

Factors affecting the relationship between seed removal and seed mortality

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Abstract: S.B. Vander Wall et al. (*Ecology*, **86**: 801–806 (2005)) criticized seed dispersal studies that use seed removal as a proxy for seed predation, because secondary dispersal processes following removal are important to seed fates for many plants. We compared seed removal rates with direct estimates of seed mortality and another mortality index, based on a 3-year experiment that included five temperate deciduous tree species and four enclosure treatments designed to identify effects of different seed consumer groups. Patterns of seed removal rates generally did not match patterns of mortality. Removal and mortality rates were both highest in seed-poor years, indicative of response to food limitation, but annual food abundance interacted with seed type differently for removal rates than for mortality rates. The effect of enclosure type (access by different consumers) on removal rates was opposite its effect on mortality rates; seeds were removed fastest from enclosures that allowed access to tree squirrels (genus *Sciurus* L., 1758), but these seeds had the lowest mortality because *Sciurus* is an important seed disperser. We discuss types of studies in which seed removal may be a reasonable index of seed mortality, and we stress the importance of justifying assumptions concerning links between removal and predation.

Résumé : S.B. Vander Wall et al. (*Ecology*, **86**: 801–806 (2005)) ont critiqué les études sur la dispersion des graines qui utilisent le retrait des graines comme variable de remplacement pour la prédation des graines, parce que, chez de nombreuses plantes, les processus de dispersion secondaire subséquents au retrait des graines sont importants pour expliquer le sort des graines. Nous avons comparé les taux de retrait des graines avec des estimations directes de la mortalité des graines et avec un autre coefficient de mortalité, dans une expérience de 3 années, qui impliquait cinq espèces d'arbres tempérés à feuillage décadu et quatre traitements en enclos, destinée à identifier les effets des différents groupes de consommateurs de graines. En général, les patrons de retrait des graines ne s'accordent pas avec les patrons de mortalité. Les taux de retrait et de mortalité sont tous les deux plus élevés les années de faible production de graines, ce qui indique une réaction à la pénurie de nourriture; cependant, l'abondance annuelle de nourriture interagit avec le type de graines de façon différente dans le cas des taux de retrait et celui des taux de mortalité. Les effets du type d'enclos (accès par des consommateurs différents) sur les taux de retrait sont à l'inverse de ceux sur les taux de mortalité; le retrait des graines se fait plus rapidement dans les enclos qui permettent l'accès aux écureuils arboricoles (du genre *Sciurus* L., 1758), mais ces graines ont la mortalité la plus basse car les *Sciurus* sont connus pour faire une importante dispersion des graines. Nous discutons des types d'études dans lesquelles le retrait des graines peut être un indice acceptable de la mortalité des graines et nous insistons sur l'importance de justifier les présuppositions faites concernant les liens entre le retrait et la prédation.

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Introduction

Seed dispersal is a multistep process. Chambers and MacMahon (1994) generalized the movements experienced in the “life of a seed” into two main types: phase I dispersal, which includes initial movement of seeds from the plant to some surface, and phase II dispersal, which may include multiple additional horizontal and vertical movements. It is now widely appreciated that the latter phase — often called secondary dispersal — may be equally or more important in determining seed fate and patterns of plant dispersion for many species (e.g., Chambers and MacMahon 1994; Jansen

et al. 2004; Forget et al. 2005; Roth and Vander Wall 2005; Vander Wall et al. 2005a). For example, the role of scatterhoarding rodents and corvids as secondary dispersers of nut-bearing plants has been well studied (Vander Wall 1990; Steele and Smallwood 2002; den Ouden et al. 2005). Similarly, ants, rodents, and dung beetles in the tropics are recognized as important secondary dispersers of seeds following primary dispersal through the passage of frugivores' guts (Vander Wall and Longland 2004; Andresen and Feer 2005; Pizo et al. 2005; Vander Wall et al. 2005b).

An important conclusion from these types of studies — where seeds depend in whole or part on animals to be dispersed away from parent plants — is that seed fates must be monitored beyond their initial removal from a primary dispersal location to make inference about recruitment dynamics. Assuming a direct relation between rates of seed removal and seed mortality often is inappropriate (Vander Wall et al. 2005a). However, in spite of ever-increasing awareness that seed fates are determined by complex processes, many recent studies have made this or similar assumptions when the relationship between removal and final seed fate was unknown (e.g., Boman and Casper 1995; Mo-

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les et al. 2003; Beckage and Clark 2005; Haas and Heske 2005; López-Barrera et al. 2005; Jurado et al. 2006; Salvande et al. 2006; Lopez and Terborgh 2007).

