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 199.1. 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 (*Contopns* virens), indigo bunting (*Passerine cyanea),* least flycatcher (*Empido-na:r_* minimus), yellow-billed 'cuckoo (*Coccyzus* americanus), or cerulean warbler (*Dendroica cernlea)* at densities >7.9 deer/km2 and the eastern phoebe (Sayornis *phoebe),* and American robin (Turdus rnigratorius) were not observed at 24.9 deer/km^2. Threshold deer density for effect on habitat and songbirds within managed (100-yr rotation) forests was between 7.9 and 14.9 deer/km=.

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Key words: habitat alteration, neotropical migrants, *Odocoileus* virginianus, Pennsylvania, songbirds, white-tailed deer.

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/km^2 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). Fre?lob 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 vegetation (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/km^2) and an adjacent area with lower deer density (10-20/km^2). 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 ruhrz.L.m), 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 stern density of hardwood 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/km.^{2} for 10 years. I simulated the 4 white-tailed deer densities by maintaining 1 deer in a 26-ha enclosure (3.7 deer/km^2), 1 deer in a 13--ha enclosure (7.8 deer/km^2), 2 deer in a 13-ha enclosure (15.6 deer/km^2), and 4 deer in a 13-ha enclosure (31.2 deer/km^2). This range of deer densities encompassed estimated presettlement white-tailed deer densities in North America (2-8/krn^2; McCabe and McCabe 1984:27, Alverson et al. 1988) and recent deer densities in northwestern Pennsylvania (31/km^2; 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 corn-posing 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 (_SD) across the 4 areas for the study were 3.7 (±0.2), 7.9 (±0.1), 14.9 (±0.1), and 24.9 (±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 ilvicultural management using combinations of lean-cutting and thinning incorporated in the :udy design (Marquis et al. 1992).

If sustained forestry is practiced on longer otations to produce more mature stands, and neven-aged management is the silvicultural ystem of choice, the cycle of timber harvest *is*)nger, and the amount cut at each entry is *less,* roducing less forage and resulting in greater ffect of deer on forest regeneration at given ensities. Actually, intensity of clear-cutting and dinning on the ANF (which represented local onditions) was 4-8% clear-cutting and 12% :inning at 10-year intervals because of the lack f adequate advance regeneration caused by igh resident deer density (B. B. Nelson, Alleheny Natl. For., Warren, Pa., pers. commun.).

ETHODS

I sampled woody and herbaceous vegetation rom systematically spaced 4-m^2 regeneration dots located in each enclosure. I located 25 such lots within clear-cut treatment areas, 15 in ninned treatment areas, and 20 in uncut treataent areas. Vegetation was sampled 0, 1, 3, 5, nd 10 years after silvicultural treatments. I es:mated percent ground cover ocularly on each egeneration plot and averaged it within treattent areas. I recorded height of tallest sapling or every regeneration plot and averaged it fithin treatment areas.

I conducted point counts of birds (Verner 985) 5 times/site from 15 May to .31 July 1991 iithin the 16 deer enclosures. Because cleartits were small, I placed only 1 bird count sta.on at the center of these areas. Thinned sites /ere twice as large and I randomly located 2 :ations in each. I randomly located 3 stations Within each uncut site. All stations were ^ 30 m rom any interface with a site receiving a difBrent silvicultural treatment. During each count, recorded all birds identified aurally or visually ;30 m from a station. I categorized songbirds s ground nesting (CN), intermediate canopy esting (ICN, nesting 0.5-7.5 m aboveground), r upper canopy nesting (UCN, nesting above .5 m; DeGraaf et al. 1991, Appendix).

During each count, I recorded species richess and abundance (sum of birds identified on irvey stations) for each songbird category at ach white-tailed deer enclosure. Unequal samle sizes from songbird counts among silviculsral treatments made it unsound to compare)ngbird responses among silvicultural treatTalents. 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 A.NOVA. 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 identifled 2,912 individual songbirds among the 4 sites (658-789/site).

