Management and Conservation Note

Indirect Effects of a Keystone Herbivore Elevate Local Animal Diversity

KATHERINE R. GREENWALD,[1] *Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 300 Aronoff Laboratory, 318 W 12th Avenue, Columbus, OH 43210, USA*

LISA J. PETIT, *Cuyahoga Valley National Park, 15610 Vaughn Road, Brecksville, OH 44141, USA*

THOMAS A. WAITE, *Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 300 Aronoff Laboratory, 318 W 12th Avenue, Columbus, OH 43210, USA*

ABSTRACT We quantified indirect effects of white-tailed deer (*Odocoileus virginianus*) on ground-dwelling herpetofauna and invertebrates in Cuyahoga Valley National Park, Ohio, USA. We placed cover boards at 12 sites, each consisting of a 10 × 10-m fenced (exclosure) plot and an unfenced (control) plot. Periodically, during May–December 2004 and May–September 2005, we counted salamanders, snakes, and a variety of invertebrate taxa. Salamander, snake, and gastropod abundance as well as invertebrate richness (no. of species or higher level taxa) were higher in control than exclosure plots. Our findings suggest that management actions taken to regulate deer densities could have the unintended effect of reducing local animal diversity. (JOURNAL OF WILDLIFE MANAGEMENT 72(6):1318–1321; 2008)

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Understanding indirect species interactions is critical to evaluate effects of habitat modification by large herbivores. A potentially major factor impacting faunal communities is the burgeoning number of white-tailed deer (*Odocoileus virginianus*) in the eastern United States. Deer overabundance can impact communities at multiple levels (Rooney and Waller 2003), for example by changing nutrient-cycling regimes (Singer and Schoenecker 2003), physically modifying the substrate (Belsky and Blumenthal 1997), and decreasing abundance and diversity of plants (Horsley et al. 2003), birds (DeCalesta 1994), and small mammals (Smit et al. 2001). The rapid population growth of white-tailed deer has placed their management at high priority on many public lands, and a great deal of work has gone into addressing this problem (McShea et al. 1997, Porter and Underwood 1999, Fulton et al. 2004). Populations of white-tailed deer in northeastern Ohio (USA) have been growing since the 1980s and are now at densities (18–36 deer/km^2) that may negatively impact ecosystem function (Fulton et al. 2004).

Effects of high deer densities on invertebrate taxa are complex and differ markedly among focal organisms. In some cases both abundance and diversity decrease in grazed areas (Suominen 1999, Miyashita et al. 2004, Allombert et al. 2005), whereas in other cases both measures increase (e.g., Carabid beetles; Suominen et al. 2003). Herbivores may impact abundance and diversity differentially. For example, Suominen et al. (1999*a*) showed that moose browsing resulted in decreased abundance but increased diversity of arthropods. Finally, some work has shown no impact at all of grazing on target fauna (e.g., litter-dwelling invertebrates; Allombert et al. 2005). These negative results are likely more common than their representation in the literature suggests.

Few studies have addressed indirect effects of large-mammal herbivory on herpetofauna. Plethodontid salamanders are considered important indicators of ecosystem health and are frequently surveyed as indicators of disturbance (Welsh and Droege 2001). An observational study identified no latent effects of historic deer density on red-backed salamander (*Plethodon cinereus*) populations in New England, USA (Brooks 1999). A cover board study with paired exclosures and controls found no effect of herbivory on species composition or abundance even at the highest deer density treatment (0.3 deer/ha); Pauley and Mitchell suggest that densities included might have been too low to detect treatment effects (Pauley and Mitchell 1999). The Great Plains, a region from which feral horses were removed, had greater reptile species richness, with abundance showing a nonsignificant trend in the same direction (Beever and Brussard 2004). In a recent experimental study, the African savanna-dwelling lizard (*Lygodactylus keniensis*) was found to be less abundant in areas grazed by ungulates (Pringle et al. 2007). Thus, research to date has been equivocal regarding invertebrates and amphibians, but it does suggest that grazing can be detrimental to species richness and abundance of reptiles.