If seeds are removed exclusively by animals that are only seed predators (i.e., they provide no dispersal benefit to the plant), then removal rates and mortality rates may be directly related. However, if some species within a granivore community also act as important dispersal agents, then the relationship between removal and mortality rate should depend on complex interactions between several factors that govern each of these. Interactions between conventionally evaluated factors (e.g., seed type, seed size, annual variation in food abundance) have been shown to be important for understanding both seed survival and caching behavior of rodents (Vander Wall 2002; Jansen et al. 2004; Moore and Swihart 2007; Moore et al. 2007). Additional factors may include but are not limited to the following: seed-consumer community composition (Schnurr et al. 2002; Fedriani et al. 2004; Asquith and Mejía-Chang 2005; Moore and Swihart 2007); plant species (seed type) composition (Schnurr et al. 2002, 2004; Moles et al. 2003); dietary preferences and food-handling abilities of different consumers (Goheen and Swihart 2003; García et al. 2005; Briones-Salas et al. 2006); whether different seed types are favored for immediate consumption or for storage (Gendron and Reichman 1995; Kotler et al. 1999); and temporal or spatial variation in food abundance (Schnurr et al. 2002, 2004; Jansen et al. 2004; Xiao et al. 2005; Moore and Swihart 2007).

We compared seed removal rates with estimates of seed mortality during 3 years for five temperate deciduous tree species that produce hard mast (nuts) known to be consumed and hoarded by several rodent species in the Central Hardwoods region, USA. Exclosure experiments allowed differential access to seeds by different members of the granivore community. Rodent species in our study area vary in the extent to which they may contribute to tree dispersal; most are considered primarily to be seed predators (including southern flying squirrel (*Glaucomys volans* (L., 1758)), eastern chipmunk (*Tamias striatus* (L., 1758)), North American red squirrel (*Tamiasciurus hudsonicus* (Erxleben, 1777)), and white-footed mouse (*Peromyscus leucopus* (Rafinesque, 1818); but see Moore et al. 2007 and Moore and Swihart 2007), whereas tree squirrels (eastern gray squirrel (*Sciurus carolinensis* (Gmelin, 1788)) and fox squirrel (*Sciurus niger* L., 1758)) act as both seed predators and seed dispersers (Steele and Smallwood 2002). Additionally, blue jays (*Cyanocitta cristata* (L., 1758)) are the only important avian seed disperser. Species in this granivore community vary in their dietary preferences and abilities to use the seed types we studied (Smith and Follmer 1972; Ivan and Swihart 2000; Moore and Swihart 2006), and the seed types vary in their utility to tree squirrels as instant-consumption versus long-term storage items (Hadj-Chikh et al. 1996; Steele et al. 1996; Smallwood et al. 2001). Annual seed production varied widely during the study.

Our study enabled us to determine how these factors and their interactions affected the relationship between removal rates and direct estimates or other indices of seed mortality. We expected that whether removal rates could serve as a proxy for seed mortality would depend on the seed types used, which animal species were utilizing the different seed

types, and ambient food availability. Specifically, we predicted that for seed types with high storage potential, removal rates would be inversely correlated with mortality rates when they were accessible to scatter-hoarding rodents known to play important seed dispersal roles (i.e., *Sciurus* species). In other words, fast removal of seeds by *Sciurus* would enable seeds to escape even greater predation threats (i.e., other granivores that do not benefit seeds) and would lead to some seed survival (since some cached seeds would not be reclaimed). This relationship should manifest primarily in years of high seed production, whereas in low-seed years we expected high seed mortality across the board.

