
Managing the Abundance and Diversity of Breeding Bird Populations through Manipulation of Deer Populations

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Abstract: *Deer densities in forests of eastern North America are thought to have significant effects on the abundance and diversity of forest birds through the role deer play in structuring forest understories. We tested the ability of deer to affect forest bird populations by monitoring the density and diversity of vegetation and birds for 9 years at eight 4-ha sites in northern Virginia, four of which were fenced to exclude deer. Both the density and diversity of understory woody plants increased following deer exclosure. The numerical response of the shrubs to deer exclosure was significantly predicted by the soil quality (ratio of organic carbon to nitrogen) at the sites. Bird populations as a whole increased following exclosure of deer, particularly for ground and intermediate canopy species. The diversity of birds did not increase significantly following exclosure of deer, however, primarily because of replacement of species as understory vegetation proceeded through successional processes. Changes in understory vegetation accounted for most of the variability seen in the abundance and diversity of bird populations. Populations of deer in protected areas are capable of causing significant shifts in the composition and abundance of bird communities. These shifts can be reversed by increasing the density and diversity of understory vegetation, which can be brought about by reducing deer density.*

Manejo de la Abundancia y Diversidad de Aves Reproductoras Mediante la Manipulación de Poblaciones de Venados

Resumen: *Se considera que las densidades de venados en los bosques del Este de Norte América tienen efectos significativos en la abundancia y diversidad de aves debido al papel que el venado juega en la estructuración del sotobosque. Evaluamos la habilidad del venado para afectar las poblaciones de aves mediante el monitoreo de la densidad y diversidad de la vegetación y las aves por nueve años en ocho sitios de 4 ha de extensión en el norte de Virginia, cuatro de los cuales fueron cercados para excluir a los venados. Tanto la densidad como la diversidad de las plantas leñosas del sotobosque incrementaron después de la exclusión de los venados. La respuesta numérica de los arbustos a la exclusión de venados fue pronosticada significativamente por la calidad del suelo (proporción de carbono orgánico/nitrógeno) en los sitios. Las poblaciones de aves en su conjunto incrementaron después de la exclusión de venados, particularmente las especies del suelo y de dosel intermedio. Sin embargo, la diversidad de aves no incrementó significativamente después de la exclusión de venados, primariamente debido al remplazo de especies al pasar la vegetación del sotobosque por los procesos sucesionales. Los cambios en la vegetación del sotobosque fueron responsables de la mayoría de la variabilidad observada en la abundancia y diversidad de poblaciones de aves. Las poblaciones de venados en áreas protegidas son capaces de causar cambios significativos en la composición y la abundancia de comunidades de aves. Estos cambios pueden ser revertidos al incrementar la densidad y diversidad de la vegetación del sotobosque, lo cual puede llevarse a cabo mediante una reducción en la densidad de venados.*

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Introduction

Ungulate populations have strong direct and indirect impacts on forest plant communities (Augustine & McNaughton 1998). These changes are brought about both by browsing (Alverson et al. 1988; Tilghman 1989; Augustine & Frelich 1998) and by the indirect cycling of nutrients and energy flow (Pastor & Naiman 1992; Hobbs 1996). The result of these activities is to change the species composition and relative abundance of both herbaceous and woody plants within forest ecosystems. In the United States, most states report deer densities that exceed all previous estimates for the century (McCabe & McCabe 1997). This increase is the direct result of conservation efforts to increase the number of these and other game species. How planned increases in large herbivores affect other forest animal species is unknown. White-tailed deer (*Odocoileus virginianus*), however, may play an increasing role in the structuring of forest ecosystems and should be considered a significant factor in plans for protected forest management plans (Porter & Underwood 1999).

Food webs are complex interactions between species that regulate the transfer of nutrients and energy across trophic levels (Polis & Strong 1996). Dominant or keystone organisms not only influence adjacent trophic levels but have effects that are measurable throughout an ecosystem (Power 1992; Power et al. 1996). If habitat characteristics influence the distribution of most animal species, and if ungulates shape habitat characteristics, then ungulates may have an important role in complex food webs throughout multiple trophic levels. Food web links have been demonstrated between white-tailed deer and small mammals (Ostfeld 1997; McShea 2000) and among white-tailed deer, white-footed mice (*Peromyscus leucopus*), and ticks (*Ixodes scapularis*) (Jones et al. 1998). These linkages suggest that the foraging behavior of deer may structure forest populations of other animal species.

Bird species are particularly sensitive to changes in vegetation volume and composition (Mills et al. 1991). Direct positive correlations have been found between bird diversity and vegetation volume in tropical forest systems (Bell 1982) and spatial heterogeneity in temperate forests (Roth 1976). Forest models that predict vegetation volume have been used to predict the structure of bird populations (Urban & Smith 1989). Proposed mechanisms by which understory vegetation could affect bird populations include: (1) determining the density of foliage-dependent larva (Lynch & Whigham 1984) and (2) influencing the efficiency of nest predators (Martin & Roper 1988).

