

Research Paper

Songbird community varies with deer use in a fragmented landscape

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HIGHLIGHTS

- We found higher deer use at our coastal study sites than our inland sites.
- Coastal sites had more than twice the amount of deer-promoting forest edge.
- There was a negative correlation between deer use and deer-sensitive songbirds.
- Some common songbird species were positively associated with deer.
- Land use practices that promote deer may impact local bird community composition.

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ABSTRACT

Consumption of understory foliage by abundant ungulates can reshape forest structure and thus induce corresponding ecosystem changes. In forest songbirds, a negative response to deer browsing was documented for species that use understory foliage, although this association remains poorly understood at the community level. Such knowledge is especially important in eastern North America where deer populations have recently increased substantially. Our primary objective was to examine correlations between deer and songbirds in coastal Virginia ($n = 92$ sites, 2010–2013), a region with heavy forest fragmentation and abundant deer. The secondary objectives were to compare coastal surveys to an inland region ($n = 99$ sites, 2012) with fewer deer and lower fragmentation, and to explore links between fragmentation and deer. We predicted that densities of songbirds that use understory foliage (“deer-sensitive”) would correlate negatively with deer fecal pellets – our measure of relative deer use. The estimate of median pellets inland (0 ha^{-1} , range $0\text{--}19,600 \text{ pellets ha}^{-1}$) was significantly lower than on the coast ($2,014 \text{ ha}^{-1}$, range $0\text{--}28,193 \text{ ha}^{-1}$). We found a negative correlation with deer-sensitive birds on the coast ($r_s = -0.35$, $P = 0.002$), whereas inland, no correlation was evident. Coastal sites had approximately twice as much fragmented forest, which favors deer. Of 26 songbirds in our species-level analysis, we found negative correlations for three species, including one of high conservation concern. These results are consistent with the hypothesis that habitat modification by over-abundant deer promotes measurable changes in bird communities, with conservation implications for declining songbirds.

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1. Introduction

Ungulates have the potential to restructure forest by consuming herbaceous and woody vegetation. Populations of both native and invasive deer have increased in many places worldwide, prompting several recent studies on ecosystem influence of abundant deer in Europe and North America (Côté, Rooney, Tremblay, Dussault, & Waller, 2004; Knox, 1997). Uncontrolled browsing by deer can

generate considerable and rapid change in plant communities, leading to simplification and reduction of biomass in understory vegetation (Fuller, 2001; Martin, Stockton, Allombert, & Gaston, 2010; Stockton, Allombert, Gaston, & Martin, 2005), especially when foraging selectivity decreases at high ungulate densities (Augustine & McNaughton, 1998). Such vegetation changes have been implicated in subsequent declines in foliage-dwelling invertebrates (Allombert, Stockton, & Martin, 2005). Vegetation volume is particularly important for many breeding songbird species (Mills, Dunning, & Bates, 1991). Thus, high deer numbers can affect bird populations – especially those that are associated with lower forest strata – by changing both habitat structure and food availability.

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In the eastern United States, White-tailed Deer (*Odocoileus virginianus*; henceforth deer) numbers have increased dramatically over the past century (Côté et al., 2004). For example, between 1931 and early 1990, the deer population in Virginia was estimated to have grown 36-fold to nearly 1 million individuals (Knox, 1997). Extirpation of predators, urbanization of expansive areas where deer hunting formerly occurred, and human-induced forest fragmentation have all contributed to this population boom (Lovely, McShea, Lafon, & Carr, 2013; McShea, Underwood, & Rappole, 2003). Fragmented forested landscapes provide deer with high-quality habitat because deer have immediate access to abundant forage at sunlit edges between forest and roadsides, grasslands, agricultural fields, or residential neighborhoods, while providing protective cover in nearby forest (Augustine & de Calesta, 2003; Lovely et al., 2013).

Several studies have suggested a link between deer browsing and songbird populations. Species richness and abundance declined with increased deer densities in Pennsylvania (deCalesta, 1994) and Massachusetts (DeGraaf, Healy, & Brooks, 1991). Off-shore of southern British Columbia, islands with high densities of Black-tailed Deer (*Odocoileus hemionus*) had lower densities of Rufous Hummingbirds (*Selasphorus rufus*), Song Sparrows (*Melospiza melodia*), and Fox Sparrows (*Passerella iliaca*) compared to deer-free islands (Martin, Arcese, & Scheerder, 2011). Further north in British Columbia, on the Haida Gwaii archipelago, long-term declines in abundance and diversity of understory birds were connected to the depletion of understory vegetation by introduced Black-tailed Deer (Chollet, Bergman, Gaston, & Martin, 2014). Following experimental deer enclosure in Virginia, abundance of ground-nesting and intermediate canopy-nesting birds increased with regenerating understory vegetation (McShea & Rappole, 2000). In a study by Holt, Fuller, and Dolman (2013), in Britain, Eurasian Blackcaps (*Sylvia atricapilla*), which prefer early successional forest, were more abundant, settled earlier each spring, and acquired better body condition on sites where Roe Deer (*Capreolus capreolus*) and introduced Reeves's Muntjac (*Muntiacus reevesi*) were experimentally excluded. Two studies have examined the effects of deer browsing on breeding songbirds at a larger scale. With analysis at the state and provincial scales, Chollet and Martin (2013) found a connection between deer populations and declines of understory-nesting and foraging birds detected with the North American Breeding Bird Survey (BBS). Another study of deer and forest songbirds, on a regional scale in Britain, found that several species, including two of high conservation concern, may have been heavily impacted by the spread of introduced Fallow Deer (*Dama dama*) and Reeves's Muntjac (Newson, Johnston, Renwick, Baillie, & Fuller, 2012). These impacts of deer on birds, delivered primarily through browsing on understory foliage, can be magnified in forest fragments as deer concentrate activity in forested patches that comprise a smaller proportion of the deer home range (Augustine & de Calesta, 2003). Whether examining individual birds at a local scale, or population trends at a regional scale, high deer numbers appear to be linked to both the abundance and composition of forest songbird communities.

