

Post-dispersal losses to seed predators: an experimental comparison of native and exotic old field plants

C.S. Blaney and P.M. Kotanen

Abstract: Invasions by exotic plants may be more likely if exotics have low rates of attack by natural enemies, including post-dispersal seed predators (granivores). We investigated this idea with a field experiment conducted near Newmarket, Ontario, in which we experimentally excluded vertebrate and terrestrial insect seed predators from seeds of 43 native and exotic old-field plants. Protection from vertebrates significantly increased recovery of seeds; vertebrate exclusion produced higher recovery than controls for 30 of the experimental species, increasing overall seed recovery from 38.2 to 45.6%. Losses to vertebrates varied among species, significantly increasing with seed mass. In contrast, insect exclusion did not significantly improve seed recovery. There was no evidence that aliens benefitted from a reduced rate of post-dispersal seed predation. The impacts of seed predators did not differ significantly between natives and exotics, which instead showed very similar responses to predator exclusion treatments. These results indicate that while vertebrate granivores had important impacts, especially on large-seeded species, exotics did not generally benefit from reduced rates of seed predation. Instead, differences between natives and exotics were small compared with interspecific variation within these groups.

Key words: aliens, exotics, granivores, invaders, old fields, seed predators.

Résumé : L'invasion par les plantes adventices est plus plausible si ces plantes ont peu d'ennemis naturels, incluant les prédateurs post-dispersion des graines (granivores). Les auteurs ont examiné cette idée lors d'une expérience sur le terrain, conduite près de Newmarket en Ontario, dans laquelle ils ont expérimentalement empêché les prédateurs de graines, vertébrés et insectes terrestres, d'avoir accès aux graines de 43 espèces de plantes indigènes ou exotiques, de vieilles prairies. La protection contre les vertébrés augmente significativement la survie des graines; l'exclusion permet de récupérer plus de graines comparativement aux témoins chez 30 espèces de plantes expérimentales, avec une augmentation générale de récupération allant de 38.2 à 45.6%. Les pertes occasionnées par les vertébrés varient selon les espèces, augmentant significativement avec la grosseur des graines. Au contraire, l'exclusion des insectes n'augmente pas significativement les nombres de graines récupérées. Ils n'y a pas de preuve que les adventices auraient bénéficié d'une réduction du taux de prédation post-dispersion des graines. Les impacts des prédateurs de graines ne diffèrent pas significativement entre les espèces indigènes et introduites, qui montrent au contraire des réactions très similaires aux traitements d'exclusion des prédateurs. Ces résultats indiquent que bien que les granivores vertébrés aient des impacts importants, surtout sur les espèces à grosses graines, les plantes introduites ne bénéficient généralement pas de taux réduits de prédation des graines. Au contraire, les différences entre les plantes indigènes et les plantes introduites sont petites comparativement à la variation interspécifique à l'intérieur de chacun de ces groupes.

Mots clés : adventices, exotiques, granivores, envahisseurs, vieilles prairies, prédateurs de graines.

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Introduction

The spread of non-native plants has changed the composition, structure, and function of many ecosystems around the world (Elton 1958; Drake et al. 1989; Pyšek et al. 1995; Vitousek et al. 1996; Williamson 1996; Mack et al. 2000). Exotic plants currently contribute 25% or more of the spe-

cies of many regional floras (Heywood 1989; Vitousek et al. 1996; Whitney 1994), in some cases nearly replacing native vegetation (e.g., U.S. Congress 1993; Vitousek et al. 1996; Mack et al. 2000). Still, such examples represent only a small minority of potential invaders; the majority of newly arriving plant species fail to become established, or remain scarce even if they do (Williamson 1996; Williamson and Fitter 1996a, 1996b; Mack et al. 2000). Many researchers have attempted to develop rules to identify the minority of species which become successful invaders (e.g., Elton 1958; Baker 1974; Drake et al. 1989; Mack 1996), but these efforts have achieved few significant advances (Perrins et al. 1992; Lodge 1993; Mack 1996; Williamson 1996).

One hypothesis which has gained some support is that invasion may be more likely if the potential invader enjoys an unusually low risk of predation. There are two distinct ways

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this could occur. First, invaders might lose their natural enemies when they are transported to a new region (the predator escape hypothesis; Elton 1958; Crawley 1986, 1987). Second, species intrinsically resistant to damage might be less likely to be eliminated by natural enemies before they can establish viable populations (the predator filter hypothesis). The first hypothesis is one of the foundations of biological control, which often attempts to replace “missing” predators (e.g., recent efforts to control *Lythrum salicaria* (Malecki et al. 1993)). The second has been used to explain why plants from regions with long histories of vertebrate grazing can be better invaders of rangelands than plants from islands or continental regions lacking native grazers (e.g., Crosby 1986; Mack 1989).

