White-tailed Deer: Dispersers or Predators of American Ginseng Seeds?

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ABSTRACT.—As a result of game management practices and alterations in habitat, white-tailed deer populations (*Odocoileus virginianus* Z.) have increased to all time highs within the last century. Large herd numbers are having negative impacts at multiple levels in forest ecosystems, although there are many aspects that have not yet been investigated. One of the least understood impacts is the effect of deer browsing on the fate of valuable harvested understory species such as American ginseng (*Panax quinquefolius* L.). The objectives of this study were to quantify the natural frequency at which fruit-bearing ginseng plants are browsed by deer, to determine the amount of ginseng seeds consumed by deer and with feeding trials, to determine if white-tailed deer are seed dispersers or seed predators of American ginseng. Our results showed that fruits are frequently browsed in natural populations and that browsed seeds are most likely destroyed during the digestive process. The loss of ginseng seeds to deer browsing can negatively impact the seed bank and ultimately affect long term population growth and viability. Although white-tailed deer and American ginseng are managed species, effective growth of deer populations is adversely affecting ginseng, as well as other valuable forest species.

INTRODUCTION

The loss of large carnivores and the fragmentation of the landscape, coupled with effective game management practices, have led to a sharp increase in white-tailed deer (*Odocoileus virginianus*) populations. As keystone herbivores in the eastern deciduous forests, large deer herds can alter biotic communities within forest ecosystems (Waller and Alverson, 1997). Research on the effects of this overabundant species show that white-tailed deer are having a negative impact on multiple trophic levels of the forest community including trees and shrubs (*see* review Russell *et al.*, 2001), herbaceous plants (*see* review Miller *et al.*, 1992; Anderson, 1994; Balgooyen and Waller, 1995; Rooney and Dress, 1997; Augustine and Frelich, 1998; Rooney and Waller, 2001) and even birds (deCalesta, 1994; McShea *et al.*, 1995; McShea and Rappole, 1997) and other small mammals (Ostfeld *et al.*, 1996; Flowerdew and Ellwood, 2001). Many studies have demonstrated negative effects of deer browsing on regeneration, growth and survival of valuable tree species (Alverson *et al.*, 1988; Rooney, 2001; *see* also review Russell *et al.*, 2001). Fewer studies have assessed the impact of deer browsing on herbaceous species although those studies again have demonstrated dramatic reductions in growth, survival and abundance due to deer browsing (Anderson, 1994; Rooney and Dress, 1997; Augustine and Frelich, 1998; Rooney and Waller, 2001). The potential effects of deer on less understood plant processes like seed dispersal have rarely been studied (but *see* Welch, 1985; Dinerstein, 1989; Malo and Suarez, 1995; Gill and Beardall, 2001; Vellend *et al.*, 2003).

Large herbivores such as white-tailed deer can serve as dispersal agents in two ways. First, seeds may disperse passively as hitch-hikers attached to fur (Stiles, 1992; Chambers and MacMahon, 1994). This is probably rare for seeds surrounded by a fleshy exocarp and certainly not a major mode of dispersal for many fruit producing woodland species. Second,

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white-tailed deer may eat fruit and seeds outright as a source of autumn forage (Gee *et al.*, 1991). Fruit and seed consumption may also occur incidentally as a consequence of browsing the foliage of the plant (Chambers and MacMahon, 1994). In the latter situation, seed dispersal is the consequence of serendipitous mixing of the animal's forage with seed and subsequent fortuitous survival of the hazardous trip through the digestive process (Janzen, 1984). Regardless of whether ingestion is deliberate, if seeds survive, deer can help perform the two major functions of seed dispersal: (1) removal of seeds from the parent shadow and (2) colonization of a new, potentially better, site (Janzen, 1971). The newly deposited seed might have an environmental advantage over its undigested counterparts by being deposited in fertile fecal material (Stiles, 1992). Plants that most likely benefit from deer browsing are those plants which produce small, hard seeds that are located within close proximity to the foliage. Deer have been shown to serve as dispersal agents for many grasses as well as members of the Leguminosae, Scrophulariaceae and Amaranthaceae families (Stiles, 1992). Malo and Suarez (1995) and Welch (1985) showed that many grasses and legumes are successfully dispersed by red deer (*Cervus elaphus*) and fallow deer (*Dama dama*). Vellend *et al.* (2003) recovered viable seeds of *Trillium grandiflorum* Michx. from deer pellets.

