

EFFECT OF WHITE-TAILED DEER ON SONGBIRDS WITHIN MANAGED FORESTS IN PENNSYLVANIA

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Abstract: White-tailed deer (*Odocoileus virginianus*) populations have been maintained at high densities in Pennsylvania for several decades with unknown effects on songbirds and their habitats. I evaluated effects of white-tailed deer density on songbird species richness, abundance, and habitat. I simulated 4 deer densities (3.7, 7.9, 14.9, and 24.9 deer/km²) within individually fenced enclosures on 4 65-ha forest areas in northwestern Pennsylvania. Within all enclosures, 10% of the area was clear-cut and 30% was thinned. Enclosures were subjected to 10 years of deer browsing, 1980–90, at the 4 simulated densities. I conducted bird counts in 1991. Varying deer density had no effect ($P > 0.1$) on ground- or upper canopy-nesting songbirds or their habitat, but species richness of intermediate canopy-nesting songbirds declined 27% ($P = 0.01$) and abundance declined 37% ($P = 0.002$) between lowest and highest deer densities. I did not observe the eastern wood pewee (*Contopus virens*), indigo bunting (*Passerina cyanea*), least flycatcher (*Empidonax minimus*), yellow-billed cuckoo (*Coccyzus americanus*), or cerulean warbler (*Dendroica cerulea*) at densities >7.9 deer/km², and the eastern phoebe (*Sayornis phoebe*), and American robin (*Turdus migratorius*) were not observed at 24.9 deer/km². Threshold deer density for effect on habitat and songbirds within managed (100-yr rotation) forests was between 7.9 and 14.9 deer/km².

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Declines in populations of migratory songbirds have been associated with forest fragmentation in breeding and wintering ranges and with silvicultural practices that alter forest structure by eliminating old-growth characteristics (Robbins et al. 1989, Finch 1991, Hagan and Johnston 1992, Schneider and Pence 1992). White-tailed deer densities >7 /km² have been reported in the northeastern United States (Alverson et al. 1988, Burke and Ferrigno 1989, Palmer 1989). In Pennsylvania, the white-tailed deer population has increased since 1970 and

averaged >11 /km² statewide in 1992 (Witmer and deCalesta 1992). At these densities, species richness and abundance of herbaceous and woody vegetation decline (Behrend et al. 1970, Alverson et al. 1988, Tilghman 1989). Frelich and Lorimer (1985) and Tilghman (1989) documented an inverse relationship between deer density and density of woody vegetation <1.5 m in height. Species richness and abundance of forest songbirds have been positively correlated with species abundance, composition, and vertical structure of woody and herbaceous vege-

tation (MacArthur and MacArthur 1961, Karr and Roth 1971, Hooper et al. 1973, DeGraaf et al. 1991). By affecting vegetation, deer might alter songbird habitat and negatively affect songbird populations.

McShea and Rappole (1992) demonstrated a positive correlation between understory vegetation density and songbird species richness and abundance and noted that deer densities were higher in areas with reduced understory vegetation. Casey and Hein (1983) compared differences in bird occurrence and abundance between an area affected by 27 years of ungulate (including white-tailed deer) browsing (100 browsing animals/km²) and an adjacent area with lower deer density (10–20/km²). Ten species of ground-nesting or intermediate canopy-nesting birds were absent or occurred at lower frequencies in the area with higher ungulate density.

From 1980–90, personnel of the Warren Laboratory of the U.S. Forest Service, Northeastern Forest Experiment Station, studied the effect of varying white-tailed deer densities on regeneration of woody vegetation (Tilghman 1989). I tested whether relationships existed among deer density, songbird habitat, and songbird species richness and abundance at these sites in 1991.

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STUDY AREA

Four 65-ha study sites were located in northwestern Pennsylvania on and adjacent to the ANF in Warren, Forest, Elk, and McKean counties: all were within 100 km of each other. All were 50–60-year-old Allegheny hardwood stands dominated by black cherry (*Prunus serotina*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), and beech (*Fagus grandifolia*) (Tilghman 1989). Sites represented a gradient of low-to-high potential for successful regeneration (species composition and stem density of hard-

wood seedlings sufficient to replace existing trees after removal harvest) (Marquis et al. 1992).