Evidence for the impacts of deer on songbirds comes primarily from studies on isolated or small forested sites. Only two studies have inspected effects of deer on avian communities at the scale beyond the forest patch, and we are not aware of any research that has examined the connection between deer and forest songbirds on a regional scale using fine-grained deer and bird density estimates. The present study provides an opportunity to examine such deer-songbird association in two landscapes that varied in deer use. Our primary objective was to determine whether deer have influenced the forest songbird community at a study area in coastal Virginia where, based on a priori field observations, we determined deer to be abundant. By quantifying deer pellet and songbird densities

across a large region in coastal Virginia over four years, we tested the prediction that densities of species that nest and forage in the lowest stratum of forest foliage (i.e., vegetation on the ground and in the understory) negatively correlates with intensity of deer use across sites. The secondary objective was to conduct matching surveys at an inland Virginia study area with fewer deer, to determine if the link between deer and songbirds was retained under lower deer pressure. Lastly, we used hunter harvest data in addition to our deer pellet density estimates to test for a predicted difference in deer use between the two study areas, and conducted land cover analyses to explore the possibility that high deer numbers in the coastal region are associated with more deer-promoting edge habitat, as reported previously in Virginia (Lovely et al., 2013). Overall, we explored the linkages between forest fragmentation, relative deer use, and songbird densities.

2. Methods

2.1. Study areas

We measured deer use and forest songbird densities at two study areas in Virginia, USA (Fig. 1). Our primary survey region ("Coastal Virginia") was the Virginia and Middle Peninsula on the coastal plain of southeastern Virginia from Newport News to West Point, and contained 92 sites surveyed three times annually over four years (2010–2013). Dominant trees in the canopy layer were *Pinus taeda*, *Liriodendron tulipifera*, *Liquidambar styraciflua*, and *Quercus alba*, whereas the subcanopy layer was typified by *Liquidambar styraciflua*, *Ilex opaca*, *Acer* spp., *Fagus grandifolia*, and *Liriodendron tulipifera*, respectively (Jirinec, Isdell, & Leu, 2016). We randomly placed survey locations in wooded areas stratified by land ownership that consisted of 13 private, city, county, state, and federally owned tracts. Deer appeared to be highly abundant at Coastal Virginia sites. We added a second study region, "Inland Virginia", where we observed that deer population appeared to be lower, to contrast with Coastal Virginia. This study area with lower expected density of deer was located approximately 200 km west of the Coastal Virginia region, and encompassed the Shenandoah River Valley from Stuarts Draft to Harrisonburg with 99 sites surveyed three times each, in 2012 only. All sites were primarily forested and comprised a mix of private lands, city and town parks, state and national forests, and the lower elevations of Shenandoah National Park. Sites were selected opportunistically based on access to forested sites in this heavily agricultural region, with the goal of even spatial coverage. Forest types varied but the most abundant canopy tree genera were *Quercus*, *Acer*, *Carya*, *Fraxinus*, *Tilia*, *Liriodendron* and *Nyssa*, with scattered *Pinus* and an understory dominated by numerous species of shrubs including *Vaccinium* and *Kalmia* species. Sampling sites in Inland Virginia were a minimum of 300 m apart as in Coastal Virginia and were at <600 m in elevation to increase similarity of bird communities sampled between the two study regions. Nevertheless, we wish to clarify that the two communities were not identical nor did this inconsistency affect our conclusions about the effect of deer on understory songbirds because all deer and bird analyses were carried out within region.

We assessed the level of forest fragmentation between the two study areas with the LANDFIRE dataset (Landfire, 2012), and used the amount of forest edge as a measure of fragmentation. To compile land cover classes relevant to deer, we extracted forest, grassland, row crop, and rural pixels (Appendix A) across each of the two study regions at 30-m resolution. We report results as mean edge length per 1 km² plot for forest edge with grassland, row crop, or rural land, which we obtained by converting minimum convex polygons delineated by survey sites to a squared-km grid (Fig. 1). In addition to land cover, we calculated road density (road km

