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Interactions between mammals and trees: predation on mammal-dispersed seeds and the effect of ambient food

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Abstract The Janzen-Connell escape hypothesis predicts that the success of tree propagules increases with distance from the parent tree. Fleshy fruits that are transported in the guts of frugivores are believed to have evolved to facilitate the wide dispersal of seeds. However, some frugivores deposit seeds in latrines, thus creating aggregations of seeds that are large enough to attract seed predators and negate the advantages of dispersal. Raccoons (*Procyon lotor*) often produce large seed deposits since they habitually defecate in latrines. The survival of wild black cherry (*Prunus serotina*) seeds in simulated raccoon latrines was monitored in areas with natural levels of food availability and in areas to which supplemental food had been supplied to the primary seed predators. Dispersal of seeds by raccoons did not necessarily provide effective protection from post-dispersal seed predation at natural food levels. Once the resident seed predators had located the latrines, the majority of the seeds were quickly removed. However, seed removal from raccoon latrines was reduced significantly and dramatically by the addition of alternative food. This implies that raccoon latrines may represent safe sites for tree recruitment during periods of high food availability such as during masting events, thus providing conditional support for the escape hypothesis.

Keywords Escape hypothesis · Frugivory · Granivory · *Procyon lotor* · Seed predation

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Introduction

Patterns of recruitment by forest trees are strongly influenced by the distribution of natural enemies of seeds and seedlings. In both tropical and temperate forests, predators and pathogens of tree seeds and seedlings tend to concentrate near parent trees, resulting in high mortality and low recruitment of tree propagules that fail to disperse (Augsburger 1983; De Steven and Putz 1984; Howe et al. 1985; Packer and Clay 2000). This pattern is consistent with the predictions of the escape hypothesis (Janzen 1970; Connell 1971) which states that the success of tree propagules should increase with distance from the parent. The evolution of fleshy fruits by forest trees is widely considered an adaptation to attract vertebrate frugivores that will disperse seeds away from parent trees, to sites where survival is more likely (Howe and Smallwood 1982; Crawley 1983; Fenner 1985; Tamboia et al. 1996). In particular, large frugivorous mammals can facilitate tree recruitment via scarification of seed coats in the digestive tract, dispersal of seeds away from concentrations of natural enemies, and provision of fertilizer in fecal deposits (Traveset and Willson 1997; Manson et al. 1998; Cypher and Cypher 1999).

Small granivorous mammals are capable of strongly inhibiting seed survival and tree recruitment in both temperate and tropical forests (Whelan et al. 1991; Forget 1993; Ostfeld et al. 1997; Hulme and Borelli 1999). Small mammals are often attracted to concentrations of seeds and in some cases exhibit their highest attack rates where seeds are most concentrated, such as under the canopies of parent trees (Howe et al. 1985; Manson et al. 1998). Consequently, seed dispersal by large mammalian frugivores may function to reduce the inhibitory effects of small mammalian granivores by redistributing seeds away from parent trees. However, some frugivorous mammals habitually defecate in localized sites, called latrines, resulting in secondary concentrations of seeds. The net effect of frugivorous seed dispersers on seed survival and tree recruitment may thus depend on the de-

gree to which deposition of seeds in feces results in escape from, versus attraction of, seed predators.

Temperate forest mammals are known to consume large numbers of fruits of such canopy and understory trees as *Prunus* (cherry), *Cornus* (dogwood), and *Viburnum*, as well as the fruits of shrubs and vines such as *Rubus* and *Vitis* species; however, their role as seed dispersers has not been well studied. This study investigates the survival of raccoon dispersed seeds of wild black cherry, *Prunus serotina*, a widespread native in eastern deciduous forests of the United States. Although *P. serotina* is often described as bird-dispersed, its fruits are consumed in great numbers by omnivorous mammals such as raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), coyotes (*Canis latrans*) and black bears (*Ursus americana*) (Whitaker and Hamilton 1998), and these animals may serve as important seed dispersers. Raccoons in particular are known to habitually defecate in latrines (Giles 1939, 1940; Page et al. 1998, 1999), which may create a potential food resource for seed predators that is predictable in space and time.