I divided each 65-ha site into 4 deer enclosures and approximated and maintained white-tailed deer densities of 4, 8, 16, and 31/km² for 10 years. I simulated the 4 white-tailed deer densities by maintaining 1 deer in a 26-ha enclosure (3.7 deer/km²), 1 deer in a 13-ha enclosure (7.8 deer/km²), 2 deer in a 13-ha enclosure (15.6 deer/km²), and 4 deer in a 13-ha enclosure (31.2 deer/km²). This range of deer densities encompassed estimated presettlement white-tailed deer densities in North America (2–8/km²; McCabe and McCabe 1984:27, Alverson et al. 1988) and recent deer densities in northwestern Pennsylvania (31/km²; J. S. Jordon, U.S. For. Serv., Northeast. For. Exp. Stn., Warren, Pa., pers. commun.). Estimates of overwinter deer density during the study averaged 12 deer/km² (W. L. Palmer, Pa. Game Comm., Harrisburg, pers. commun.) in the 4 county area composing the forest. All sites were within large blocks of contiguous second-growth forest. The forest canopy was opened by clear-cuts and thinnings created by the study design, and by forest roads, gas wellheads and pipelines, and clear-cuts and thinnings on adjacent lands. I constructed enclosures of 2.4-m-tall woven-wire livestock fence.

I fitted deer with radio collars equipped with mortality sensors and stocked them in enclosures. Deer that were lost from enclosures through winter starvation, escape, poaching, and predation were replaced the following spring. Occasionally, wild deer infiltrated the enclosures, resulting in temporary (2–6 weeks) overstocking until they could be removed. Thus, actual densities varied; average deer densities (\pm SD) across the 4 areas for the study were 3.7 (\pm 0.2), 7.9 (\pm 0.1), 14.9 (\pm 0.1), and 24.9 (\pm 2.3) deer/km².

Each of the 16 enclosures was subdivided into 3 silvicultural treatment areas at study initiation: 10% of each enclosure was harvested to remove all trees except seedlings, 30% was thinned to effect a 40% reduction in relative density, and 60% was left uncut. This treatment simulated a 100-year rotation, representing standard silvicultural practice on Allegheny hardwood forests managed for multiple resources (Marquis et al. 1992). Allegheny hardwood stands reach financial maturity at 90–120 years (Marquis and Gearhart 1983) and, in the presence of high deer densities, sustained yields of timber can be produced only by even-aged

silvicultural management using combinations of clear-cutting and thinning incorporated in the study design (Marquis et al. 1992).

If sustained forestry is practiced on longer rotations to produce more mature stands, and uneven-aged management is the silvicultural system of choice, the cycle of timber harvest is longer, and the amount cut at each entry is less, producing less forage and resulting in greater effect of deer on forest regeneration at given densities. Actually, intensity of clear-cutting and thinning on the ANF (which represented local conditions) was 4–8% clear-cutting and 12% thinning at 10-year intervals because of the lack of adequate advance regeneration caused by high resident deer density (B. B. Nelson, Allegheny Natl. For., Warren, Pa., pers. commun.).

METHODS

I sampled woody and herbaceous vegetation from systematically spaced 4-m² regeneration plots located in each enclosure. I located 25 such plots within clear-cut treatment areas, 15 in thinned treatment areas, and 20 in uncut treatment areas. Vegetation was sampled 0, 1, 3, 5, and 10 years after silvicultural treatments. I estimated percent ground cover ocularly on each regeneration plot and averaged it within treatment areas. I recorded height of tallest sapling for every regeneration plot and averaged it within treatment areas.