We and others have proposed that a link exists between white-tailed deer population densities and the abundance of certain bird species in deciduous forests

(McShea & Rappole 1992, 1997; deCalesta 1994; McShea et al. 1995). This hypothesis is based on the facts that deer are often the principal agent of structural change within forests and that many species of birds are sensitive to such changes. Deer are not the only cause of forest alteration, but within protected forests most other factors (e.g., timber harvest and wildfires) have been eliminated.

Earlier studies have found circumstantial evidence that bird populations are sensitive to deer densities. Declines in Ovenbirds in a western Maryland preserve (Boone & Dowell 1986) and declines in understory birds in New York (Baird 1990) were attributed to high deer densities, and lower numbers of individuals in all bird guilds in a Pennsylvania preserve were attributed to large herbivores (Casey & Hein 1983). These studies, however, noted only that declines in bird species and numbers of individuals coincided with more deer. Kentucky Warbler (*Oporornis formosus*) densities were tracked for 10 years at the National Zoo's Conservation and Research Center in Virginia, and over that period the distribution of territories shifted to areas that maintained low deer densities (McShea et al. 1995). The most complete study was deCalesta's (1994) bird survey of several deer enclosures in Pennsylvania. After 10 years at predetermined deer densities, point-count surveys revealed higher encounter rates for intermediate canopy birds within areas with the lowest deer densities. The experiment, however, was designed primarily to examine the effects of deer on forestry practices, so bird densities were not monitored during the first 10 years of the study, and the enclosures contained a mixture of managed and unmanaged forest. DeGraaf et al. (1991) examined the interaction between high deer density and forest management on forest bird communities. They found that the effects of thinning were more obvious than those of deer densities, but Hermit Thrushes (*Catharus guttatus*) were more abundant and Eastern Towhees were less abundant at low deer densities. These studies point to the need to quantify how forest birds respond to changes in deer density in order to manage effectively a group of species that has been declining over the same period that deer densities have been increasing. Efforts by government agencies to increase a single species such as deer may impede efforts to conserve other species.

We report on the long-term enclosure of deer from 4-ha plots within extensive tracts of protected forest. We compared these sites to control areas that initially contained similar understory and deer densities and report on the changes in vegetation and bird communities that occurred. Our purpose was to test whether deer can serve as agents of structural change in protected forests and whether manipulation of deer numbers can affect bird populations, with understory vegetation as the short-term link between these two trophic levels.

Methods

Study Sites and Deer Densities

Eight sites were located within 25 km of Front Royal, Virginia (lat 38°54N, long 78°09W), in large forest tracts in either the Shenandoah National Park (SNP) or the Smithsonian Institution's Conservation and Research Center (CRC). These plots contained mature oak (*Quercus* spp.), hickory (*Carya* spp.), white ash (*Fraxinus americana*), yellow poplar (*Liriodendron tulipifera*), and understory shrubs of flowering dogwood (*Cornus florida*), spicebush (*Lindera benzoin*), and redbud (*Cercis canadensis*) (SAF Type 52, Eyre 1980). All sites were 4 ha in size, either 200 × 200 m or 160 × 250 m in shape, and separated by at least 1 km. No sites were adjacent to forest edges or contained human-made structures that might be considered internal edges.

Soil samples were obtained at 10 points on each site. Nitrogen and organic carbon components were measured by flash combustion with a Carlo Erba NA-1500 Elemental Analyzer (Verardo et al. 1990). We used the ratio of organic carbon to nitrogen as an indicator of soil productivity (Van Miegroet & Johnson 1993).

Sites were paired based on similar understory vegetation, as measured in 1990, and one site of each pair was fenced in early 1991. The 3-m fence, composed of 1.5 m of farm fencing (25 × 25 cm mesh at bottom) topped with high-tensile wire, did not exclude small to medium-sized vertebrates (Leimgruber et al. 1994). We constructed fences without removing canopy trees along the site boundaries. Deer density in the region, based on line-transect surveys (Burnham et al. 1980), remained high throughout the period (>25 deer/km²), about twice the state-wide density estimates (Knox 1997). Along the boundary of each site, six 2 × 20 m areas were cleared of deer fecal pellet groups and resurveyed eight times between 1992 and 1996. There was no difference in the number of fecal pellet groups found between control and enclosure sites after variation due to sampling period was accounted for (partial $F = 0.26$, $df = 8,332$, $p = 0.61$). Deer hunting is prohibited in both SNP and CRC.

Vegetation Density

In 1990 three 24 × 24 m quadrats were established at each site, and all woody plants >1 m in height and <4 cm in diameter were identified to species and counted. This survey was repeated at the same quadrats in 1994 and 1997. Vegetation density at each site was also estimated each July with a coverboard (Nudds 1977). The 2 × 0.5 m board was divided into four equal sections, with each section divided into 25 squares of equal size. The board was placed 16 m from the observer, and the number of

squares containing green vegetation were counted for each section. Readings were taken at each corner of the three quadrats established for each site and averaged. Only the two center sections (0.5–1.5 m above ground) were used because these segments were the least affected by woody debris or overhanging limbs. We tested the relationship between these coverboard values and the density of understory shrubs for the 3 years when both measures were obtained (1990, 1994, 1997). The number of woody stems was significantly correlated with the average coverboard value for each site ($F = 84.3$, $df = 1, 30$, $r^2 = 0.74$, $p < 0.001$).

