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RESEARCH ARTICLE

Are There Too Many Deer in a Large Private Park in Westcentral Indiana?

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ABSTRACT: Overabundant white-tailed deer (*Odocoileus virginianus*) can have significant effects on forest understory vegetation, especially in parks where hunting is not permitted. The DePauw Nature Park is a large (210 ha) private park located in west-central Indiana; hunting was prohibited in the park when the park was established in 2003. The park is mostly forest habitat but is surrounded by a rural landscape consisting of a mix of agricultural fields and forest fragments. We assessed the effects of deer on forest understory vegetation in the park using exclosures and control plots and estimated the size of the deer population in the park using infrared digital game cameras. There were almost no changes in forest understory vegetation during the first four years after the exclosures were established. The estimated population size of deer in the park ranged from 46 to 66 deer per km². Although no observations were made outside park boundaries, we believe that the deer often move in and out of the park, feeding in surrounding fields and returning to the park for shelter. Effects of a large population of deer on forest understory vegetation are mediated by movement of deer in and out of the park as well as hunting pressure outside the park. We conclude that deer are having minimal effects on forest understory vegetation in the exclosures and control plots during future years.

Index terms: forest understory vegetation, Indiana, white-tailed deer

INTRODUCTION

White-tailed deer (Odocoileus virginianus) populations have gone through a bustand-boom cycle in the eastern United States during the last 150 years (Russell et al. 2001; Côté et al. 2004). Deer were extirpated in parts of the eastern United States 100 to 150 years ago, but populations became re-established during the mid-20th century. The absence of predators, the absence or reduction of hunting pressure, and changes in landscapes have contributed to an explosion of deer populations during the last 50 years. Deer have become superabundant and have, in turn, contributed to dramatic changes in vegetation within some landscapes.

Deer-induced changes in forest vegetation have been well documented. At high population levels, deer overbrowse vegetation and cause shifts in the composition of understory plant communities (Tilghman 1989; Horsley et al. 2003; Goetsch et al. 2011), declines in the cover, diversity, and density of forest understory vegetation (Webster and Parker 1997; McShea and Rappole 2000; Boucher et al. 2004; Asnani et al. 2006; Goetsch et al. 2011), and regeneration failure of canopy tree species (Marquis 1974; Tilghman 1989; Horsley et al. 2003) Native wildflowers may be extirpated and replaced by non-native plant species (Augustine and Frelich 1998; McGraw and Furedi 2005; Knight et al. 2009). Deer also facilitate the spread of invasive and non-native plant species by

carrying seeds in their feces, on their fur, or attached to their hooves (Cavers et al. 1979; Vellend 2002; Williams and Ward 2006; Eschtruth and Battles 2008, 2009; Knight et al. 2009).

Effects of deer on vegetation are most dramatic in forest reserves and parks where deer are superabundant and hunting is prohibited (Webster et al. 2005; Asnani et al. 2006; Killmaster et al. 2007). Hunting was prohibited in state parks in Indiana until the 1990s when park managers began observing extensive damage to vegetation due to high deer populations. Controlled hunts were initiated on a limited basis to reduce deer populations in the parks (Webster and Parker 1997, 2000). Controlled hunts have been continued on a regular basis in Indiana state parks and are now mandated by state law (Mitchell et al. 1997). Annual hunting can be effective at controlling deer populations, but often hunting alone fails to achieve population goals or forest recovery goals (Royo et al. 2010). Regardless of effectiveness, the decision to introduce hunting within a reserve or park is not without controversy or complications (Kilpatrick et al. 1997; Brown et al. 2000).

These same issues apply to management of the DePauw Nature Park, a 210-ha private park in west-central Indiana. Hunting is prohibited in the park, but occurred before the park was established in 2003 and currently occurs in properties surrounding the park. In 2005, an advisory board, responsible for ecological restoration and stewardship of the park, expressed concern about overabundance of deer and health of the vegetation in the park. The advisory board considered the question of whether hunting should be permitted on a controlled basis to reduce the deer population. To address the concerns of the advisory board, we conducted a study to assess the effects of deer on forest understory vegetation and estimate the size of the deer population in the park. We set up deer exclosures and monitored vegetation for four years in the exclosures and adjacent unfenced areas. We used infrared digital game cameras to estimate deer populations in the park.