I conducted point counts of birds (Verner 1985) 5 times/site from 15 May to 31 July 1991 within the 16 deer enclosures. Because clear-cuts were small, I placed only 1 bird count station at the center of these areas. Thinned sites were twice as large and I randomly located 2 stations in each. I randomly located 3 stations within each uncut site. All stations were ≥ 30 m from any interface with a site receiving a different silvicultural treatment. During each count, I recorded all birds identified aurally or visually ≤ 30 m from a station. I categorized songbirds as ground nesting (GN), intermediate canopy nesting (ICN, nesting 0.5–7.5 m aboveground), or upper canopy nesting (UCN, nesting above 7.5 m; DeGraaf et al. 1991, Appendix).

During each count, I recorded species richness and abundance (sum of birds identified on survey stations) for each songbird category at each white-tailed deer enclosure. Unequal sample sizes from songbird counts among silvicultural treatments made it unsound to compare songbird responses among silvicultural treat-

ments. Rather, I summed songbird population parameters collected during the 5 separate surveys and pooled across clear-cut, thinned, and uncut survey stations within each of the 4 deer density enclosures at each of the 4 study areas.

I used analysis of variance (ANOVA) to test whether differences of independent variables (species richness and abundance for the 3 songbird categories, height of woody vegetation, and percent ground cover) occurred among study sites and deer densities and whether there were study area by deer density interactions. I also used ANOVA to determine whether thresholds existed for effect of deer density on independent variables. I considered a threshold to exist if differences in dependent variables occurred ($P < 0.05$) between consecutive deer densities. I used the Bonferroni procedure to test for thresholds within dependent variable categories (Wilkinson 1984). If ANOVA indicated differences existed among dependent variables over the range of deer densities, but not between consecutive deer densities, then I determined that the effect of deer densities on dependent variables was continuous (without a defined threshold) rather than discrete (with a defined threshold). Because bird species richness and abundance and sampling height were not block variables, I used regression analysis to determine whether sapling height and bird species richness and abundance were related.

RESULTS

I detected 48 songbird species among the 4 study sites (Appendix). Number of species at individual sites ranged from 31 to 43. I identified 2,912 individual songbirds among the 4 sites (658–789/site).

Deer Density and Vegetation

Percent ground cover was not affected by deer ($F = 1.764, 1.692, \text{ and } 0.843; 3, 384, 3, 224, \text{ and } 3, 304 \text{ df}; P = 0.375, 0.170, \text{ and } 0.471$, respectively, for clear-cut, thinned, and uncut sites [Fig. 1]). There were changes in species composition of ground cover; increasing deer densities were associated with decreases in flowering plants and increases in fern and grasses (deCalesta, unpubl. data).

Mean sapling height was reduced by deer on clear-cut ($F = 34.16; 3, 377 \text{ df}; P < 0.001$), thinned ($F = 14.27; 3, 220 \text{ df}; P < 0.001$), and uncut sites ($F = 19.61; 3, 297 \text{ df}; P < 0.001$; Fig. 2). Mean sapling height on clear-cut,

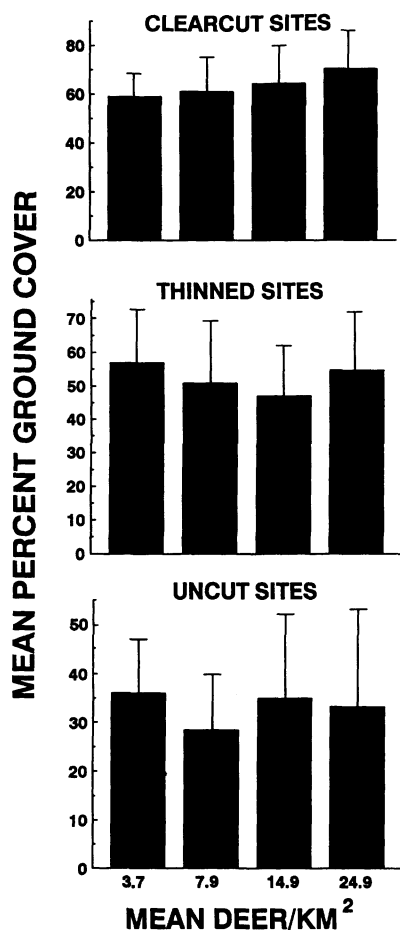


Fig. 1. Mean (\pm SE) percent ground cover by white-tailed deer density on clear-cut, thinned, and uncut sites in northeastern Pennsylvania, 1991. There were no differences ($P > 0.05$) among percent cover values within clear-cut, thinned, or uncut sites.