Bird Populations

Breeding bird populations were estimated through mist-netting from 1990 through 1998. Each year we expended 1000 net hours of effort at each site by using 25 nets (12 × 2 m, 36 mm mesh) distributed in a grid with 40 m between nets. The nets were strung between trees, and the same trees were used each year, except when one tree of the set died. All netting was conducted between 30 May and 30 June, with nets generally opened from dawn to dusk and monitored for 3 consecutive days. During the first 3 years of the study, 1500 net hours were expended each site, but a graph of net hours versus species and individuals captured indicated that 1000 net hours were sufficient. For data from these first 3 years, only captures during the first 1000 net hours were considered. All captured birds were identified to species, sexed, assessed for reproductive condition, given a uniquely numbered U.S. Fish and Wildlife Service band, and released. Only the first capture of each individual was counted during each breeding season. For diversity and abundance measures, we included for analysis only the 25 species with at least 20 captures during the study period.

Species were designated as guild members based on life-history characteristics (Ehrlich et al. 1988), specifically distance of migration and mean foraging height (Table 1). The three migration categories were resident species, species that migrate within the continental United States, and species that migrate to South or Central America. The three nesting categories were <2 m above ground, >2 m above ground but below the canopy, and in the canopy. Two species, Brown-Headed Cowbirds and Chipping Sparrows, were difficult to classify and were placed into the resident guild based on lack of affinity with the other two guilds. To gauge the conservation value of each bird species, we used values obtained for our physiographic region from Partners in Flight. Partners in Flight is a national program concerned with migrant bird issues that produces a conservation priority list for each physiographic region based on multiple criteria (for details see www.partnersinflight.org) A high Part-

Table 1. Bird species with at least 20 captures over 9 years of sampling at eight sites in Northern Virginia.

Species ^a	Migration distance	Forage/nest height	Forest guild	PIF score ^b
Hooded Warbler (<i>Wilsonia citrina</i>)	long	low	low	21
Ovenbird (<i>Seiurus aurocapillus</i>)	long	ground	low	18
Worm-eating Warbler (<i>Helminthos vermivorus</i>)	long	low	low	25
Gray Catbird (<i>Dumetella carolinensis</i>)	long	low	low	19
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	long	low	low	19
Veery (<i>Catharus fuscescens</i>)	long	low	low	17
Wood Thrush (<i>Hylocichla mustelina</i>)	long	low/mid-canopy	low	25
Indigo Bunting (<i>Passerina cyanea</i>)	long	low	low	16
Red-eyed Vireo (<i>Vireo olivaceus</i>)	long	mid-canopy	intermediate	15
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	long	mid-canopy	intermediate	18
American Redstart (<i>Setophaga ruticilla</i>)	long	mid-canopy	intermediate	16
Acadian Flycatcher (<i>Empidonax virens</i>)	long	mid-canopy	intermediate	21
Eastern Wood-Pewee (<i>Contopus virens</i>)	long	mid-canopy	intermediate	22
Cerulean Warbler (<i>Dendroica cerulea</i>)	long	canopy	intermediate	27
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	long	canopy	intermediate	17
Scarlet Tanager (<i>Piranga olivacea</i>)	long	canopy	intermediate	20
Blue Jay (<i>Cyanocitta cristata</i>)	resident	mid-canopy	resident	11
Downy Woodpecker (<i>Picoides pubescens</i>)	resident	mid-canopy	resident	14
Tufted Titmouse (<i>Baccolophus bicolor</i>)	resident	mid-canopy	resident	14
Northern Cardinal (<i>Cardinalis cardinalis</i>)	resident	low/mid-canopy	resident	13
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	resident	mid-canopy	resident	14
Hairy Woodpecker (<i>Picoides villosus</i>)	resident	mid-canopy	resident	15
Brown-headed Cowbird (<i>Molothrus ater</i>) ^c	short	all	resident	13
Carolina Wren (<i>Troglodytes ludovicianus</i>)	resident	low	resident	14
Chipping Sparrow (<i>Spizella passerina</i>) ^c	short	low	resident	15

^a Species are listed by forest guild, which was based on migration distance and forage/nesting height.

^b Partners in Flight (PIF) score indicates degree of conservation concern.

^c Guild designation based on personal observations.

ners in Flight score means a high priority for conservation effort for that species.

Statistics

Tests for significance were conducted with a standard statistical package (SAS version 6.2). Analysis of variance for repeated measures was used to test differences in bird populations on control and experimental sites over the study period. For individual species, the relationship between number captured and vegetation density was tested with linear regression. Analysis of covariance was used to test for relationships between vegetation abundance and diversity measures and soil quality and exclosure status (i.e., control or experimental site). Cover-board values were log-transformed prior to analysis. Significance values reported for repeated analysis of variance (ANOVA) were adjusted to meet the assumptions of a sphericity test (SAS Institute 1987). Species richness was considered the total number of species captured or counted at each site. Species evenness was measured with the Shannon-Weiner diversity index ($H' = -\sum p_i \ln(p_i)$), where p_i is the proportion that species contributed to total abundance. Diversity was also measured with a modified Simpson diversity index (number of species \times number of individuals; Peet 1974). In measures of

vegetation diversity, no attempt was made to differentiate between *Rubus* sp.