We evaluated the indirect trophic effects of deer overabundance on ground-dwelling herpetofauna and invertebrates. We conducted an exclosure experiment to determine whether heavy browsing by deer was associated with elevated or depressed local animal diversity. We ask whether deer management plans could have the unintended effect of altering local diversity of some animal taxa.

STUDY AREA

The study took place in Cuyahoga Valley National Park (CVNP) in northeastern Ohio (41°14′28″N, 81°33′10″W). The park stretched along the course of the Cuyahoga River and was bounded to the north and south by Cleveland and

[1] *E-mail: greenwald.35@osu.edu*

Table 1. Abundance and species richness in exclosures versus control plots in Cuyahoga Valley National Park, Ohio, USA, in 2004 and 2005.

Effect	Herpetofauna		Invertebrates				
	P. cinereus	*T. sirtalis*	Isopoda	Myriapoda	Gastropoda	Lumbricina	Species richness
Yr	0.219	0.250	0.204	0.635	0.835	0.777	0.607
Treatment	0.031*	0.016*	0.519	0.970	0.002*	0.241	0.009*

* Significant *P*-values following sequential Bonferroni correction.

Akron, Ohio, respectively. The total area within the park boundary was 13,355 ha.

The CVNP was authorized as a National Recreation Area in 1974 and was changed to National Park status in 2000. Two interstate highways, 2 state routes, and numerous local roads crossed through the park. The heterogeneity of the region led to a patchy distribution of forest habitat, with a high ratio of edge-to-core habitat. White-tailed deer are known to do well in such edge-dominant, successional environments and, indeed, deer densities in CVNP are extremely high (Alverson et al. 1988). Underwood and Coffey (1999) estimated densities as high as 0.17–0.35 deer/ha in 1998. Extrapolation suggests that the park may contain a population of 2,300–4,600 deer.

The National Park Service erected 12 10 × 10-m deer exclosures in the winter of 1999. A stratified random-sampling scheme was used to select locations for 3 exclosure sites in each of 4 habitat types: upland field, bottomland field, upland forest, and bottomland forest. Each exclosure was paired with a nearby 10 × 10-m unfenced (control) plot. Exclosure-control pairs did not differ in forest cover type, soil type, contour, slope, or aspect (Dengg 2002). Dengg's (2002) study showed that deer-browsing significantly decreased foliage in all habitats. Herbivory also negatively impacts growth and maximum height of seedlings in bottomland sites, as well as diversity of native groundcover in upland forests. In contrast, diversity and density of groundcover in upland fields was enhanced in grazed areas.

METHODS

We placed 5 30 × 30 × 5-cm red oak (*Quercus rubra*) cover boards in each plot ($n = 120$) in March 2005, using a stratified random design. We divided plots into 5 rows (A through E) and 5 columns (1 through 5), each 2 m wide. We randomly chose a column for each row and placed the board in that quadrant (e.g., Terra Vista Exclosure: A1, B4, C5, D1, E2; Terra Vista Control: A1, B1, C2, D3, E2). We repeated this process for each plot. We surveyed the boards every 3–4 weeks from May through December 2004 (10 visits total) and monthly from May through September 2005 (5 visits total).

For vertebrates, we restricted statistical analysis to the 2 most common species, the red-backed salamander and garter snake (*Thamnophis sirtalis*). We saw other snake species infrequently and observed only one other amphibian (northern spring peeper [*Pseudacris crucifer*]). For both *P. cinereus* and *T. sirtalis* we summed the number of individuals under all 5 cover boards for each plot. We then used a Wilcoxon signed-rank test to detect any differences between the 2 years. Because we found no such differences, we averaged the count data across all visits to test for treatment effects.

We counted all invertebrates encountered during surveys and analyzed abundance and diversity. We identified invertebrates to morphospecies, which has been described as a suitable method for approximating species richness across habitats (Oliver and Beattie 1996). We identified myriapods to class; we encountered both Chilopoda (centipedes) and Diplopoda (millipedes). We identified other noninsects to order, which included Isopoda (pill-bugs), Opiliones (harvestmen), Araneae (spiders), Pulmonata (slugs), and suborder Lumbricina (earthworms). We identified insects to order, which included Coleoptera, Orthoptera, Lepidoptera, Hymenoptera, Dermaptera, and Hemiptera.