One possible, and as yet unmeasured, factor affecting the behavior of seed predators is the availability of alternative and possibly more attractive foods. Small mammals are known to be selective in the foods that they consume (Jensen 1993; Hulme 1994; Hadj-Chikh et al. 1996; Manson and Stiles 1998). Thus, post-dispersal seed survival could be strongly influenced by the availability of other more desirable or more accessible foods. In the forests and old-fields of eastern North America, the dominant seed predator is the white-footed mouse, *Peromyscus leucopus* (Myster and Pickett 1993; Ostfeld et al. 1997; Manson and Stiles 1998). White-footed mice are known to forage in raccoon latrines (Page et al. 1999, 2001a; LoGiudice 2001) and consume *P. serotina* seeds (Whitaker and Hamilton 1998). In a series of experiments, Janzen (1971, 1982a, 1982b) showed that some small mammals actively seek out fecal piles as possible seed sources. However, *P. leucopus* avoid seeds embedded in raccoon feces when clean seeds or seeds embedded in other substrates are available (Bermejo et al. 1998; LoGiudice 2001). This observation implies that seed dispersal by frugivores may be advantageous despite the build-up of relatively large concentrations of seeds. This study investigates the role of raccoon latrines as possible safe sites for tree seeds and looks at seed removal from the latrines at two levels of ambient food availability. Our primary goal was to understand the conditions under which seeds deposited by frugivores in secondary concentrations, such as latrines, would have a high probability of escaping predation by seed consumers.

Materials and methods

Study sites

This research was conducted in March and April of two consecutive years. In 1998, the work was conducted in the Hutchinson Memorial Forest and Kilmer Preserve, field stations of Rutgers

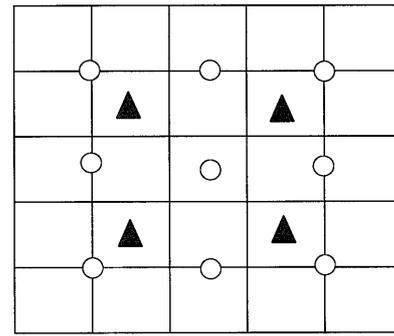


Fig. 1 Layout of trapping grids. *Triangles* represent simulated raccoon latrines, *circles* represent feeders (food addition grids only). Each intersection is a trapping station (10 m spacing)

University in central New Jersey and in 1999 on the grounds of the Institute of Ecosystem Studies in southeastern New York. Late winter/early spring was chosen because it is generally a season of low food availability for small mammals, so the effects of food addition are likely to be most readily observed. Thus, if seed predators eschew raccoon latrines during a season with so few alternative foods, it is likely that the response will be similar, or even magnified, during a natural masting event since these occur at times when there may be many alternative foods available.

In 1998, 12 trapping grids of 0.25 ha were established in mature forest (8 grids in Hutchinson Memorial Forest and 4 in Kilmer Preserve) in a 6×6 array of traps with 10 m spacing. In 1999, 3 pairs of grids were established with identical spacing dimensions in the Institute of Ecosystem Studies. All grids were separated by at least 100 m to insure that there was no regular crossover of mice from one grid to another. During the course of the experiments there was little or no snow cover on the grids during either year.

Simulated raccoon latrines

Within every trapping grid, four simulated latrines were created (Fig. 1), each consisting of two raccoon scats. This is equal to a latrine density of 16 per hectare, and is consistent with densities observed in the wild (Page et al. 2001b). Simulated latrines were placed within 3 m of the grid locations on downed logs, tree bases or stumps and other areas typical of raccoon latrines (Page et al. 1998). Raccoon feces used in these experiments were collected from a captive raccoon that was fed a diet of dog food and vegetables. Feces were homogenized, mixed with seeds and re-formed into cylinders approximately 10×2 cm and weighing approximately 35 g (35.2±0.3 SD). Each scat contained 50 wild black cherry seeds. Scats were less than 30% seeds by weight, which is consistent with literature values for wild raccoon scat (Giles 1940) and with scats observed in the wild in the late summer and fall when raccoons are feeding on fruits (K. LoGiudice, personal observation).

In 1998, foraging at the latrines was measured qualitatively, by inspecting the latrines and rating the amount of disturbance on a scale of 3, with 1 being no disturbance, 2 being some signs of foraging (including general disturbance of the feces and the presence of empty seed coats) and 3 being all seed removed. Feces were placed in the latrines and monitored for 8 weeks. Fresh feces were added in the 5th week. In 1999, seed predation was measured quantitatively by removing one of the two scats in each simulated latrine each week and replacing it with a fresh scat, so that each scat was in the latrine for 2 weeks. The areas surrounding the latrines were also searched for signs of foraging such as empty *P. serotina* seed coats. Seeds that remained in scats were recovered by softening each scat in a beaker with water and then straining the contents through a fine sieve while flushing with additional

water. Twenty scats were randomly chosen before being put into latrines, and seeds were counted to check for accuracy of counts and seed recovery procedures. This random check recovered 99.9% of the seeds, indicating a high degree of counting accuracy with little seed loss during the recovery process.