STUDY AREA

Our study was conducted in the DePauw Nature Park, located in Putnam County, west-central Indiana. The DePauw Nature Park was established in 2003 and is 210 ha in size. Hunting has not been permitted within the park since 2003, but hunting does occur on properties adjacent to the park. Approximately 62 percent of the park consists of mature deciduous forest. The park also includes developed areas (parking lots, buildings, mowed lawns), old fields undergoing forest succession, and an abandoned limestone quarry (Table 1, Figure 1). There are no agricultural fields in the park. The area surrounding the DePauw Nature Park is mostly rural and is a mix of agricultural fields, forest fragments, and developed areas (Table 1, Figure 1).

METHODS

We set up exclosures and adjacent control sites at two forested sites in the DePauw Nature Park, Creekside Trail, and Quarry South (Figure 1). We chose these two sites because of the presence of active deer trails, spring wildflowers, and distance from human-used trails in the park. We set up four exclosures and four control plots at Creekside Trail during 2006, and set up four exclosures and four control plots at Quarry South in 2008. All exclosures and control plots were set up in closed-canopy forests. Soil conditions, slope, and forest composition and structure were similar among the exclosures and control plots within each site. Each exclosure was 5 m × 5 m in size and was surrounded by 2.5-m tall mesh fencing. Each control plot was $5 \text{ m} \times 5 \text{ m}$ in size, located within 5 m of each exclosure, and marked with stakewire flagging.

We monitored vegetation within four subplots inside each exclosure and control plot. Each subplot was $1 \text{ m} \times 1 \text{ m}$ in size and was located 1 m from each corner of the exclosure or control plot (Figure 2). Within each subplot, we counted the number of plants (or plant stems) by species and estimated percent cover of vegetation. Vegetation measurements were conducted twice a year, during spring (late April, early May) and fall (mid-October) for four years, from 2008 to 2011.

Vegetation data were analyzed using a repeated measures analysis of variance

Table 1. Habitat types (percent of total area) in the DePauw Nature Park and within a 1-km buffer surrounding the DePauw Nature Park, estimated from analysis of a 2010 aerial photo using ArcMap software.

Habitat type	Nature Park	1 km buffer
Developed	9%	26%
Fields	0	32
Shrubs, young forest	15	6
Mature forest	62	31
Water	5	1
Old quarry	9	0

(RM-ANOVA) model. The RM-ANOVAs tested for effects of time (season and year), treatment (control vs. exclosure), and time × treatment interaction on percent cover of vegetation and number of plants for each plant species or groups of plant species. A significant treatment \times year interaction was interpreted as a significant treatment effect because our experimental design incorporated both the effects of treatment and time since the exclosures and control plots were initially established. A significant interaction effect thus indicated that the change in vegetation differed between exclosures and control plots over time. This approach prevented the potential problem of identifying any effects that were due to initial differences between the control plots and exclosures. We ran separate RM-ANOVAs for two sites, Creekside Trail and Quarry South. We calculated averages of the four subplots within each plot and used the averages from each of the four plots as the replicates in the analysis. We used alpha of 0.05 as the threshold for significance. We did not adjust alpha based on the number of tests run to ensure that we did not commit type II errors (i.e., to ensure that we did not overlook any potential treatment effects).

We used infrared digital game cameras (Moultrie Gamespy I-35 and I-40, www. moultriefeeders.com) to estimate the number of deer in the park. We divided the forest habitat within the park into five similarsized parts, and set up one camera within each of the five parts to ensure complete coverage of the forest habitat. Within each area, cameras were subjectively placed along active deer trails to maximize the likelihood of "capturing" deer with the cameras. The estimated camera density was one camera per 42 ha, which was below the minimum camera density (one camera per 65 ha) recommended by Jacobson et al. (1997). The cameras were set up from October through December in 2008, 2009, and 2011. The cameras automatically recorded the date and time on each photograph. The infrared sensor was sensitive to motion within 15 m. Photographs were taken at intervals of one minute. We checked the cameras every three to four weeks and downloaded the photos onto laptop computers for analysis.



