

All frugivores are not equal: exploitation competition determines seed survival and germination in a fleshy-fruited forest herb

Eric C. Niederhauser · Glenn R. Matlack

Received: 5 May 2015 / Accepted: 2 July 2015 / Published online: 21 August 2015
© Springer Science+Business Media Dordrecht 2015

Abstract Multiple-frugivore systems are common in deciduous forest communities, but multiple dispersal has rarely been examined from the perspective of plant fitness. We compare the consequences of fruit consumption by two co-occurring vertebrate frugivores (*Odocoileus virginianus*, white-tailed deer, and *Procyon lotor*, raccoon) for a fleshy-fruited forest herb (*Podophyllum peltatum*, mayapple). Shoot emergence, flowering, and fruit removal were monitored in natural populations in southeastern Ohio, USA. Survival of ingestion was tested in feeding trials. Germinability of ingested and non-ingested seeds was tested by experimental planting. Only 2.6 % of mayapple shoots flowered. All flowers appeared to initiate fruit, but 66 % aborted after 1–2 weeks. Of the fruits remaining, 82 % were removed unripe, evidently by deer. Only 5.5 % of fruit survived to ripen in mid-July at which time all were quickly removed. In feeding trials, 28 % of seeds survived ingestion by raccoons but only ca. 1 % survived ingestion by deer. Seeds hand harvested from unripe fruits had a lower proportion germinating in the following spring than those taken from ripe fruits as a result of significantly lower over-winter seed survival. Seeds ingested by

raccoons showed significantly higher germination than non-ingested seeds and were more likely to be taken by secondary dispersers. It appears raccoons have the capacity to disperse a large proportion of mayapple seeds, whereas deer are primarily seed predators. By removing unripe fruit in early summer, deer are preempting late-summer consumption by raccoons thereby reducing the net fitness benefit to the forest herb. Frugivore service appears to be additive, potentially reducing herb fitness in proportion to consumption by the inferior dispersal agent.

Keywords Deer · Frugivory · Mayapple · Raccoon · Seed dispersal

Introduction

Do forest herbs benefit from fruit consumption by multiple frugivore species? Endozoochory is common in temperate deciduous forest herbs, probably because it is well suited to dispersal of large seeds (Whigham 2004), because seeds move long distances relative to other dispersal modes (Matlack 1994a), and ingestion potentially enhances germination and establishment (Traveset et al. 2007). Most endozoochorous herb species appear to be dispersal generalists consumed by several, or perhaps many, frugivore species in a diffuse mutualistic interaction (e.g., Levey et al. 2006; Loiselle et al. 2007; Brodie et al. 2009). Feeding behaviors and patterns of defecation vary considerably

Communicated by William E. Rogers.

E. C. Niederhauser · G. R. Matlack (✉)
Department of Environmental and Plant Biology, Ohio
University, 405 Porter Hall, Athens, OH 45701, USA
e-mail: matlack@ohio.edu

among frugivore species, potentially leading to differences in seed deposition and probability of seedling establishment (Traveset et al. 2007; Schupp et al. 2010). The reproductive success of the parent plant can be viewed as the cumulative result of service provided by each of the individual frugivore species. It is unclear, however, to what extent differences in frugivore life histories and feeding habits actually translate into detectable dispersal effects because multi-vector systems have rarely been examined from the perspective of plant reproduction.

The net result of dispersal by multiple vectors may theoretically be complementary, supplementary, or subtractive relative to a single vector. Two or more frugivore species potentially complement each other by depositing seeds in different microhabitats (Thayer and Vander Wall 2005; Jordano et al. 2007; García-Robledo and Kuprewicz 2009; Amato and Estrada 2010) thereby broadening the habitat diversity experienced by seeds relative to a single frugivore species. Alternatively, frugivore contributions can be additive within the same habitat type, which may be important to plant fitness if vector density is low (e.g., Santos et al. 1999; Loiselle et al. 2007; Garcia and Martinez 2012) or fruit density is high (Herrera and Jordano 1981). It is also possible that a frugivore species providing inferior dispersal service could decrease plant fitness by denying access to a more effective dispersal vector (Jordano 1983, and see Celedon-Neghme et al. 2013). There are few published examples, however, and the relative importance of such interactions is unclear.