Food supplementation

In both years, half of the grids were randomly assigned to a food treatment. Supplemental food was provided in nine feeders that were evenly distributed in each food addition grid (Fig. 1). Feeders consisted of stainless steel boxes (30×15×18 cm) fitted with wooden covers containing two access holes (2.5 cm square), which allowed entry of mice, but excluded most larger granivores such as squirrels. The feeders were wired to trees or staked to the ground to prevent disturbance and were kept filled with seeds (crimped oats in 1998 and sunflower in 1999) for the duration of the experiment. Food was added 2 weeks before the placement of the latrines.

In both years, mouse density was monitored as a covariate since this factor may affect seed predation in latrines. Following an initial 2 night trapping session to determine baseline densities, grids were trapped on a rotating basis so that each grid was trapped for 2 consecutive nights in 2 out of every 3 weeks. A Sherman trap (9×8×23 cm; wrapped with plastic bubble wrap for added insulation) was placed at each trapping station and provisioned with rolled oats, sunflower seeds and pressed cotton bedding. Traps were set at dusk and checked within 2 h of sunrise on nights with temperatures above -7°C . In 1998, trapping was conducted regardless of temperature and traps were checked once during the night (approximately 6 h after sunset) and again within 2 h of sunrise. Animals were marked for individual identification using Monel ear tags (National Band and Tag Company). Probability of capture in the marked populations was high (0.90 ± 0.07), so minimum number alive (MNA) was used as a relative index of mouse density (Hilborn et al. 1976; Wolff 1985; Slade and Blair 2000).

Statistical analysis

In order to determine whether food availability affected seed predation at the latrines, the 1998 data were simplified into two categories: latrines showing evidence of foraging and undisturbed latrines. The proportions of latrines showing evidence of foraging in the food supplemented and unsupplemented grids were compared using an unpaired *t*-test.

The 1999 experiment was designed as a repeated measures analysis of variance, with food (a fixed factor) and grid pair (a blocking factor) as the main effects, and the number of seeds removed from the latrines as the response variable (PROC ANOVA; SAS 1996). Data were non-normal (Shapiro-Wilk Test; $W=0.87$; $P=0.006$; PROC Univariate; SAS 1996), so they were also analyzed using non-parametric methods including rank transformation (Scheirer-Ray-Hare extension of the Kruskal-Wallis test; Sokal and Rohlf 1995) and log-linear analysis (SAS 1985). The data appeared to be bimodal (all or most of the seeds were either missing or present). Because analysis of variance is generally robust enough to tolerate this type of departure from the underlying assumptions (Scheffé 1959), parametric statistics are reported here. However, the effects observed were quite strong, and the results were virtually identical when analyzed using the non-parametric methods outlined above.

In a second analysis, the time effect was removed by averaging the number of seeds remaining in each latrine across time (each data point is the mean of 7 weekly measurements) and the data were subjected to an analysis of covariance. Food treatment (a fixed factor) and grid pair (a blocking factor) were the main effects and mouse density was included as a covariate.

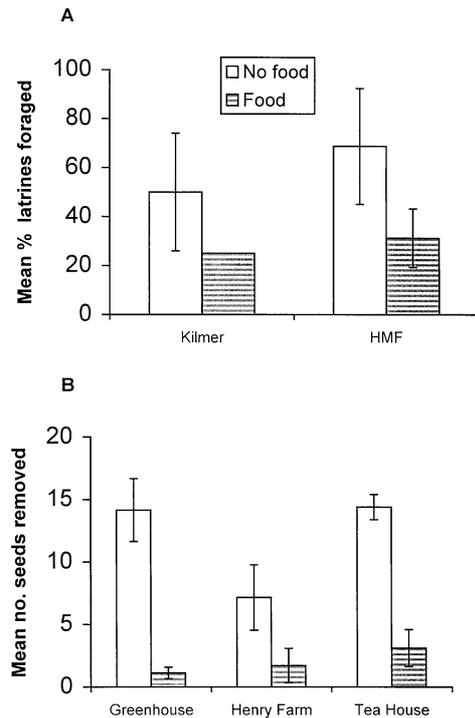


Fig. 2 The effect of food addition on the mean proportion (\pm SE) of simulated raccoon latrines showing signs of foraging in 1998 (a) and the mean number (\pm SE) of seeds removed from simulated raccoon latrines averaged across time in 1999 (b)