Figure 1. Habitat types within the DePauw Nature Park and within a 1-km radius surrounding the park. Big Walnut Creek forms the western boundary of the park. Developed areas within the park include an abandoned limestone quarry, parking lots, buildings, and mowed lawns. Developed areas surrounding the park include the city of Greencastle (north and east of the park) and rural farmhouses, other buildings, and mowed lawns. CKT (Creekside Trail) and QS (Quarry South) indicate the two sites in the park where data were collected in exclosures and adjacent control plots.

We used methods recommended by Jacobson et al. (1997) to estimate the deer population. For each year of photos, we identified individual bucks based on antler configurations to estimate the buck population (E_{buck}). The doe to buck ratio, N_{doe}/N_{buck} , was estimated as the total number of antlerless deer (N_{doe}) in the photos divided by the total number of antlered deer in the photos (N_{buck}). The estimated

doe population (E_{doe}) was calculated as $E_{buck} \times (N_{doe}/N_{buck})$, or the estimated buck population multiplied by the doe to buck ratio. The total deer population (E_{total}) was calculated as $E_{doe} + E_{buck}$.



Figure 2. Experimental design of exclosures (left) and control plots (right). Solid lines are fenced; dashed lines are unfenced. Vegetation data were collected in four 1-m² subplots within each exclosure and control plot. Subplots were located 1 m from each corner of the exclosure and control plot.

RESULTS

At Creekside Trail, there was a significant time × treatment interaction effect on the total number of understory plants ($F_{7,42} = 2.8, p = 0.02$). The total number of plants was higher in control plots than exclosures during spring 2009, and did not differ be-

tween control plots and exclosures during other time periods (Figure 3a). At Quarry South, there was no time × treatment interaction effect on the total number of understory plants ($F_{7, 42} = 0.8$, p = 0.6), but there was a significant effect of time on the total number of plants ($F_{7, 42} = 25.9$, p < 0.001), with higher numbers of plants observed during spring 2011 compared to other time periods (Figure 3b).

There was no significant time × treatment interaction effect on the percent cover of understory vegetation at Creekside Trail ($F_{7, 42} = 2.8, p = 0.3$) or Quarry South ($F_{7, 42} = 1.9, p = 0.09$). Percent cover of vegetation varied significantly by time at both sites (Creekside Trail, $F_{7, 42} = 22.3, p < 0.001$; Quarry South, $F_{7, 42} = 22.3, p < 0.001$). Percent cover of vegetation varied among years and was consistently higher during spring than fall each year (Figure 3c,d).

We observed a total of 32 plant species or groups of species at the two sites. Snakeroot (*Sanicula canadensis*) was the most abundant plant species at both sites (Table 2). Other abundant plant species included Miami mist (*Phacelia purshii*), sweet cicely (*Osmorhiza longistylis*), wild chervil (*Chaerophyllum procumbens*), and stinging nettle (*Urtica dioica*).



Figure 3. Density (top; number of plants per m², mean and standard error) and percent cover (bottom) of forest understory vegetation in exclosures and control plots at Creekside Trail (left) and Quarry South (right) during spring (S) and fall (F) 2008-2011.

Table 2. Density of plants (number per m², averaged for all time periods and treatments combined) and p-values from RM-ANOVAs testing for effects of time (spring, fall, 2008-2011), treatment (control, exclosure), and time × treatment interaction. Bold font indicates $p \le 0.05$. Data were analyzed separately for the two sites, Creekside Trail and Quarry South. The top section of the table shows plants that occurred during both spring and fall (df time = 7, 42; df trt = 1, 6; df time × trt = 7, 42). The bottom section of the table shows plants that only occurred during spring or fall (df = 3.48. df = 1.6; df time × trt = 7, 42). The bottom section of the table shows plants that only occurred during spring or fall (df = 3.48.)

