$p(\cdot), \lambda(\cdot)$	3	4.27	0.05
$p(\cdot), \lambda(\text{litter})$	4	4.77	0.04
$p(\cdot), \lambda(\text{forb})$	4	4.95	0.04
$p(\cdot), \lambda(\text{rubus})$	4	5.05	0.04
$p(\cdot), \lambda(\text{vacc})$	4	6.04	0.02
$p(\cdot), \lambda(\text{fern})$	4	6.44	0.02