Deer may be seed predators for some plant species. Seed predation can occur when seeds are directly destroyed during mastication or broken down in the gut during digestion. Larger seeds with soft coats are more susceptible to chewing and digestive damage. Several studies have reported evidence of seed predation by deer. Sargent (1990) noted that although the fruits of *Viburnum dentatum* L. were consumed by white-tailed deer, intact seeds were not recovered from deer pellets collected at the study sites. Dinerstein (1989) found that seeds were destroyed instead of dispersed in his examination of over 40,000 deer pellets from four Asian deer.

For rare plants that are often preferred browse species by white-tailed deer, it is important to understand the impact of deer consumption on seed fates. The focus of this study is American ginseng (*Panax quinquefolius* L.), which is considered rare due, in part, to harvesting of the root by humans for medicinal sales on the Asian market and due to loss of suitable habitat (Charron and Gagnon, 1991). American ginseng is often browsed by white-tailed deer though it is unclear how often ginseng seeds are consumed and whether seeds remain viable after being ingested. Although the timing of browse varies among years, browsing occurs late in the growing season when fruits are still present on the plants (M. A. Furedi, pers. obs.). In some wild populations in West Virginia, browsing rates are so intense that nearly all fruiting plants are defoliated. *A priori* it is not easy to predict whether ginseng seeds will successfully survive the chewing and digestive processes of deer. On the other hand, at ca. 3 mm (Lewis and Zenger, 1982), the seeds are relatively large. However, the seed coat is relatively hard and resistant at the time of dispersal, probably to protect the embryo through the 18+ mo dormancy period.

In this study we addressed three key questions regarding the role of deer as possible dispersal agents of American ginseng seeds: First, in seven wild populations, we asked what is the frequency of browsing of leaves and/or fruits of fruit-bearing plants by white-tailed deer? Second, of the plants browsed by deer, what fraction had fruits (and seeds) consumed? Third, after ingestion, what is the fate of these seeds? In summary, do deer act as dispersers or predators when consuming ginseng seeds?

STUDY SPECIES AND METHODS

Study species.—American ginseng is a long-lived, perennial herb that can live for more than 20 y once established as a seedling (Charron and Gagnon, 1991). Ginseng is found in the understory community of deciduous forests in the eastern United States and southern

TABLE 1.—The population size, number of reproductive individuals and the deer browsing rates of reproductive plants found in seven natural populations of American ginseng from 2001–2003

Population	Population size			Number of reproductive individuals			Browsing rates of reproductive plants (%)		
	2001	2002	2003	2001	2002	2003	2001	2002	2003
BG	44	64	75	22	26	22	27.3	23.1	13.6
BN	45	44	34	7	6	2	100	100	50
CR	9	6	11	1	2	0	0	100	0
P4	102	129	121	27	18	14	57.1	61.1	88.9
P5	317	365	379	51	62	73	41.1	83.9	45.2
W2	59	112	102	5	17	24	50	75	28.6
W4	26	31	28	8	4	7	60	23.5	62.5

Canada. The range of American ginseng extends from southern Quebec to northern Georgia and from the East Coast states to Missouri (Anderson *et al.*, 1993; Robbins, 1998). In the central Appalachian region, American ginseng is often associated with rich, north-facing, coves although McGraw *et al.* (2003) found that ginseng occupies a broader niche than previously thought.