	CKT	p-values			QS	p-values		
pring and fall	Density	Time	Trt	Time x trt	Density	Time	Trt	Time x trt
Alliaria petiolata	0.6	0.003	0.1	0.01	0	ı	ı	I
Asarum canadense	0.3	0.5	0.5	0.4	0	ı		ı
Asimina triloba	0.3	0.1	0.9	0.9	0.2	0.6	0.9	0.6
Equisetum hyemale	0	·	ı	·	0.4	0.1	0.2	0.5
Hydrophyllum appendiculatum	1.3	0.02	0.3	0.5	0	ı	·	ı
Osmorhiza longistylis	1.5	0.02	0.6	0.9	17.2	< 0.001	0.7	0.7
Ribes uva-crispa	0.1	0.6	0.7	0.3	0	ı	ı	I
Sanicula canadensis	16.5	0.001	0.9	0.9	61.2	< 0.001	0.9	0.9
Smilax spp.	0.3	0.02	0.05	0.009	0	ı	·	ı
Symphoricarpos orbiculatus	0	·	ı	·	1.2	0.1	0.3	0.1
Urtica dioica	9.1	< 0.001	0.9	0.9	0.3	0.007	0.7	0.4
Viola sororia	1.1	0.2	0.8	0.9	8.4	0.04	0.9	0.9
Graminoids (unidentified)	12.0	< 0.001	0.9	0.9	10.6	< 0.001	0.7	0.8
Tree seedlings	3.1	0.002	0.5	0.9	0.2	0.008	0.9	0.3
Herbaceous seedlings (unidentified)	19.8	0.02	0.3	0.8	30.4	< 0.001	0.4	0.2
ring								
30ehmeria cylindrica	0	ı	ı	ı	0.4	0.1	0.9	0.7
Chaerophyllum procumbens	4.7	0.00	0.8	0.9	13.3	0.005	0.7	0.9
Claytonia virginica	6.5	0.3	0.5	0.8	3.1	0.1	0.5	0.6
Cardamine concatenata	7.3	0.2	0.9	0.9	0.1	ı		I
Erythronium americanum	4.0	0.4	0.4	0.5	0	ı		I
Galium aparine	6.9	0.02	0.5	0.7	6.1	0.006	0.04	0.4
Impatiens capensis	1.7	0.2	0.6	0.4	5.9	0.03	0.2	0.1
Lamium purpureum	1.0	0.3	0.5	0.3	0	ı	·	ı
Phacelia purshii	4.5	0.5	0.7	0.4	19.0	0.7	0.3	0.4
Podophyllum peltatum	1.1	0.4	0.5	0.5	0.1	0.4	0.4	0.4
Polygonatum biflorum	1.8	0.8	0.6	0.9	0.4	0.5	0.2	0.6
Ranunculus arbortivus	0.3	0.1	0.4	0.7	1.0	0.01	0.5	0.1
Sanguinaria canadensis	0.2	0.4	0.4	0.4	0	I	ı	I
Senecio aureus	0.9	0.2	0.6	0.8	0	ı	·	I
Stellaria media	3.5	0.1	0.8	0.9	0	I	ı	I
Frillium sessile	1.7	0.4	0.9	0.4	0	I	ı	I
Π								
		1						

There was a significant time \times treatment interaction effect for two plant species (Table 2). Abundance of greenbrier (*Smilax* spp.) at Creekside Trail was similar in the control plots and exclosures in 2008, and increased in abundance in the control plots but not the exclosures from 2008 to 2011 (Figure 4a). Abundance of garlic mustard (*Alliaria petiolata*) at Creekside Trail was low in the exclosures in all years and varied in abundance among years in the control plots (Figure 4b).

There was a significant effect of time for 13 plant species or groups of species (Table 2). Abundance of these plants varied among years and between spring and fall, as shown for stinging nettle (Figure 4c), snakeroot (Figure 4d), and tree seedlings (Figure 4e) at Creekside Trail. Abundance of one plant species at Quarry South, jewelweed (*Impatiens capensis*), increased over time in exclosures and remained low in control plots (Figure 4f), but the time × treatment interaction effect was not significant (Table 2).