Ideally, a rigorous evaluation of dispersal effectiveness would consider the entire process from maturation of seeds to establishment of the vegetative plant (Schupp et al. 2010) but such a broad scope is often logistically difficult. Most studies of multiple dispersal have chosen to focus on the spatial aspects of seed movement. However, fruit removal and digestion are also relevant to dispersal effectiveness and must be considered (e.g., Valenta and Fedigan 2009; Koike et al. 2007). In this paper, we quantify the effect of fruit removal and ingestion on seed survival and germination in a fleshy-fruited forest herb, *Podophyllum peltatum* (mayapple), by two mammal species. *Odocoileus virginianus* (white-tailed deer) and *Procyon lotor* (raccoon) have substantially different feeding behaviors, digestive processes, movement patterns, and range sizes potentially affecting patterns of seed

distribution. We ask (a) how each frugivore species affects the reproductive fitness of the forest herb in terms of seed survival and germination, and (b) how their individual patterns of frugivory combine to determine fitness in a real plant community. Specifically, we ask whether they complement or detract from one another as agents of mayapple dispersal.

Methods

Mayapple phenology was monitored in Strouds Run State Park in southeastern Ohio, USA (39°21'6.39"N, 82°2'5.54"W). Natural vegetation of the region is a mixed-mesophytic deciduous forest typical of Braun's (1950) Low Hills belt. Dominant tree species include *Quercus* spp., *Carya* spp., *Acer* spp., and *Fagus grandifolia*. *Liriodendron tulipifera* is prominent in disturbed areas. Study sites were situated in long-established second-growth stands on mildly acidic sandy and silty loam soils typical of mature forest (Lucht et al. 1985). The highly dissected ridge-and-ravine topography supports a diverse understory and herb community, and robust populations of raccoons and deer.

Mayapple (*Podophyllum peltatum* L.) is a shade-tolerant perennial herb common in deciduous forests of eastern North America. In the study area, it is typically found in clusters of 10–100s of shoots in mid-slope positions. In early March, a rhizome section produces either a single peltate leaf or a sexual shoot with a flower bud in the axil of two leaves. The solitary white flowers are pollinated by various bee species in late April (Rust and Roth 1981; Laverty 1992). Developing fruits (unicarpellate berries) are green and odorless with a hard white mesocarp. Upon ripening in mid-summer, the color changes to yellow over the course of 2–3 days with a noticeable odor and a marked softening of the mesocarp. Fruit are globular with a mean diameter of ca. 3 cm and 19 seeds/fruit (± 13 SD, $n = 74$ fruits). Mature seeds weigh 37.5 mg (± 8.3 SD, $n = 110$ seeds). Both raccoons and deer have been observed removing mayapple fruits in the study area (Philhower and Matlack in preparation) and, hence, are potential dispersal agents. Eastern box turtles (*Terrapene Carolina*) have been reported to disperse mayapple seeds elsewhere in the eastern United States (Rust and Roth 1981; Braun and Brooks 1987) and are common in the study area.

Raccoons (*Procyon lotor* L.) are medium-sized (5–7 kg) omnivorous mammals with a home range of 40–100 ha, implying a maximum movement distance of 700–1100 m (Lotze and Anderson 1979; Ghert 2003). Consistent with a broadly diversified diet, raccoons have a dental index of 3.1.4.2 with relatively few and narrow molars (Zevloff 2002). They have a simple stomach, no cecum, and non-complex colons. Ingested material is retained in the gut for ca. 24 h (Clemens and Stevens 1979). Raccoons are known to disperse a variety of tree and shrub species by ingestion and defecation of seeds (Willson 1993; Cypher and Cypher 1999; LoGiudice and Ostfeld 2002).

White-tailed deer (*Odocoileus virginianus*, Zimmerman) are large cervids (40–100 kg) common in forests across eastern North America. White-tailed deer (hereafter “deer”) are generalist herbivores known to disperse many plant species including several deciduous-forest herbs (Vellend et al. 2003; Myers et al. 2004; Williams et al. 2008; Blyth et al. 2013). As ruminants, they have large well-developed molars and a four-chamber stomach. Ingested food is fermented and re-chewed to reduce structural carbohydrates (Ditchkoff 2011). Multi-stage food processing results in fine shredding of ingested foliage with gut retention times of up to 64 h (Mautz and Petrides 1971; Ditchkoff 2011). Deer are highly mobile with ranges as large as 3.2 km in diameter (Walter et al. 2009).

Phenology

To place mayapple reproduction and fruit removal in a seasonal context, clonal shoots were monitored through the growing season. In March 2010, seven 3 × 3 meter plots were established within mayapple colonies just after the beginning of shoot emergence. Plots were positioned to include ca. 100 stems apiece and situated at least 500 m apart to ensure independence. All plots were at least 50 m from a forest margin to avoid edge effects (Matlack 1994b). Anthesis, fruit initiation, spontaneous abortion, and fruit removal were recorded weekly from early March through senescence of the last shoot in mid-August. Only a small proportion of stems actually produced flowers in 2010. To allow closer examination of reproductive behavior, fifty-six sexual shoots were specifically selected for monitoring in March 2011.