Materials and methods

Experimental design

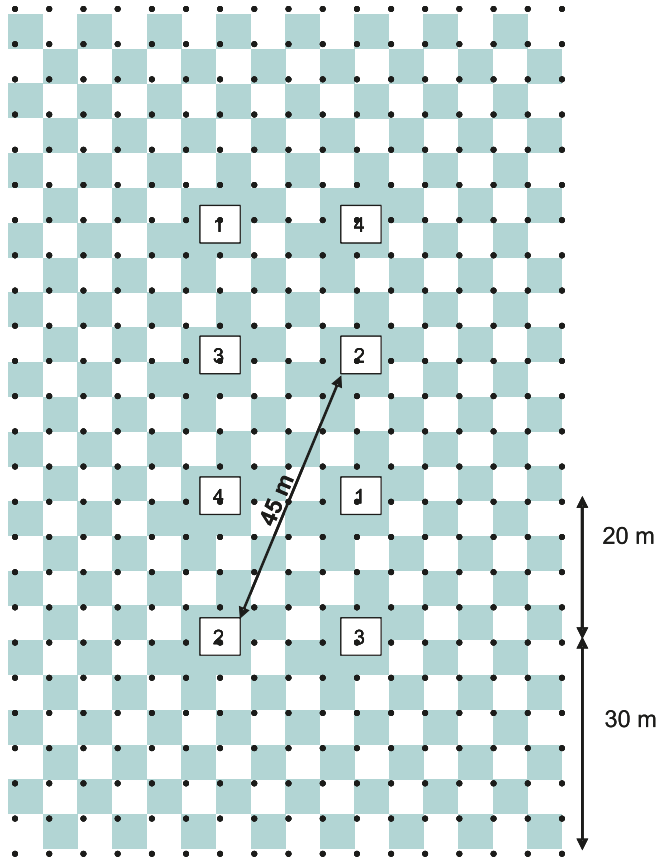
We established 11, 10, and 8 study plots in autumn 2002, 2003, 2004, respectively, in forest patches within an agriculturally dominated landscape of north-central Indiana. Ambient seed production across the study region was low in 2002, extremely high in 2003, and extremely low in 2004. A study plot consisted of a 25 × 17 grid of wire-pin flags spaced at 5 m (Fig. 1). The grid facilitated a systematic search for dispersed seeds (see below). We placed one exclosure box (1 m × 1 m base) filled with seeds at eight locations in each grid. Boxes at each site comprised four treatments (two boxes per treatment) allowing access to the following: (1) white-footed mice; (2) mice, eastern chipmunks, southern flying squirrels, and red squirrels; (3) all forest rodents in the community, including gray squirrels and fox squirrels; and (4) all rodents and similar-sized consumers such as blue jays, but not larger consumers such as white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)). Boxes were ≥20 m from each other (45 m apart for boxes of the same treatment), and 30 m from the nearest edge of a study grid. See Moore and Swihart (2007) and Moore et al. (2007) for more detail about the exclosure and experimental design.

In late October of each year, we filled each box with 50 (2003, 2004) or 65 (2002) black walnuts (*Juglans nigra* L., except for treatment 1, since white-footed mice do not consume these), shagbark hickory nuts (*Carya ovata* (Mill.) K. Koch), northern red oak acorns (*Quercus rubra* L.), pin oak acorns (*Quercus palustris* Muenchh.), and white oak acorns (*Quercus alba* L.). We did not use white oak in autumn 2004 (no seed crop to collect), and white oaks were included at only 6 of 11 sites in 2002. Most viable seeds germinate in the first spring–summer following drop, with white oak germinating immediately following drop during the same autumn. In total, we placed ~53 900 seeds in exclosures. Before placement, we inserted a small metal tag (13–19 mm wire nail) into each seed. Different nail types and colors were used to identify different seed types and treatments.

Seed removal

Following placement, we visited sites daily (every other day in autumn 2004) and recorded the number of seeds of each type remaining in each box. We visited sites for up to about 2 weeks in 2002 and 2004, or for up to 41 days in 2003 (visited once per week after the first 13 days). We

Fig. 1. Experimental study grid layout used to test for effects of various factors on seed survival in forest fragments of north-central Indiana. Points represent flags, separated by 5 m, arranged in a 25×17 grid. Numbered boxes (not to scale) indicate locations of eight semi-permeable enclosures, comprising four experimental treatments (see text). Shaded quadrats represent areas searched by metal detector in an ideal case.



used a Cox proportional hazards model (Klein and Moeschberger 1997; Williams et al. 2002) to assess effects of year, box type, seed type, and study plot on hazard ratios, which reflect the relative risk of “failure”, defined in this case as removal from a box by a consumer. We also estimated effects of year \times treatment and year \times seed-type interactions on hazard ratios. Removal of nuts within the same box may not constitute independent events, so we emphasize that estimated removal rates are specific to experimental seeds and may not reflect removal rates of naturally fallen seeds.

Mortality estimates

We compared removal rates to mortality estimates based on survival analyses described in Moore and Swihart (2007), which we describe only briefly here. For study sites that we established in autumn 2003 and 2004, we used metal detectors (Fisher 1225-X) in the following spring seasons (April–June 2004 and 2005) to search for seeds that rodents had removed from enclosures. At each study site, we tried to search ~50% of the $5 \text{ m} \times 5 \text{ m}$ quadrats (in checkerboard fashion) that were delineated by flags on the study grids. The search radius in all directions around each enclosure was $\geq 30 \text{ m}$ (up to $>100 \text{ m}$ in some directions for some ex-

closures). These search distances were sufficient to include a vast majority of scatter-hoarded seeds, which had median removal distances of ~5–15 m for all seed types in most years (Moore et al. 2007; also see Abbott and Quink 1970; Sork 1984). Upon finding a tag, we recorded the seed type, treatment from which it came, and fate (buried uneaten, unburied uneaten, eaten). Because each grid was sampled rather than censused, we applied correction factors to estimate the true number of seeds surviving to late spring. This correction factor (Moore et al. 2007) was $CF_{fibr} = 1/(q_f/4) \times 1/d_{t,b} \times l_r$, where q_f is the number of quadrats searched around a particular flag f (varies from 1 to 4), $d_{t,b}$ is the estimate of detectability for a given tag type t that was buried ($b = 1$), and $l_r = 1.5$ for seeds found 30–50 m from their sources or 3 for seeds found $>50 \text{ m}$ from their sources. We used hierarchical generalized linear models (HGLM) with a logit-link function to estimate effects of year, seed type, treatment, and interactions (year \times treatment and year \times seed type) on mortality (Moore and Swihart 2007).