Deer Density and Vecetation

Percent ground cover was not affected by deer (F = 1.764, 1.692, and 0.843; 3, 384, 3, 224, and 3, 304 df; P = 0.375, 0.170, 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 flowerin9.-, 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 df; $P < 0.001$), thinned ($F = 14.27$; 3, 220 df; $P < 0.001$), and uncut sites ($F = 19.61$; 3, 297 df; $P < 0.001$; Fig. 2). Mean sapling height on clear-cut,

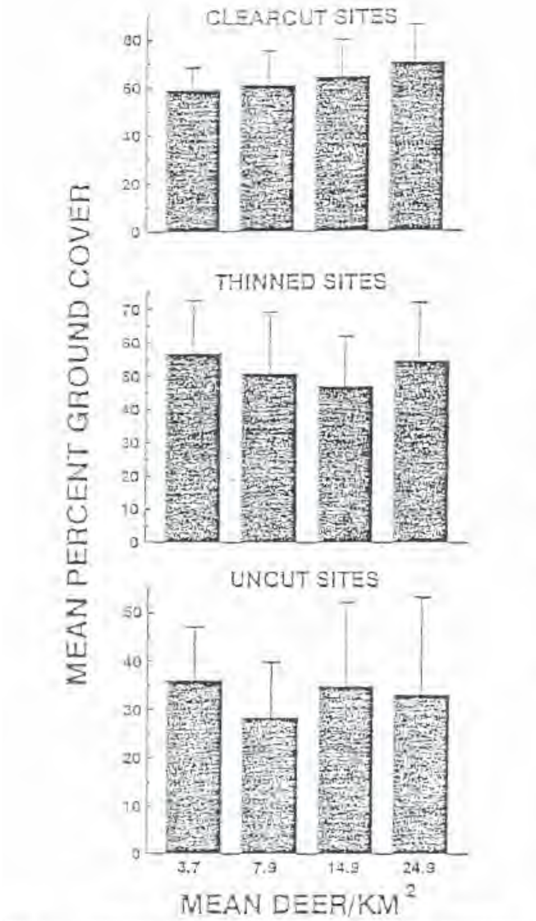


Fig. 1. Mean (± SE) percent ground cover by white-tailed deer density on clear-cut, thinned, and uncut sites in northeastern Pennsylvania, 1991. There were no differences ($P > 0.05$) among percent cover values within clear-cut, thinned, or uncut sites.

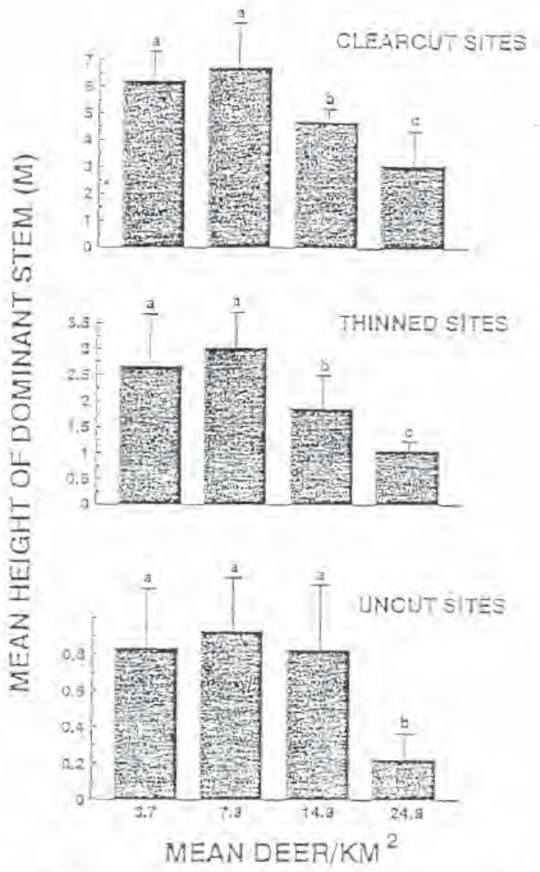


Fig. 2. Mean (± SE) sapling height by white-tailed deer density on clear-cut, thinned, and uncut sites in northwestern Pennsylvania, 1991. Bars with dissimilar letters, within sites, were different ($P < 0.05$).