Natural enemies may be especially important if they affect a critical life history stage; for invaders, seeds may represent such a stage. Abundant seed production, dispersal, and accumulation in the seed bank may aid in the invasion of new areas while reducing the risk of extinction for small colonizing populations (Baker 1969, 1974; Venable and Brown 1988; Rees and Long 1992; Rees 1993; Stöcklin and Fischer 1999). For example, invasiveness in *Pinus* and other woody plants is correlated with large seed crops, animal dispersal, and small seed size, which is also believed to be correlated with dispersability (Rejmánek 1995, 1996; Rejmánek and Richardson 1996). Similarly, many invaders produce significant seed banks (Holm et al. 1977). Crawley et al. (1996) found that British aliens were more likely than natives to have persistent seed banks, though Thompson et al. (1995) found that this was less true for aliens than for invasive native species. The ability of invaders to form seed banks actually may be improved by the invasion process. For example, seed banks of *Mimosa pigra* are approximately 100 times larger in Australia, where it is non-native, than in its native Mexico (Lonsdale and Segura 1987). Numerous *Acacia* spp. develop much larger seed banks in South Africa than in their native Australia, in response to the loss of pre-dispersal seed predators and gall rusts (Dean et al. 1986). Finally, seed banks of the reciprocally invasive *Acacia longifolia* (native to Australia) and *Chrysanthemoides monilifera* (native to South Africa) respectively were increased 44 and 1316 times in their new regions (Weiss and Milton 1984). For *A. longifolia* this difference was primarily the result of reduced seed production due to a weevil in its native range; for *C. monilifera*, the explanation lay with differences in the survival of buried seeds.

In this paper, we use a suite of 43 native and exotic species occurring in old fields to (1) quantify losses of seeds to vertebrate and terrestrial insect post-dispersal seed predators (granivores), and (2) experimentally examine the hypothesis that seeds of aliens are less susceptible than seeds of natives to predation. We focus on seed predation after dispersal but before incorporation into the long term seed bank.

Methods

Study site

This experiment was conducted at the Dead Man’s Curve old field of the University of Toronto Joker’s Hill field station (<http://www.erin.utoronto.ca/~w3pkota/jh.html>), Regional Municipality of York, Ontario (44°02'25"N, 79°32'00"W). This is a dry-mesic meadow on a south facing slope and has been abandoned

from any agricultural use for at least 30 years. Vegetation is a diverse mix of native and alien species, typical of southern Ontario old fields (e.g., Maycock and Guzikowa 1984). Grasses dominate the site with the aliens *Bromus inermis* Leyss. and *Poa pratensis* L. important in mesic areas. Drier portions of the site are dominated by the natives *Poa compressa* L. and *Danthonia spicata* (L.) Beauv. Common native herbs include *Solidago canadensis* L., *Solidago nemoralis*, *Antennaria neglecta* Greene, *Aster urophyllus* Lind. and *Aster novae-angliae* L. The most common alien herbs are *Hieracium piloselloides* Vill., *Hieracium caespitosum* Dumort., *Melilotus alba*, *Medicago lupulina* L., *Daucus carota*, *Hypericum perforatum* L. and *Chrysanthemum leucanthemum*. Tree and shrub cover is approximately 10%. See Blaney (1999) for further details. See Table 1 for authorities not given for the species mentioned above.

Experimental species

Seeds of 22 native and 21 regionally non-native forbs and graminoids (Table 1) were selected from a pre-existing collection of southern Ontario seeds. For both aliens and natives, the species used represent a taxonomically broad and overlapping range of families, reducing the chances that any alien–native difference is attributable to phylogeny (Kotunen et al. 1998). All of the species chosen occur primarily, or entirely, in open, upland habitats and forest edges. Most occur naturally within the Joker’s Hill property (Table 1); all have wild populations within in the Regional Municipality of York (Riley 1989). With four exceptions, seeds had been bulk-collected from wild populations in southern Ontario between June 1996 and June 1997, and stored dry in a freezer until use. Seeds of *Digitaria ischaemum* were collected from greenhouse plants grown from local, wild seed in 1997. Seeds of *Bromus kalmii*, *Elymus trachycaulus* and *Sorghastrum nutans* were purchased from the Pterophylla Farm, Walsingham, Ontario, where they had been grown in 1996 from plants originating from wild seed stock.

Treatments

Six experimental plots (1.5 × 6.5 m) were established in July 1997, at approximately the peak time of seed dispersal. Plots were distributed evenly along the 30 m elevational gradient of the Dead Man’s Curve site but otherwise were randomly placed. Each contained sixteen 14 × 1 cm Petri dishes filled with 180 g of locally collected sand. A mixture of 20 seeds per species of a random subset of 10–11 of the 43 experimental species was placed on the surface of the sand in each dish; all 43 species were not used in each dish in order to avoid unmanageably high seed densities, but all were present in each treatment in each plot.