Based on the camera surveys, the estimated number of deer in the park during fall was 97 to 138. Given the size of the Nature Park (2.1 km^2) , these estimates are equivalent to 46 to 66 deer per km² (Table 3).

DISCUSSION

One of the goals of our study was to document changes in forest understory vegetation during a four year period (from 2008 to 2011) after deer exclosures and control plots were set up in the DePauw Nature Park. A significant treatment × year interaction effect would have been interpreted as a significant treatment effect because our experimental design incorporated the effects of treatment (control vs. exclosure) and time (four years) since the treatments were established. We observed almost no changes in forest understory vegetation during the four year period since the exclosures were set up. There was a significant time × treatment effect on the total number of plants at one of the sites (Creekside Trail), but the pattern of change was not indicative of an effect of deer overbrowsing. There were no other significant

interaction effects on the total number of plants or percent cover of vegetation.

There were significant time \times treatment effects on the abundance of two plant species, greenbrier and garlic mustard. Greenbrier appeared to be positively affected by deer, showing an increased abundance in control plots over time, but the overall change was relatively minor, with average densities of less than one greenbrier plant per square meter in control plots. Garlic mustard, a non-native and invasive plant species, varied in abundance among years in the control plots and was nearly absent in the exclosures. Deer are known to be responsible for the spread of non-native and invasive plant species (Vellend 2002, Williams and Ward 2006), but our results are probably due to the biennial growth habit and stage-structured populations of garlic mustard. Most of the garlic mustard populations in the park are dominated by one life history stage, with an abundance of adult garlic mustard plants occurring during even-numbered years (spring 2008, spring 2010; V. Fox, pers. observ.). The significant interaction effect may not have been due to the combination of time and treatment, but instead, the differences between the control plots and exclosures may have existed before we initiated the experiment.

Abundance of jewelweed increased in exclosures and remained low in control plots during the four year period. The treatment × time interaction effect was not significant, but the patterns suggest that jewelweed is being affected by deer overbrowsing in the park. Leaves and stems of jewelweed are known to be a preferred food item for deer (Nixon et al. 1970; Williams et al. 2000), and this plant species has been recommended as an indicator of deer browsing intensity (Williams et al. 2000).

The second goal of our study was to estimate the size of the deer population occurring in the park. Our camera surveys indicate that the deer population ranged from 46 to 66 deer per km². These estimates are comparable to population levels observed in other areas where hunting is not permitted (Kilpatrick et al. 1997; Porter and Underwood 1997; Morrison and Brown

2004; Asnani et al. 2006; Killmaster et al. 2007).

We can answer the question, "Are there too many deer in the DePauw Nature Park?" in several different ways. One answer is "No, there aren't too many deer," because our observations in the exclosures and control plots have shown that there were almost no effects of deer overbrowsing on understory vegetation. A second answer is "Yes, there are too many deer," because the camera surveys showed very high population levels of deer in the park. How do we resolve these two opposing answers?

One important aspect to consider is the landscape context of the park. Previous studies have shown that vegetation in parks surrounded by contiguous forest is affected by deer more than vegetation in parks surrounded by rural landscapes (DeCalesta and Stout 1997; Augustine and Jordan 1998; Hurley et al. 2012). Deer readily move between sheltered forests and open fields (Nixon et al. 1991), and are unlikely to remain in forest habitats when agricultural fields are located nearby (Augustine and Jordan 1998). For example, Brown County State Park, located in southern Indiana, is a large block of contiguous forest (over 60 km²) and is surrounded by mostly forest. Deer in Brown County State Park have fewer opportunities to visit open fields for foraging, are not exposed to hunting pressure within the park, and thus exert stronger grazing pressure on understory vegetation in the park (Hurley et al. 2012). The DePauw Nature Park, in comparison, is mostly forest, but is surrounded by a mix of forest fragments and agricultural fields. Although no observations were made outside park boundaries, we believe that the deer often move in and out of the park, feeding in surrounding fields and returning to the park for shelter. Effects of a large population of deer on forest understory vegetation are mediated by movement of deer in and out of the park as well as hunting pressure outside the park.