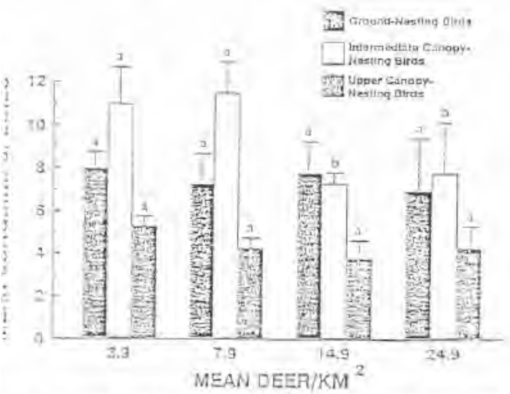
thinned, and uncut sites also differed among study areas (F = 4.04, 4.89, and 7.59; 3, 377, 3, 220, and 3, 297 df; $P < 0.05$ for all sites). There were study area by deer density interactions (F = 4.88, 3.29, and 2.81; 9, 377, 9, 220, and 9, 297 df; $P < 0.005$), respectively, for clear-cut, thinned, and uncut sites. A threshold for reduction in sampling height occurred between 7.9 and 14.9 deer/km22 (F = 25.90 and 14.51; 1, 377 and 1, 200 df; $P < 0.001$, for clear-cut and thinned sites, respectively); for uncut sites the threshold occurred between 14.9 and 24.9 deer/km' (F = 35.09; 1, 297 df; P < 0.001).

Sapling Height and Eird Species Richness and Abundance

Richness and abundance of CN and UCN species were not related to sapling height on 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 cif; P < 0.001). Threshold for deer effect occurred between 7.9 and 14.9 deer km2 (F = 15.17; 1, 64 df; $P < 0.001$). Four IC species (eastern wood pewee, indigo bunting.



g. 3. Mean (±SE) number of songbird species by white-iled deer density across pooled clear-cut, thinned, and uncut tes in northwestern Pennsylvania, 1991. Bars with dissimilar tters within bird groupings (ground nesting, intermediate can-y nesting, upper canopy nesting) were different ($P < 0.05$).

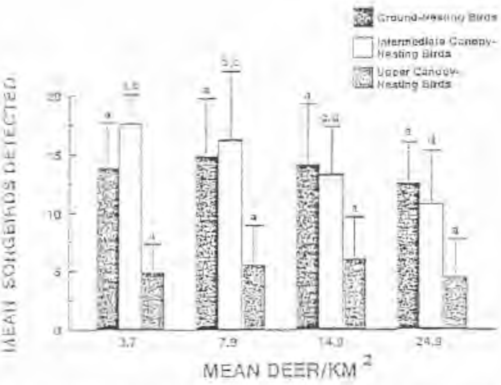


Fig. 4. Mean (±SE) abundance of songbirds by white-tailed deer density across pooled clear-cut, thinned, and uncut sites in northwestern Pennsylvania, 1991. Bars with dissimilar letters within bird groupings (ground nesting, intermediate canopy nesting, upper nesting) were different ($P < 0.05$).

ast Ovcatcher, and yellow-billed cuckoo) were at detected at densities >7.9 deer/km" on sites here they had been detected at deer densities :7.9 deer/km'". The American robin and east-7ri phoebe were not detected at deer densities • 14.9 deer/km^2 on sites where they had been etected at densities ·_ 14.9 deer/Km'.

