

DO SMALL-SEEDED SPECIES HAVE HIGHER SURVIVAL THROUGH SEED PREDATION THAN LARGE-SEEDED SPECIES?

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Abstract. Seed ecologists have often stated that they expect larger-seeded species to have lower survivorship through postdispersal seed predation than smaller-seeded species. Similar predictions can be made for the relationship between survivorship through predispersal seed predation and seed mass. In order to test these predictions, we gathered data regarding survivorship through 24 hours of exposure to postdispersal seed predators for 81 Australian species, and survivorship through predispersal seed predation for 170 Australian species. These species came from an arid environment, a subalpine environment, and a temperate coastal environment. We also gathered data from the published literature (global) on survivorship through postdispersal seed predation for 280 species and survivorship through predispersal seed predation for 174 species.

We found a weak positive correlation between seed mass and the percentage of seeds remaining after 24 hours of exposure to postdispersal seed predators at two of three field sites in Australia, and no significant relationship across 280 species from the global literature, or at the remaining field site. There was no significant relationship between seed mass and survivorship through predispersal seed predation either cross-species or across phylogenetic divergences in any of the vegetation types, or in the compilation of data from the literature. Postdispersal seed removal was responsible for a greater percentage of seed loss in our field studies than was predispersal seed predation. On average, 83% of diaspores remained after 24 hours of exposure to postdispersal seed removers, whereas 87% of seeds survived all predispersal seed predation that occurred between seed formation and seed maturity. Mean seed survival was higher in the field studies than in the literature compilations, and species showing 100% survival were heavily underrepresented in the literature. These differences may be due to biases in species selection or publication bias. Seed defensive tissue mass increased isometrically with seed mass, but there was no significant relationship between the amount of defensive tissue per gram of seed reserve mass and survivorship through postdispersal seed predation.

Key words: *Australia; postdispersal seed predation; predispersal seed predation; publication bias; seed defense; seed mass; seed predation vs. seed size.*

INTRODUCTION

Plants around the world make seeds in an impressively wide range of sizes, from the dust-like seeds of orchids that weigh only one millionth of a gram, to the huge seeds of the double coconut that can weigh an awesome 20 kg each (Harper et al. 1970). Even within plant communities, there are usually 5–6 orders of magnitude of variation in seed mass across species (Leishman et al. 2000). These differences in seed mass can have substantial effects on the chances that seeds will survive the different threats to which they are exposed in the course of their development, dispersal, and establishment as seedlings (Westoby et al. 1996, Leishman et al. 2000). One hazard that seeds must survive is seed predation.

There are two main types of seed predation: (1) predispersal seed predation, which occurs while seeds are still on their mother plant, and (2) postdispersal seed predation, which occurs once seeds have dispersed away from their parent. Predispersal seed predation is largely carried out by invertebrates such as coleoptera, diptera, lepidoptera, and hymenoptera (Crawley 1992, Hulme 1998b), many of which develop inside the seeds. Postdispersal seed predation is largely carried out by larger organisms such as rodents, but ants are also important postdispersal seed predators (Crawley 1992, Hulme 1998b).

In this paper, we use a combination of field estimates of survivorship through seed predation (across many species in three Australian vegetation types) and a compilation of previously published estimates of survivorship through predation (global) to investigate relationships between seed mass and survivorship through exposure to pre- and postdispersal seed predation (henceforth referred to as pre- and postdispersal survivorship). We also investigate relationships between seed defenses, seed mass, and pre- and postdispersal survivorship.

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Seed mass and postdispersal survivorship

There is a general expectation that large seeds will have lower postdispersal survivorship than small seeds (Louda 1989, Blate et al. 1998, Kollmann et al. 1998). A number of reasons have been put forward to explain why this might be the case. First, large seeds might be more apparent to predators (Feeny 1976), and thus more likely to be encountered by a seed predator. Second, large seeds might spend longer on or near the soil surface than small seeds, because it is more difficult for large seeds to become incorporated into the soil profile through the action of rain or organisms such as earthworms (Thompson et al. 1994, Bekker et al. 1998). This would mean that larger seeds would be exposed to the action of seed predators over a longer period than small seeds (Bekker et al. 1998). Third, optimal foraging theory suggests that it might be more efficient for a seed predator to search for a few large seeds rather than many small seeds, given equal handling time for small and large seeds. (Charnov 1976, Hoffmann et al. 1995, Blate et al. 1998).