Four treatments were used: 1) control, 2) vertebrate exclusion, 3) insect exclusion, and 4) vertebrate + insect exclusion. Vertebrate exclusion was accomplished by enclosing the Petri dish in a wire mesh cage (1-cm gauge) secured by ground staples; the depth of these cages would have made their contents inaccessible to most granivorous birds. Exclusion of terrestrial insects was accomplished by covering the outer edge of the Petri dish with Tangle-trap Insect Trap Coating (The Tanglefoot Company, Grand Rapids, Mich.). This substance is usually most effective at excluding small crawling insects (like ants), while birds and rodents retained access to these dishes. Vertebrate exclusion + insect exclusion was accomplished by combining these treatments (i.e., protecting dishes with both screening and Tangle-trap). The height of each dish was small compared to the height of the surrounding vegetation (ca. 50 cm), ensuring that all dishes were well within the surface boundary layer. In the control and vertebrate exclusion treatments, Petri dishes were sunk into the ground leaving the edges flush with the soil surface to allow easy access to crawling insects. The depth of all dishes remained constant at 1 cm.

Table 1. Experimental species.

Natives				Aliens			
Family	Species	weight (mg) ^a	JH ^b	Family	Species	weight (mg)	JH
Asclepiadaceae	<i>Asclepias syriaca</i> L.	5.2	+	Apiaceae	<i>Daucus carota</i> L.	0.7	+
Asteraceae	<i>Artemisia campestris</i> L.	0.1		Asteraceae	<i>Arctium minus</i> (Hill) Bernh.	9.8	+
Asteraceae	<i>Solidago nemoralis</i> Ait.	0.1	+	Asteraceae	<i>Chrysanthemum leucanthemum</i> L.	0.3	+
Boraginaceae	<i>Hackelia virginiana</i> (L.) Johnst.	2.6	+	Boraginaceae	<i>Echium vulgare</i> L.	2.5	+
Brassicaceae	<i>Arabis glabra</i> (L.) Bernh.	0.1	+	Brassicaceae	<i>Alyssum alysooides</i> (L.) L.	0.3	+
Caryophyllaceae	<i>Silene antirrhina</i> L.	0.1	+	Caryophyllaceae	<i>Silene vulgaris</i> (Moench) Garcke	1.1	+
Cyperaceae	<i>Carex muhlenbergii</i> Schk.	2.1	+	Chenopodiaceae	<i>Chenopodium album</i> L.	0.5	+
Fabaceae	<i>Desmodium canadense</i> L. DC.	6.3	+	Cyperaceae	<i>Carex spicata</i> Hudson	2.0	+
Fabaceae	<i>Lespedeza capitata</i> Michx.	3.6		Dipsacaceae	<i>Dipsacus sylvestris</i> Hudson	2.2	
Lamiaceae	<i>Hedeoma hispida</i> Pursh	0.2	+	Fabaceae	<i>Melilotus alba</i> Medikus	2.0	+
Lamiaceae	<i>Monarda fistulosa</i> L.	0.3	+	Fabaceae	<i>Vicia cracca</i> L.	12.3	+
Onagraceae	<i>Oenothera biennis</i> L. (s.l.)	0.4	+	Lamiaceae	<i>Leonurus cardiaca</i> L.	0.8	+
Plantaginaceae	<i>Plantago rugellii</i> Decne.	0.5	+	Lamiaceae	<i>Nepeta cataria</i> L.	0.6	+
Poaceae	<i>Bromus kalmii</i> A. Gray	3.2		Plantaginaceae	<i>Plantago major</i> L.	0.2	+
Poaceae	<i>Elymus trachycaulus</i> (Link) Gould	4.6		Poaceae	<i>Bromus tectorum</i> L.	3.0	
Poaceae	<i>Panicum linearifolium</i> Scrib.	0.4	+	Poaceae	<i>Digitaria ischaemum</i> (Schreb.) Schreb.	0.5	+
Poaceae	<i>Sorghastrum nutans</i> (L.) Nash	1.7		Poaceae	<i>Elymus repens</i> (L.) Gould	3.4	+
Ranunculaceae	<i>Anemone cylindrica</i> A. Gray.	1.1	+	Polygonaceae	<i>Rumex crispus</i> L.	1.5	+
Ranunculaceae	<i>Ranunculus rhomboideus</i> Goldie	1.3		Rosaceae	<i>Geum urbanum</i> L.	1.5	+
Rosaceae	<i>Geum aleppicum</i> Jacq.	1.0	+	Rosaceae	<i>Potentilla recta</i> L.	0.2	+
Rosaceae	<i>Potentilla arguta</i> Pursh	0.1	+	Scrophulariaceae	<i>Verbascum thapsus</i> L.	0.1	+
Scrophulariaceae	<i>Penstemon hirsutus</i> (L.) Willd.	0.1					

Total: 43 species (22 native, 21 alien)

Note: Origin (native vs. alien) follows Morton and Venn (1990) and nomenclature follows Gleason and Cronquist (1991).