The seasonal phenological progression of American ginseng begins each spring after the tree canopy has partially or fully developed (Lewis and Zenger, 1982). Plants emerge from winter dormancy in late April to early May (Hackney and McGraw, 2001). Anthesis is reached in mid-May and continues until late July. Berry development and maturation begins in late June and ends by October (Carpenter and Cottam, 1982). Fruit maturation is marked by the bright red color of the exocarp. Mature berries contain from one to three seeds (Lewis and Zenger, 1982; Anderson *et al.*, 1993).

Natural rates of deer frugivory.—In order to understand the frequency with which American ginseng seeds are ingested by white-tailed deer, we followed the fate of all fruit-bearing plants found in seven natural populations of American ginseng. The seven populations were located in north-central West Virginia in mid-successional mixed Allegheny hardwood stands dominated by oak species (*Quercus* spp.), yellow-poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marsh) and black cherry (*Prunus serotina* Ehrh.). All stands shared a common history of logging that occurred around the turn of the 20th century. The populations represented a wide range of sizes (6 to 379) in a variety of aspects (north to northwest and south to southeast) and elevations (580.4 m to 805.6 m) (Table 1). Precise locations are withheld for conservation reasons.

Beginning in May 2001, all plants within each population were located and cryptically marked with an identification number engraved on the flat head of a 6.4 cm aluminum nail. Each engraved nail was carefully placed belowground at the base of the sympodium so as not to damage the root, but to obscure the nail head from view. In the event of complete deer browsing, the identification tag could be relocated using a metal detector. New plants discovered in 2002 and 2003 were marked and added to the study. All plants were censused in mid-July to determine which plants would produce fruit. After fruiting individuals were identified, the number of seeds produced per plant was recorded. All fruiting individuals were then monitored every 3 wk to determine whether or not the plants had been browsed by deer. Damage due to deer browsing results in the partial or almost complete loss of aboveground plant biomass and is identified by the rough cut of the sympodium or petiole (Augustine and Frelich, 1998). Deer browsing sometimes results in a fraction of plant biomass being removed. In other instances, the entire plant is completely browsed,

including the fruit cluster. For plants that were deer browsed, we recorded whether or not the fruits were consumed with the foliage. If a plant was completely browsed, the area around the plant was inspected for fruits that may have fallen during the browsing episode. If no fruits or remnants of seed coats were found on the ground, we assumed that all fruits had been consumed by deer. This monitoring of all fruiting plants continued until October when most of the fruits had been dispersed and plants had begun to senesce. The natural rates of frugivory were monitored for three growing seasons, 2001–2003. From these data, we were able to determine the percentage of fruiting plants browsed by deer, the percentage of browsing resulting in loss of fruit to deer consumption and the overall percentage of seeds consumed by deer. Log-likelihood analyses were used to test for differences in deer frugivory with population and year as the main effects (SAS JMP, V.5.0, SAS, Inc., 2002). The CR population was excluded from the analyses because no data existed for 2001 and 2003 since all reproductive individuals in that population were browsed prior to fruit set in 2001 and no fruits were produced in 2003.

Feeding trials.—Since fruit production in natural populations is low, cultivated fruits were substituted for natural ones to obtain a sufficient sample size. Ripe ginseng fruits for the feeding trials were collected from 'wild simulated' plants grown by a ginseng cultivator in Preston County, West Virginia. Fruits were collected 23 August 2001 and stored at 24 C in plastic bags until their use in the feeding trials.

Feeding trials began 28 August 2001 at the West Virginia Wildlife Center located in French Creek, West Virginia. The selection of individuals to be used in the feeding trials was based on availability of resident deer at the wildlife center. Eight individuals were used for the feeding trials, four yearlings, two does and two bucks. These animals were kept in separate enclosures adjacent to a larger enclosure where the deer were normally maintained. All deer were placed in their new enclosure for 4 d prior to the start of the feeding trials to allow for acclimation to the new surroundings.