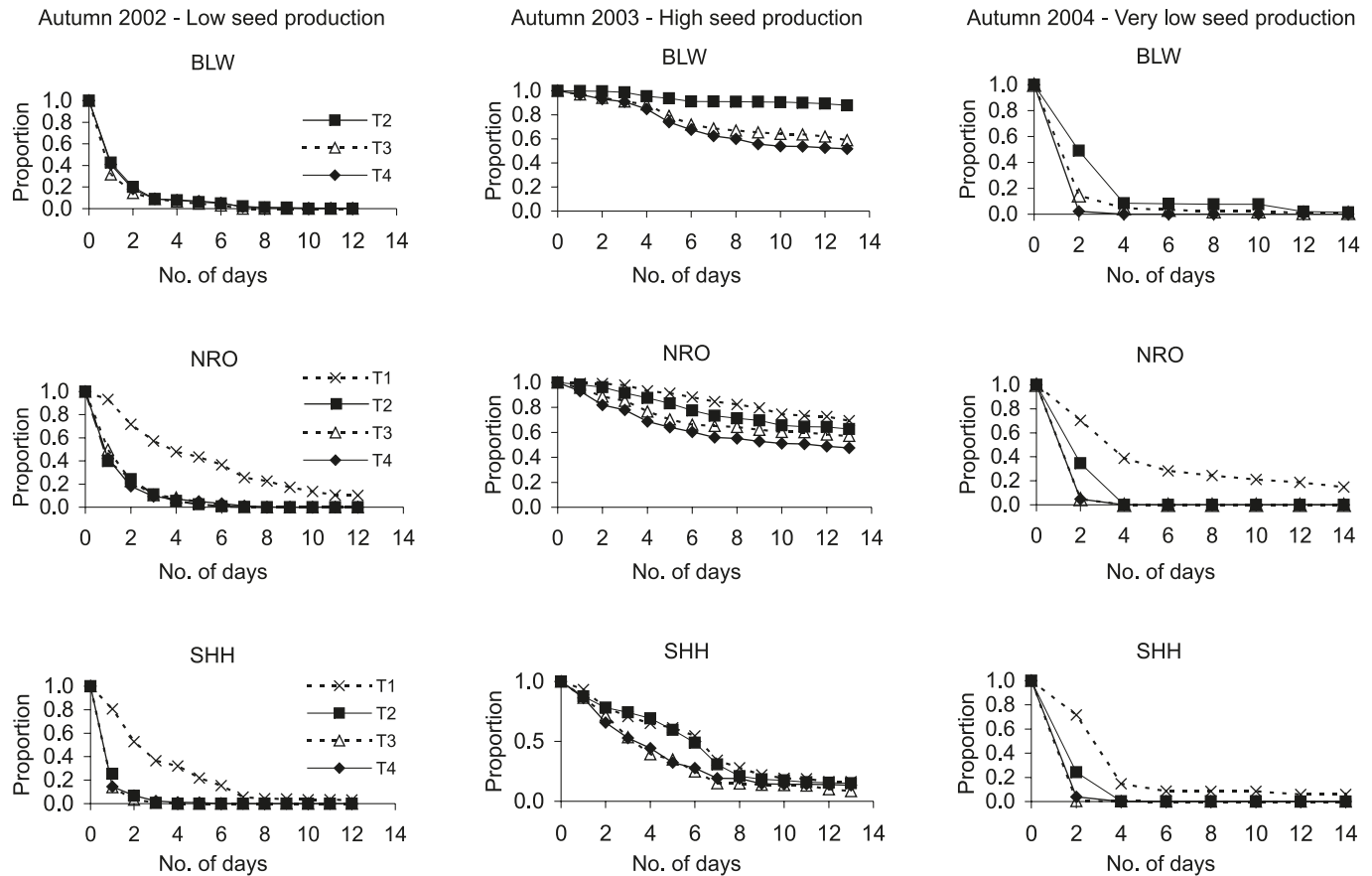
Mortality index

For sites established in autumn 2002, we sampled study grids with metal detectors, but we expended roughly half of our search effort for each grid immediately after seed removal in autumn, with the other half expended in the following spring. Moreover, we only searched half of each grid in this year (total seeds searched for ~11 400). Thus, survival data from the first year were not comparable with data from subsequent years. Therefore, for search data collected in spring 2003, we calculated a mortality index as the number of tags that we found from eaten seeds divided by the total number of tags that we found (with correction factors applied). This index only reflects relative mortality of scatter-hoarded seeds across years or treatments; it does not account for annual variation in the number of seeds larder-hoarded in burrows, tree cavities, etc. Therefore, the mortality index underestimates the true mortality. We calculated the mortality index for all 3 years, and used a generalized linear model (GLM) with logit link (binomial error distribution) to model it as a function of the same factors that we used to model seed mortality. We included an overdispersion term in the GLM; this inflated standard errors that were artificially small because of intrasite correlation in seed fates.