There are two important lines of indirect evidence for larger seeds having lower postdispersal survivorship than small seeds. (1) Seed-eating organisms faced with a range of seeds will generally take the largest seeds that they can physically process (Davidson 1977, Nelson and Chew 1977, Chew and De Vita 1980, Abramsky 1983, Moegenburg 1996, Hulme 1998a; but see Smith 1987 and Osunkoya et al. 1994). (2) Cages that exclude seed predators can result in increased recruitment of large-seeded species, but no increase in the establishment of small-seeded species (Brown and Heske 1990, Reader 1993).

Despite these arguments and indirect evidence that large seeds are more likely to be eaten by postdispersal seed predators than are small seeds, direct evidence for a negative relationship between seed size and postdispersal survivorship is limited. A few multispecies studies have shown the predicted negative relationship between seed mass and postdispersal survivorship (e.g., Hulme [1998a] for 19 herbaceous taxa from Europe; Kiviniemi [2001] for 11 species of Rosaceae in Sweden; and Reader [1997] for six old-field species). However, other studies have found no significant relationship (e.g., Moles and Drake [1999] for 11 large-seeded species from New Zealand; Hau [1997] for 16 species from Hong Kong; Kollmann et al. [1998] for 12 species from Europe; Holl and Lulow [1997] for 10 species from Costa Rica; and Meiners and Stiles [1997] for nine American species), or even a positive relationship (e.g., Blate et al. [1998] for 40 Southeast Asian rain forest species, and Osunkoya [1994] for 12 Australian rain forest species).

Seed mass and predispersal survivorship

Less attention has been paid to the possible relationship between seed mass and predispersal survi-

vorship than to the relationship between seed mass and postdispersal survivorship. However, theories based on apparency and optimal foraging ideas make the same predictions for negative relationships between seed mass and predispersal survivorship as for postdispersal survivorship. In addition, large seeds might be exposed to predispersal seed predation from a wider range of seed predators than small seeds, as large seeds can be colonized by both large and small seed predators, but small seeds can only be colonized by small seed predators (Greig 1993, Mucunguzi 1995). Large seeds might also be exposed to predispersal seed predation for a longer time, as large seeds take longer to complete development than small seeds (Moles and Westoby 2003).

There is a small amount of evidence to suggest that large-seeded species might have lower predispersal survivorship than small-seeded species. For instance, Moegenburg (1996) showed that some predispersal seed predators preferentially oviposit on larger seeds. As with postdispersal survivorship, results from existing cross-species studies are mixed. Greig (1993) found a negative relationship between seed mass and predispersal survivorship across five species of *Piper* (Piperaceae). Janzen (1969) showed that across 36 species of Fabaceae, species attacked by bruchids had significantly smaller seeds than those that were not attacked. Auld (1983) found no significant relationship between seed mass and predispersal survivorship for 28 Australian Fabaceae, and there was a positive relationship between seed mass and predispersal survivorship across nine species of *Yucca* (Keeley et al. 1984).

In this study, we aimed to provide a broad survey to test the hypothesis that pre- and postdispersal survivorship might be higher in small-seeded than in large-seeded species.

What is the magnitude of seed loss to pre- and postdispersal seed predation?