Results

Vegetation

The exclusion of deer increased the density of understory woody shrubs relative to control sites. Repeated-measures ANOVA showed a significant interaction between time and exclosure for both the measure of vegetation cover ($df = 8, 48$, $F = 2.53$, $p = 0.049$) and for the number of woody stems ($df = 2, 12$, $F = 5.34$, $p = 0.037$). Soil productivity, as measured by the ratio of organic carbon to nitrogen, was not correlated with the abundance of woody stems at each site in the beginning of the study ($p > 0.05$), but an analysis of covariance with exclosure status and soil quality as covariables found a positive relationship in 1994 ($F = 10.64$, $df = 3, 4$, $p = 0.022$, $r^2 = 0.89$) and again in 1997 ($F = 23.50$, $df = 3, 4$, $p = 0.005$, $r^2 = 0.95$).

Diversity measures for understory woody plants showed a significant effect of deer exclosure (Table 2). Although sites were not significantly different at the start of the study, species richness increased within the exclosure areas over the course of the study, as evidenced by the significant interaction term of time and

exclusion in the repeated-measures ANOVA. Species evenness, which we measured using the Shannon-Weiner diversity index, did not show significant changes in enclosure sites relative to control sites. The significant interaction between time and enclosure in the repeated-measures ANOVA indicates that the modified Simpson diversity index did increase significantly in enclosure sites relative to control sites. When soil quality was added to enclosure status as a covariable in an analysis of covariance, it was not a significant predictor of the modified Simpson diversity index at the start of the study ($p > 0.05$) but was significant in 1994 ($F = 6.95$, $df = 3,4$, $p = 0.046$, $r^2 = 0.84$) and in 1997 ($F = 21.50$, $df = 3,4$, $p = 0.006$, $r^2 = 0.94$). No significant interactions were found between species richness or evenness and soil quality ($p > 0.05$).

Bird Populations and Vegetation

Twenty-five bird species were captured at least 20 times during the study and were distributed into three forest guilds (Table 1). The exclusion of deer affected the number of individuals captured at each site, as shown by the significant interaction between time and enclosure status in the repeated-measures ANOVA (Table 3). This effect was significant when all three guilds of forest birds

were combined. The exclusion of deer, however, increased the number of low and intermediate birds and decreased, although not significantly, the abundance of resident birds. No measures of species richness, evenness, or diversity showed significant changes in response to exclusion of deer (Table 2).

A linear regression for each bird species between abundance and the density of understory vegetation, as measured by the coverboard, revealed that most species (15/25) responded positively to the increase in vegetation that resulted from deer exclusion (Table 4). Eleven species showed a significant correlation between understory vegetation and abundance. For six species, there was still a significant effect of deer enclosure, even after the variability due to vegetation cover was accounted for. One measure of bird species diversity, the modified Simpson diversity index, was significantly correlated with measures of shrub density and diversity (Table 5). Bird species richness was significantly correlated with coverboard density. (Table 5).

More than one pattern of change in bird populations was observed, and these patterns are best described by three species (Fig. 1): (1) species that prefer open understory (e.g., Chipping Sparrows) declined on enclosure plots; (2) species that prefer a dense herbaceous ground cover (e.g., Indigo Buntings) immediately increased within enclosure sites but then declined as her-

Table 2. Repeated-measures analysis of variance for changes in bird and shrub diversity at four control and four deer enclosure sites in Northern Virginia from 1990 to 1998.

Organism	Diversity measure ^a	Covariable	df	MS	F ^b
Birds	species richness	time	8	5.81	0.70
		enclosure	1	3.12	0.08
		enclosure × time	48	2.78	0.38
		error		7.26	
	species evenness	time	8	0.04	0.74
		enclosure	1	0.00	0.00
		enclosure × time	48	0.05	1.03
		error		0.05	
	modified Simpson diversity	time	8	11.96	1.35
		enclosure	1	47.71	0.44
	enclosure × time	48	13.97	1.58	
	error		8.83		
Shrubs	species richness	time	2	2.54	0.58
		enclosure	1	54.0	1.72
		enclosure × time	12	82.62	18.95**
		error		4.36	
	species evenness	time	2	0.09	1.39
		enclosure	1	0.00	0.01
		enclosure × time	12	0.11	1.62
		error		0.06	
	modified Simpson diversity	time	2	145.72	2.72
		enclosure	1	770.25	3.62
	enclosure × time	12	261.37	4.87*	
	error		53.66		

^a Species evenness is based on Shannon-Weiner diversity index ($H' = -\sum p_i \ln(p_i)$). Modified Simpson diversity index = number of species × number of individuals.

^b * $p < 0.05$; ** $p < 0.001$.

Table 3. Repeated-measures analysis of variance for changes in abundance of 25 bird species captured at least 20 times at four control and four deer enclosure sites in Virginia from 1990 to 1998.