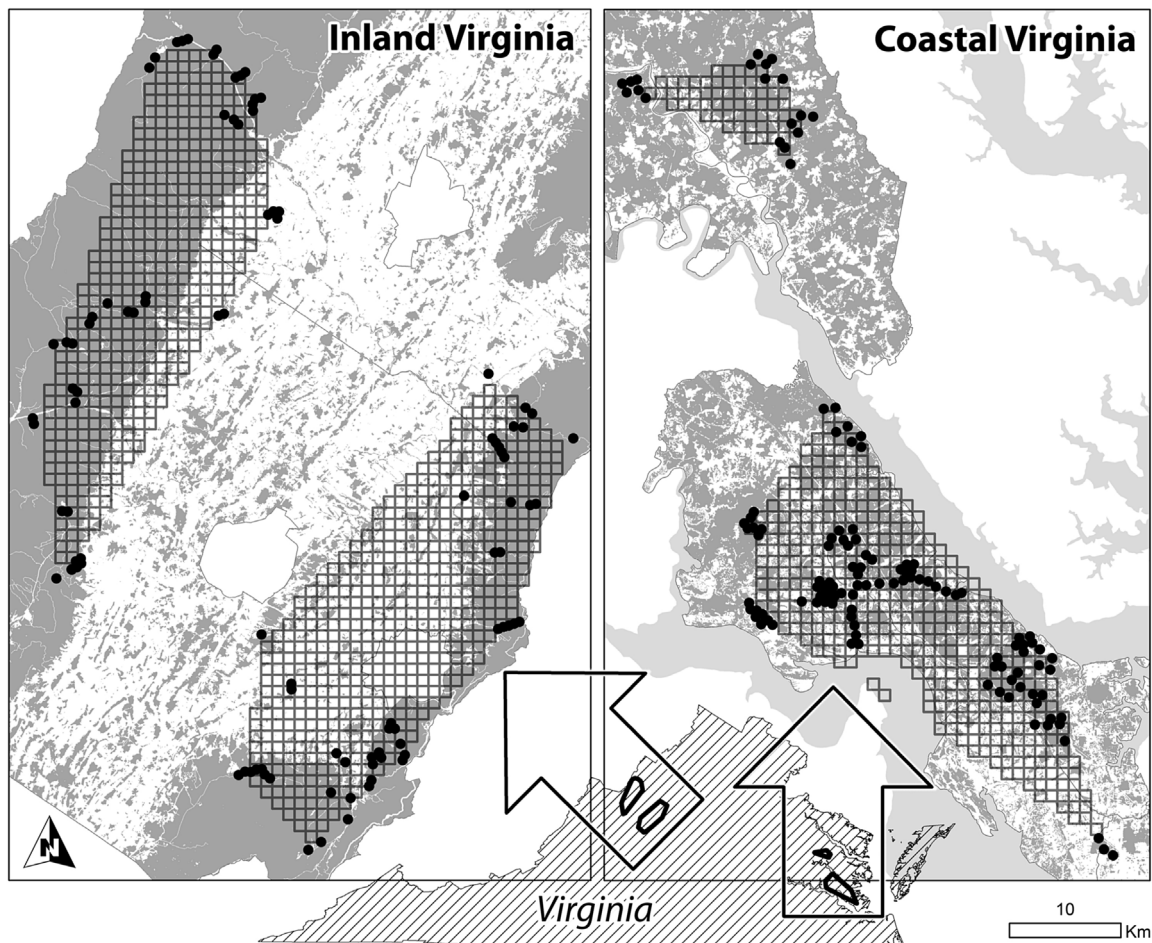


Fig. 1. Survey site locations. We estimated deer use levels and bird densities at sites (black dots) in Inland Virginia ($n = 99$; 2012 only) and Coastal Virginia ($n = 92$; 2010–2013). To assess deer habitat quality in the two study areas, we measured forest edge length in 1-km² plots (gray grid) inside minimum convex polygons in Inland Virginia and Coastal Virginia ($n = 1,018$ and 507, respectively). To obtain an index of deer abundance, we divided the number of hunter-killed deer within counties intersecting our survey sites by county forest cover area (dark gray zones).

per km²; TIGER, US Census Bureau 2014) for each study region as another category of forest fragmentation, as road density has been shown to be a good proxy for deer density (Lovely et al., 2013). Grid construction and edge delineation was conducted in Geospatial Modeling Environment (Beyer, 2011), while edge density was calculated in ArcGIS (ArcMap 10.1; ESRI, Redlands, California, USA).

We used hunting data to obtain an independent index of deer abundance for the two study regions by dividing the number of harvested deer by forest area in each county intersecting our survey sites (Fig. 1). We included Augusta and Rockingham counties (Inland Virginia), and Hampton, James City, King and Queen, King William, Newport News City, Williamsburg City, and York counties (Coastal Virginia). A decade of annual county-based deer harvest data (2004–2013) was provided by the Virginia Department of Game and Inland Fisheries (M. Knox, unpublished data).

2.2. Bird and deer surveys

We used distance sampling to quantify deer pellets and forest songbirds. Eight-minute variable-distance point counts were used to survey birds (Coastal Virginia: $n = 92$ sites; Inland Virginia: $n = 99$ sites). Point counts in Coastal Virginia were conducted in late May and June over four years (2010–2013) with three visits to each site every year. Inland Virginia sites were surveyed three times each in June 2012. All point counts were conducted between 15 min after sunrise and 10:00 EDT on days with no rain. For

each observation we estimated the distance between the observer and the bird using a laser range finder (400 LH; Opti-Logic, Tullahoma, Tennessee, USA), whether birds were detected aurally or visually. We also recorded ambient temperature (°C) and wind speed (m s^{-1}) using a hand-held weather station (Kestrel 2000, NK, Boothwyn, Pennsylvania, USA), and wind speed in the canopy (Beaufort scale: 0 = calm, smoke rises vertically, 1 = smoke drifts, sporadic leaf rustling, 2 = leaves rustling, can feel wind on face, 3 = leaves and twigs move around, small flags extend, 4 = moves thin branches, raises loose papers, 5 = small trees swaying) and ambient noise (0 = no appreciable effect [e.g. owl calling], 1 = slightly affecting sampling [e.g. distant traffic, dog barking, 1 car passing], 2 = moderately affecting sampling [e.g. nearby traffic, 2–5 cars passing], 3 = seriously affecting sampling [e.g. continuous traffic nearby, 6–10 cars], 4 = profoundly affecting sampling [e.g. continuous traffic passing, construction noise]).

Following avian surveys, we counted deer fecal pellets along two 60-m transects randomly placed within 0–150 m of point count locations in Coastal Virginia, or centered on the point count location in Inland Virginia, to estimate relative site use by deer. We assumed that pellet density reflected deer use at each site, such that sites with higher pellet counts were used by deer more heavily. Observers slowly walked tape-delineated transects counting all pellets differentiated as either singletons or clusters (defined as pellets grouped within a circle of 15-cm radius) and measuring distance (in cm), using a tape measure, from the transect to

each singleton or center of pellet cluster. We encountered pellets 0–273 cm from transects, thus surveying a swath of up to 328 m² per transect.

Following McShea and Rappole (2000), we used Partners in Flight Species Assessment Database scores to provide a measure of bird conservation importance (Partners in Flight Science Committee, 2012). These scores correspond to bird conservation region 27 (Southeastern Coastal Plain) that overlaps our Coastal Virginia study area. We used the regional combined score for the breeding season (RCS-b) that incorporates the species' breeding distribution, population size, regional population trend, relative breeding density, and regional threats to reproduction, with higher scores indicating higher conservation concern.

2.3. Analysis

We employed two tests to assess differences in deer use between the two study regions. Test choice and parameters were based on tests of normality (Shapiro & Wilk, 1965) and homogeneity of variance (Levene, 1960) assumptions after histogram and boxplot evaluation. To assess differences in 2012 deer pellet estimates between Coastal Virginia and Inland Virginia, we utilized the Wilcoxon rank sum test. To evaluate differences in deer harvest rates between regions, we used a paired *t*-test. We used overlap of 95% confidence intervals to determine whether edge amount significantly differed between Coastal Virginia and Inland Virginia.