Feeding trials were conducted for a period of 3 wk. On a daily basis, fruits were fed to captive white-tailed deer by adding 100 intact fruits to their usual feed of corn and grain. During the 21 d period, a total of 16,800 fruits were fed to the deer. Those fruits not consumed from the previous day were removed and replaced with fresh ones each morning.

Along with the feeding trials, all fecal pellets were collected on a daily basis for a period of 5 wk. This provided a sufficient time period for all consumed fruit to pass through the digestive tract of each deer. After collection, all fecal pellets were dissolved in water and filtered through a #30 standard testing sieve to retain any undigested matter. The material retrieved from the sieve was then inspected for intact seeds using a dissecting microscope.

RESULTS

Natural rates of herbivory and frugivory.—The difference among populations in herbivory of reproductive plants depended on the year ($\chi^2 = 24.286$, P = 0.0069). Although the proportion of fruit-bearing plants browsed was variable among populations and years, a general pattern emerged for some populations (Table 1) (Fig. 1a). For example, the BG population had the lowest proportion of browsed fruit-bearing individuals compared to the other populations (27.3%, 23.1% and 13.6% in 2001, 2002 and 2003, respectively) and this browsing proportion decreased over the 3 y (Fig. 1a). Similarly, the BN population experienced a decrease in the proportion of fruit-bearing plants browsed in 2003 (50%) although browsing occurred at a constant and greater proportion in 2001 and 2002 (100% for both years). In contrast, the P4 population experienced a gradual increase in the proportion of browsed fruit bearing individuals during the 3-y duration of this study (Fig. 1a). Browsing of reproductive plants differed among populations ($\chi^2 = 25.491$, P < 0.0001),
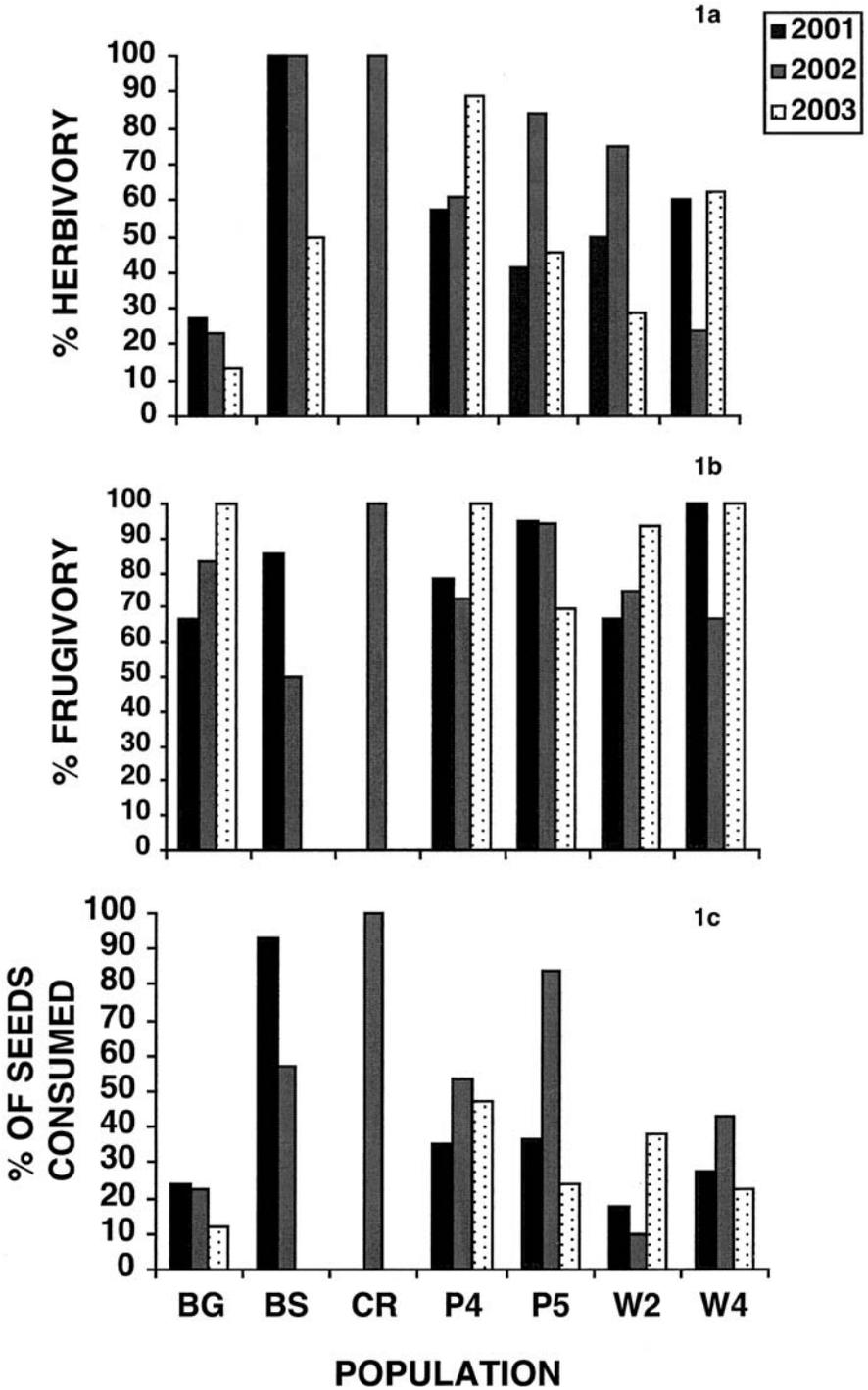
but not among years ($\chi^2 = 0.172$, P = 0.9178). During the 3-y census period, we found that the browsing frequency of fruit-bearing plants ranged from 13.6% to 100% with the exception of the CR population (Fig. 1a). In 2001 all reproductive individuals in the CR population were completely browsed prior to fruit production. In 2003 no fruits were produced.