It is not uncommon for plants to lose 90–100% of a given seed crop to seed predators (Louda 1989, Crawley 1992, Hulme 1998b). These losses can result in significantly reduced seedling establishment (Brown et al. 1979, Inouye et al. 1980, De Steven and Putz 1984, Hobbs 1985, Louda 1989, Heske et al. 1993, Asquith et al. 1997, Cornett et al. 1998, Feller and Klinka 1998). A previous literature compilation found an average of 55% predispersal survivorship, and 50% postdispersal survivorship (Crawley 1992). In this study, we were interested in quantifying and comparing pre- and postdispersal survivorship across the full suite of species setting seed at a few sites, and in determining whether postdispersal survivorship values reported in the literature were comparable to those found in our own cross-species studies in Australian ecosystems.

Other factors explaining variability in pre- and postdispersal survivorship across species

Seed mass is not expected to explain all (or even the majority) of the variation in pre- or postdispersal sur-

ivorship across species. Many other traits might influence a species' survivorship, including the amount of time seeds spend exposed to seed predators, and chemical and physical seed defenses. Quantification of the time spent exposed to seed predators was beyond the scope of this study, but we know from previous studies that large seeds spend longer exposed to predispersal seed predators (Moles and Westoby 2003). Large seeds may also remain on the soil surface exposed to postdispersal seed predators for longer than small seeds (Bekker et al. 1998). Investigations of chemical defense of seeds were also beyond the scope of this study. However, we were able to investigate the relationship between postdispersal survival and species' physical defenses.

It has been proposed that higher investment in seed coat tissue and fruit tissue dispersed with seeds might increase a species' postdispersal survivorship (Mazer 1998). Some evidence supports this idea. *Pinus flexilis* allocates more energy to seed defense in environments where seed predation is present than where it is absent (Benkman 1995). Postdispersal survivorship was positively associated with seed coat thickness and hardness for 40 species from Southeast Asia (Blate et al. 1998). Similarly, Rodgerson (1998) found a positive relationship between seed strength and survivorship through seed predation by the ant *Rhytidoponera metallica* for 17 plant species from Sydney, and Gathua (2000) noted that hard seed pods prevented some seed predators from accessing *Aflezia quanzensis* seeds. However, Auld (1983) found no consistent relationship between physical defenses of developing legume seeds and predispersal survivorship for 28 Australian legume species. Thus, our final aim was to quantify the relationship between postdispersal survivorship and physical defenses across a wide range of species.

In summary, the questions addressed in this paper are: (1) Is there a relationship between postdispersal survivorship and seed mass? (2) Is there a relationship between predispersal survivorship and seed mass? (3) What percentage of seeds survive pre- and postdispersal seed predation in Australia? (4) Do species with a high ratio of protective tissue to seed reserve mass have greater postdispersal survivorship than those with relatively less investment in protection?

METHODS

Study sites

Field sites were located in three very different ecosystems in New South Wales, Australia (Appendix A): Sturt National Park (an arid area in northwestern New South Wales that supports chenopod shrublands and grassland; sites around 29°10' S; 141°37' E), Ku-ring-gai Chase National Park (a temperate coastal environment near Sydney that supports fire-prone forest and heath; sites around 33°37' S; 151°15' E) and Kosciuszko National Park (an alpine to subalpine environment

that supports subalpine forests, grasslands, and alpine herbfields; sites around 36°22' S; 148°26' E). These different ecosystems were chosen in order to maximize the total number of species studied and to determine whether patterns observed in field trials were generalizable across ecosystems.

Species selection at field sites

To be included, a species had to be represented by at least five fruiting individuals, carrying a combined total of at least 150 ripe seeds at the time of fieldwork. Species studied for predispersal survivorship had to have at least 50 ripe fruits that had not begun to dehisce. Species studied for postdispersal survivorship had to have seeds large enough to be reliably relocated after placement on the soil surface, and could not possess adaptations for wind dispersal. We included all species that had sufficient suitable seeds at the time of fieldwork at each site, but excluded species with elaiosomes from analyses involving postdispersal seed removal, as removal of these seeds might not be very tightly associated with seed predation. This resulted in postdispersal survivorship data for 81 Australian species and predispersal survivorship data for 170 Australian species. Lists of the species studied for pre- and postdispersal seed predation at each site, as well as seed mass, percentage survival, and phylogenetic trees, can be found in Appendices B–G.