Mean richness of ON and UCN species did .)t differ among deer densities (F = 1.128 and 105; 3, 64 df; P = 0.813 and 0.948, resoc• vely), but I did not observe the cerulean war er at deer densities >14.9/km^2. Richness 2N and GN species differed among study site: L = 3.690, and 2.798; 3, 64 df; P 0.02 awl 05, respectively), but I detected no interacti(etween study site and deer density (F = 0.8f;" ad 1.128; 9, 64 df; P = 0.56 and 0.36, resort vely, for ICN and ON species). Richness ,,j CN species was not related to study site (F 710; 3, 64 df; P = 0.521).

eer Density and Scngbird Abundance

Abundance of ICN species declined 37% Emil) west to highest deer density (F 7.90; 3, f%• P 0.002; Fig. 4), whereas that of ON CN species did not differ among deer densit = 1.32 and 0.709; 3, 64 df; P = 0.123 aril 424, respectively). There was no defini-, l :oshold effect of deer density on ICN speci, Abundances of ICN , ON , and L;(. lu ncian ce tries differed among study sites (F =4. :z7,, 63, and 3.21; 3, 64 df; P = 0.008, 0.017, 023, respectively). There was no interactif/P tween study site and de,.r density for N, or UCN species (F = 0.7^9, 1.51, and 64 df; P = 0.69, 0.16, and 0.24, respectively,-

DISCUSSION

White tailed deer densities >7.9/km^2 reducted ICNspecies richness and abundance wemingly by reducing height of woody veget:ition in the intermediate canopy <7.5 m on thinned and clear-cut sites. Ground-nesting ;ougbirds were unaffected by differences in deer iciisity, perhaps because percent ground cover was not affected by deer. Presumably, UCN ;pecies were not affected by deer density because their habitat (upper canopy forest) was eyond the reach of deer.

A threshold for negative effect on ICN species richness clearly occurred between densities of 7.9 and 14.9 deer/km^2. However, I may not have fully assessed the effect of deer densities <12 deer/km" on ICN species richness. The full component of ICN species may not have been present because high deer density (average of 12 deer/km^2) 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 LIdovicianus*], warbling vireo [*Vireo gilvust* yellow-breasted chat *Ucteria oirens*]) or 2 ON species (golden-winged warbler [*Vermivora chrysoptera*], worm-eating warbler [*Helmitheros* vermi.vorus]) 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/km^2. 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/km^2, I may have detected effects at lower densities. Likely, ION 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 ION species richness remained stable when deer density increased from 3.7 to 7.9 deer/km^2, 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/km'.

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/km^2 suggested by Alverson et al. (1988).

Factors other than white-tailed deer may affect height of woody vegetation and ION species richness and abundance. In this study, ION 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 silvicuitural practices. Deer effect is on habitat quality of ION species and so would exacerbate and be additive to habitat fragmentation or elimination.

Smith et al. (1993) noted declines in abundance of several ION 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 ION 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 (Behrenci 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 -5_4 deer/km^2 (Alverson 1988, Warren 1.991, 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 relate'-u to white-tailed deer density.

Ground-nesting songbirds: black-and-white warbler *(Mniotilta caria)*, common yellowthroat *(Geothylpis trichas)*, dark-eyed junco *(junco hyemalis)*, hermit thrush (Catharus *guttatus)*, *'mourning* warbler *(Oporornis phitadelphia.)*, ovenbird *(Seiuru.s aurocapillus)*, painted redstart *;:viyioborus pietus)*, ufou -sided towhee *erythroph thalmus)*, song sparrow *(Melospiza raeiodia)*, veery *(Catharus forcestens)*, and vesper sparrow *(Pooecetes i:zrarnineas)*.

Intermediate canopy-nesting songbirds (birds nesting 0.5–7.5 m aboveground): black-throated blue warbler *(Dendroica caerulescens)*, blackbilled cuckoo *(Coccyzus erythropthalmus),* brown creeper (Certhia *americana),* chestnut-sided warbler *(Dendroica pens ylvanica),* gray catbird *(Dumetella carolinensis),* hooded warbier (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/km^2. Eastern wood pewee, indigo bunting, least flycatcher, and yellow-billed cuckoo were species missing on >=2 sites with deer densities of >15 deer/km^2.

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 *(Piranha olir,acea),* and yellow-throated vireo *(Vireo fiavifrons).* Cerulean warbier 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 *(Qu.iscalus 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.