Shoots were selected as available in and near the 3 × 3 meter plots used in the previous year.

Gut passage and germination

In July 2010, we fed wild-collected fruits to captive white-tailed deer and raccoons to examine gut passage. All applicable institutional and national guidelines for the care and use of animals were followed. In all cases, the scale of the trials was limited by the number of seeds and fruits available in local populations. A two-year-old doe was fed ten ripe mayapple fruits. Because fully developed fruit sometimes contain no seeds, each fruit was cut beforehand to verify the presence of seeds. Assuming 19 seeds per fruit, the deer was fed ca. 190 seeds. The deer’s enclosure was cleared of fecal pellets prior to feeding and all pellets were collected for 72 h after feeding, a period chosen to ensure complete gut passage. Pellets were gently mashed and washed through a sieve to recover seeds. Because only a small number of seeds were recovered, seeds were not systematically tested for germination.

Each of five captive raccoons was fed two ripe fruits, equivalent to a total of ca. 190 seeds. Feces were collected for 30 h after feeding and washed through a sieve to recover seeds. Seed germination after gut passage was compared to germination of non-ingested ripe seeds and seeds from unripe fruits harvested 3–4 weeks earlier. Seeds from unripe fruit showed the same firmness, moisture, and size as ripe seeds; we assume they were live embryos at an earlier developmental stage. To test germination, seeds were sown in flats of potting soil mixed with sand and a small amount of forest soil. Flats were kept outdoors over winter and covered with 50 % shade cloth to simulate natural light conditions. Seeds were checked weekly for appearance of seedlings and watered as needed to stay imbibed.

The numbers of ingested and non-ingested seeds surviving to spring 2011 were compared using a Chi-square test with the null hypothesis that ingestion and survival were independent. Similarly, non-ingested ripe and unripe seeds were compared on the basis of survival to spring 2011, and ripe and unripe germination was compared in surviving seeds.

A second germination trial was begun in 2011 because many seeds sown in 2010 appeared to have been removed by small animals. Six raccoons were fed 16 ripe fruits equivalent to ca. 304 seeds. Recovered

seeds were sown outdoors in flats caged with wire mesh to prevent seed removal. To examine the effects of ingestion, non-ingested ripe seeds were sown in the same flats. As before, the interaction of ingestion and survival over winter was assessed by a Chi-square test. Among surviving seeds, the interaction of ingestion condition (ingested or non-ingested) and germination was similarly tested.

Results

Mayapple shoots emerged rapidly in late March and early April (Fig. 1). Most vegetative shoots were present for 6–8 weeks and then senesced over a period of ca. 4 weeks in June. Sexual shoots and a small number of vegetative shoots remained green until early August. In 2010, only fifteen (2.6 %) of the 593 shoots produced flowers in our plots. Flowers opened in early May and fruit was initiated in all sexual shoots 1–2 weeks later (Fig. 1). However, seven fruits (47 %) were aborted (indicated by drying, shriveling, and browning) within 2 weeks of anthesis (Fig. 2a). Five developing fruits were removed before June 17 while still hard and green. The three remaining fruit were removed upon ripening at the end of July and early August leaving a 10- to 20-cm stem.

In 2011, fruit abortion was again concentrated in the first two weeks but continued at low levels until July 19, nine weeks after anthesis (Fig. 2b). Only 14 fruits (25 %) continued development and 13 of these

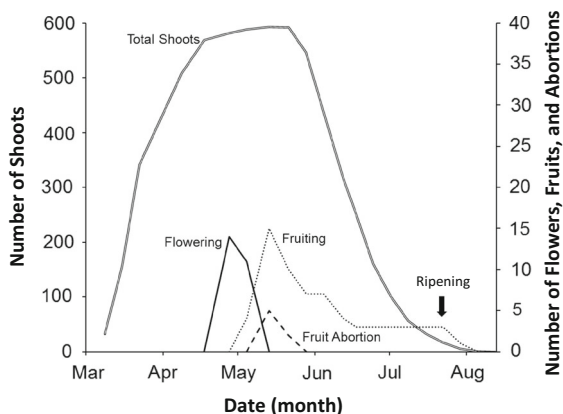


Fig. 1 Phenology of mayapple (*Podophyllum peltatum*) at seven forested sites in southeastern Ohio in 2010. A maximum of 593 total shoots were recorded in mid-May. The numbers of sexual shoots are shown on the right-hand axis for clarity