Postdispersal survivorship

Twenty depots were established for each species. At each depot, five seeds were placed into a depression in the ground to reduce the chance that seeds would be blown away by wind. We used naturally formed depressions wherever possible in order to minimize soil and litter disturbance. Seeds were set directly on the soil surface in order to mimic the natural situation as closely as possible. Seeds were set out complete with whatever protective tissues would normally accompany them after natural seed dispersal. Thus, diaspores (rather than seeds) were the actual unit of study for postdispersal survivorship. Structures that are usually lost during seed dispersal (such as the flesh of fleshy-fruited species) were removed before postdispersal survivorship trials. At each depot, seeds were placed within 5 cm of a wooden toothpick, and a larger marker (a labeled aluminum tag on a peg pushed into the ground) was established 1 m from the toothpick. Seed depots were established every 10 m along transect lines within the vegetation type from which the seeds were collected. Depots for the different species at each site were arranged haphazardly along the transect lines. Seeds were set out within two days of collection. Thus, postdispersal survivorship was monitored in the natural environment in which the species occurred, and at the time of year at which seeds of that species would normally be available. The number of seeds remaining at each depot was censused 24 hours after they had been

set out. Seeds were considered to have been removed if they could not be found within 30 cm of the toothpick, or if they had been damaged to such an extent that germination seemed unlikely. It is important to note that we have measured seed removal, not seed predation. Seed removal may largely correspond to seed predation, but it is not possible to be certain about that. Nearly all published estimates of postdispersal "predation" actually estimate removal in this same manner.

In Sturt and Kosciuszko National Parks, postdispersal survivorship was estimated over a single 24-hour period for each species. However, in Ku-ring-gai Chase National Park we were able to spread the trials over four study days for each species.

Where the vegetation is very open, secondary dispersal of the seeds by the wind could be a major issue (Manson and Stiles 1998). Species considered likely to have been affected by the wind and those with seeds that were too small to be reliably found on the soil surface were excluded from the postdispersal survivorship study, as were species with elaiosomes. Consequently, the range of taxa and seed masses represented was narrower for postdispersal survivorship than for predispersal survivorship.

Predispersal survivorship

For each species, at least 100 mature seeds from a minimum of five plants were collected and checked for damage. In the case of species with many-seeded fruits, seeds were taken from at least 50 fruits. Seeds were considered to have been preyed upon when there was clear evidence, i.e., if the seeds showed entry/exit holes, or if invertebrates, frass, or fragments of damaged seed coat were present in place of a seed. If all of the seeds in a multi-seeded fruit had been completely destroyed by a seed predator (i.e., were not able to be counted), then the number of seeds preyed upon in that fruit was taken to be the mean number of seeds set per fruit for that species. Considering any seed with predation damage to be inviable means that we may have slightly overestimated postdispersal seed predation, as some seeds (especially large seeds) can germinate despite partial consumption (Steele et al. 1993, Ollerton and Lack 1996, Dalling et al. 1997, Hobbs and Young 2001). On the other hand, seeds that were aborted before maturity were not counted as preyed upon, although this may sometimes have been due to predators feeding on nearby stem or fruit tissue. Predispersal seed predation by taxa that remove the entire fruit from the plant was not assessed.

Seed mass

Twenty seeds of each species were oven-dried at 60°C for at least three days, and then weighed on a Cahn microbalance (Cahn Instruments, Cerritos, California, USA). For predispersal seed predation, true seeds were the unit of study (rather than diaspores).

For postdispersal seed removal, diaspore mass was used. The dry mass of protective structures for at least 10 diaspores of each species was also recorded. Protective structures were defined as all tissue surrounding the embryo and endosperm after dispersal (including fruit tissue not removed during dispersal, seed coats, and pods). Accessories that provided no protection from seed predation, such as wings for dispersal and structures that lie below the seeds (e.g., receptacles in Asteraceae and *Isopogon*), were not included in protective structure mass.