When fruiting plants were browsed, the fruits themselves were not always consumed. Therefore, we separately analyzed the incidence of frugivory in browsed plants. Differences among populations in the proportion of browsed plants experiencing frugivory depended on the census year ($\chi^2 = 28.736$, P = 0.0014) (Fig. 1b). Both the BG and W2 populations exhibited a similar pattern of increasing frugivory in the 3 y, although the BG population experienced a greater proportion in 2002 and 2003 (83.3% and 100%, respectively) (Fig. 1b). In contrast, the P5 and BN populations both showed a decrease in frugivory as the three years progressed (Fig. 1b), and the decrease was more pronounced in the BN population. Frugivory differed significantly among populations ($\chi^2 = 21.150$, P = 0.0008), but not among years ($\chi^2 = 0.132$, P = 0.9360). We found that the proportion of fruiting plants experiencing complete deer browsing ranged from 0% where plants had been partially browsed and fruits not consumed (BN, 2003) to 100% where all fruit bearing plants were completely browsed in several populations/years (Fig. 1b).

To describe the net effect of deer browsing on seed production, we estimated the proportion of seeds (not just fruit) consumed by deer. Seed consumption patterns across years differed among populations ($\chi^2 = 83.774$, P < 0.0001). P5, P4 and W4 had comparable patterns of seed consumption over the 3 y with the greatest rate being seen in 2002 (Fig. 1c). In contrast, W2 experienced the least amount of seed consumption (10%) by deer in 2002 (Fig. 1c). Although the proportion of seeds ingested by deer did not differ among years ($\chi^2 = 2.511$, P = 0.2849), the overall rate of seed consumption did vary among populations ($\chi^2 = 80.382$, P < 0.0001). The proportion of seeds consumed by deer ranged from 0% (BN, 2003) where plants had been partially browsed but fruits remained, to 100% (CR, 2002) where all seeds were consumed by deer (Fig. 1c).