Forest guild ^a	Covariables	df	MS	F (partial) ^b
All birds	species	24	320.92	7.65***
	enclosure	1	75.64	1.80
	time	8	13.30	3.59***
	time × species	192	4.80	1.29**
	time × enclosure	8	14.64	3.95***
	error	1392	3.71	
Low	species	7	709.86	8.67***
	enclosure	1	159.39	1.95
	time	8	22.19	4.02***
	time × species	56	5.59	1.01
	time × enclosure	8	13.13	2.38*
	error	440	5.52	
Intermediate	species	7	162.96	3.92**
	enclosure	1	40.11	0.96
	time	8	8.54	1.88
	time × species	56	6.22	1.37
	time × enclosure	8	13.27	2.93**
	error	440	4.54	
Resident	species	8	8.35	1.38
	enclosure	1	11.41	1.89
	time	8	1.61	1.27
	time × species	64	1.69	1.34*
	time × enclosure	8	2.09	1.65
	error	496	1.27	

^a See Table 1 for explanation of forest guilds.

^b * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 4. The relationship between understory density, as measured by a coverboard, and the abundance of birds captured at four deer exclosure and four control sites in Virginia.

Species ^a	Number of captures	Cover		Exclosure		r ²
		MS	F (partial) ^b	MS	F (partial) ^b	
Hooded Warbler ^c	48	150.62	169.7***	0.46	0.58	+0.72
Ovenbird ^c	336	870.90	61.3***	24.87	1.75	+0.48
Worm-eating Warbler ^c	67	2.57	0.72	0.17	0.05	+0.01
Gray Catbird ^c	32	4.63	1.52	0.56	0.18	+0.02
Eastern Towhee ^c	162	134.28	33.01***	0.56	0.14	+0.32
Veery ^c	77	36.87	11.82***	3.38	1.08	+0.16
Wood Thrush ^c	703	747.95	19.15***	71.98	1.84	+0.23
Indigo Bunting ^c	240	17.11	1.35	71.79	5.65*	+0.09
Red-eyed Vireo ^d	188	123.11	30.59***	4.32	1.07	+0.31
Rose-breasted Grosbeak ^d	51	1.44	0.54	0.37	0.14	0.00
American Redstart ^{df}	334	1418.20	63.80***	4.16	0.19	+0.48
Acadian Flycatcher ^d	127	47.23	7.24***	37.04	5.68*	+0.16
Eastern Wood-Pewee ^d	215	16.51	3.05	16.96	3.13	-0.08
Cerulean Warbler ^d	24	1.31	2.62	0.06	0.12	+0.04
Great Crested Flycatcher ^d	48	0.31	0.35	8.21	9.22***	+0.12
Scarlet Tanager ^d	164	0.83	0.24	10.83	3.13	+0.04
Blue Jay ^e	29	4.05	4.04*	0.08	0.09	-0.05
Downy Woodpecker ^e	55	0.35	0.34	2.10	2.00	-0.04
Tufted Titmouse ^e	96	27.62	13.81***	16.34	8.17***	-0.24
Northern Cardinal ^e	41	6.48	3.94*	9.62	5.84*	-0.12
White-breasted Nuthatch ^e	57	1.87	0.85	0.59	0.27	-0.02
Hairy Woodpecker ^e	30	0.18	0.34	0.00	0.01	0.00
Brown-headed Cowbird ^e	46	1.63	1.46	0.03	0.03	+0.02
Carolina Wren ^e	21	0.72	1.11	3.34	5.15*	-0.08
Chipping Sparrow ^e	79	12.46	2.40	1.79	0.35	-0.04

^a See Table 1 for explanation of forest guilds.

^b*p < 0.05; **p < 0.01; ***p < 0.001.

^c Low forest guild.

^d Intermediate forest guild.

^e Resident forest guild.

Table 5. The relationship between measurements of bird diversity and shrub diversity as determined by linear regression.

Bird diversity measure ^a	Shrub diversity/density measure		F ^b	r ²
		df		
Species richness	Species richness	1,22	1.12	0.05
	species evenness	1,22	0.43	0.02
	modified Simpson's	1,22	3.14	0.12
	coverboard density	1,70	7.63***	0.10
	stem density	1,22	2.95	0.12
Species evenness	species richness	1,22	0.07	0.00
	species evenness	1,22	0.29	0.01
	modified Simpson's	1,22	0.17	0.01
	coverboard density	1,70	1.51	0.02
	stem density	1,22	0.07	0.00
Modified Simpson's	species richness	1,22	3.32	0.13
	species evenness	1,22	0.79	0.03
	modified Simpson's	1,22	17.18***	0.44
	coverboard density	1,70	21.79***	0.23
	stem density	1,22	16.72***	0.43

^a Species evenness is based on Shannon-Weiner diversity index ($H' = -\sum p_i \ln(p_i)$). Modified Simpson diversity index = number of species × number of individuals.

^b ***p < 0.001.

baceous species were replaced by woody vegetation; and 3) species that preferred a dense, woody understory (e.g., Ovenbirds) gradually increased following deer exclosure.