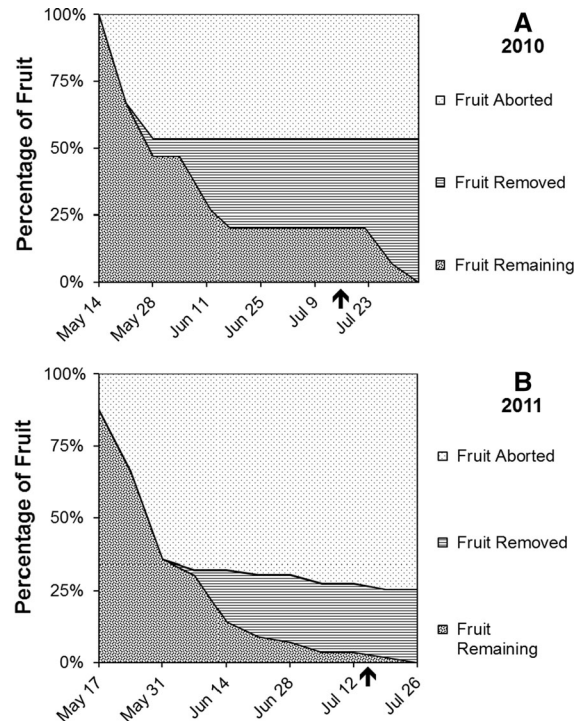


Fig. 2 Fate of mayapple fruit through the fruiting season at plots in southeast Ohio ($N = 15$ fruit) and in 2011 (56 fruit). Chart begins on the date of peak fruit number. In 2011, seven fruit aborted before the peak at May 17 and, so, are not shown here. Arrows indicate the approximate beginning of fruit ripening

were eaten unripe in June or the first week of July. In June, fruit removal was accompanied by loss of leaves, clipping of the stem at 10–20 cm, and removal of many surrounding vegetative shoots, suggesting deer grazing. The single remaining fruit ripened and was quickly removed at the end of July, leaving an erect 10- to 20-cm stem. Of all sexual shoots encountered in 2010 and 2011, 65.6 % failed to produce fruit due to abortion and only 5.5 % of fruit eventually ripened.

Ingested seeds

Only two seeds were recovered from the 10 fruits fed to the deer, representing ca. 1 % of ingested seeds. Both seeds were excreted between 24 and 48 h after consumption. The two seeds recovered both appeared to be viable, remaining firm, moist, light-brown, and free from fungi (indeed, one of the seeds germinated in the lab). However, the small sample size prevented systematic testing of germination.

In the 2010 feeding trial, 53 seeds (ca. 28 % of seeds ingested) were recovered from the five raccoons, all within 30 h of consumption. In the germination trial many seeds decayed, were eaten by slugs or millipedes, or simply disappeared within the first few months (Table 1a). No raccoon-ingested seeds survived to the spring of 2011. In contrast to ingested seeds, 61 % of non-ingested ripe seeds survived, showing a strongly significant ingestion \times survival interaction ($\chi^2 = 10.75$, 1 df, $P = 0.001$). Failure to survive was largely caused by the high rate of disappearance of ingested seeds (63 %) relative to non-ingested ripe seeds (22 %). In contrast to disappearance, similar proportions of raccoon-ingested seeds (12.5 %) and ripe non-ingested seeds (10.2 %) decayed.

Sufficient non-ingested seeds survived to compare seeds from ripe and unripe fruit (Table 1a). Ripe seeds were more likely to survive until spring than unripe seeds ($\chi^2 = 11.64$, 1 df, $P = 0.001$), primarily due to the higher rate of decay of unripe seeds (36.5 and 10.2 % decayed; $\chi^2 = 9.55$, 1 df, $P = 0.002$). Germination of surviving seeds was independent of fruit ripeness ($\chi^2 = 1.19$, 1 df, $P = 0.28$). Six ripe seeds survived an additional year and germinated in 2012, bringing the total germination of hand-harvested ripe seeds to 40.7 %. In contrast, only 13.5 % of unripe seeds eventually germinated and none germinated in 2012.

In the 2011 feeding trial, 83 seeds were recovered from raccoon feces, representing 27 % of seeds ingested. Recovered ingested seeds were sown beside ripe non-ingested seeds in the wire cages. As in 2010, many seeds appeared to have been eaten or decayed, but no seeds disappeared (Table 1b). Ingestion of seeds and survival to spring 2012 were independent ($\chi^2 = 0.18$, 1 df, $P = 0.67$) with little difference in proportional survival. However, germination of surviving raccoon-ingested seeds was significantly higher (100 %) than surviving non-ingested seeds (61 %; $\chi^2 = 11.3$, 1 df, $P = 0.0007$).