Results

In the 12 grids trapped in 1998, 118 white-footed mice were captured 372 times in 3,800 trapnights. In the 6 grids trapped in 1999, 240 white-footed mice were captured 643 times in 2,664 trapnights. The mean capture success was 10.4% and 35.8% in 1998 and 1999, respectively, and the average MNA per grid in 1998 and 1999 was 5.4 and 20.8, respectively. Simulated dispersal of seeds by raccoons did not guarantee protection from secondary predation. Overall, 46% and 53% of all the latrines showed signs of being foraged by seed predators in 1998 and 1999, respectively. There were marked differences in latrine foraging between the food supplemented versus unsupplemented grids. In 1998, 63% (15 of 24) of the latrines showed signs of foraging in the unsupplemented grids versus 29% (7 of 24) in the supplemented grids (unpaired *t*-test; $P=0.05$; 10 *df*; Fig. 2a). In both years it was common for all 50 seeds to be removed from latrines on the control grids while this was relatively rare in the food-supplemented grids (Table 1).

In 1999, the repeated measures analysis of variance revealed significant time and food effects ($F_{5, 14}=5.57$; $P=0.005$; $F_{1, 18}=39.24$, $P=0.0001$, respectively), and a significant time-by-food interaction ($F_{5, 14}=7.71$, $P=0.001$). In the unsupplemented grids, seed predation at the latrines increased with time. In the food-supplemented grids, however, seed predation remained consistently low throughout the entire study period (Fig. 3). During

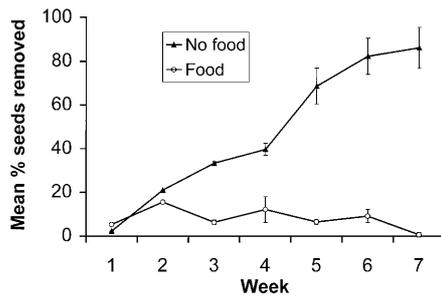


Fig. 3 The timing of seed removal from simulated raccoon latrines in the three unsupplemented grids (*triangles*) and the three food-addition grids (*circles*) in the 1999 experiment (*error bars* \pm SE). There were significant time, food and time \times food effects ($P < 0.005$)

Table 1 Thoroughness of removal of *Prunus serotina* seeds from simulated raccoon latrines. In 1998, latrines were qualitatively assessed at 3 week intervals. In 1999, seed removal was assessed quantitatively by replacing scats at 2 week intervals

Year	Latrines with all seeds removed (%)		Latrines with no seeds removed (%)		Trapping success (%)	
	Food	Control	Food	Control	Food	Control
1998	8.3	41.7	70.8	37.5	14.4	6.4
1999	0.0	72.2	77.8	8.3	34.8	36.9

the final week of the study, when the seed removal rate was the highest, 86.2% (± 7.4 SE) and 0.7% (± 0.6 SE) of the available seeds were removed from latrines in the control and food addition grids, respectively.

When the time effect was removed by averaging across time, significantly fewer seeds were removed from latrines in food-supplemented grids than in unsupplemented grids (ANCOVA; Food-treatment: $F_{1, 29} = 19.22$; $P < 0.0001$; Fig. 2b). Over the entire period of the experiment, seed removal in the control grids averaged 47.6% ($\pm 13.4\%$ SE) of the total seeds available, while 7.6% ($\pm 3.8\%$ SE) of the seeds were removed from the latrines in the food-supplemented grids. No significant grid effects or food \times grid interactions were observed. Regression analysis indicated that there was no relationship between mouse density and seed removal ($r^2 = 0.002$; $P = 0.79$) in 1999. It appeared that fewer seeds were taken in 1998, when mouse densities were lower (Table 1), but due to the differences in methods between the 2 years, no direct comparison is possible.