Results

Seed removal rates varied greatly with year (seed production), treatment (effective granivore community structure), and seed type. In autumn 2002 and 2004 (seed-poor years), most seeds disappeared within a few days (Fig. 2). In 2003 (seed-rich year), by contrast, most boxes took at least 2 weeks to empty, and many were still not empty when we stopped checking after 41 days. All effects included in the proportional hazard model were highly significant ($P < 0.001$, based on χ^2 tests, for at least one level of each factor). On average, seeds were removed much more slowly from boxes only accessible by white-footed mice (treatment 1) than from boxes accessible by all rodent species (treatments 3 and 4; see Fig. 2 and compare hazard ratios in Figs. 3A–3C). Removal rates from treatment 2 often were intermediate between these. Thus, removal rate was posi-

Fig. 2. Seed removal rates exemplified by three seed types (BLW, black walnut (*Juglans nigra*); NRO, northern red oak (*Quercus rubra*); SHH, shagbark hickory (*Carya ovata*)) in four enclosure treatments during 3 years. T1, access by white-footed mice (*Peromyscus leucopus*) only; T2, access by all rodents except *Sciurus* species; T3, access by all rodents; T4, access by all rodents and birds (blue jays, *Cyanocitta cristata*). Plots show the proportion of seeds remaining in an enclosure (averaged across all sites in the year) after each day, out to 12–14 days following start of the experiment.



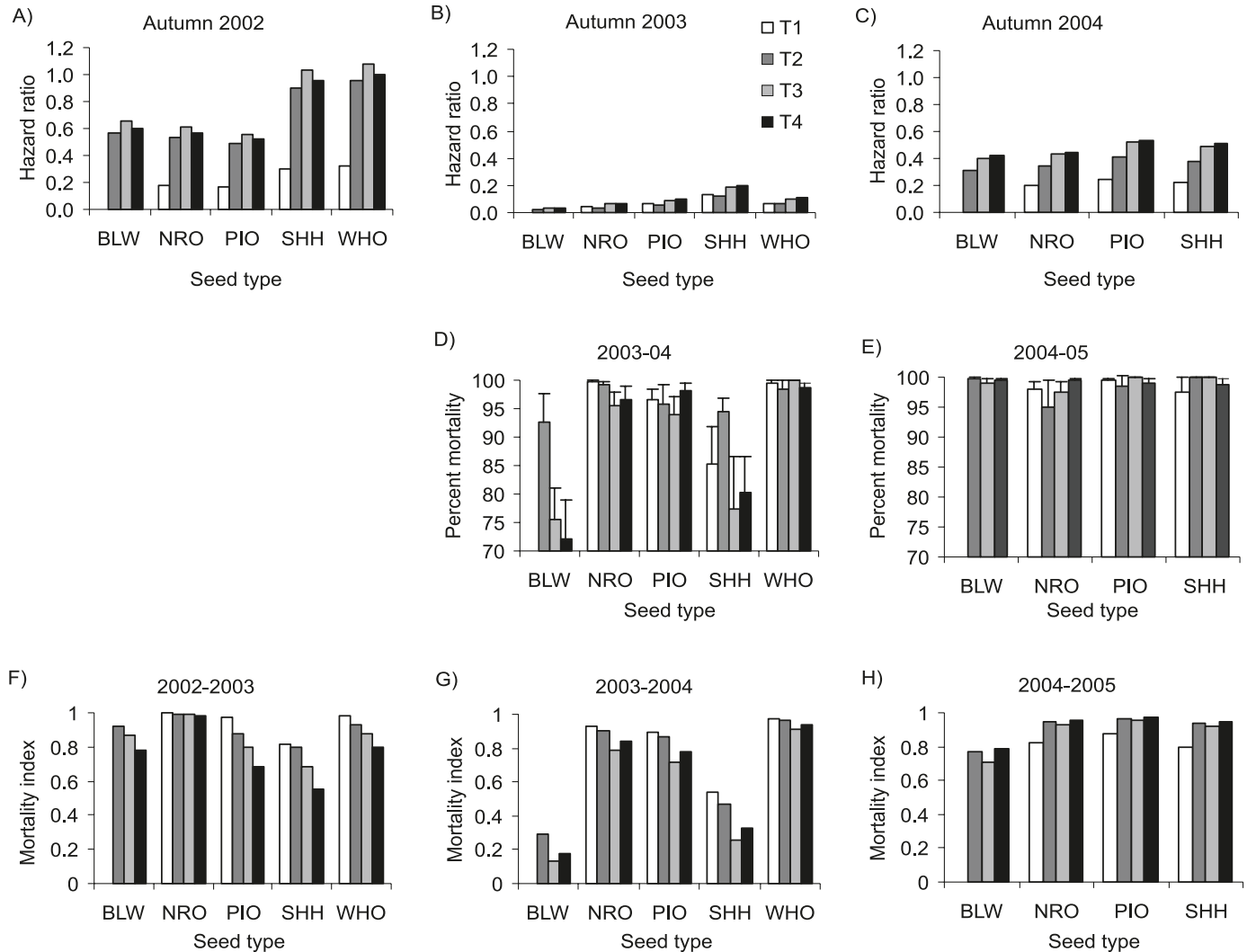
tively related to the proportion of rodent community that could access seeds. Hazard ratios reflect that, in 2002, hickory nuts and white oak acorns were removed faster than other species (Fig. 3A). In 2003, hickory nuts again were removed the fastest and black walnuts were removed the slowest (Fig. 3B). In 2004, all seed types were removed at comparable rates (Fig. 3C).