Compilation of data from the literature

We compiled data regarding the pre- and postdispersal survivorship from all of the papers cited in reviews by Crawley (1992) and S. A. Cunningham (*unpublished data*; 138 species). These sources provided a relatively complete search of the literature up to 1992 (Crawley) and 1994 (Cunningham). We then searched *Current Contents* (January 1993–July 2002) for articles in English containing the words "seed" and "predation" in the title or abstract. Because seed fate has rarely been measured in studies of postdispersal seed "predation," we have been forced to review the percentage of seeds remaining after 24 hours of exposure to seed predators rather than the percentage of seeds surviving postdispersal seed predation per se. Pre- and postdispersal survivorship were averaged over all sites, times, and densities to find a mean survival rate for each species. Results from studies that quantified the percentage of seeds remaining after >24 hours of exposure to postdispersal seed predators were converted to a 24-hour basis assuming an exponential rate of seed removal (exponential seed removal would result from the removal of a constant percentage of seeds each day, and has commonly been observed in seed predation studies; e.g., Blate et al. 1998). Studies that did not report sample sizes were necessarily excluded from analyses, as were studies that quantified the percentage of fruits showing damage without quantifying the percentage of seeds preyed upon. Only studies and treatments that allowed access to all types of predators were included. A full description of the methods used to compile data from the literature can be found in Moles and Westoby (2003). Lists of the species included in literature compilations of pre- and postdispersal seed predation, as well as seed mass, percentage survival, habitat type, study location, data sources, and phylogenetic trees used in phylogenetic regressions, can be found in Appendices H and I.

Seed mass data were gathered from the same papers as survivorship data wherever possible, or from other published sources. If seed mass could not be found in either of those ways, species were excluded from this compilation. Habitat types were assigned based on the vegetation classification scheme provided by Udvardy (1975).

TABLE 1. Results of cross-species and phylogenetic regressions on the relationships between seed mass and survivorship through pre- and postdispersal seed predation.

Site	Cross-species regression				Phylogenetic regression			
	No. species	<i>P</i>	Mean slope (95% CI)	Species effect	df	<i>P</i>	<i>R</i> ²	Slope
Postdispersal predation								
Sturt	44	<0.001	1.18 (0.59–1.81)	1.19	1, 25	<0.001	0.36	1.05
Ku-ring-gai	24	<0.001	2.30 (1.35–3.32)	1.38	1, 17	0.001	0.48	1.98
Kosciuszko	13	0.21	–1.18 (–3.04–0.71)	1.61	1, 7	0.55	0.05	–0.67
Literature	280	0.06	0.13 (0.00–0.28)	1.9	1, 147	0.59	<0.01	0.04
Predispersal predation								
Sturt	80	0.08	–0.92 (–1.98–0.11)	2.66	1, 43	0.39	0.018	–0.39
Ku-ring-gai	41	0.995	0.004 (–1.27–1.40)	3.26	1, 31	0.86	0.001	–0.07
Kosciuszko	49	0.65	–0.29 (–1.64–1.00)	4.13	1, 27	0.16	0.07	–0.82
Literature	174	0.47	–0.16 (–0.50–0.28)	1.8	1, 72	0.27	0.02	–0.23

Notes: Cross-species regressions were performed using random effects logistic regressions. Phylogenetic regressions were performed on logit-transformed survivorship data (see *Methods* for details on statistical techniques). To account for the large number of regressions performed here, Bonferroni corrections were applied; thus, we did not consider a relationship to be significant unless its *P* value was <0.0125 (0.05/4) for each regression.