^aSeed weights represent seeds as used in experiment (one seed plus any accessory structures naturally with the seed at the time of dispersal).

^bPresence on Joker's Hill research station property (JH) is indicated by "+."

The contents of the Petri dishes were recovered in August 1997, after a month in the field. Seedlings of study species in, or immediately around, the Petri dishes were also recorded at this time. The contents (seeds + sand) of each dish were then returned to the lab where they were passed through a 0.5-mm sieve to recover all but the smallest seeds. The sieved sand was then weighed to provide an independent measure of loss due to wind, rain or handling. The sand from each Petri dish was then spread thinly (ca. 0.25 cm) over potting mix in a 12 × 20 cm tray and was kept moist in a greenhouse for 3 months. Seedlings were recorded after 1.5 months and at 3 months. Seeds were recorded as recovered if seedlings were detected in the field, if seeds were found by sieving, or if seedlings were observed in the greenhouse. Any seeds trapped in the Tangle-trap were excluded from all analyses. We observed no evidence that Tangle-trap was toxic or otherwise harmful to seeds other than those actually trapped.

Analysis

Before analyses, results were corrected for abiotic losses of seeds using the following formula:

$$[1] \quad \text{corrected proportion of seeds recovered} = \frac{\text{number of seeds recovered}}{(\text{number of seeds initially added} - \text{number lost to Tangle-trap}) \times (\text{proportion of sand recovered})}$$

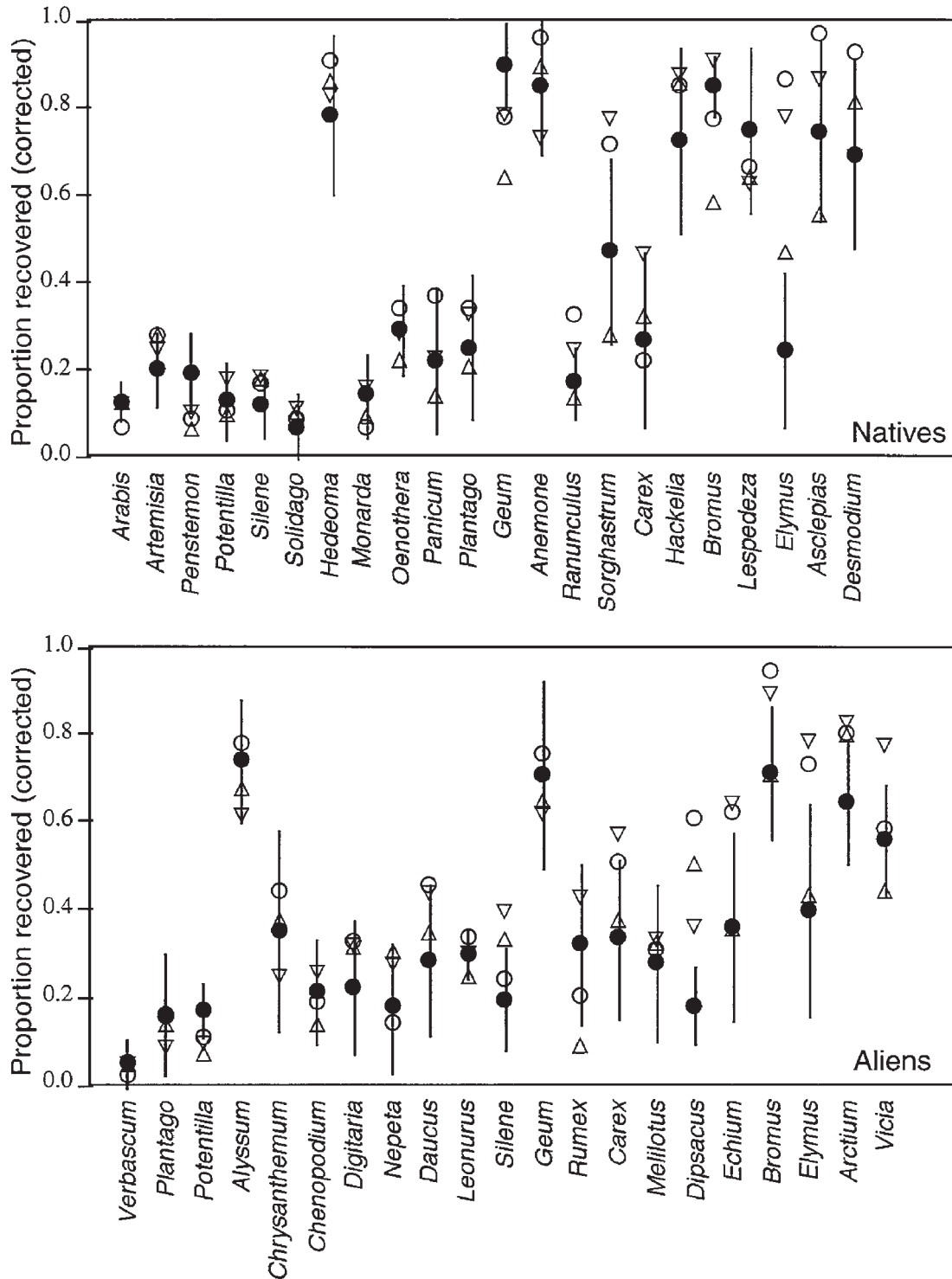
These corrected values were then arcsin transformed to improve normality (Kirk 1982).