We recorded number of specimens of each morphospecies encountered across all cover boards (hereafter, abundance) within a plot for the 4 most-abundant invertebrate taxa (isopods, myriapods, slugs, and earthworms). Other taxa were too rare to be included in the analysis. We also analyzed alpha-level species density, defined by Gotelli and Colwell (2001) as the number of species (or higher level taxa) encountered per sampling unit (plot, in this case). We tallied total number of arthropod morphospecies encountered across all cover boards in each plot for the species density measure. We analyzed abundance and species density using a Wilcoxon signed-ranks test as described above. We used SPSS v. 14.0 (SPSS Inc., Chicago, IL) routines for all analyses.

Table 2. Snake abundance in Cuyahoga Valley National Park, Ohio, USA, in 2004 and 2005.

Species	Exclosures	Controls	Total
Garter snakes[a]	6	33	39
Brown snakes	1	3	4
Green snakes	0	1	1
Ring-necked snakes	0	1	1
Total	7	38	45

[a] We included only garter snakes in statistical analysis.

RESULTS

We did not find any differences between years for any of the focal taxa (Table 1), so we averaged count data across all visits to test for treatment effects. We captured nearly 3 times as many red-backed salamanders in control plots versus exclosures ($P = 0.031$; Table 1; Fig. 1). We observed 45 snakes over all visits (Table 2), including 39 garter snakes, 4 brown snakes (*Storeria dekayi*), 1 eastern smooth

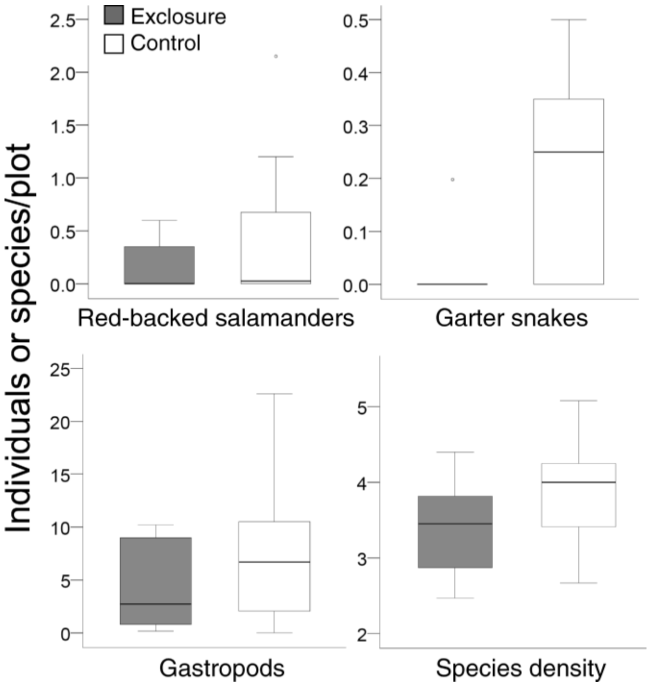

Figure 1. Abundance of red-backed salamanders, garter snakes, and gastropods, and invertebrate morphospecies density, in exclosures (gray bars) and control plots (white bars), in Cuyahoga Valley National Park, Ohio, USA, May through December 2004 and May through September 2005. Bars represent the interquartile interval, thick lines indicate the median of means, and vertical lines show the maximum and minimum means (circles indicate outliers). We caught more salamanders, snakes, and gastropods in control plots than in exclosures. Invertebrate species density was higher in control plots than in exclosures. Other focal taxa showed no significant effect of treatment (data not shown).

green snake (*Opheodrys vernalis*), and 1 northern ring-necked snake (*Diadophis punctatus*). We found 38 in control plots and 7 in exclosure plots. We captured >5 times more garter snakes in control plots than exclosures ($P = 0.016$; Table 1; Fig. 1). Among invertebrates, only gastropods showed a significant trend, with abundance 11% higher within the controls ($P = 0.002$; Table 1; Fig. 1).