Partners in Flight conservation scores ranged from 11 to 27 for species we examined (Table 1). When cover values increased following deer exclosure, bird species that significantly increased in number had higher conservation scores than species that significantly decreased in numbers ($\bar{x} = 19.0$ and 12.6 , respectively; $F = 10.01$, $df = 1,9$, $p = 0.011$).

Discussion

Reduction in deer density changed the composition of bird populations over the 9 years of this study. This change coincided with changes in both the density and diversity of understory vegetation. For the majority of bird species, bird numbers increased following reduced deer density. Migrant birds that foraged either in the understory or higher in the canopy responded positively to the increases in vegetation density and diversity that followed deer reduction. This finding agrees with deCal-

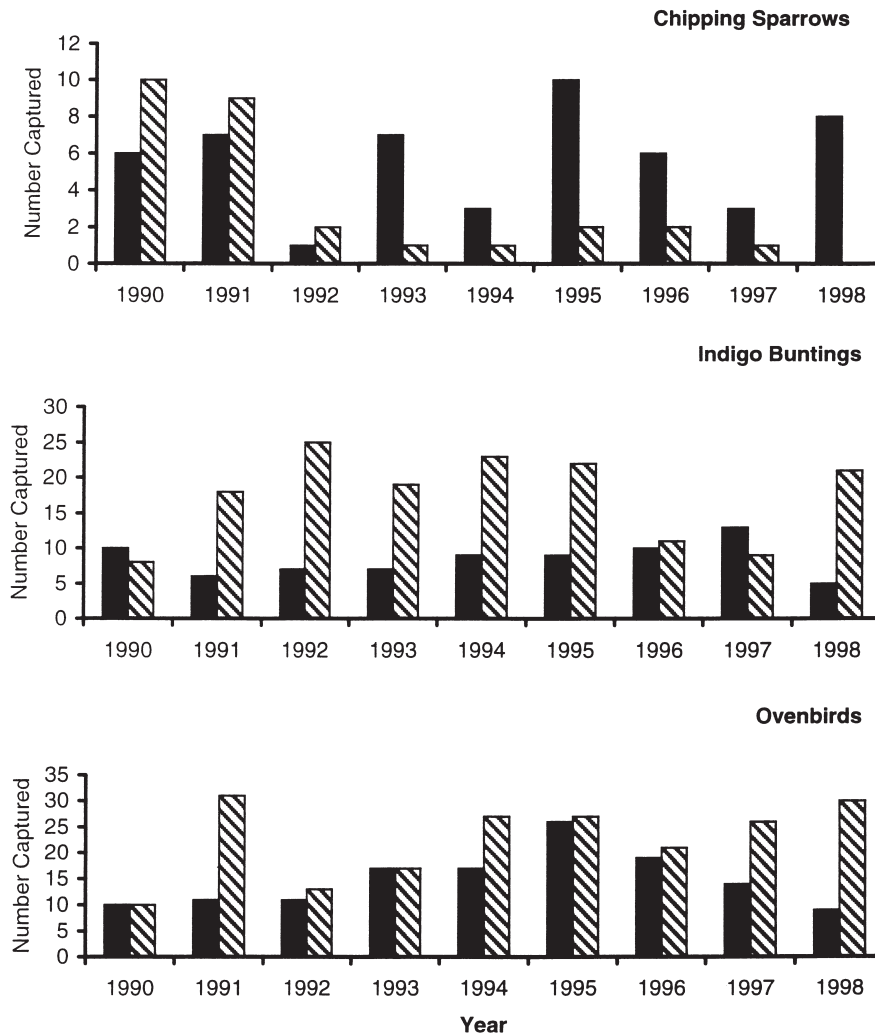


Figure 1. Abundance of three representative bird species at four deer exclusion sites (hatched bars) and four control sites (solid bars).

esta's (1994) report of higher densities of intermediate canopy birds at lower deer densities, but he did not find higher densities of ground-dwelling birds as we did. The difference may be due to different sampling techniques (i.e., mist-netting vs. point counts) or to the fact that each of his sites was a combination of forest management types and ours were all within protected forest. There are also vegetation differences between Pennsylvania and Virginia. Ground cover in sites with high deer densities in Virginia tends to be dominated by grass species (personal observation), whereas ground cover at sites of high deer density in Pennsylvania tends to be dominated by hay-scented fern (*Dennstaedtia punctilobula*; Tilghman 1989).

A simple measure of understory density, the coverboard, was sufficient to explain the variability seen between sites in bird abundance for 11 species. For 6 species there was additional variability due to the exclusion of deer that was not explained by coverboard data. It is

possible that these species responded to other layers of understory outside the 0.5–1.5 m height used in our measurements or that deer foraging causes changes not reflected by simple vegetation measures.

As opposed to the migrant guilds, several resident birds, such as Tufted Titmouse, Blue Jay, Northern Cardinal, Carolina Wren, showed marked decreases in abundance in response to deer removal. These species tend to have stable or increasing populations in national surveys and are not normally of management concern, as indicated by their lower mean scores in the Partners in Flight ranking.