Mortality estimates and removal rates were not related to each other, especially in the seed-rich year (2003–2004; Fig. 4A) when mortality varied greatly with various factors. Seed mortality estimates from autumn to late spring varied with seed type and treatment in 2003–2004 (Fig. 3D), but were uniformly high in 2004–2005 (Fig. 3E; Moore and Swihart 2007). This latter point is in contrast with treatment-dependent removal rates in autumn 2004 (Fig. 3C). From 2003 to 2004, mortality of all acorn types was higher than for black walnuts or shagbark hickory nuts, and was highest for white oak (Fig. 3D). This is consistent with removal rates of all species in 2003 except shagbark hickory, which had the highest removal rates in this year (Fig. 3B). For black walnut, red oak, and shagbark hickory, mortality was higher for seeds from treatments 1 and 2 than for those from treatments 3 and 4 (Fig. 3D). This contrasts with the opposite pattern of removal rates for these treatments (Fig. 3B).

All factors included in the GLM of the mortality index were statistically significant ($P < 0.05$ for at least one level of all main-effect variables; $P < 0.01$ for at least one level of all interaction variables). Consistent with removal rates (hazard ratios) and mortality estimates, the mortality indices for all species were higher in 2002–2003 and 2004–2005 than in 2003–2004 (Figs. 3F–3H). In 2003–2004, model estimates of the mortality index seemed to reflect mortality estimates reasonably well, both across treatments and seed types (Fig. 4B). In 2004–2005, however, this was not the case. In this year, mortality indices were consistent with variation in mortality estimates across all species except black walnut; the index suggested that mortality was lower for this seed type, whereas mortality estimates did not suggest a difference (compare Figs. 4D and 4G). Also, the mortality index in 2004–2005 suggested that mortality was lower for seeds in treatment 1, which was not the case according to mortality estimates.

The pattern of mortality indices and hazard ratios were quite different from each other in 2002–2003 (Figs. 3A, 3F, 4C). In autumn 2002, removal rates were highest for white oak and shagbark hickory, lower for red oak, pin oak, and black walnut, and lower from treatment 1 than other treatment types (Fig. 3A). In contrast, the mortality index for this year suggested shagbark hickory and black walnut

Fig. 3. Three metrics of seed mortality for five seed types in four enclosure treatments (T1–T4) during 3 years. TOP PANELS: mean hazard ratios (across sites) based on estimates from Cox proportional hazards regression model fitted to seed removal data. Ratios indicate the relative failure rate (relative probability of being removed) for seeds in a particular year \times treatment \times seed-type combination, compared with that of white oak (WHO) seeds in treatment 4 during 2002 (intercept model: hazard ratio = 1). MIDDLE PANELS: estimates of seed mortality from autumn to spring (2003–2004 and 2004–2005) based on Moore and Swihart (2007). Bars show mean \pm 1 SE of observed estimates (adjusted by correction factors) across sites. BOTTOM PANELS: mortality index estimates (number of tags from eaten seeds divided by total number of tags found) based on generalized linear model fitted to the index data. Seed types: BLW, black walnut (*Juglans nigra*); NRO, northern red oak (*Quercus rubra*); PIO, pin oak (*Quercus palustris*); SHH, shagbark hickory (*Carya ovata*); WHO, white oak (*Quercus alba*).