Discussion

Development of mayapple in our plots was similar to other early-spring perennials such as *Hydrastis canadensis* L. (Eichenberger and Parker 1976) and *Trillium* spp. (Lubbers and Lechowicz 1989; Sage et al. 2001) in which stored reserves are used to promote rapid leaf expansion, and flowers open shortly thereafter. The peak in mayapple shoot number and the beginning of fruit expansion roughly corresponded to canopy closure in mid-May. After canopy closure, fruit development continued through the summer supported by stored resources and a portion of current assimilate (Kudo et al. 2008).

Table 1 Fate of mayapple seeds ingested by raccoon and non-ingested seeds collected from ripe and unripe fruit

A. 2010 Trial	Total seeds sown Aug 2010	Seeds eaten, missing, decayed	Seeds surviving Feb 2011	Germinated Feb 2011 (% of surviving)	Surviving Fall 2011	Germinated Apr 2012
Raccoon ingested	24	6, 15, 3	0	0	0	0
Ripe fruit non-ingested	59	4, 13, 6	36 (61 %)	18 (50 %)	12	6
Unripe fruit non-ingested	52	7, 12, 19	14 (27 %)	7 (50 %)	7	0
B. 2011 Trial	Total seeds sown Aug 2011		Seeds surviving Apr 2012	Germinated Apr 2012 (% of surviving)	Surviving Fall 2012	Germinated Apr 2013
Raccoon-Ingsted	83	–	26 (31 %)	26 (100 %)	0	–
Ripe fruit non-ingested	125	–	44 (35 %)	27 (61 %)	0	–

A. Seeds sown in 2010 (not caged)

B. Seeds sown in 2011 (caged)

In 2011 no seeds were missing, and seed decay and predation were not differentiated

Infrequent flowering and low fruit set observed here may reflect the expense of reproduction in the low-light forest environment (Rust and Roth 1981; Sohn and Policansky 1977). Alternatively, reproduction is often pollen-limited in mayapple (Swanson and Sohmer 1976; Crants 2008), potentially causing the high level of abortion observed in our plots. A similar survey in southeastern Kentucky found 63 % of sexual shoots produced no fruit (Krochmal et al. 1974) possibly due to inadequate pollination (Stephenson 1981). Consistent with our observations, studies in Wisconsin and Indiana reported only ca. 3 % of mayapple shoots flowering and fewer than 10 % of flowers producing fruit (Swanson and Sohmer 1976; Geber et al. 1997). The infrequency and inferred expense of seed set suggests that the fitness cost of inappropriate dispersal is quite high.

Frugivory

Of those fruits not aborted, most (82 %) were removed in June while still unripe. Intensive grazing associated with June fruit removal suggests that unripe fruits were removed by deer, consistent with a previous photo-monitoring study which showed deer grazing of mayapple narrowly concentrated in June (Philhower and Matlack, unpublished). Unripe seeds were less likely to survive over winter than ripe seeds and less likely to germinate in the third year. Thus, early removal by deer is probably of little dispersal value to the plant because it results in distribution of low-viability seeds.

Ripe mayapple seeds were destroyed in the digestive process by both raccoons and deer, but deer caused a much greater reduction in seed numbers. Deer also consume a co-occurring forest herb *Panax quinquefolius* L. (American ginseng), apparently ingesting the relatively large seeds as they graze the foliage. No viable seeds were recovered from 16,800 deer-consumed fruits (Furedi and McGraw 2004), consistent with our observation of seed destruction in mayapple. Indeed, the captive deer used in this study was also fed corn to supplement herbaceous forage available during the feeding trial. Only a few recognizable corn kernels were identified in 3 days' worth of feces, indicating the food processing efficiency of the deer. Paradoxically, many species have been observed to survive deer digestion at sites in western New York, southern Connecticut, and central Ohio

(Myers et al. 2004; Williams et al. 2008; Blyth et al. 2013). However, these are almost entirely small, hard-coated species typical of open habitats. The degree of seed destruction appears to depend on seed size and exocarp hardness (Vellend et al. 2003) suggesting that many forest herb species cannot be dispersed by deer because their seeds are too large and/or soft to survive gut passage. It is worth noting that two viable seeds were recovered from fecal pellets in our feeding trial so occasional dispersal cannot be ruled out. With long gut-retention times and movement distances measured in kilometers, deer may potentially move seeds long distances (Vellend et al. 2003) with demographic consequences out of proportion to the low dispersal frequency (Neubert and Caswell 2000).