The basic analyses were 3-factor randomized block factorial ANOVAs (Type III sums of squares), with blocking by plot, and with vertebrate exclusion, insect exclusion, and species as factors. For these analyses, a non-interactive model was used as recommended by Newman et al. (1997), so that the residual was used as the error term. Of the 1032 experimental values, 9 were discarded because of problems in distinguishing seedlings of certain species when they co-occurred in a seed combination; these cells were interpolated using treatment × species means, adjusting degrees of freedom accordingly (Underwood 1997). Treatment effects were further investigated by calculating the following contrasts (Kirk 1982):

$$[2] \quad \Psi_{\text{vertebrate}} = \text{vertebrate exclusion effect} \\ = (\text{mean}_{\text{vertebrate exclusion}} - \text{mean}_{\text{control}}) + (\text{mean}_{\text{insect \& vertebrate exclusion}} - \text{mean}_{\text{insect exclusion}})$$

$$[3] \quad \Psi_{\text{insect}} = \text{insect exclusion effect} \\ = (\text{mean}_{\text{insect exclusion}} - \text{mean}_{\text{control}}) + (\text{mean}_{\text{insect \& vertebrate exclusion}} - \text{mean}_{\text{vertebrate exclusion}})$$

Fig. 1. Recovery of experimental seeds, subdivided by species. Points represent the mean proportion of seeds recovered ± 2 SE (controls only), corrected for physical losses. Species are arranged in rank order of increasing seed weight; see Table 1 for complete species names and seed weights. Treatments are controls (●), insect exclusion (Δ), vertebrate exclusion (∇), and insect exclusion + vertebrate exclusion (○). For both natives and aliens, mean recovery and treatment effects differed significantly among species; see Table 2 for details.



We also performed a Split-plot Factorial ANOVA to compare mean responses of natives and aliens, treating species as random blocks, treatments as fixed effects, and using blocks and their interactions as error terms (Kirk 1982). Means are reported ± 1 SE.

Results

The uncorrected rate of seed recovery averaged $37.5 \pm 0.1\%$, while $89.5 \pm 0.9\%$ of sand was recovered, leading to a

Table 2. Results of 3-factor randomized block factorial ANOVAs on the recovery of experimental seeds.

Factor	Natives			Aliens		
	df	MS	<i>F</i> value	df	MS	<i>F</i> value
Plot	5	0.733	3.412**	5	1.131	4.713***
Vertebrate exclusion	1	6.947	32.336***	1	5.335	22.232***
Insect exclusion	1	0.038	0.177	1	0.033	0.138
Species	21	13.501	62.843***	20	7.844	32.688***
Vertebrate exclusion × insect exclusion	1	1.330	6.191*	1	0.040	0.167
Vertebrate exclusion × species	21	0.666	3.100***	20	0.443	1.846*
Insect exclusion × species	21	0.444	2.067**	20	0.393	1.638*
Vertebrate exclusion × insect exclusion × species	21	0.243	1.131	20	0.240	1.000
Error	431	0.215	—	410	0.240	—

Note: "Plot" was treated as the blocking factor, and the residual was used as the error term.