We estimated both bird and deer pellet densities (individuals and pellets ha⁻¹, respectively) in Distance 6.0 software (Thomas et al., 2010) using Multicovariate Distance Sampling (MCDS). Program Distance allowed us to account for imperfect detection and further adjust bird and deer pellet density estimates based on effects of survey-specific covariates (e.g., birds: observer, temperature, wind speed, date, time of day, and day within breeding season [May 25 = day 1]; deer: observer, time of year [May 25 = day 1], and days since rainfall for the Coastal Virginia sites). We first evaluated model fit (e.g., hazard rate-cosine or half normal-cosine; Thomas et al., 2010) of distances from observer to objects based on Goodness of Fit tests, and evaluated model fit of covariates in MCDS ranking models using AICc (Thomas et al., 2010). We used overlap of 95% confidence intervals to determine whether detection probabilities significantly differed between species and guilds. Lastly, we estimated site-specific bird and deer pellet densities based on the best model and the detection probability based on all sites. We thus believe that our estimates adequately reflect densities of birds and relative deer use at each site.

We tested for associations between deer use and birds at both the species and guild levels. For guild analyses, we grouped birds into three guilds. The primary guild of interest were species that nest in understory shrubs and glean understory foliage ("deer-sensitive" guild), which we predicted to have a negative association with deer use via the loss of nesting and foraging substrate within the deer browse stratum (ground to 1.5–2 m, Allombert et al., 2005; Bressette, Beck, & Beauchamp, 2012). On the other hand, we predicted a positive relationship with deer for canopy-nesting open ground feeders ("deer-beneficial" guild), through the expansion of foraging areas for these species. Lastly, we assigned birds for which we could not determine an a priori connection with deer to the "deer-neutral" guild: canopy-nesting species that were either canopy feeders or aerial salliers or cavity-nesting canopy feeders. We based guild assignments on foraging and nesting descriptions found in Ehrlich, Dobkin, and Wheye (1988), and our region-specific guild assignments can be found in Appendix B. Some species (e.g., *Vireo olivaceus* and *Seiurus aurocapilla*) were not assigned to guilds as they feed and nest across forest structures, or their foraging and nesting ecology predicted conflicting relationship with deer. In guild analyses, we pooled within-guild detections and assumed

equal within-guild detection probabilities. We believe this was reasonable as species within a guild occur in the same forest structure and therefore have similar factors influencing detection. We tested this assumption by comparing species detection probabilities within guilds. In species analyses, only forest-nesting passerines with ≥60 detections were included for optimal density estimates (Thomas et al., 2010). This restriction limited our species-level analysis to Coastal Virginia only. Lastly, we used Spearman's rank correlation in program R (R Core Team, 2014) to test for associations between deer and bird density estimates.

We present two types of *P*-values in the correlation coefficient (*r_s*) results tables: uncorrected and corrected for multiple comparisons. When multiple *P*-value-based tests are conducted, the number of significant results obtained by chance (leading to Type I error) increases with the number of tests (Rice, 1989). Thus, methods such as the popular Bonferroni correction procedure have been developed to adjust *P*-values based on the number of tests conducted (Cabin & Mitchell, 2000). However, Bonferroni correction has a number of undesirable consequences (see review in Moran, 2003). Importantly, biologists conducting ecological research with high variability and small replicate number are either forced to limit the scope of their study or report results with greatly inflated Type II error. Because of this phenomenon and persistent debate about where to apply Bonferroni correction, it is desirable to report both uncorrected and corrected *P*-values (Moran, 2003), and thus we do so in this study.

3. Results

In order to account for imperfect detection (Kéry & Schmid, 2004), we estimated detection probability as a nuisance parameter to adjust pellet and bird densities. Deer pellet detection probability was significantly lower in Coastal Virginia (0.37, CI=0.35–0.39) compared to Inland Virginia (0.55, CI=0.51–0.58). Bird and guild detection probabilities were all ≤0.34. For individual bird species, detection probability was highest (0.34, CI=0.30–0.38) for the Yellow-throated Warbler (*Setophaga dominica*) and lowest (0.11, CI=0.09–0.13) for the Eastern Towhee (*Pipilo erythrophthalmus*; Appendix C). For Coastal Virginia, guild detection probabilities did not differ from average detection probabilities of species within that guild: deer-sensitive guild 0.14 (CI=0.10–0.19) vs. 0.18 (CI=0.10–0.26), deer-beneficial guild 0.19 (CI=0.18–0.20) vs. 0.22 (CI=0.05–0.39), and deer-neutral guild 0.19 (CI=0.17–0.21) vs. 0.19 (CI=0.16–0.22). There was no difference in guild detection probabilities between Coastal Virginia and Inland Virginia for the deer-sensitive guild (0.08, CI=0.04–0.15), but detection probabilities were significantly lower at Inland Virginia sites for the deer-beneficial guild (0.11, CI=0.08–0.14) and the deer-neutral guild (0.14, CI=0.12–0.15).

Average forest edge extent in Coastal Virginia was generally more than twice the amount present inland. This pattern held for edge delineated by roads, as well as the three land cover types (Fig. 2). Specifically, edge extent was higher coastal than inland for forest-road, forest-grassland, forest-row crop, and forest-rural land edges, by 232%, 346%, 176% and 252%, respectively.