We assume the late-removed fruits were consumed by raccoons. Camera-trap data show that raccoons ignore unripe mayapple fruits early in the summer but quickly consume fruits when they ripen in late July (Philhower and Matlack, unpublished) possibly cued by odor. Removal of fruits 10–20 cm above the ground is inconsistent with turtle activity, but easily achieved by raccoons. Although raccoons destroyed most seeds in the feeding trials, a substantial number survived ingestion potentially allowing dispersal. Ingestion may actually improve fitness of surviving seeds. Those defecated by raccoons germinated at a higher rate than un-ingested seeds in the 2011 trial, perhaps due to the removal of a germination inhibitor (Krochmal et al. 1974; Cypher and Cypher 1999). Loss of raccoon-ingested seeds from uncaged sowing sites was higher than non-ingested seeds, apparently due to removal of seeds by small vertebrates. If raccoon ingestion makes seeds more attractive to cache-forming seed predators, the benefits of secondary dispersal may also increase fitness of ingested seeds (LoGiudice and Ostfeld 2002; Niederhauser and Matlack, unpublished). In contrast to deer, consumption by raccoons appears to have several benefits for the mayapple notwithstanding the destruction of a portion of seeds in digestion.

Other studies report that box turtles commonly consume mayapple fruits, passing a higher proportion of viable seeds than raccoons and leading to greater germination (Rust and Roth 1981; Braun and Brooks 1987). We found no direct evidence of turtle frugivory (nor did Philhower and Matlack, unpublished), but the abundance of turtles in the study area suggests that they contribute at least occasionally to dispersal.

Cumulative fitness effects

Multiple frugivory appears to have a negative effect on the dispersal component of mayapple fitness in our study area. Raccoons discovered 100 % of ripe fruits but only 28 % of seeds survived gut passage implying a 72 % reduction in reproductive fitness at the dispersal stage. Assuming a hypothetical clone produced ten ripe fruits, raccoon frugivory would result in ca. 53 seedlings. In a second scenario, only deer consume mayapple fruits. In contrast to raccoons only ca. 1 % of deer-ingested seeds survived digestion (these are likely to be low-quality seeds collected before maturity) but they failed to find 18 % of fruits, with a net result of 82 % reduction in reproductive fitness. Thus, in the case of deer frugivory the hypothetical clone could potentially produce ca. 34 seedlings. However, the surviving 18 % of fruits would not be dispersed and seedlings would potentially experience some form of compensatory mortality at high density around the parent plants (Giladi 2006). Thus, the realized number of seedlings would probably be much less than the 34 seeds which escaped deer predation.

In a third scenario, more realistically corresponding to observations in the field, the fruits surviving deer predation are subsequently discovered and consumed by raccoons, compounding the fitness reduction. Of the 18 % escaping deer predation, seed number would be reduced a further 72 % by raccoons resulting in a cumulative 5 % survival of seeds, equivalent to ca. 10 seedlings in the hypothetical clone. Comparison of the hypothetical seedling numbers suggests that deer predation reduces mayapple reproductive fitness by preventing raccoon (and possibly turtle) dispersal. Complementary or supplementary interactions are precluded by the near-complete destruction of seeds by deer.

Preemption of raccoon frugivory in late summer is a form of exploitation competition in which deer dominate by virtue of earlier fruit consumption. The situation is analogous to the classic study of *Ficus*-consuming parrots in lowland Costa Rica (Jordano 1983), in which competitive dominance was expressed as greater numerical abundance of the inferior dispersal agent (see also Amato and Estrada 2010). The contrast between deer and raccoon dispersal is particularly important to mayapple fitness because successful fruit set is relatively uncommon (only 2.6 % of shoots reproduced in 2010 and 66 % of these were lost

to spontaneous abortion). If reproduction is limited by slow accumulation of resources at the forest floor (Whigham 2004) loss of even a small number of seeds to inappropriate frugivores may substantially reduce reproductive success on a scale of years or decades.

Conclusion

The negative effects demonstrated here are probably common in the deciduous forest community because multiple frugivory is common among forest herbs, and individual frugivore species differ in the character of seed and fruit processing (e.g., Bonaccorso et al. 2006; Brodie et al. 2009). On an evolutionary time scale, variation in dispersal-vector quality potentially exerts selective pressure for fruit traits that specifically attract beneficial frugivores and avoid less helpful species. In the short term, white-tailed deer populations are currently at historically high levels within the range of mayapple (Iverson and Iverson 1999; Côté et al. 2004), suggesting unprecedented pressure on mayapple reproduction and perhaps reproduction of other species as well. The potential damage to forest herb populations provides an additional reason for controlling white-tailed deer.