Discussion

Many aspects of frugivore seed dispersal, such as relocation away from the parent plant where natural enemies are common, and the application of nitrogen-rich feces, appear to facilitate tree regeneration. This may be especially true in the case of raccoon-dispersed seeds, as raccoon latrines commonly occur in treefall gaps (Page et

al. 1998) which present abiotic conditions favorable for the establishment of seedlings, as well as possible relief from seed predation pressure (Webb and Willson 1985). Furthermore, passage through the raccoon gut has been shown to enhance the germination rates of some tree seeds (Cypher and Cypher 1999). However, the results of this study demonstrate that seed dispersal by raccoons does not always favor escape from seed predation. During the last weeks of the experiments after the seed predators had presumably discovered the locations of the latrines, the majority (63% and 92% in 1998 and 1999, respectively) of the latrines in the control grids showed signs of foraging. Although we did not monitor undispersed seeds for a direct comparison, this is comparable to pre-dispersal seed predation levels under parent trees that have been reported by other investigators (from 68% to 99% of seeds removed; Webb and Willson 1985; Schupp 1988; Bermejo et al. 1998; Manson et al. 1998). In most cases, mice either found and removed every seed that was present, or failed to remove any seeds at all (79.2% of the latrines in both years).

In the unsupplemented grids, mice removed progressively more seeds with time since latrine establishment and we presume that this reflects a period during which mice were discovering the locations of the latrines. This explanation is consistent with the observations of Page et al. (1999), who found that seeds were removed at a greater rate from established raccoon latrine sites than from newly established artificial latrines. If this assumption is correct, it implies that newly established raccoon latrines (i.e., those not yet discovered by seed predators) may provide short-term refuge from seed predators regardless of ambient food levels. Such a refuge would be particularly significant for seeds that are protected from predator activity by immediate germination, secondary dispersal, or burial in soil or litter. However, this and other studies (Page et al. 1999, 2001a) indicate that established raccoon latrines (i.e., those that seed predators have previously learned to associate with a food resource) are sites of high seed predator activity.

Our food addition experiments demonstrate that ambient food levels can greatly influence seed removal from fecal concentrations. Significantly fewer seeds were removed from latrines in food-supplemented grids than from those in unsupplemented grids, and this pattern was consistent across years and locations despite a large variation in mouse density. This dramatic reduction in seed predation in areas with high ambient food availability implies that any positive effects of mammalian seed dispersal may be contingent on the temporal dynamics of seed production by other forest trees. Masting by species such as oaks (*Quercus* spp.), American beech (*Fagus grandifolia*), hickories (*Carya* spp.) and conifers causes dramatic interannual changes in the amount of winter food available to granivores (Ostfeld and Keesing 2000). Thus, in heavy mast years, the profusion of attractive, easily accessible foods is likely to deflect seed predator activity from raccoon latrines, increasing the probability that seeds in latrines will escape predation. A

large fall masting event may, in effect, provide protection for seeds in raccoon latrines that may last well into the winter. Conversely, during times of winter food shortage, such as years of mast failure, raccoon latrines are not likely to represent safe sites for seeds, as they are easily located and readily used by small mammal seed predators. This may be particularly true when a heavy mast year, which would elevate mouse densities (Ostfeld et al. 1996; Wolff 1996; Jones et al. 1998; McShea 2000), is followed by a year of mast failure.

Our experiment was conducted during late winter/early spring, a time of relatively low ambient levels of food for white-footed mice. Thus, we expected that visitation to raccoon latrines, which are present all year, would be particularly high. Our food supplementation experiment was intended to mimic a relatively sudden increase in food availability, a phenomenon that can occur at virtually any time of year [e.g., red maple (*Acer rubrum*) seed dispersal in spring, insect outbreaks in spring or summer or bud-burst in early spring], that may distract seed predators from mammal dispersed seeds.

This deflection of seed predators from raccoon latrines during times of high food availability may be an alternative mechanism by which predator satiation might be observed, albeit one that favors heterospecifics, as fleshy fruited trees such as *P. serotina* do not typically exhibit masting behavior. These results offer conditional support for the escape hypothesis (Janzen 1970; Clark and Clark 1984) whereby dispersal away from the parent plant favors seed survival, but only in years of high availability of alternative foods.

In order to escape predation and germinate, there are two critical periods through which seeds must survive, the period from production to dispersal and the period from dispersal to germination or incorporation into the seed bank. Fall fruiting species such as *P. serotina*, must produce seeds that persist not only through the fall, but also through the winter, a period of low food availability for seed predators. Although there may be some consistent advantages to mammalian dispersal such as escape from concentrations of soil pathogens (Packer and Clay 2000), these do not unconditionally include protection from seed predators. Our research has shown that a large infusion of food such as a masting event may distract seed predators from mammal-dispersed seeds and provide a window of opportunity for the establishment of seeds. The probability of escaping predation ultimately depends upon the interaction of many factors including the identity of the disperser, the dispersal location, the activity level of seed predators and the assemblage of alternative foods available to the predators.

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