We found deer use to be greater in Coastal Virginia (Fig. 3). In 2012, the median estimate of pellet density in Coastal Virginia (2,013.8 pellets ha⁻¹, range 0–28,193 ha⁻¹) was significantly higher than in Inland Virginia (0 pellets ha⁻¹, range 0–19,600 pellets ha⁻¹), Wilcoxon rank sum test: *W* = 5462, *P* = 0.01. For Inland Virginia, the majority (57%) of survey sites contained no pellets at all, whereas only 38% of Coastal Virginia sites had zero pellets. In 2004–2013, hunters harvested a mean of 4.73 (CI=4.45–5.00, *n* = 10) deer year⁻¹ ha⁻¹ of forest in Coastal Virginia, which was 58% higher

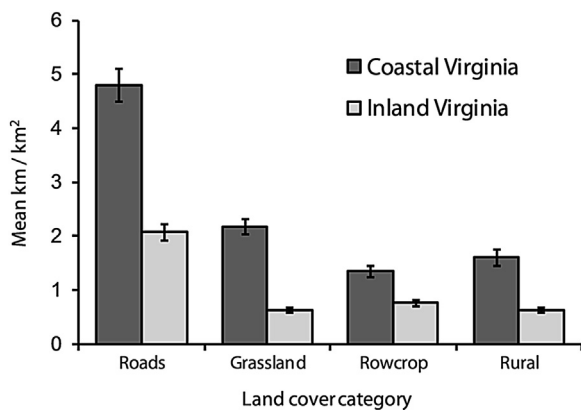


Fig. 2. Mean forest edge length in our study areas. To evaluate habitat quality for White-tailed Deer, we measured forest edge length delineated by roads and three land cover categories in 1 km² plots (depicted in Fig. 1). Mean forest edge length was higher at plots in Coastal Virginia ($n = 507$) than in Inland Virginia ($n = 1,018$), suggesting better habitat for deer, which prefer fragmented forests, in Coastal Virginia. Error bars represent 95% confidence intervals.

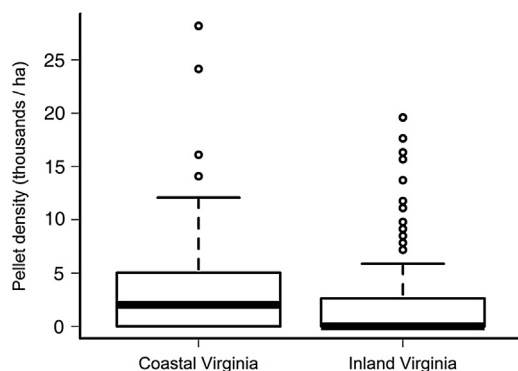


Fig. 3. Deer pellet density at survey plots in Coastal Virginia ($n = 92$) and Inland Virginia ($n = 99$) estimated from data collected in 2012. Median pellet density in Coastal Virginia ($2,013.8$ pellets ha^{-1}) was significantly higher than in Inland Virginia (0 pellets ha^{-1} , Wilcoxon rank sum test: $W = 5462$, $P = 0.01$).

than the annual harvest in Inland Virginia (2.99 deer $\text{year}^{-1} \text{ha}^{-1}$, $CI = 2.79\text{--}3.19$, $n = 10$; paired t -test: $t_9 = 11.1$, $P < 0.001$).

In Coastal Virginia, avian community varied with deer use at the guild level (Table 1; Fig. 4). Supporting our prediction, we found a negative correlation between deer use and the deer-sensitive guild (shrub-nesting foliage gleaners) in Coastal Virginia ($r_s = -0.35$, $P = 0.002$). Interestingly, we found a positive correlation between deer use and the deer-neutral guild (canopy-nesting species that are either canopy feeders or aerial salliers, plus cavity-nesting canopy feeders; $r_s = 0.27$, $P = 0.03$). We detected no relationships between bird guilds and deer use in Inland Virginia.

Avian densities varied with deer use in Coastal Virginia at the species level of analysis (Table 2). Birds with a significant negative correlation with deer use, employing P -values uncorrected for multiple comparisons, were the White-eyed Vireo (*Vireo griseus*), Red-eyed Vireo (*Vireo olivaceus*), Black-and-white Warbler (*Mniotilta varia*), Hooded Warbler (*Setophaga citrina*), Prairie Warbler (*Setophaga discolor*), and Scarlet Tanager (*Piranga olivacea*). We detected a positive correlation between deer use and densities for the following species: Eastern Wood-Pewee (*Contopus virens*), Acadian Flycatcher (*Empidonax virens*), Blue Jay (*Cyanocitta cristata*), Carolina Chickadee (*Poecile carolinensis*), and White-breasted Nuthatch (*Sitta carolinensis*). Bonferroni-corrected P -values ($n = 26$) remained significant for the White-eyed Vireo and Prairie and Hooded Warblers (negative relationship with deer), as

well as for the Carolina Chickadee and White-breasted Nuthatch (positive relationship with deer).

4. Discussion

Our study is consistent with a growing body of evidence implicating deer as important habitat engineers for birds. Thus far, relevant literature has connected deer to songbird populations through studies ranging from relatively small experimental deer enclosures (e.g., Cardinal, Martin, Tremblay, & Côté, 2012; McShea & Rappole, 2000) to examinations of broad trends using citizen-science data (Chollet & Martin, 2013). To our knowledge, this is the first study to investigate the deer-bird relationship on a regional scale while employing rigorous, plot-specific, multi-year estimates of deer use and bird densities. By utilizing detection probabilities corrected for survey-specific covariates, we were able to adjust density estimates for imperfect detection for both birds and deer pellets. Our results match those of other studies – woodland songbirds that depend on foliage below the browse line show an inverse relationship with deer (e.g., Cardinal et al., 2012).

We detected significant correlations between deer use and densities of forest birds for species utilizing habitat below the deer browse line. At the guild level, we found a negative correlation between deer use and shrub-nesting foliage gleaners (Table 1; Fig. 4). Using P -values corrected for multiple comparisons, the species-level analysis revealed a negative correlation for the White-eyed Vireo, Hooded Warbler, and the Prairie Warbler, a bird listed among species of highest conservation concern at the continental scale by Partners in Flight (Rosenberg et al., 2016). White-eyed Vireos are associated with low shrubby vegetation and high foliage density, preferring habitat with expansive undergrowth, brambles, and saplings (Hopp, Kirby, & Boone, 1995). Local populations of the Hooded Warbler, an understory shrub-nesting bird, have declined heavily with shrub layer disappearance (for review see Chiver, Ogden, & Stutchbury, 2011). Similarly, the Prairie Warbler typically breeds in forests with open canopy and shrubby undergrowth (Nolan, Ketterson, & Buerkle, 1999). Association with forest understory makes both the Prairie Warbler and the White-eyed Vireo deer-sensitive species. Over-browsed areas associated with high deer densities tend to be devoid of vegetation cover below the browse line (Martin et al., 2010), and it should be noted that direct depredation of songbird nests by deer has also been documented (Luepold, Hodgman, McNulty, Cohen, & Foss, 2015). Following removal of deer, experimental plots in Virginia saw gradual increase of Hooded Warblers as understory vegetation recovered (McShea & Rappole, 2000). Another study found no Hooded Warblers in plots with artificially inflated ungulate densities, even though they were detected in surrounding areas (Casey & Hein, 1983).