Fates of ingested seeds.—The deer used in the feeding trials consumed all of the fruits added to their daily feed. We observed that the fruits were often selectively removed from the corn and grain mixture and were consumed first. No intact seeds were recovered from the fecal pellets although one partial seed coat was identified.

Discussion

Although the frequency of browsing of fruit-bearing plants, complete consumption of all plant parts including fruits and the proportion of seeds consumed by deer varied among populations and years, this variability is not unexpected since large differences in local deer densities, vegetation and accessibility can exist from one location to the next and from one season to another. While we did not find significant differences among years, the year-to-year variation in environmental conditions such as precipitation can also influence deer browsing patterns, more so in some populations than others.

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Fig. 1.—Browsing effects in seven natural populations of American ginseng over three growing seasons, including: (a) the proportion of fruiting plants that were either partially or completely browsed by deer, (b) the proportion fruiting plants whose fruits were consumed by deer and (c) the proportion of all forming or ripe seeds that were consumed by deer

To our surprise, for a majority of the populations followed in this study, deer completely browsed 50% or more of the fruit-bearing plants. In some populations, deer consumed a substantial proportion (47.4% to 100%) of the seeds produced in that season. Although we have seen evidence that seeds can be predated upon by small rodents, we were careful to look for the remains of seed coats under plants when determining if in fact deer had consumed the seeds. For small populations with few reproductive individuals such as the CR population, consumption of even a small number of seeds can significantly decrease input into the seed bank. In 2001 the single reproductive plant in the small CR population was browsed before seed set. In 2002 the only two reproductive plants were completely browsed and in 2003, no fruits were produced. For this particular population, this means that no seeds were produced in 3 y. The results from this study not only provided clear evidence that white-tailed deer actively consume American ginseng fruit, but also have the potential to strongly impact the yearly seed rain of American ginseng. This study focused solely on those fruit-bearing plants that were browsed, but the impact on seed contribution may actually be greater than this. Reproductive plants are often browsed prior to fruit production as seen in the CR population in 2001 (Fig. 1b).

Since our data showed that white-tailed deer could consume a large majority of seeds produced in a population, it is essential to further understand seed fate after consumption. The results of the feeding trials suggest that white-tailed deer are seed predators of American ginseng, not seed dispersers. The destruction of all 16,800 seeds may have been facilitated by the mastication process deer employed while consuming the corn and grain diet. In their natural environments, depending on the season, their diet would contain more roughage, which could result in less destructive chewing of fruits. However, an inspection of deer pellets collected from each population revealed no evidence of ginseng seeds nor any other seeds successfully passing through the gut. Our findings are supported by other studies that have examined the fate of large seeds consumed by deer (Dinerstein, 1989; Sargent, 1990; but also *see* Vellend *et al.*, 2003). Thus, we feel it is reasonable to conclude that deer are primarily seed predators of American ginseng.

These results may seem illogical, given the location and coloration of ginseng fruits that suggests adaptation to animal dispersal. The fruits of American ginseng are located on an elevated peduncle at the juncture of the prongs and the sympodium, thus making them apparent to potential dispersers. The seeds of American ginseng are surrounded by a fleshy exocarp that turns bright red when the fruit is ripe. Fruit coloration is considered a primary cue to attract dispersers (Stiles, 1992) and white-tailed deer can distinguish longer wave-lengths of color such as orange and red (VerCauteren and Pipas, 2003). The color of ginseng fruits may in fact serve as a cue for potential avian and mammalian dispersers, but incidentally also attract deer, which are not effective dispersal agents. Other woodland species such as jack-in-the-pulpit (*Arisaema triphyllum* L.) and spicebush (*Lindera benzoin* L.) have bright colored fruits similar to ginseng and are dispersed and predated upon by fruit-eating birds, rodents, etc. (Bierzychudek, 1982).