* $p < 0.01$

** $p < 0.001$

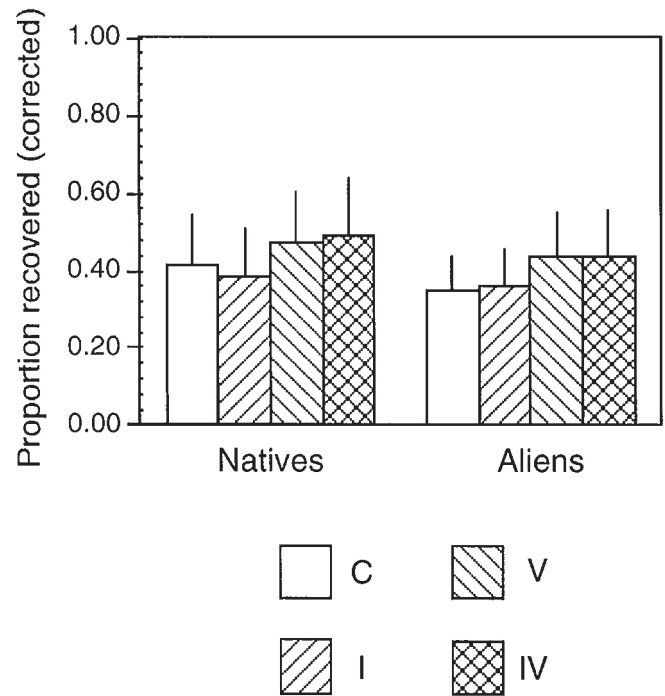
*** $p < 0.0001$

corrected seed recovery rate of $41.4 \pm 1.0\%$. Recovery rates varied significantly among species (Table 2), with corrected rates ranging from 85.5% in *Anemone cylindrica* to 4.0% in *Verbascum thapsus* (Fig. 1). Mean recovery declined with decreasing seed size ($r_{\text{Pearson}} = 0.431$, $p < 0.005$; $r_{\text{Spearman}} = 0.625$, $p < 0.001$; $n = 43$; Fig. 1). Most seed recovery (85.1%) was accomplished by sieving; 7.2% of recovered seeds germinated in the Petri dishes in the field, 5.1% of recovered seeds germinated in the greenhouse, and 2.7% of recovered seeds were found as seedlings outside of Petri dishes in the field. Five native species (*S. nemoralis*, *Arabis glabra*, *Penstemon hirsutus*, *Potentilla arguta*, *Artemisia campestris*), and one exotic (*V. thapsus*) were recorded primarily or entirely by greenhouse germination; these were all small-seeded species, for which overall recovery was low (Fig. 1).

For most species, controls had lower rates of seed recovery than vertebrate granivore exclusion treatments. Vertebrate exclusion produced higher recovery than controls for 30 of the 43 experimental species (Fig. 1), resulting in a highly significant vertebrate exclusion effect (Table 2) which increased overall seed recovery from 38.2 (controls) to 45.6% (vertebrate exclusion) (Fig. 2). Some species showed much larger effects than this average (Fig. 1); as a result, vertebrate exclusion × species interactions also were significant (Table 2). Contrasts of vertebrate exclusion treatments versus other treatments ($\Psi_{\text{vertebrate}}$; eq. 2) indicated that the magnitude of the vertebrate exclusion effect was positively correlated with seed size ($r_{\text{Pearson}} = 0.419$, $p = 0.005$; $r_{\text{Spearman}} = 0.616$, $p < 0.001$; $n = 43$); the recovery of larger seeds was improved more by caging than the recovery of smaller seeds. Overall, nine of the ten species with the greatest increases in recovery as a result of vertebrate exclusion had seed weights above the median of 1.0 mg. Insect exclusion produced higher seed recovery in 20 of 43 species (Fig. 1), slightly less than the 50% of species predicted by random chance. Accordingly, insect exclusion had no overall effect (Table 2), though insect exclusion × species interactions were significant (Table 2; Fig. 2). These results imply that insect exclusion had different effects on different species: some species had improved recovery, while recovery in others was reduced, possibly because of physical losses. Contrasts of insect exclusion treatments versus other treat-

ments (Ψ_{insect} ; eq. 3) indicated that the magnitude of the insect exclusion effect was unrelated to seed size ($r_{\text{Pearson}} = -0.028$, $p = 0.860$; $r_{\text{Spearman}} = 0.011$, $p = 0.941$; $n = 43$).

Natives and aliens did not differ in their susceptibility to predation. An ANOVA comparing mean recovery for native and alien species again found a significant vertebrate exclusion effect (Table 3) but no evidence of a native–exotic difference or interactions. Instead, the general pattern of treatment effects was very similar for natives and exotics, especially when considered relative to the large among-species differences (Table 2; Fig. 1). When natives and exotics were



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Table 3. Results of a Split-plot Factorial ANOVA comparing mean recovery of seeds of native and exotic species.