thinned, and uncut sites also differed among study areas ($F = 4.04, 4.89, \text{ and } 7.59; 3, 377, 3, 220, \text{ and } 3, 297 \text{ df}; P < 0.05$ for all sites). There were study area by deer density interactions ($F = 4.88, 3.29, \text{ and } 2.81; 9, 377, 9, 220, \text{ and } 9, 297 \text{ df}; P < 0.005$), respectively, for clear-cut, thinned, and uncut sites. A threshold for reduction in sampling height occurred between 7.9 and 14.9 deer/km² ($F = 25.90 \text{ and } 14.51; 1, 377 \text{ and } 1, 200 \text{ df}; P < 0.001$, for clear-cut and thinned sites, respectively); for uncut sites the threshold occurred between 14.9 and 24.9 deer/km² ($F = 35.09; 1, 297 \text{ df}; P < 0.001$).

Sapling Height and Bird Species Richness and Abundance

Richness and abundance of GN and UCN species were not related to sapling height on

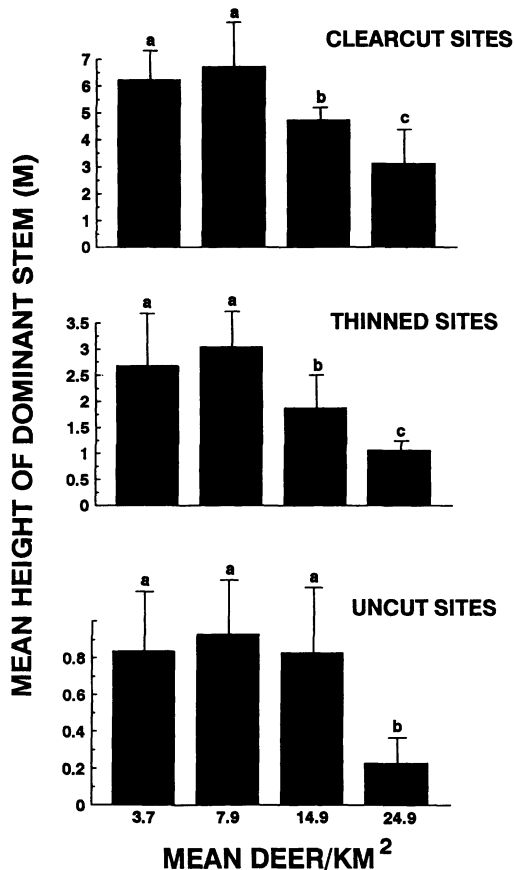


Fig. 2. Mean (\pm SE) sapling height by white-tailed deer density on clear-cut, thinned, and uncut sites in northwestern Pennsylvania, 1991. Bars with dissimilar letters, within sites, were different ($P < 0.05$).

clear-cut, thinned, or uncut sites ($P > 0.75$). Species richness of ICN species was weakly correlated with sapling height on clear-cuts ($P = 0.118, r^2 = 0.166$), moderately correlated with sapling height on thinned sites ($P = 0.01, r^2 = 0.39$), and not correlated with height on uncut sites ($P > 0.50$). Abundance of ICN species was correlated with sapling height on thinned ($P = 0.05, r^2 = 0.326$) and on clear-cut sites ($P = 0.001, r^2 = 0.60$), and not correlated with sapling height on uncut sites ($P > 0.50$).