The 4-ha exclusion sites created for our study were small islands within large forest tracts that contained high densities of deer. Although 4 ha is a large site size for an exclusion study, it is sufficient to incorporate only three or four territories for most migrant species. Despite the small size of the exclusions, we produced measurable results by excluding deer. Most management

guidelines for white-tailed deer operate at a larger scale (Porter & Underwood 1999), in part because state wildlife programs have only limited control of the movements of hunters. This larger scale is appropriate because bird populations appear to function at a regional scale (Robinson et al. 1995).

Earlier investigators of the effects of deer on natural resources have made deer density recommendations based on their results (Alverson et al. 1988; deCalesta 1994). We contend that there are at least three reasons for using vegetation measures rather than deer density for measuring progress toward bird management goals. First, deer densities are notoriously difficult to measure (Burnham et al. 1980), certainly more difficult than the coverboard and stem density counts we used to measure vegetation density. Second, deer management by state agencies operates at a county or district level (Knox 1997) that might contain multiple units of conservation land with multiple conservation objectives. Third, bird species respond to vegetation volume, not deer density. Control sites located in close proximity to each other maintained either high or low densities of birds because of differences in vegetation volume, not densities of deer. Soil and presumably moisture traits at each site determined the rate at which the vegetation responded to reduced deer densities. Productive sites can tolerate higher deer densities, whereas sites with low soil potential and/or no canopy opening will respond slowly to deer reduction. DeGraaf et al. (1991) showed that vegetation parameters, in their case forest thinning, took precedence over deer densities in predicting bird numbers. Lowering deer densities is one means to increase vegetation density and diversity, but there can be no target deer density; rather, vegetation measurements will determine when the deer densities at that site are sufficient to allow a vegetation response.

It is difficult to provide a specific vegetation index that would gauge deer effect. A long-term index would measure the density and diversity of understory shrubs, but changes in these values will occur over 5–10 years, not on the annual basis needed for deer management decisions. An annual index should not be based on seedling densities, because these values showed great annual variation (personal observation). It is possible to use an index based on the proportion of browsed twigs for favored tree species (Balgooyen & Waller 1995). There is often variability in the relative abundance of preferred trees, and this may dilute the sensitivity of the index. Plants within the Liliaceae or Orchidaceae families are common throughout the eastern United States, and both the number of plants and the proportion flowering are sensitive to changes in deer densities (Balgooyen & Waller 1995; Augustine & Frelich 1998; Fletcher 1999).

Shifts in the abundance and diversity of the bird community at our sites were dynamic, with birds responding to annual changes in site condition. Release from deer

browsing caused rapid successional changes in the forest understory as vegetation progressed from grasses to forbs to *Rubus* spp. to woody saplings. These changes corresponded to a shift in bird species composition from Chipping Sparrows to Indigo Buntings to Hooded Warblers to Ovenbirds. This successional process, in combination with site differences, makes it difficult to say whether or not a particular species will increase in response to lower deer densities, because the answer depends on the site characteristics and time span involved. For example, Indigo Buntings responded immediately to removal of deer but then declined at exclosure sites until the ninth year, when an ice storm opened the canopy and resulted in a second pulse of herbaceous vegetation and a second pulse of birds (Fig. 1).

Because of species replacement, our measures of bird diversity did not show increases. Spatial and structural heterogeneity are the keys to understanding bird diversity (MacArthur & MacArthur 1961; Karr & Roth 1971; Roth 1976). Under conditions of high browsing pressure from deer, low disturbance rates, and low plant productivity due to poor soil quality, the heterogeneity of a site is reduced and bird diversity is lower. These three traits often characterize protected forests in the eastern United States. Our sites did not demonstrate a high spatial heterogeneity because the disturbance event—release from deer browsing—occurred equally across the site. Additional time may result in an increase in bird diversity within these sites because much of the disturbance within eastern deciduous forests occurs at the microscale of single tree falls (Runkle 1982), and over time these types of disturbance would lead to spatial heterogeneity. An effect of white-tailed deer is to prevent the formation of these microsites through concentrated feeding activity in these small openings and thereby reduce heterogeneity (Veblin et al. 1989). Again, our sites may be too small to demonstrate spatial heterogeneity because disturbance events larger than single tree falls would serve to reset the successional process of the entire site.

The theory of food webs points to the complexity of forest ecosystems (Polis & Strong 1996; Ritchie et al. 1998). Within many terrestrial food webs, large ungulates are landscape engineers (Pastor et al. 1997; Stromayer & Warren 1997). Deer are dominant herbivores within forest systems of the eastern United States and have measurable effects on forest vegetation (Pastor et al. 1997; Augustine & Frelich 1998). Changes in understory vegetation diversity and density translate into increased numbers for some bird species, but not necessarily increased diversity, at least at the scale we measured.