Factor	df	MS	F
origin	1	0.444	0.317
species	41	1.398	—
Vertebrate exclusion	1	1.489	21.577***
Vertebrate exclusion × origin	1	0.001	0.014
Vertebrate exclusion × species	41	0.069	—
Insect exclusion	1	0.000	0.006
Insect exclusion × origin	1	0.004	0.077
Insect exclusion × species	41	0.051	—
Vertebrate exclusion × insect exclusion	1	0.023	0.782
Vertebrate exclusion × insect exclusion × origin	1	0.058	1.978
Vertebrate exclusion × insect exclusion × species	41	0.029	—

Note: “origin” refers to native vs. exotic origins; “species” was used as the blocking factor; blocks and their interactions were used as the error terms.

* $p < 0.01$.

** $p < 0.001$.

*** $p < 0.0001$.

considered separately, plot and species had highly significant effects on seed recovery for both (Table 2). For both natives and aliens, vertebrate exclusion had a highly significant positive effect on seed recovery, and there were significant interactions of insect exclusion × species and vertebrate exclusion × species (Table 2; Fig. 2).

Discussion

Predator identity

Our results suggest that vertebrates are more important than terrestrial insects as post-dispersal seed predators for the majority of species at our study site. Many other studies in similar habitats tend to support this conclusion (summarized in Janzen 1971; Thompson 1987; Louda 1989; Crawley 1992; Chambers and MacMahon 1994; Baskin and Baskin 1998). In temperate grasslands and old fields, mammals (primarily rodents) often are important as seed predators (e.g., Mittelbach and Gross 1984; Gill and Marks 1991; Hulme 1994; Ostfeld et al. 1997; Manson and Stiles 1998; Edwards and Crawley 1999). Many temperate zone birds are also granivores, and also may have important impacts on seed survival in grassland habitats (Howe and Brown 1999). Invertebrates tend to be less important (Mittelbach and Gross 1984; Hulme 1994), though Reader and Beisner (1991) found that ants, not rodents or birds, were significant seed predators at a site similar to ours and only 75 km distant. Slugs and snails (Newell 1967; Crawley 1997), and winged insects, including carabid beetles (Kjellson 1985) and lygaeid bugs (Collins and Uno 1985), also can feed on seeds and small seedlings at the soil surface.

Occasional droppings observed in the Petri dishes during our experiment confirmed the presence of birds and rodents. The common occurrence of seed husks and damaged seeds in these dishes suggests that many seeds were consumed by birds and rodents on site rather than being cached, as also was found in a similar study in old field habitats (Mittelbach and Gross 1984). Commonly observed seed eating birds at our study site were field sparrow (*Spizella pusilla*), song sparrow (*Melospiza melodia*), northern cardinal (*Cardinalis cardinalis*), indigo bunting (*Passerina cyanea*), and Ameri-

can goldfinch (*Carduelis tristis*). Granivorous deer mice (*Peromyscus* spp.) are abundant at this site, and other seed and seedling predators such as meadow vole (*Microtus pensylvanicus*), meadow jumping-mouse (*Zapus hudsonius*), and eastern chipmunk (*Tamias striatus*) also occur. Ants were the only seed-eating insects commonly found adhering to the Tangle-trap-coated dishes, and a single observation of ants removing seeds also was made. None of the seeds used in the study had eliasomes, and thus any seed removal by ants was likely for consumption of the seed itself. Lygaeids and carabids were likely not important post-dispersal seed predators at our site since none of these ground-foraging taxa (Kjellson 1985) were found among the many insects stuck to the Tangle-trap; however, snails and slugs are locally common, and slime trails indicated that they occasionally entered experimental dishes.

Some losses to predators may have occurred shortly after germination; as a result, some of the losses we observed may have been seedling predation, rather than seed predation. It is very difficult to determine whether a missing or shelled seed was killed before or after germination; however, since a very small proportion of seeds are known to have germinated in the field (2.7% of all experimental seeds), we feel justified in interpreting our results as primarily reflecting seed predation. Nonetheless, some of the predators involved in this experiment (e.g., molluscs; Crawley 1997) may have specialized primarily on germinating seeds.

Rates of seed removal

The magnitude of seed removal in this experiment was considerably lower than values reported for most comparable studies (Thompson 1987; Louda 1989; Crawley 1992; Chambers and MacMahon 1994; Baskin and Baskin 1998). It is not surprising that predation rates were lower than those found in studies in arid landscapes, which have numerous specialist granivorous rodents and ants; however, our measured rates of removal were also low compared to other temperate-habitat studies. We found vertebrates removed <10% of seeds in 1 month (in excess of control values), and insect removal was negligible. In comparison, Mittelbach and Gross (1984) and Hulme (1994) investigated post-dispersal