The high frequency of fruit consumption by deer, coupled with the subsequent possible destruction of consumed seeds during the digestive process, can have a direct negative impact on contributions to the seed bank and ultimately the recruitment rates of American ginseng. Reduced seed bank size may be particularly important for population recovery from harvest. Lewis (1988) found that the recovery of a harvested population of American ginseng in Missouri was due mostly to an accumulation of viable seeds in the seed bank. Van der Voort *et al.* (2003) reported a similar dependence on viable propagules in the seed bank to aid in the partial recovery of a harvested West Virginia population of American ginseng. Indeed, the reduced seed bank caused by deer browsing may be adequate to explain why the

seed rain was insufficient to allow full population recovery after harvest in the populations reported by Lewis (1988) and Van der Voort *et al.* (2003). Although Charron and Gagnon (1991) found that population growth of ginseng populations was more sensitive to a decrease in the survival of plants in larger size classes than a reduction in seed production, for small populations (6 of the 7 followed in this study), loss of even a slight proportion of seeds can dramatically influence population growth. This same pattern is likely to affect other understory species' ability to recover from disturbances as well. In the early stages of deer overpopulation, the negative effects may be largely reversible: a lowering of deer populations can be expected to allow full recovery and re-establishment of the seed bank. However, once deer browsing has continued for too long, extinction of species can be expected, as resistance to other disturbances is lost. It is important for wildlife and land managers to understand these collateral costs associated with the overabundance of white-tailed deer.

LITERATURE CITED

ALVERSON, W. S., D. M. WALLER AND S. L. SOLHEIM. 1988. Forest too deer: edge effects in Northern Wisconsin. *Con. Bio.,* **2**:348–358.

ANDERSON, R. C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecol. Appl.,* **4**:104–109.

———, J. S. FRALISH, J. E. ARMSTRONG AND P. K. BENJAMIN. 1993. The ecology and biology of *Panax quinquefolium* L. (Araliaceae) in Illinois. *Am. Midl. Nat.,* **129**:357–372.

AUGUSTINE, D. J. AND L. E. FRELICH. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Con. Bio.,* **12**:995–1004.

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. *Nat. Areas J.,* **15**:308–318.

BIERZYCHUDEK, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecol. Monographs.,* **52**:335–351.

CARPENTER, S. G. AND G. COTTAM. 1982. Growth and reproduction of American ginseng (*Panax quinquefolius*) in Wisconsin, U.S.A. *Can. J. Bot.,* **60**:2692–2696.

CHAMBERS, J. C. AND J. A. MACMAHON. 1994. A day in the life of a seed: movement and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics,* **25**:263–292.

CHARRON, D. AND D. GAGNON. 1991. The demography of northern populations of *Panax quinquefolium* (American ginseng). *J. Ecol.,* **79**:431–445.

DECALESTA, D. S. 1994. Effects of white-tailed deer on songbirds within managed forests in Pennsylvania. *J. Widl. Manage.,* **58**:711–718.

DINERSTEIN, E. 1989. The foliage-as-fruit hypothesis and the feeding behavior of South Asian ungulates. *Biotropica.,* **21**:214–218.

FLOWERDEW, J. R. AND S. A. ELLWOOD. 2001. Impacts of woodland deer on small mammal ecology. *Forestry,* **74**:277–287.

GEE, K. L., M. D. PORTER, S. DEMARAIS, F. C. BRYANT AND G. VAN VREEDE. 1991. White-tailed deer: their foods and management in the cross timbers. A Samuel Roberts Noble Foundation Publication, Ardmore, Okla. 8–9 p.

GILL, R. M. A. AND V. BEARDALL. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry,* **74**:209–218.

HACKNEY, E. E. AND J. B. McGRAW. 2001. Experimental demonstration of an allee effect in American ginseng. *Con. Bio.,* **15**:129–136.