A third answer to the question "Are there too many deer in the DePauw Nature Park?" is "We don't know." The four- to six-year time span since we set up the exclosures may not have been sufficient for recovery



Figure 4. Density (number of plants per m², mean and standard error) of (a.) greenbrier (*Smilax* spp.) (b.) garlic mustard (*Alliaria petiolata*), (c.) stinging nettle (*Urtica dioica*), (d.) snakeroot (*Sanicula canadensis*), and (e.) tree seedlings at Creekside Trail during spring (S) and fall (F) 2008-2011, and (f.) jewelweed (*Impatiens capensis*) at Quarry South during spring (S) 2008-11.

$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		2008	2009	2011
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	E _{buck} ¹	26	19	23
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	N _{buck} ²	56	63	89
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	N _{doe} ³	239	259	351
E _{doe} ⁵ 112 78 9	P _{doe} ⁴	4.3	4.1	3.9
	E _{doe} ⁵	112	78	91
E_{total} 138 97 11	E _{total} ⁶	138	97	114
E_{total}/km^2 66 46 5	E_{total}/km^2	66	46	54
	$^{3}N_{\text{buck}}$ = total number of anticred deer	occurrences in photographs		
$^{3}N_{\text{buck}}$ – total number of anticided deer occurrences in photographs	$^{4}P_{\text{tot}}$ = ratio of does to bucks, calculate	ed as N ₁₁₁ /N ₁₁₁₁		
$^{3}N_{\text{doe}}$ = total number of antieried deer occurrences in photographs $^{4}P_{\text{ture}}$ = ratio of does to bucks, calculated as N _{tu} /N _{ture} .	${}^{5}E_{4,2}$ = estimated total doe population	calculated as $E_{\text{buck}} \times P_{\text{doc}}$		
$^{3}N_{doe}$ = total number of antiered deel occurrences in photographs $^{4}P_{doe}$ = ratio of does to bucks, calculated as N_{doe}/N_{buck} $^{5}E_{doe}$ = estimated total doe population, calculated as $E_{buck} \times P_{doe}$	$\mathbf{D}_{000} = \mathbf{c}_{000}$			

Table 3. Estimated deer population during fall 2008, 2009, and 2011 in the DePauw Nature Park, west-central Indiana, based on surveys using infrared trail cameras.

of vegetation to have occurred. Several other studies have shown no differences in vegetation between exclosures and control areas, perhaps because recovery of vegetation from overbrowsing is slow or delayed (Kraft et al. 2004; Webster et al. 2005; Collard et al. 2010; Tanentzap et al. 2012). Slow or delayed recovery may be caused by slow plant growth, slow seed dispersal, reduced seed availability, or presence of browse-tolerant vegetation that outcompetes other plant species (Tanentzap et al. 2012).

There are other potential explanations for why we did not detect any differences in forest understory vegetation between the exclosures and control plots. Our sample size may have been too small to detect any differences. Alternatively, the observed variation between years and seasons may indicate that forest understory vegetation is affected more by climate and weather than by deer, or that the effects of climate and weather mask any effects of deer (Collard et al. 2010). We also recognize that other features of the vegetation could be measured to detect potential effects of deer, such as plant height, flower and fruit production, and browse intensity on shrubs and saplings (Fletcher et al. 2001; Augustine and DeCalesta 2003; Kraft et al. 2004). In addition, it is important to point out that hunting was permitted within the

boundaries of the park until 2003 when the park was officially established. Perhaps the eight years since the park was established and since the no-hunting policy was implemented have not been long enough for any significant changes in vegetation to occur.