seed predation in old fields in Michigan and England. They found predation rates of 5% per day and 24% per day over 6 days and 3 days respectively. This discrepancy might be attributable to differences between the timing and duration of these studies; however, one might expect that the July–August scheduling of our experiment would be ideal for detecting effects of both insects and resident birds, while its one-month duration was longer than that of most similar studies. Instead, the low rates in our study may reflect low predator abundances, but probably are also partly attributable to our use of numerous seeds weighing <1 mg (Table 1). Seed predators often tend to prefer large seeds (Thompson 1987; Hulme 1994, 1996), and studies by Kelrick et al. (1986), Mittelbach and Gross (1984) and Reader (1993) suggest that seeds below 1–3 mg tend to escape predation by a wide range of vertebrates. In our study, impacts of vertebrate predators increased with seed size, supporting this interpretation. In contrast, effects of insect predation did not vary regularly with seed size; seed chemistry and surface characteristics may have been more important than size in determining losses to insects.

Controls sometimes had higher rates of recovery than exclusion treatments; we attribute this both to uncontrolled losses from exclusion treatments (see below) and to random error associated with high among-sample variance. Such results should bias against the detection of predator exclusion effects, making tests of predator impacts more conservative. Conversely, we observed surprisingly high rates of loss (>50%) from Petri dishes protected from both vertebrate and terrestrial insect predators. There are several possible sources for this loss. First, the correction factor for physical loss of seeds based on the recovery of sand was probably an underestimate; seeds may have blown out of dishes or washed out in rainfall more readily than the sand beneath them. This may have been especially true for smaller seeds, explaining their generally low rates of recovery. Second, inviable or dormant seeds may not have been detected by germination tests. Again, this may have been an especially serious problem for smaller seeds, which were more likely to escape visual detection. Finally, the methods used to exclude seed predators may not have been effective against all taxa. Though caging probably excluded both rodents and the majority of seed-eating birds, a few long-beaked species may have had access to some caged dishes, while Tangle-trap may fail against invertebrates other than small, crawling insects. In particular, molluscs did not become trapped in the Tangle-trap, and may have been able to enter some dishes. Since these factors would have led to losses of seeds from all experimental treatments, they cannot explain our detection of highly significant exclusion treatment effects. However, they may have contributed to lower rates of recovery for some species (especially those with small seeds), and may have obscured exclusion treatment effects by removing seeds from “protected” treatments.

Differences among species

Consistent differences in recovery rates among species probably reflect both physical (weight, buoyancy) and biological (dormancy) characteristics. More interesting are the species–treatment interactions; different species responded differently to the predator exclusion treatments. In particular,

larger seeds were distinctly more susceptible to vertebrate predation; this agrees with work in shrub steppe by Kelrick et al. (1986), and in old fields by Mittelbach and Gross (1984) and Reader (1993). One taxonomic trend in predation rates was also evident: graminoids were overrepresented among the seeds favoured by vertebrates. The six species exhibiting the most improved recovery with vertebrate exclusion included four grasses and one sedge, out of only nine graminoids in our study; much of this trend may be explained by the relatively large size of these seeds.

Aliens versus natives

Aliens and natives did not differ in their susceptibility to seed predation. There was no evidence that aliens benefitted from a substantially reduced rate of post-dispersal seed predation, as predicted by both the predator escape and predator filter hypotheses. Instead, aliens and natives apparently suffered similar rates of predation by vertebrates, and very little predation by insects. The predator escape hypothesis requires the existence of species specific natural enemies, which are lost when the host plant migrates to a new region. Vertebrate herbivores tend to be much less specialized in their diets than insects (Strong et al. 1984; Crawley 1989); given that vertebrates were the important predators of these seeds, it is perhaps not surprising that the predator escape hypothesis did not apply to our results. In contrast, the predator filter hypothesis does not require specialist enemies, only that successful exotics tend to be more predator-resistant than species which fail to establish; species with seeds unattractive to granivores because of size, structure, or chemical characteristics might make better invaders than species with highly palatable seeds. Our results reject this hypothesis as well. Although recovery varied significantly among species, there was no evidence that exotics were, on average, less palatable than natives. Instead, any differences between seeds of exotics and natives apparently were trivial relative to the interspecific variation within these groups. For example, the smallest and largest seeds in this experiment differed in weight by more than two orders of magnitude, but on average natives and exotics differed in weight by only about 36% (natives= 1.60 mg, aliens= 2.17 mg); since vertebrate predation varied with seed size, it is perhaps not surprising that losses to vertebrates varied more strongly within than between these groups. These conclusions further support the view that aliens and natives often do not differ in predictable ways (e.g., Perrins et al. 1992; Thompson et al. 1995; Williamson 1996); instead, colonization by natives and by exotics are likely to be favoured by similar characteristics, meaning that exotics and natives in the same habitat are also likely to be ecologically similar.

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