JANZEN, D. H. 1971. Escape of *Cassia grandis* beans from predators in time and space. *Ecology,* **52**:964–979.

———. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *Am. Nat.,* **123**:338–353.

LEWIS, W. H. 1988. Regrowth of a decimated population of *Panax quinquefolium* in a Missouri climax forest. *Rhodora,* **90**:1–5.

——— AND V. E. ZENGER. 1982. Population dynamics of the American ginseng *Panax quinquefolium* (Araliaceae). *Am. J. Bot.,* **69**:1483–1490.

MALO, J. E. AND F. SUAREZ. 1995. Herbivorous mammals as seed dispersers in a Mediterranean *dehesa. Oecologia,* **104**:246–255.

McGRAW, J. B., S. M. SANDERS AND M. VAN DER VOORT. 2003. Distribution and abundance of *Hydrastis canadensis* L. (Ranunculaceae) and *Panax quinquefolius* L. (Araliaceae) in the central Appalachian region. *J. Torr. Bot. Soc.,* **130**:62–69.

McSHEA, W. J., M. V. McDONALD, E. S. MORTON, M. ROSE AND J. H. RAPPOLE. 1995. Long–term trends in habitat selection by Kentucky warblers. *Auk.,* **112**:375–381.

———, AND J. H. RAPPOLE. 1997. Herbivores and the ecology of forest understory birds, p. 298–309. *In:* W. J. McShea, H. B. Underwood and J. H. Rappole (eds.). The science of overabundance: deer ecology and population management. Smithsonian Press, Washington, D.C.

MILLER, S. G., S. P. BRATTON AND J. HADIDIAN. 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. *Nat. Areas J.,* **12**:67–74.

OSTFELD, R. S., C. G. JONES AND J. O. WOLF. 1996. Of mice and mast. *Bioscience,* **46**:232–330.

ROBBINS, C. S. 1998. American ginseng: the root of North America's medicinal herb trade. TRAFFIC North America. Washington, D.C. 94 p.

ROONEY, T. P. 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry,* **74**: 201–208.

——— AND W. J. DRESS. 1997. Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old growth forest in Pennsylvania, USA. *Nat. Areas J.,* **17**:297–305.

——— AND D. M. WALLER. 2001. How experimental defoliation and leaf height affect growth and reproduction in *Trillium grandiflorum. J. Torrey Bot. Soc.,* **128**:393–399.

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. *Am. Midl. Nat.,* **146**:1–26.

SARGENT, S. 1990. Neighborhood effect on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology,* **71**:1289–1298.

SAS, INSTITUTE. 2002. JMP. Version 5.0. SAS Institute, Cary, N.C.

STILES, E. W. 1992. Animals as seed dispersers, p. 105–156 *In:* M. Fenner (ed.). Seeds: the ecology of regeneration in plant communities. Wallingford, UK. CAB.

VAN DER VOORT, M. E., B. BAILEY, D. E. SAMUEL AND J. B. McGRAW. 2003. Recovery of populations of goldenseal (*Hydrastis canadensis* L.) and American ginseng (*Panax quenquefolius* L.) following harvest. *Am. Midl. Nat.,* **149**:282–292.

VELLEND, M., J. A. MYERS, S. GARDESCU AND P. L. MARKS. 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology,* **84**:1067–1072.

VERCAUTERN, K. C. AND M. J. PIPAS. 2003. A review of color vision in white-tailed deer. *Wildlife Soc. Bul.,* **31**:684–691.

WALLER, D. M. AND W. S. ALVERSON. 1997. The white-tailed deer: a keystone herbivore. *Wildlife Soc. Bul.,* **25**:217–226.

WELCH, D. 1985. Studies in the grazing of heather moorland in north-east Scotland. IV. Seed dispersal and plant establishment in dung. *J. App. Ecol.,* **22**:461–472.