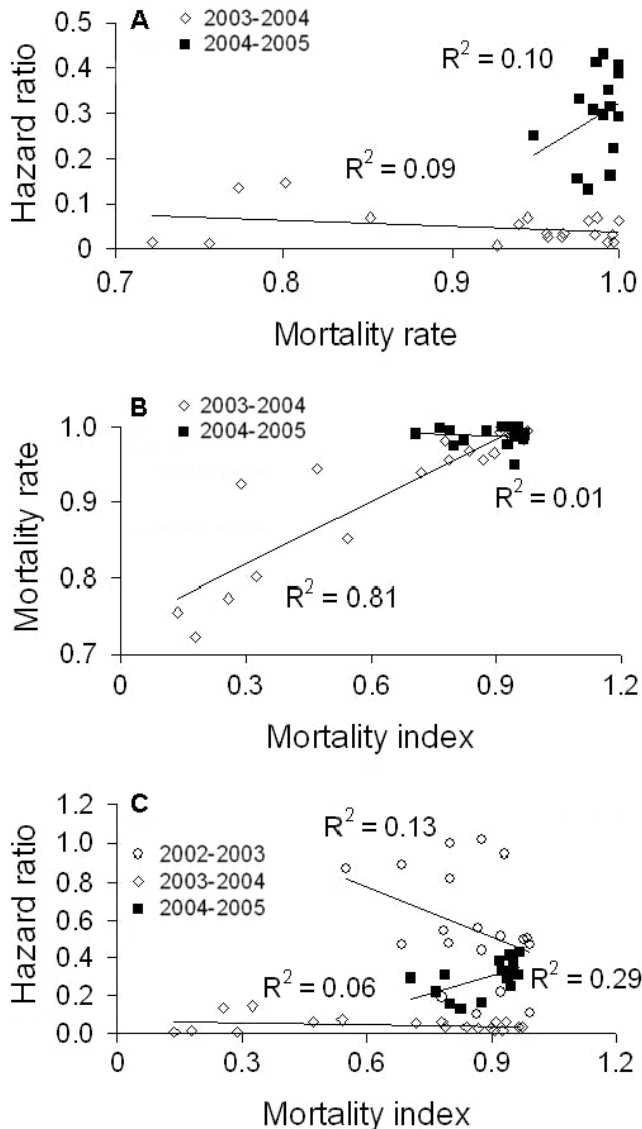
had the lowest mortality (consistent with the index and mortality estimates for 2003–2004), and that mortality of red oak and pin oak acorns were more similar to that of white oak (also similar to the 2003–2004 results) (Fig. 3F). The mortality index also suggested that mortality was greater for seeds from treatments 1 and 2 than from treatments 3 and 4 (consistent with results from the 2003–2004 index and actual mortality estimates). Mortality indices and hazard ratios were positively related in 2003–2004, but were unrelated to each other in 2004–2005 (Fig. 4C).

Discussion

Our study highlights the potential for removal rates to mislead as indices of seed predation rates, and provides empirical support for the suggestion of Vander Wall et al.

(2005a) that seed removal is not always justified as a proxy for seed predation. We found that factor-dependent patterns of removal rates of nuts generally did not match factor-dependent mortality. With respect to annual (food abundance) effects, the hazard ratios suggested radically reduced removal rates for all seed types in 2003 (seed-rich year) compared with 2002 and 2004 (seed-poor years), whereas mortality estimates and indices showed that only for black walnut and shagbark hickory was mortality very much lower in 2003–2004 than in the other 2 years. With respect to seed-type effects, removal data would have led us to believe that hickory nuts suffered highest predation rates during 2 years of our study when in fact hickory nuts appeared to have among the lowest mortality during these years. Removal data in 2002 also appeared to underestimate seed predation of pin oak and red oak acorns rel-

Fig. 4. Scatter plots showing relationships between (A) mortality estimates and hazard ratios (removal rates), (B) mortality index and mortality estimates, and (C) mortality index and hazard ratios. Separate regression lines are fitted for each year's data within a scatter plot. Each point represents the mean estimate for a given site \times treatment \times seed type within a year. The overall R^2 values for a line fitted to all points (not controlling for year) are 0.12 (A), 0.79 (B), and 0.04 (C).



ative to white oak acorns. Finally, removal rate data completely misrepresented the effects of box treatment type — a proxy for altered granivore community structure — on seed mortality. Removal rates appeared to simply reflect the varying degrees of accessibility granted by the different enclosure types. Seeds disappeared most slowly from treatments 1 and 2, apparently because only a subset of rodent species in the community could access seeds from these enclosures. If we had viewed removal as a proxy of predation, we would have concluded that a greater abundance of rodent species is bad for seed survival. However, the rodent species excluded from treatments 1 and 2, i.e., fox squirrels and eastern gray squirrels, are those considered most beneficial to seed dispersal in our study system (Steele and Smallwood 2002;

Steele et al. 2005), and survival data indicated that the treatment effect on mortality was opposite that which would have been concluded from removal rate experiments. Seeds from treatments 3 and 4 were removed the fastest, but they were taken largely by tree squirrels (genus *Sciurus*) who subsequently scatter-hoarded and failed to retrieve a number of seeds.