Deer Density and Songbird Species Richness

Mean richness of ICN species declined 27% from lowest deer density to the highest (Fig. 3) ($F = 10.46; 3, 64 \text{ df}; P < 0.001$). Threshold for deer effect occurred between 7.9 and 14.9 deer/km² ($F = 15.17; 1, 64 \text{ df}; P < 0.001$). Four ICN species (eastern wood pewee, indigo bunting,

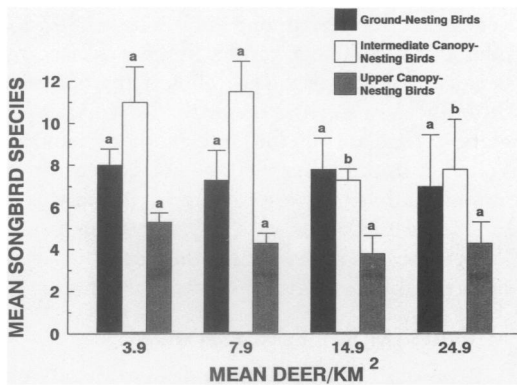


Fig. 3. Mean (\pm SE) number of songbird species by white-tailed deer density across pooled clear-cut, thinned, and uncut sites in northwestern Pennsylvania, 1991. Bars with dissimilar letters within bird groupings (ground nesting, intermediate canopy nesting, upper canopy nesting) were different ($P < 0.05$).

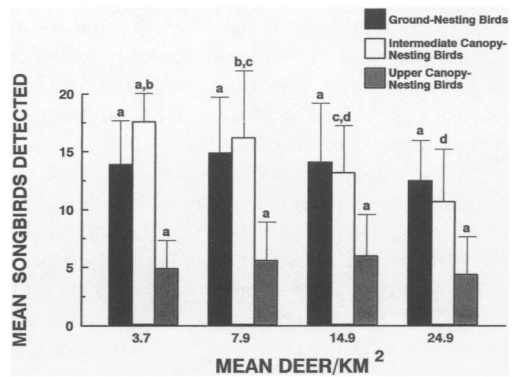


Fig. 4. Mean (\pm SE) abundance of songbirds by white-tailed deer density across pooled clear-cut, thinned, and uncut sites in northwestern Pennsylvania, 1991. Bars with dissimilar letters within bird groupings (ground nesting, intermediate canopy nesting, upper nesting) were different ($P < 0.05$).

least flycatcher, and yellow-billed cuckoo) were not detected at densities >7.9 deer/km² on sites where they had been detected at deer densities ≤ 7.9 deer/km². The American robin and eastern phoebe were not detected at deer densities >14.9 deer/km² on sites where they had been detected at densities ≤ 14.9 deer/km².

Mean richness of GN and UCN species did not differ among deer densities ($F = 1.128$ and 0.105 ; 3, 64 df; $P = 0.813$ and 0.948 , respectively), but I did not observe the cerulean warbler at deer densities >14.9 /km². Richness of ICN and GN species differed among study sites ($F = 3.690$ and 2.798 ; 3, 64 df; $P = 0.02$ and 0.05 , respectively), but I detected no interaction between study site and deer density ($F = 0.869$ and 1.128 ; 9, 64 df; $P = 0.56$ and 0.36 , respectively, for ICN and GN species). Richness of UCN species was not related to study site ($F = 0.710$; 3, 64 df; $P = 0.521$).

Deer Density and Songbird Abundance

Abundance of ICN species declined 37% from lowest to highest deer density ($F = 7.90$; 3, 64 df; $P = 0.002$; Fig. 4), whereas that of GN and UCN species did not differ among deer densities ($F = 1.32$ and 0.709 ; 3, 64 df; $P = 0.123$ and 0.424 , respectively). There was no defined threshold effect of deer density on ICN species abundance. Abundances of ICN, GN, and UCN species differed among study sites ($F = 4.26$, 3.63 , and 3.21 ; 3, 64 df; $P = 0.008$, 0.017 , and 0.023 , respectively). There was no interaction between study site and deer density for ICN, GN, or UCN species ($F = 0.72$, 1.51 , and 1.33 ; 9, 64 df; $P = 0.69$, 0.16 , and 0.24 , respectively).