Acknowledgments We thank Susan Shibley of Forever-Wild Wildlife Rehabilitation Center, and Leland Green of Green Family White-Tails for their generous assistance in the feeding trials. Two anonymous reviewers made helpful comments on the manuscript. Thank you!

References

- Amato KR, Estrada A (2010) Seed dispersal patterns in two closely related howler monkey species (*Alouatta palliata* and *A. pigra*): a preliminary report of differences in fruit consumption, travelling behavior, and associated dung beetle assemblages. *Neotrop Primates* 17:59–66
- Blyth LH, Ouborg LJ, Johnson DM, Anderson LJ (2013) The short-term germination and establishment success of deer-dispersed seeds in mesic temperate forests. *J Torrey Bot Soc* 140:334–348
- Bonaccorso FJ et al (2006) Evidence for exploitative competition: comparative foraging behavior and roosting ecology of short-tailed fruit bats (Phyllostomidae). *Biotropica* 39:249–256
- Braun EL (1950) *Deciduous forests of Eastern North America*. The Blackburn Press, Caldwell
- Braun J, Brooks GR (1987) Box turtles (*Terrapene carolina*) as potential agents for seed dispersal. *Am Midl Nat* 117: 312–318

- Brodie JF, Helmy OH, Brockelman WY, Maron JL (2009) Functional differences within a guild of tropical mammalian frugivores. *Ecology* 90:688–698
- Celedon-Neghme C, Traveset A, Calvino-Cancela M (2013) Contrasting patterns of seed dispersal between alien mammals and native lizards in a declining plant species. *Plant Ecol* 214:657–667
- Clemens ET, Stevens CE (1979) Sites of organic acid production and patterns of digesta movement in the gastro-intestinal tract of the raccoon. *J Nutr* 109:1110
- Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. *Annu Rev Ecol Evol Syst* 35:113–147
- Crants JE (2008) Pollination and pollen limitation in mayapple (*Podophyllum peltatum* L.), a nectarless spring ephemeral. Ph.D. thesis, Department of Ecology and Evolutionary Biology, University of Michigan
- Cypher BL, Cypher EA (1999) Germination Rates of Tree Seeds Ingested by Coyotes and Raccoons. *Am Midl Nat* 142:71–76
- Ditchkoff SS (2011) Anatomy and physiology pp. In: Hewitt DG (ed) *Biology and management of white-tailed deer*. Taylor and Francis Group, Boca Raton, pp 43–73
- Eichenberger MD, Parker GR (1976) Goldenseal (*Hydrastis Canadensis* L.) distribution, phenology and biomass in an oak-hickory forest. Ohio Academy of Science
- Furedi MA, McGraw JB (2004) White-tailed deer: dispersers or predators of American ginseng seeds? *Am Midl Nat* 152:268–276
- Garcia D, Martinez D (2012) Species richness matters for quality of ecosystem services: a test using seed dispersal by frugivorous birds. *Proc R Soc B* 279:3106–3113
- García-Robledo C, Kuprewicz EK (2009) Vertebrate fruit removal and ant seed dispersal in the neotropical ginger *Renealmia alpinia* (Zingiberaceae). *Biotropica* 41:209–214
- Geber MA, De Kroon H, Watson MA (1997) Organ preformation in mayapple as a mechanism for historical effects on demography. *J Ecol* 85:211–223
- Ghert SD (2003) Raccoon (*Procyon lotor* and allies) pp. In: Feldhamer GA, Thompson BC, Chapman JA (eds) *Wild mammals of North America*. Johns Hopkins University Press, Baltimore, pp 611–634
- Giladi I (2006) Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos* 112:481–492
- Herrera CM, Jordano P (1981) *Prunus mahaleb* and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. *Ecol Monogr* 51:203–218
- Iverson AL, Iverson LR (1999) Spatial and temporal trends of deer harvest and deer-vehicle accidents in Ohio. *Ohio J Sci* 99(4):84–94
- Jordano P (1983) Fig-seed predation and dispersal by birds. *Biotropica* 15:38–41
- Jordano P, García C, Godoy JA, García-Castaño JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proc Natl Acad Sci* 104:3278–3282
- Koike S, Kasai S, Yamazaki K, Furubayashi K (2007) Fruit phenology of *Prunus jamasakura* and the feeding habit of the Asiatic black bear as a seed disperser. *Ecol Res* 23:385–392
- Krochmal A, Wilkins L, Van Lear D, Chien M (1974) Mayapple (*Podophyllum peltatum* L.). USDA Forest Service NE-296
- Kudo G, Ida TY, Tani T (2008) Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. *Ecology* 89:321–331
- Lavery TM (1992) Plant interactions for pollinator visits: a test of the magnet species effect. *Oecologia* 89:502–508
- Levey DJ, Tewksbury JJ, Cipollini ML, Carlo TA (2006) A field test of the directed deterrence hypothesis in two species of wild chili. *Oecologia* 150:61–68
- LoGiudice K, Ostfeld RS (2002) Interactions between mammals and trees: predation on mammal-dispersed seeds and the effect of ambient food. *Oecologia* 130:420–425
- Loiselle BA, Blendinger PG, Blake JG, Ryder TB (2007) Ecological redundancy in seed dispersal systems: a comparison between manakins (Aves: Pipridae) in two tropical forests. In: Dennis AJ, Green RJ, Westcott DA (eds) *Seed Dispersal: Theory and its Application in a Changing World*. CAB International, Cambridge, pp 178–195
- Lotze JH, Anderson S (1979) *Procyon lotor*. Mammalian Species:1–8
- Lubbers AE, Lechowicz MJ (1989) Effects of leaf removal on reproductions vs Belowground storage in *Trillium Grandiflorum*. *Ecology* 70:85–96
- Lucht TE, Anderson KM, Brown DL, Martin NH (1985) Soil Survey of Athens County Ohio. Soil Conservation Service, US Department of Agriculture, Government Printing Office, Washington DC
- Matlack GR (1994a) Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75:1491–1502
- Matlack GR (1994b) Vegetation dynamics of the forest edge—trends in space and successional time. *J Ecol* 82:113–123
- Mautz WW, Petrides GA (1971) Food passage rate in the white-tailed deer. *J Wildl Manag* 35:723
- Myers JA, Vellend M, Gardescu S, Marks PL (2004) Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139:35–44
- Neubert MG, Caswell H (2000) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81:1613–1628
- Rust RW, Roth RR (1981) Seed production and seedling establishment in the mayapple *Podophyllum peltatum* L. *Am Midl Nat* 105:51
- Sage TL, Griffin SR, Pontieri V, Drobac P, Cole WW, Barrett SC (2001) Stigmatic self-incompatibility and mating patterns in *Trillium grandiflorum* and *T. erectum* (Melanthiaceae). *Ann Bot* 88:829–841
- Santos T, Tellería JL, Virgós E (1999) Dispersal of Spanish juniper *Juniperus thurifera* by birds and mammals in a fragmented landscape. *Ecography* 22:193–204
- Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytol* 188:333–353
- Sohn J, Policansky D (1977) The Costs of Reproduction in the Mayapple *Podophyllum peltatum* Berberidaceae. *Ecology* 58:1366–1374
- Stephenson AG (1981) Flower and fruit abortion: proximate causes and ultimate functions. *Annu Rev Ecol Syst* 12:253–279