Most seeds removed by animals are consumed. In this sense, faster removal can mean greater predation, as both will often be related to ambient resource limitation. But when comparing differences across seed types or treatments, we found that removal and mortality rates of nuts were governed by different processes. Removal rates (within a year) were determined by the number of animal species able to use different seeds, whereas predation rates (and hence mortality) depended on those species that actually removed the various seed types. Given the importance of secondary dispersal processes in a number of animal-plant systems, it is prudent when making conclusions from removal rate data to consider that removal from a primary dispersal location by certain consumers can be good for the seed (Chambers and MacMahon 1994; Vander Wall and Longland 2004; Vander Wall et al. 2005b). For plants that depend on granivores for dispersal, resource limitation probably will have negative effects on seed survival, but a lack of granivores can be equally detrimental for these plants, in which case low removal may reflect poor survival as seeds succumb to rot, desiccation, or other predators that provide no dispersal benefit.

One caveat of our study is that final fates were not determined for all seeds. It is likely that many seeds which were still uneaten at the end of our search period ultimately succumbed to mortality, so our estimates of seed mortality are minimal rates and are uncertain. Fortunately, our conclusions do not depend on knowing final fates of all seeds. To reject the conventional assumption that seed predation and seed removal rates are correlated, we only need to show that seeds removed more quickly suffer predation rates lower than or equal to seeds removed more slowly. Our data, which document seed survival from the removal period to the start of germination period approximately 6 months later (for most seed types), provide clear evidence to refute the conventional assumption. That is, we have shown that seeds removed faster did not have correspondingly higher predation rates; indeed, their ultimate predation rates (e.g., probability of being consumed before germinating) could only have been lower than or equal to seeds removed more slowly. This result alone is sufficient to support our primary conclusions. Moreover, given the viability schedule of seeds in relation to the duration of our study, it seems likely that survivorship from around October to May should be correlated with survivorship to germination stage.

When might seed removal be a good proxy for seed predation? Clearly, not all seed consumers benefit seeds, so there may be cases in which seed removal reasonably indexes seed mortality. We can think of two types of studies that fit these scenarios. In one type, seed consumers are known and exert only negative effects on seeds. For example, Herrera (1995) identified ungulates as consumers of all acorns placed in certain experimental treatments. García et

al. (2005) were able to attribute all seed removal in their experiments to rodents that exclusively larder-hoarded seeds in sites unsuitable for germination. Li and Zhang (2003) collected detailed data on acorn fates and found that, in addition to high consumption rates by rodents, scatter-hoards were placed in locations unsuitable for establishment. Where such information is known, it seems that removal may be a decent index of predation.

In the second type of study, seeds are placed by the researcher in germination- and seedling-favorable environments likely to have been “found” by a different stage of the dispersal process than the removal mechanism being studied. For example, Orrock et al. (2003) scattered pokeweed (*Phytolacca americana* L.) seeds in suitable germination sites in a manner that mimicked primary dispersal by frugivorous birds. Postdispersal consumers of these seeds included granivorous birds (which do not scatter-ward), invertebrates, and rodents (principally white-footed mice). In this type of situation, one knows that these seed predators were not responsible for the seeds initially reaching favorable sites, and that some percentage of seeds removed from these favorable sites will perish, so removal constitutes a neutral or negative effect for all seeds (net negative) in terms of germination and establishment probability. Orrock et al. (2003) did not confirm that removed seeds were actually depredated. In fact, white-footed mice showed signs of some caching behavior when given pokeweed seeds in feeding experiments by McDonnell et al. (1984). However, given that experimental locations of seeds represented suitable germination sites for this plant, it was probably safe to conclude that additional secondary removal of these seeds had a more negative effect on recruitment than if all seeds escaped discovery by postdispersal consumers. Moreover, Orrock et al. (2003) found that natural seedling densities were negatively correlated with rodent densities, and the high toxin levels in pokeweed fruits are assumed to be adaptations against mammalian consumers (McDonnell et al. 1984). For this type of system, seed removal may have been a suitable index of seed mortality.

Removal studies may or may not provide direct insight to seed predation or the seed dispersal process. Such studies may be useful for understanding seed preferences and which seed types are removed by which animal species. If seed predators do not provide any dispersal benefit to the plant, removal may be a reasonable proxy for predation. But often, the relationship between seed removal and seed mortality is much more complex. Researchers should make every attempt to be explicit in their assumptions concerning the links between removal and predation, and to justify those assumptions.

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