Overall, we conclude that effects of deer are minimal at this time and we do not recommend controlled hunts to reduce the deer population in the DePauw Nature Park. Despite the large numbers of deer observed in the park, we detected almost no changes in forest understory vegetation, perhaps because movement of deer in and out of the park reduces feeding pressure. We will continue to be vigilant by periodically monitoring vegetation in the exclosures and control plots during future years. We will consider adding other types of measurements such as assessment of browse intensity on shrubs and saplings. In the meantime, a higher priority for ecological restoration and stewardship may be to focus on reducing the extent and spread of nonnative plants, such as Alliaria petiolata, and restoring native plant communities within the park.

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Vanessa Fox is an Associate Professor in the Biology Department at DePauw University where she teaches ecology, evolution, and biostatistics. Her research interests are in the area of forest ecology.

Kristen Frederick, Ryan Kelly, and Emily Meadows are recent graduates from De-Pauw University (class of 2012) and were undergraduate students when this research was conducted. Kristen and Emily majored in biology and Ryan majored in economics. All three plan to continue their education through graduate studies.

LITERATURE CITED

- Asnani, K.M., R.A. Klips, and P.S. Curtis. 2006. Regeneration of woodland vegetation after deer browsing in Sharon Woods Metro Park, Franklin County, Ohio. Ohio Journal of Science 106:86-92.
- Augustine, D.J., and D. DeCalesta. 2003. Defining deer overabundance and threats to forest communities: from individual

plants to landscape structure. Ecoscience 10:472-486.

- Augustine, D.J., and L.E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conservation Biology 12:995-1004.
- Augustine, D.J., and P.A. Jordan. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. Journal of Wildlife Management 62:1076-1086.
- Boucher, S., M. Crête, J.P. Ouellet, C. Daigle, and L. Lesage. 2004. Large-scale trophic interactions: white-tailed deer growth and forest understory. Ecoscience 11:286-295.
- Brown, T.L., D.J. Decker, S.J. Riley, J.W. Enck, T.B. Lauber, P.D. Curtis, and G.F. Mattfeld. 2000. The future of hunting as a mechanism to control white-tailed deer populations. Wildlife Society Bulletin 28:797-807.
- Cavers, P.B., M.I. Heagy, and R.F. Kokron. 1979. The biology of Canadian weeds. 35. *Alliaria petiolata* (M. Bieb.) Cavara and Grande. Canadian Journal of Plant Science 59:217-229.
- Collard, A., L. Lapointe, J.P. Ouellet, M. Crête, A. Lussier, C. Daigle, and S.D. Côte. 2010. Slow responses of understory plants of maple-dominated forests to white-tailed deer experimental exclusion. Forest Ecology and Management 260:649-662.
- Côté, S.D., T.P. Rooney, J.P. Tremblay, C. Dussault, and D.M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113-147.
- DeCalesta, D.S., and S.L. Stout. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. Wildlife Society Bulletin 25:252-258.
- Eschtruth, A.K., and J.J. Battles. 2008. Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. Conservation Biology 23:388-399.
- Eschtruth, A.K., and J.J. Battles. 2009. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecological Monographs 79:265-280.
- Fletcher, J.D., W.J. McShea, L.A. Shipley, and D. Shumway. 2001. Use of common forest forbs to measure browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. Natural Areas Journal 21:172-176.
- Goetsch, C., J. Wigg, A.A. Royo, T. Ristau, and W.P. Carson. 2011. Chronic over browsing

and biodiversity collapse in a forest understory in Pennsylvania: results from a 60 year-old deer exclusion plot. Journal of the Torrey Botanical Society 138:220-224.