DISCUSSION

White-tailed deer densities >7.9 /km² reduced ICN species richness and abundance seemingly by reducing height of woody vegetation in the intermediate canopy <7.5 m on thinned and clear-cut sites. Ground-nesting songbirds were unaffected by differences in deer density, perhaps because percent ground cover was not affected by deer. Presumably, UCN species were not affected by deer density because their habitat (upper canopy forest) was beyond the reach of deer.

A threshold for negative effect on ICN species richness clearly occurred between densities of 7.9 and 14.9 deer/km². However, I may not have fully assessed the effect of deer densities <12 deer/km² on ICN species richness. The full component of ICN species may not have been present because high deer density (average of 12 deer/km²) in the surrounding area may have affected vegetation sufficiently to preclude use by the full complement of ICN species. I had no observations of 3 ICN species (Carolina wren [*Thryothorus ludovicianus*], warbling vireo [*Vireo gilvus*], yellow-breasted chat [*Icteria virens*]) or 2 GN species (golden-winged warbler [*Vermivora chrysoptera*], worm-eating warbler [*Helmitheros vermivorus*]) previously reported nesting in northwestern Pennsylvania forests (Warren 1890, Bent 1964) or the ANF (B. B. Nelson, pers. commun.).

There was no threshold effect of deer density on ICN species abundance. Rather, abundance declined linearly, beginning at 3.7 deer/km². Effect of deer density on songbird abundance

may not have been negatively affected by ambient deer density outside enclosures. Indeed, superior habitat conditions within lower deer density enclosures may have drawn in songbirds from impoverished outside habitats.

Thresholds for effect of deer density on sapling height seemingly occurred between 7.9 and 14.9 deer/km² on clear-cut and thinned sites. The threshold on uncut sites was between 14.9 and 24.9 deer/km². These thresholds are likely not fixed but rather vary with the amount of forage available to deer. In forests managed less intensively than simulated by my study, there will be less opening of the canopy and less production of deer forage.

Abundance of ICN species declined linearly. Had the study incorporated deer densities < 3.7/km², I may have detected effects at lower densities. Likely, ICN species abundance is more sensitive to deer effect than is species richness. Presumably it requires more effect to lose species from sites rather than to reduce abundance. Whether losing species or reducing abundance has more ecological significance is unclear. Whereas ICN species richness remained stable when deer density increased from 3.7 to 7.9 deer/km², abundance declined 8.4%.

Limitations of data available for evaluating effect of deer on woody vegetation also may have affected sensitivity of my analysis. As originally conceived, the study did not incorporate evaluation of condition of wildlife habitat. The only measure available for structure of the intermediate canopy was height of tallest sapling per plot. There were no data available for measuring density of all stems in the intermediate canopy. A more thorough evaluation of intermediate canopy structure and density may have indicated that deer effect on this component of wildlife habitat began at densities <7.9 deer/km².

White-tailed deer effect would likely be higher across landscapes with reduced levels of cutting. My results thus represent conservative estimates of deer effect. On sites managed less intensively, the threshold for effect of deer density on habitat and songbird populations will be lower, perhaps approximating the threshold of <4 deer/km² suggested by Alverson et al. (1988).

Factors other than white-tailed deer may affect height of woody vegetation and ICN species richness and abundance. In this study, ICN species differed among areas independent of deer density; height of intermediate-canopy woody

vegetation differed among areas interactive with deer density. These results are not surprising because study areas were chosen to represent differences in starting condition of woody vegetation that forms the intermediate canopy. Whether initial differences in woody vegetation among study sites were related to differences in deer densities prior to study initiation is unknown because pretreatment deer densities were not available for any study sites.

MANAGEMENT IMPLICATIONS

Potential for white-tailed deer to negatively affect songbirds and their habitats must be evaluated concurrently with existing habitat conditions and other effects such as forest fragmentation, nest predation and parasitism, and silvicultural practices. Deer effect is on habitat quality of ICN species and so would exacerbate and be additive to habitat fragmentation or elimination.