- Swanson SD, Sohmer SH (1976) The biology of *Podophyllum peltatum* L. (Berberidaceae), the may apple II The transfer of pollen and success of sexual reproduction. Bull Torrey Bot Club 103:223–226
- Thayer TC, Vander Wall SB (2005) Interactions between Steller's jays and yellow pine chipmunks over scatter-hoarded sugar pine seeds. J Anim Ecol 74:365–374
- Traveset A, Robertson AW, Rodríguez-Pérez J (2007) A review on the role of endozoochory on seed germination. In: Dennis AJ, Schupp EW, Green RJ, Westcott DA (eds) Seed dispersal: Theory and its application in a changing world CABI Publishing, Wallingford, UK, pp 78–103
- Valenta K, Fedigan LM (2009) Effects of gut passage, feces, and seed handling on latency and rate of germination in seeds consumed by capuchins (*Cebus capucinus*). Am J Phys Anthropol 138:486–492
- Vellend M, Myers JA, Gardescu S, Marks P (2003) Dispersal of trillium seeds by deer: implications for long-distance migration of forest herbs. Ecology 84:1067–1072
- Walter WD et al (2009) Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. Landsc Ecol 24:1405–1420
- Whigham DF (2004) Ecology of woodland herbs in temperate deciduous forests. Annu Rev Ecol Evol Syst 35:583–621
- Williams SC, Ward JS, Ramakrishnan U (2008) Endozoochory by white-tailed deer (*Odocoileus virginianus*) across a suburban/woodland interface. For Ecol Manag 255:940–947
- Willson MF (1993) Mammals as seed-dispersal mutualists in North America. Oikos 67:159–176
- Zeveloff SI (2002) Raccoons. A Natural History. Smithsonian Institution Press, Washington DC