Statistics

The main purpose of this study was to investigate relationships between survivorship and seed mass. Because survival is a binary variable (any seed will either survive or be eaten), we analyzed these data with logistic regression, which appropriately uses a binomial data structure within each species. Logistic regression models the mean–variance relationship of binomial data correctly, while fitting a model that ranges from 0% to 100% survival. If data were instead transformed and linear regression were used, it would only be possible to achieve one of these two properties: the former using arcsine-transformed proportions and the latter using logit-transformed proportions. Because only a fraction of the between-species variation in survivorship was expected to be due to seed mass, a term was included in the model to account for other sources of species-to-species variation (this term is listed as “species effect” in Table 1). Therefore, we used random effects logistic regression to estimate relationships between seed mass and pre- and postdispersal survivorship (McCulloch and Searle 2001). Each model was fitted using winBUGS version 1.3 (MRC Biostatistics Unit 2002), which uses the Monte Carlo Markov chain method (Gilks et al. 1996) for estimation. In fitting models, we used a burn-in of 1000 updates, followed by 50 000 updates. Seed or diaspore mass was \log_{10} -transformed before all calculations.

Phylogenetic regressions (Grafen 1989, Westoby 1999) were also performed on the relationships between \log_{10} seed mass and logit-transformed survivorship. Because 100% survival cannot be plotted on a logit scale (it is infinite), it was necessary to add 0.5 to the number of seeds preyed upon before calculating logit-transformed seed survivorship. This addition was only required for the phylogenetic regressions and graphs; 0% and 100% survivorship values are not a

problem for the logistic regressions used to calculate cross-species relationships. The phylogenetic trees constructed (Appendices B–I) follow Stevens (2001 onward), the APG (1998), and Kuzoff and Gasser (2000) above family level. Within families, we followed Douglas (1995) for Proteaceae, Crisp and Doyle (1995) for Fabaceae, Simon (1993) for Poaceae, and Wilson (1984) for Chenopodiaceae. We performed phylogenetic regressions using a generalized linear interactive modeling program (Phylo.glm version 1.03; Grafen 1989). Path segment lengths for the phylogenetic trees were calculated by assigning a height to each node that was one less than the number of species below or at that node in the tree (Grafen 1989). Note that the model used for the phylogenetic regression did not include a term for species effect.

The slope of the relationship between protective tissue mass and seed reserve mass was calculated using a Standardized Major Axes technique, SMA (also known as reduced major axis or geometric mean regressions; Sokal and Rohlf [1995]). Confidence intervals (CIs) for this slope were calculated using the method of Pitman (1939).

RESULTS

Postdispersal survivorship vs. seed mass

There were weak positive relationships between diaspore mass and postdispersal survivorship in Ku-ring-gai Chase National Park and in Sturt National Park, a marginally nonsignificant positive relationship across 280 species from the global literature, and no significant relationship in Kosciuszko National Park (Table 1, Fig. 1). However, the sample size at Kosciuszko was small ($n = 13$ species), so power to detect a relationship there was low. Thus, not only was the often-predicted negative relationship between seed mass and postdispersal survivorship absent from all four of our studies,