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Literature Cited

- Alverson, W. S., D. M. Waller, and S. I. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. *Conservation Biology* 2:348-358.
- Augustine, D. J., and L. E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented forests. *Conservation Biology* 12:995-1004.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165-1183.
- Baird, T. H. 1990. Breeding bird populations. New York State museum bulletin 477. State University of New York, Albany.
- Balgooyen, C. P., and D. M. Waller. 1995. The use of *Clintonia borealis* and other indicators to gauge impacts of white-tailed deer on plant communities in Northern Wisconsin, USA. *Natural Areas Journal* 15:308-318.
- Bell, H. L. 1982. A bird community of New Guinean lowland forest. 3. Vertical distribution of the avifauna. *Emu* 82:143-162.
- Boone, D. D., and B. A. Dowell. 1986. Catoctin Mountain Park bird study. CX-3000-4-0152. National Park Service, Thurmont, MD.
- Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monographs* 72.
- Casey, D., and D. Hein. 1983. Effects of heavy browsing on a bird community in a deciduous forest. *Journal of Wildlife Management* 47:829-836.
- deCalesta, D. S. 1994. Effects of white-tailed deer on song birds within managed forests in Pennsylvania. *Journal of Wildlife Management* 58:711-718.
- DeGraaf, R. M., W. M. Healy, and R. T. Brooks. 1991. Effects of thinning and deer browsing on breeding birds in New England oak woodlands. *Forest Ecology and Management* 41:179-191.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. *The birder's handbook*. Simon and Schuster, New York.
- Eyre, F. H., editor. 1980. *Forest cover types of the United States and Canada*. Society of American Foresters, Washington, D.C.
- Fletcher, D. 1999. The effects of herbivory by white-tailed deer on survival and distribution of native wildflowers. Master's thesis. University of Maryland, Frostburg.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695-713.
- Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schaubert, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* 279:1023-1026.
- Karr, J. R., and R. R. Roth. 1971. Vegetation structure and avian diversity in several New World areas. *American Naturalist* 105:423-435.
- Knox, M. W. 1997. Historical changes in abundance and distribution of deer in Virginia. Pages 27-36 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C.
- Leimgruber, P., W. J. McShea, and J. H. Rappole. 1994. Predation on artificial nests in large forest blocks. *Journal of Wildlife Management* 58:254-260.
- Lynch, J. F., and D. F. Whigham. 1984. Effect of forest fragmentation on breeding bird communities in Maryland. *Biological Conservation* 28:287-324.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594-598.
- Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* 90:51-57.
- McCabe, T. R., and R. E. McCabe. 1997. Recounting whitetails past. Pages 11-26 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C.
- McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations within oak dominated forests. *Ecology* 81:228-238.
- McShea, W. J., and J. H. Rappole. 1992. White-tailed deer as keystone species within forest habitats of Virginia. *Virginia Journal of Science* 43:177-186.
- McShea, W. J., and J. H. Rappole. 1997. Herbivores and the ecology of forest understory birds. Pages 298-309 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C.
- McShea, W. J., M. V. McDonald, G. E. Morton, R. Meier, and J. H. Rappole. 1995. Long-term monitoring of Kentucky Warbler habitat selection. *Auk* 112:375-381.
- Mills, G. S., J. B. Dunning Jr., and J. M. Bates. 1991. The relationship between breeding bird density and vegetation volume. *Wilson Bulletin* 103:468-479.
- Nudds, T. D. 1977. Quantifying the vegetation structure of wildlife cover. *Wildlife Society Bulletin* 5:113-117.
- Ostfeld, R. S. 1997. The ecology of Lyme-disease risk. *American Scientist* 85:338-346.
- Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139:690-705.
- Pastor, J., R. Moen, and Y. Cohen. 1997. Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. *Journal of Mammalogy* 78:1040-1052.
- Peet, R. K. 1974. The measures of species diversity. *Annual Review of Ecology and Systematics* 5:285-307.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *The American Naturalist* 147:813-846.
- Porter, W. F., and H. B. Underwood. 1999. Of elephants and blind men: deer management in the U.S. National Parks. *Ecological Applications* 9:3-9.
- Power, M. 1992. Top-down or bottom-up forces in food webs: do plants have primacy? *Ecology* 73:733-746.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daly, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609-620.
- Ritchie, M. E., D. Tilman, and J. M. N. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165-177.
- Robinson, S. K., F. R. Thompson III, and T. M. Donovan. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987-1990.
- Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57:773-782.
- Runkle, J. R. 1982. Patterns of disturbance in some old growth mesic forests of eastern North America. *Ecology* 63:1533-1546.
- SAS Institute. 1987. *SAS/STAT guide for personal computers*. Version 6. Cary, North Carolina.
- Stromayer, K. A. K., and R. J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin* 25:227-234.
- Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53:524-532.

Urban, D. L., and T. M. Smith. 1989. Microhabitat pattern and the structure of forest bird communities. *American Naturalist* **133**:811-829.

Van Miegroet, H., and D. W. Johnson. 1993. Nitrate dynamics in forest soils. Pages 75-96 in T. P. Burt, A. L. Heathwaite, S. T. Trudgill, editors. *Nitrate processes, patterns and management*. Wiley, Cinchester, United Kingdom.

Veblin, T. T., M. Mermoz, C. Martin, and E. Ramilo. 1989. The effect of exotic deer on forest regeneration and composition in Northern Patagonia. *Journal of Applied Ecology* **26**:711-724.

Verardo, D. J., P. N. Froelich, and A. McIntyre. 1990. Determination of organic carbon and nitrogen in marine sediments using the Carlo Erba NA-1500 analyzer. *Deep-sea Research* **37**:157-165.