Using Bonferroni-corrected P -values, we detected a positive correlation between relative deer use and densities of the Carolina Chickadee and White-breasted Nuthatch (Table 2). In oak-hickory forest in Arkansas, experimental understory vegetation removal and tree thinning was coupled with short-term increases in abundance of the White-breasted Nuthatch (Rodewald & Smith, 1998). Because our study design cannot detect a causal relationship between deer use and birds, some of our observed correlations may reflect overlap in habitat preferences between deer and certain bird species – not a bird response to deer. For example, both the Carolina Chickadee and deer thrive in wooded suburbs (Mostrom, Curry, & Lohr, 2002), possibly explaining the positive correlation between chickadees and deer in our study.

At Inland Virginia, we detected no relationship between bird guilds and deer use. We propose that this regional contrast is due to the difference in deer use between the two areas. Based on evidence from our deer pellet surveys and hunter harvest data, the lower

Table 1
Spearman's rank correlation test results for deer pellet density and density of three avian guilds: deer-sensitive (shrub-nesting foliage gleaners), deer-beneficial (canopy-nesting open ground feeders), deer-neutral (canopy-nesting species that are either canopy feeders or aerial salliers, plus cavity-nesting canopy feeders). We report the correlation coefficient (r_s) and both the original P -values (P) and Bonferroni-corrected P -values (P_{Bon}). For a list of species included in each guild see Appendix B.

Guild	Predicted direction	Coastal Virginia			Inland Virginia		
		r_s	P	P_{Bon}	r_s	P	P_{Bon}
deer-sensitive	negative	-0.35	<0.001*	0.002*	0.09	0.35	–
deer-beneficial	positive	0.08	0.44	–	0.11	0.27	–
deer-neutral	none	0.27	0.01†	0.03*	-0.14	0.16	–

* Indicates significance at $\alpha = 0.05$.

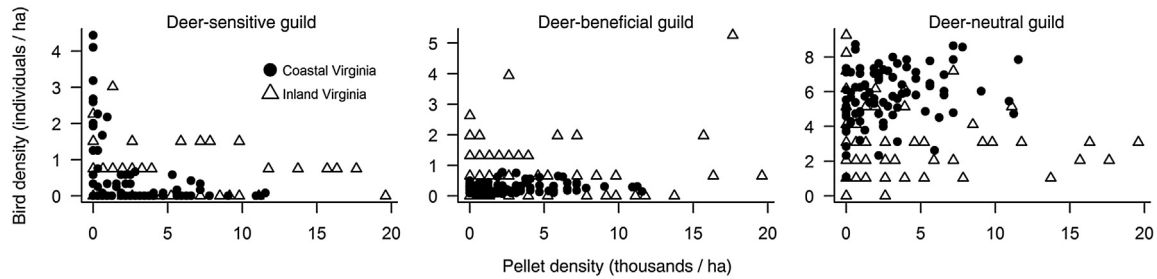


Fig. 4. Bird guild density versus deer pellet density at our two study regions. Density estimates at Coastal Virginia sites ($n = 92$) were averaged over four years (2010–2013), whereas estimates at Inland Virginia sites ($n = 99$) are based on surveys conducted in a single year only (2012). Single year (2012) pellet counts at coastal sites were higher than at inland sites (Fig. 3), suggesting more deer overall in Coastal Virginia.

Table 2
Spearman's rank correlation test results for densities of deer pellets and 26 songbird species in Coastal Virginia. Species were assigned a priori to three avian guilds: deer-sensitive (shrub-nesting foliage gleaners), deer-beneficial (canopy-nesting open ground feeders), deer-neutral (canopy-nesting species that are either canopy feeders or aerial salliers plus cavity-nesting canopy feeders). We report the correlation coefficient (r_s) and both the original P -values (P) and Bonferroni-corrected P -values (P_{Bon}). Of associations with significant original and (corrected) P -values, 6(3) were negative and 5(2) positive.