- Horsley, S.B., S.L. Stout, and D.S. DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13:98-118.
- Hurley, P.M., C.R. Webster, D.J. Flaspohler, and G.R. Parker. 2012. Untangling the landscape of deer overabundance: reserve size versus landscape context in the agricultural Midwest. Biological Conservation 146:62-71.
- Jacobson, H.A., J.C. Kroll, R.W. Browning, B.H. Koerth, and M.H. Conway. 1997. Infrared-triggered cameras for censusing white-tailed deer. Wildlife Society Bulletin 25:547-556.
- Killmaster, C.H., D.A. Osborn, R.J. Warren, and K.V. Miller. 2007. Deer and understory plant responses to a large-scale herd reduction on a Georgia State Park. Natural Areas Journal 27:161-168.
- Kilpatrick, H.J., S.M. Spohr, and G.G. Chasko. 1997. A controlled deer hunt on a stateowned coastal reserve in Connecticut: controversies, strategies, and results. Wildlife Society Bulletin 25:451-456.
- Knight, T.M., J.L. Dunn, L.A. Smith, J. David, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Natural Areas Journal 29:110-116.
- Kraft, L.S., T.R. Crow, D.S. Buckley, E.A. Nauertz, and J.C. Zasada. 2004. Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA. Forest Ecology and Management 199:219-230.
- Marquis, D.A. 1974. The impact of deer browsing on Allegheny hardwood regeneration. Research Paper NE-308, U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, Pa.
- McGraw, J.B., and M.A. Furedi. 2005. Deer browsing and population viability of a forest understory plant. Science 307:920-922.
- McShea, W.J., and J.H. Rappole. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology 14:1161-1170.
- Mitchell, J.M., G.J. Pagac, and G.R. Parker. 1997. Informed consent: gaining support for removal of overabundant white-tailed deer on an Indiana state park. Wildlife Society Bulletin 25:447-450.
- Morrison, J.A., and L. Brown. 2004. Effect of

herbivore exclosure caging on the invasive plant *Alliaria petiolata* in three southeastern New York forests. Bartonia 62:25-43.

- Nixon, C.M., L.P. Hansen, P.A. Brewer, and J.E. Chelsvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. Wildlife Monographs 118:3-77.
- Nixon, C.M., M.W. McClain, and K.R. Russell. 1970. Deer food habits and range characteristics in Ohio. Journal of Wildlife Management 34:870-886.
- Porter, W.F., and H.B. Underwood. 1997. Reconsidering paradigms of overpopulation in ungulates: white-tailed deer at Saratoga National Historical Park. Pp. 185-198 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole, eds., The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Institution Press, Washington, D.C.
- Royo, A.A., S.L. Stout, D.S. deCalesta, and T.G. Pierson. 2010. Restoring forest herb communities through landscape-level deer herd reductions: is recovery limited by legacy effects? Biological Conservation 143:2425-2434.
- Russell, F.L., D.B. Zippin, and N.L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. American Midland Naturalist 146:1-26.
- Tanentzap, A.J., K.J. Kirby, and E. Goldberg. 2012. Slow responses of ecosystems to reductions in deer (Cervidae) populations and strategies for achieving recovery. Forest Ecology and Management 264:159-166.
- Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management 53:524-532.
- Vellend, M. 2002. A pest and an invader: whitetailed deer (*Odocoileus virginianus* Zimm.) as a seed dispersal agent for honeysuckle shrubs (*Lonicera* L.) Natural Areas Journal 22:230-234.
- Webster, C.R., and G.R. Parker. 1997. The effects of white-tailed deer on plant communities within Indiana state parks. Proceedings of the Indiana Academy of Science 106:213-231.
- Webster, C.R., and G.R. Parker. 2000. Evaluation of *Osmorhiza claytonia* (Michx.) C.B. Clarke, *Arisaema triphyllum* (L.) Schott, and *Actaea pachypoda* Ell. as potential indicators of white-tailed deer overabundance. Natural Areas Journal 20:176-188.

Webster, C.R., M.A. Jenkins, and J.H. Rock. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. Biological Conservation 125:297-307. Williams, C.E., E.V. Mosbacher, and W.J. Moriarity. 2000. Use of turtlehead (*Chelone* glabra L.) and other herbaceous plants to assess intensity of white-tailed deer browsing on Allegheny Plateau riparian forests, USA. Biological Conservation 92:207-215.

Williams, S.C., and J.S. Ward. 2006. Exotic seed dispersal by white-tailed deer in southern Connecticut. Natural Areas Journal 26:383-390.