Analysis of arthropod species density included all arthropod morphospecies encountered: Chilopoda, Diplopoda, Isopoda, Opiliones, Araneae, and insect orders Coleoptera, Orthoptera, Lepidoptera, Hymenoptera, Dermaptera, and Hemiptera. Species density was 14% higher in control plots than in exclosure plots ($P = 0.009$; Table 1; Fig. 1). All significant *P*-values remained significant following sequential Bonferroni correction.

DISCUSSION

For 3 of the focal taxa, red-backed salamanders, garter snakes, and gastropods, deer herbivory had a positive, indirect effect on abundance. Arthropod species density also was significantly higher in grazed plots. A plausible mechanistic explanation of our results is bottom-up regulation, wherein grazing indirectly results in increased invertebrate species diversity, perhaps mediated by increased nutrient deposition and plant growth. Increased diversity and density of groundcover plants was previously observed at some of our grazed sites, lending support to this interpretation (Dengg 2002). Suominen et al. (1999*b*) and Suominen et al. (2003) also reported an increase in invertebrate species diversity in heavily grazed areas. The additional invertebrate species occurring in the control plots were mostly insects, mainly of the orders Coleoptera and Orthoptera. Red-backed salamanders are known to feed opportunistically on a wide variety of invertebrate prey (Jaeger 1981, Maglia 1996). Red-backed salamander presence might have driven the local abundance of garter snakes, because red-backed salamanders and gastropods are commonly preyed upon by garter snakes (Hamilton 1951). We speculate that herbivory may indirectly increase invertebrate species richness, which may attract both salamanders and snakes.

Additional data are needed to elucidate the factors mediating the increase in invertebrate species richness. We propose that future research test 2 hypotheses: 1) growth of favorable plant species is promoted by increased nutrient deposition (e.g., as described by Suominen et al. 1999*a*), and 2) a hospitable microclimate is present in terms of soil moisture content. The second hypothesis is based on an underlying assumption in many exclosure studies, which is that presence of groundcover plants and lack of trampling in ungrazed areas creates a moist, therefore favorable, micro-habitat. However, distribution of salamanders suggests that soils in grazed areas are not overly dehydrated. Plant transpiration may actually cause soil within exclosures to be less hydrated than that in controls. If this were the case it may be the driving force behind the observed increase in arthropod species density. Further research in plant community structure and soil science is needed to resolve these questions.

The simplest interpretation of our results is to accept them at face value: presence of deer in CVNP has a positive indirect effect on invertebrate species richness and herpetofaunal abundance. The most plausible explanatory hypotheses involve growth of favorable plant species in nutrient-rich soil or creation of a preferable microhabitat. However, we should consider other possible explanations. First, our sampling could be biased due to either reluctance to cross fencing or a true refuge effect. Sampling bias due to reluctance to penetrate fencing seems unlikely, given that the mesh size of the exclosure fences is >10 cm. Many herpetological studies using drift fences and pitfall traps show animals trespassing fencing even when made of solid aluminum flashing (e.g., Cook et al. 2006). Therefore, it seems unlikely that fencing with such a large mesh would create an obstacle to movement for these animals.

A second potential source of bias is the refuge effect. In this case, true densities may be similar inside and outside exclosures, but salamanders and snakes in control plots may be more likely to use cover boards, perhaps because the surrounding grazed habitat is of low quality. We think this is unlikely for both red-backed salamanders and garter snakes due to their vagility (Fitch 1980, Kleeberger and Werner 1982). To rule out the refuge effect, alternative sampling methods such as transects or timed searches could be used (but see Hyde and Simons 2001).

MANAGEMENT IMPLICATIONS

We aimed to improve understanding of indirect effects keystone herbivores have on ecosystem processes. The system we studied has broad applicability, because deer overabundance is a widespread phenomenon. Our study suggests that management of deer populations (e.g., via culling, sterilization, or carnivore reintroduction) could have the unintended effect of reducing local diversity of herpetofauna and invertebrates. Therefore, we recommend that management actions involving dramatic reduction of deer herd numbers be coupled with surveys of diversity and abundance of local herpetofauna and invertebrates. Our results suggest the counterintuitive possibility that such reductions could adversely impact some populations of common amphibians, reptiles, and invertebrates. Management plans should explicitly address this possible outcome.

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