Species	Guild ^a	PIF score ^b	r_s	P	P_{Bon}
<i>Contopus virens</i> (Eastern Wood-Pewee)	deer-neutral	14	0.27	0.008*	0.21
<i>Empidonax virens</i> (Acadian Flycatcher)	deer-neutral	15	0.30	0.004*	0.09
<i>Myiarchus crinitus</i> (Great Crested Flycatcher)	deer-neutral	11	0.10	0.36	–
<i>Vireo griseus</i> (White-eyed Vireo)	deer-sensitive	14	-0.40	<0.001*	0.002*
<i>Vireo olivaceus</i> (Red-eyed Vireo)	–	9	-0.26	0.01	0.35
<i>Cyanocitta cristata</i> (Blue Jay)	deer-beneficial	14	0.22	0.03*	0.82
<i>Corvus brachyrhynchos</i> (American Crow)	deer-beneficial	11	0.00	0.97	–
<i>Poecile carolinensis</i> (Carolina Chickadee)	deer-neutral	15	0.34	0.001*	0.02*
<i>Baeolophus bicolor</i> (Tufted Titmouse)	deer-neutral	13	0.16	0.12	–
<i>Sitta carolinensis</i> (White-breasted Nuthatch)	deer-neutral	9	0.36	<0.001*	0.01*
<i>Thryothorus ludovicianus</i> (Carolina Wren)	–	13	0.20	0.06	–
<i>Poliophtila caerulea</i> (Blue-gray Gnatcatcher)	deer-neutral	11	-0.10	0.34	–
<i>Hylocichla mustelina</i> (Wood Thrush)	deer-beneficial	16	0.04	0.69	–
<i>Turdus migratorius</i> (American Robin)	deer-beneficial	6	0.17	0.12	–
<i>Seiurus aurocapilla</i> (Ovenbird)	–	9	-0.13	0.23	–
<i>Mniotilta varia</i> (Black-and-white Warbler)	–	9	-0.22	0.03*	0.84
<i>Setophaga citrina</i> (Hooded Warbler)	deer-sensitive	14	-0.36	<0.001*	0.01*
<i>Setophaga americana</i> (Northern Parula)	deer-neutral	15	-0.13	0.22	–
<i>Setophaga pinus</i> (Pine Warbler)	deer-neutral	12	-0.18	0.08	–
<i>Setophaga dominica</i> (Yellow-throated Warbler)	–	16	-0.10	0.33	–
<i>Setophaga discolor</i> (Prairie Warbler)	deer-sensitive	17	-0.38	<0.001*	0.006*
<i>Pipilo erythrophthalmus</i> (Eastern Towhee)	–	16	-0.14	0.17	–
<i>Piranga rubra</i> (Summer Tanager)	deer-neutral	14	0.21	0.05	–
<i>Piranga olivacea</i> (Scarlet Tanager)	deer-neutral	12	-0.22	0.03*	0.84
<i>Cardinalis cardinalis</i> (Northern Cardinal)	–	12	-0.02	0.84	–
<i>Passerina cyanea</i> (Indigo Bunting)	deer-sensitive	13	-0.19	0.08	–

^a Dash indicates species was not used in guild analyses.

^b Partners in Flight Regional Combined Score for the breeding season (Partners in Flight Science Committee, 2012). Conservation assessment scores correspond to Bird Conservation Region 27 (Southeastern Coastal Plain).

* Indicates significant correlation at $\alpha = 0.05$

peninsula of the coastal plain of Virginia has a higher deer population (Fig. 3), and only here did we detect associations between deer and birds. Where deer use was lower, in the forests surrounding the Shenandoah Valley, no such relationships were evident. However, we cannot rule out the possibility that the detected regional difference was due to higher sampling effort on the coast, where we had four years of data compared to one year inland.

Our land cover analyses revealed that the high deer use in Coastal Virginia, where we detected deer-bird associations, was correlated with substantial levels of local forest fragmentation providing high-quality deer habitat. In Coastal Virginia, as is true in many other parts of Virginia (Lovely et al., 2013) and North America in general (Theobald, Miller, & Hobbs, 1997), a common land use practice is to subdivide extensive single-owner parcels into

multiple smaller lots. This rampant and expansive land use effectively reduces habitat quality for much of biodiversity (Theobald et al., 1997), but simultaneously increases habitat quality for White-tailed Deer (Stockton, Allombert, Gaston, & Martin, 2007a; Vogel, 1989) and reduces hunting pressure on deer by preventing hunter access (Brown et al., 2000; Gorham & Porter, 2011; Harden, Woolf, & Roseberry, 2005; Lovely et al., 2013; Stockton, Allombert, Gaston, & Martin, 2007b).

To reduce impacts of browsing by overabundant deer on flora and fauna, effective, continually supported, and range-wide deer management is needed, particularly in areas where traditional hunting is absent, such as exurban-suburban areas and national parks (Brown et al., 2000). To control White-tailed Deer populations, a variety of methods that includes bow hunting, sharpshooting by trained personnel, and trap-and-euthanize programs, has been successfully implemented elsewhere. Local and state governments need to maintain socially and biologically supported deer carrying capacities that allow flora and fauna to recover from excessive browsing (Brown et al., 2000). For example, Martin et al. (2011) showed that Black-tailed Deer density of <0.1 ha⁻¹ allows for vegetation recovery. Reducing deer populations also has direct benefits to human safety by reducing deer-car collisions (Bissonette, Kassar, & Cook, 2008; Wiggers, 2011) and limiting the spread of tick-borne diseases, for which deer often serve as the most important reservoir host (Paddock & Yabsley, 2007).

5. Conclusions

In this study, high deer use was correlated with low densities of birds that breed and forage in understory vegetation. Although our results are correlative, they are consistent with the hypothesis that habitat modification by deer promotes measurable changes in bird communities, with conservation implications for some declining forest songbirds. When areas with high deer densities occur near forest reserves important for bird conservation, such as where continuous forest tracts are fragmented by low-density housing, deer management should be considered a high priority (McShea, 2012).

Table B1

Region-specific guild assignments: deer-sensitive guild (shrub-nesting foliage gleaners), deer-beneficial guild (canopy-nesting open ground feeders), deer-neutral guild (canopy nesters that are either canopy feeders or aerial salliers plus cavity-nesting canopy feeders). A dash indicates species does not regularly occur in the corresponding study area.