Smith et al. (1993) noted declines in abundance of several ICN species in northeastern United States, including the eastern wood-pewee, least flycatcher, and yellow-breasted chat, species that either disappeared with increasing white-tailed deer density in my study or were absent. By altering critical nesting habitat for ICN species in fragmented forests, where they already are more exposed to predation and nest parasitism, high deer density could further endanger vulnerable ICN species.

Researchers (Behrend et al. 1970, Warren 1991, McShea and Rappole 1992, Miller et al. 1992) noted declines in species richness and abundance of woody and herbaceous vegetation directly attributable to high white-tailed deer densities. The universally recommended response has been to reduce deer densities through hunting. Recommended white-tailed deer density for successful hardwood regeneration and diversity of forest vegetation on intensively managed forests approximates 8 deer/km² (Behrend et al. 1970, Tilghman 1989); for forests under less intense management, recommended density is generally ≤ 4 deer/km² (Alverson 1988, Warren 1991, McShea and Rappole 1992). This range of deer densities is seemingly appropriate to maintain songbird species richness and abundance across the range of managed forests in the northeastern United States. Those responsible for the management of forest vegetation and wildlife, especially songbirds, should consider maintaining deer densities within these

bounds to protect and maintain populations of forest songbirds.

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APPENDIX

The following is a classification of birds identified by nest site in northwestern Pennsylvania, 1991, noting loss related to white-tailed deer density.

Ground-nesting songbirds: black-and-white warbler (*Mniotilta varia*), common yellowthroat (*Geothlypis trichas*), dark-eyed junco (*Junco hyemalis*), hermit thrush (*Catharus guttatus*), mourning warbler (*Oporornis philadelphia*), ovenbird (*Seiurus aurocapillus*), painted redstart (*Myioborus pictus*), rufous-sided towhee (*Pipilo erythrophthalmus*), song sparrow (*Melospiza melodia*), veery (*Catharus fuscescens*), and vesper sparrow (*Pooecetes gramineus*).

Intermediate canopy-nesting songbirds (birds nesting 0.5-7.5 m aboveground): black-throated blue warbler (*Dendroica caerulescens*), black-

billed cuckoo (*Coccyzus erythrophthalmus*), brown creeper (*Certhia americana*), chestnut-sided warbler (*Dendroica pensylvanica*), gray catbird (*Dumetella carolinensis*), hooded warbler (*Wilsonia citrina*), house wren (*Troglodytes aedon*), magnolia warbler (*Dendroica magnolia*), red-eyed vireo (*Vireo olivaceus*), rose-breasted grosbeak (*Pheucticus ludovicianus*), solitary vireo (*Vireo solitarius*), Swainson's thrush (*Catharus ustulatus*), wood thrush (*Hylocichla mustelina*), and yellow warbler (*Dendroica petechia*). American robin and eastern phoebe were species missing on ≥ 2 sites with deer densities of ≥ 26 deer/km². Eastern wood pewee, indigo bunting, least flycatcher, and yellow-billed cuckoo were species missing on ≥ 2 sites with deer densities of > 15 deer/km².

Upper canopy-nesting songbirds (birds nesting above 7.5 m): black-throated green warbler

(*Dendroica virens*), blackburnian warbler (*Dendroica fusca*), cedar waxwing (*Bombycilla cedrorum*), golden-crowned kinglet (*Regulus satrapa*), purple finch (*Carpodacus purpureus*), scarlet tanager (*Piranga olivacea*), and yellow-throated vireo (*Vireo flavifrons*). Cerulean warbler was missing on ≥ 2 sites with deer densities of > 15 deer/km².

Others (birds nesting in cavities or in all height intervals): blue jay (*Cyanocitta cristata*), black-capped chickadee (*Parus atricapillus*), brown-headed cowbird (*Molothrus ater*), common grackle (*Quiscalus quiscula*), downy woodpecker (*Picoides pubescens*), yellow-bellied sapsucker (*Sphyrapicus varius*), and white-breasted nuthatch (*Sitta carolinensis*). The Pileated woodpecker (*Dryocopus pileatus*) was missing from ≥ 2 sites with deer densities of > 15 deer/km².