Scientific name	Common name	Coastal Virginia	Inland Virginia
<i>Contopus virens</i>	Eastern Wood-Pewee	deer-neutral	deer-neutral
<i>Empidonax virens</i>	Acadian Flycatcher	deer-neutral	deer-neutral
<i>Myiarchus crinitus</i>	Great Crested Flycatcher	deer-neutral	deer-neutral
<i>Vireo griseus</i>	White-eyed Vireo	deer-sensitive	-
<i>Vireo flavifrons</i>	Yellow-throated Vireo	deer-neutral	deer-neutral
<i>Vireo solitarius</i>	Blue-headed Vireo	-	deer-neutral
<i>Cyanocitta cristata</i>	Blue Jay	deer-beneficial	deer-beneficial
<i>Corvus ossifragus</i>	Fish Crow	deer-beneficial	deer-beneficial
<i>Poecile carolinensis</i>	Carolina Chickadee	deer-neutral	deer-neutral
<i>Poecile atricapillus</i>	Black-capped Chickadee	-	deer-neutral
<i>Baeolophus bicolor</i>	Tufted Titmouse	deer-neutral	deer-neutral
<i>Sitta carolinensis</i>	White-breasted Nuthatch	deer-neutral	deer-neutral
<i>Poliophtila caerulea</i>	Blue-gray Gnatcatcher	deer-neutral	deer-neutral
<i>Hylocichla mustelina</i>	Wood Thrush	deer-beneficial	deer-beneficial
<i>Turdus migratorius</i>	American Robin	deer-beneficial	deer-beneficial
<i>Setophaga citrina</i>	Hooded Warbler	deer-sensitive	deer-sensitive
<i>Setophaga ruticilla</i>	American Redstart	deer-neutral	deer-neutral
<i>Setophaga americana</i>	Northern Parula	deer-neutral	deer-neutral
<i>Setophaga fusca</i>	Blackburnian Warbler	-	deer-neutral
<i>Setophaga pinus</i>	Pine Warbler	deer-neutral	deer-neutral
<i>Setophaga discolor</i>	Prairie Warbler	deer-sensitive	deer-sensitive
<i>Setophaga virens</i>	Black-throated Green Warbler	-	deer-neutral
<i>Spizella passerina</i>	Chipping Sparrow	deer-beneficial	deer-beneficial
<i>Piranga rubra</i>	Summer Tanager	deer-neutral	-
<i>Piranga olivacea</i>	Scarlet Tanager	deer-neutral	deer-neutral
<i>Passerina cyanea</i>	Indigo Bunting	deer-sensitive	deer-sensitive

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Appendix A.

See Table A1.

Table A1

LANDFIRE land cover classification crosswalk.

Land cover class	LANDFIRE value
Grassland	67, 75, 76, 81, 85, 95, 2181–2184, 2190, 2436
Row crop	60–66, 80, 82–84
Rural	13–24
Forest	2187, 2193, 2194, 2197, 2303–2318, 2320–2331, 2333–2335, 2338–2344, 2346–2357, 2361, 2362, 2368–2370, 2377, 2379, 2400, 2456, 2468, 2471–2474, 2479, 2480, 2490, 2501, 2518, 2531–2537, 2541–2549

Appendix B.

See Table B1.

Appendix C.

See Table C1.

Table C1
 Detection probabilities (p), 95% confidence interval, function (hzcoss = hazard rate cosine, hncoss = half-normal cosine, hzsp = hazard rate simple polynomial; Thomas et al., 2010), covariate (possible covariates evaluated: observer, starting time [time since sunrise], time in breeding season [May 1 = day 1], wind speed [m s^{-1} , measured on ground], year [2010–2013], wind speed in canopy [Beaufort scale: categorical 1–5, see Methods], temperature [$^{\circ}\text{C}$], and noise (categorical 1–4, see Methods), model fit improvement when covariate included (ΔAICc) to estimate detection probabilities for species with ≥ 60 observations in Coastal Virginia study site.

Scientific name	Common name	p	Confidence interval	p function	Covariate	ΔAICc
<i>Contopus virens</i>	Eastern Wood-Pewee	0.20	0.19–0.21	hzcoss	observer	176.2
<i>Empidonax virens</i>	Acadian Flycatcher	0.17	0.16–0.18	hzcoss	observer	82.0
<i>Myiarchus cinerascens</i>	Great Crested Flycatcher	0.16	0.15–0.18	hzcoss	observer	109.1
<i>Vireo griseus</i>	White-eyed Vireo	0.15	0.12–0.19	hncoss	year	10.0
<i>Vireo olivaceus</i>	Red-eyed Vireo	0.15	0.14–0.16	hncoss	year	23.6
<i>Cyanocitta cristata</i>	Blue Jay	0.26	0.24–0.28	hzcoss	observer/wind speed	5.7
<i>Corvus brachyrhynchos</i>	American Crow	0.26	0.24–0.28	hzcoss	starting time	9.7
<i>Poecetes gramineus</i>	Carolina Chickadee	0.22	0.20–0.23	hzcoss	–	–
<i>Baeolophus bicolor</i>	Tufted Titmouse	0.14	0.13–0.15	hncoss	observer	98.1
<i>Sitta carolinensis</i>	White-breasted Nuthatch	0.27	0.24–0.30	hzcoss	year	41.0
<i>Thryothorus ludovicianus</i>	Carolina Wren	0.31	0.29–0.32	hzcoss	year	31.9
<i>Poliophtila caerulea</i>	Blue-gray Gnatcatcher	0.19	0.18–0.21	hzcoss	wind speed	5.8
<i>Hylocichla mustelina</i>	Wood Thrush	0.29	0.26–0.31	hzcoss	year/observer	15.6
<i>Turdus migratorius</i>	American Robin	0.14	0.13–0.15	hzcoss	observer	28.8
<i>Seiurus aurocapilla</i>	Ovenbird	0.25	0.24–0.27	hzsp	year	61.8
<i>Mniotilta varia</i>	Black-and-white Warbler	0.19	0.15–0.24	hncoss	–	–
<i>Setophaga citrina</i>	Hooded Warbler	0.14	0.12–0.16	hzcoss	time breeding season	15.6
<i>Setophaga americana</i>	Northern Parula	0.23	0.20–0.27	hzcoss	–	–
<i>Setophaga pinus</i>	Pine Warbler	0.27	0.25–0.29	hzsp	–	–
<i>Setophaga dominica</i>	Yellow-throated Warbler	0.34	0.30–0.38	hzcoss	–	–
<i>Setophaga discolor</i>	Prairie Warbler	0.25	0.20–0.30	hzcoss	observer	18.6
<i>Pipilo erythrophthalmus</i>	Eastern Towhee	0.11	0.09–0.13	hncoss	observer	25.0
<i>Piranga rubra</i>	Summer Tanager	0.16	0.15–0.17	hzcoss	observer	86.2
<i>Piranga olivacea</i>	Scarlet Tanager	0.14	0.12–0.17	hncoss	Julian date	27.0
<i>Cardinalis cardinalis</i>	Northern Cardinal	0.20	0.19–0.21	hzcoss	observer	122.0
<i>Passerina cyanea</i>	Indigo Bunting	0.18	0.15–0.22	hzcoss	–	–

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.landurbplan.2017.01.003>.

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