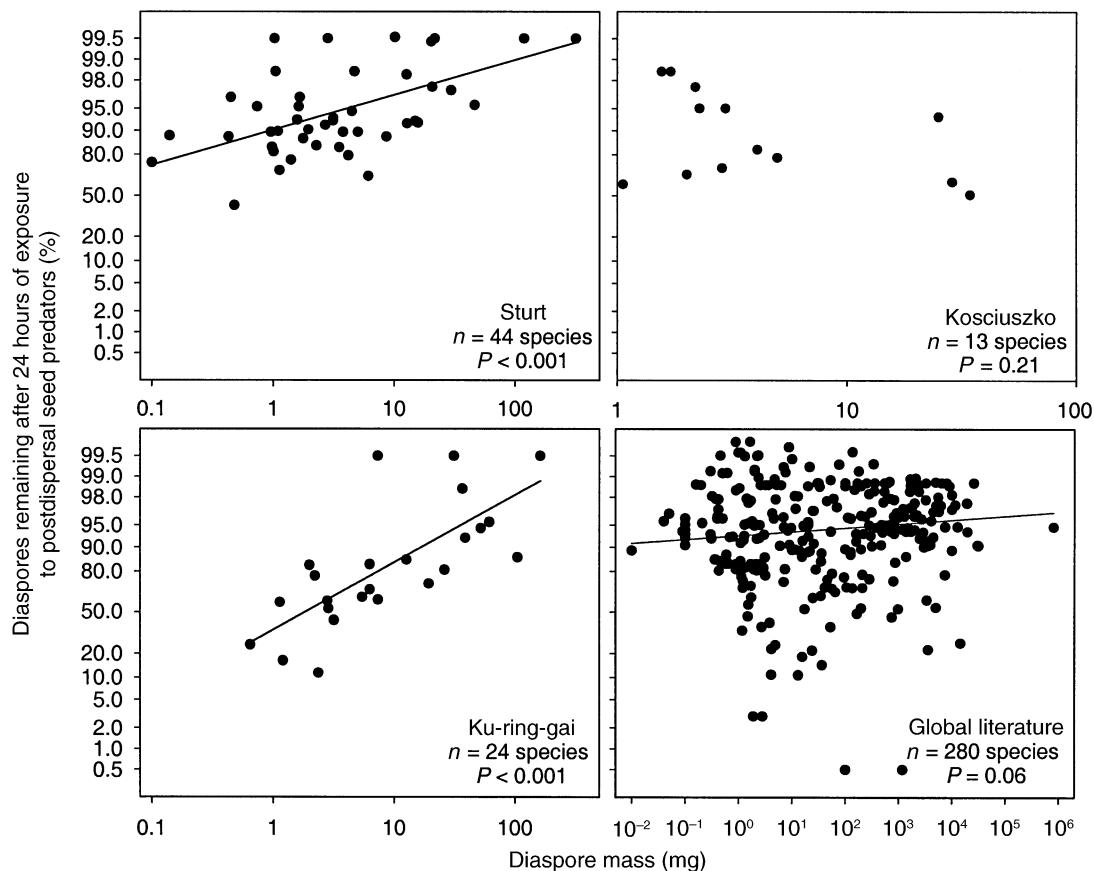


FIG. 1. Percentage of diaspores remaining after 24 hours of exposure to postdispersal seed predators (logit scale) vs. diaspore mass (log scale) from each of the three Australian habitats and from a compilation of data from previously published studies from the global literature. Kosciuszko species are from alpine and subalpine regions, Ku-ring-gai species are from dry sclerophyll vegetation, and Sturt species are from an arid environment. Each point represents the mean value for one species; P values indicate the results of random effects logistic regressions (details are in *Methods* and Table 1).

but also there was a trend toward positive relationships between postdispersal survivorship and seed mass. However, the predictive capacity (R^2) of seed mass for survivorship was low (Table 1).

Predispersal survivorship vs. seed mass

Predispersal survivorship was not significantly related to seed mass at Sturt National Park, at Ku-ring-gai Chase National Park, at Kosciuszko National Park, or in the global literature (Table 1, Fig. 2).

Phylogenetic considerations

Conceivably, there might have been a negative relationship between seed mass and survivorship within genera or families, that is across distal branch points in the phylogenetic tree, but this might have been overridden in the cross-species regression by large differences in basic natural history between families or other major clades. Most of the phylogenetic regressions were no more negative in slope than cross-species regressions (Table 1), eliminating this possibility from

consideration for most relationships. The relationship between postdispersal survivorship and seed mass for 280 species from the literature, which verged on being positive at $P = 0.06$ and slope = 0.13 in the cross species regression, weakened to $P = 0.59$ and slope = 0.04 in the phylogenetic regression, indicating that any positive relationship across species was underlain by one or a few divergences deep in the tree.

Analyses of relationships between pre- and postdispersal survivorship and seed mass within habitat types

The data from the literature span a wide range of habitats, leaving open some possibility that relationships between seed mass and survivorship might be negative within each habitat, but with this pattern being counteracted by a positive relationship across habitats. The fact that no negative relationship was found within any of the three Australian habitat-specific studies argues strongly against such an interpretation of the literature. However, previous studies have found negative

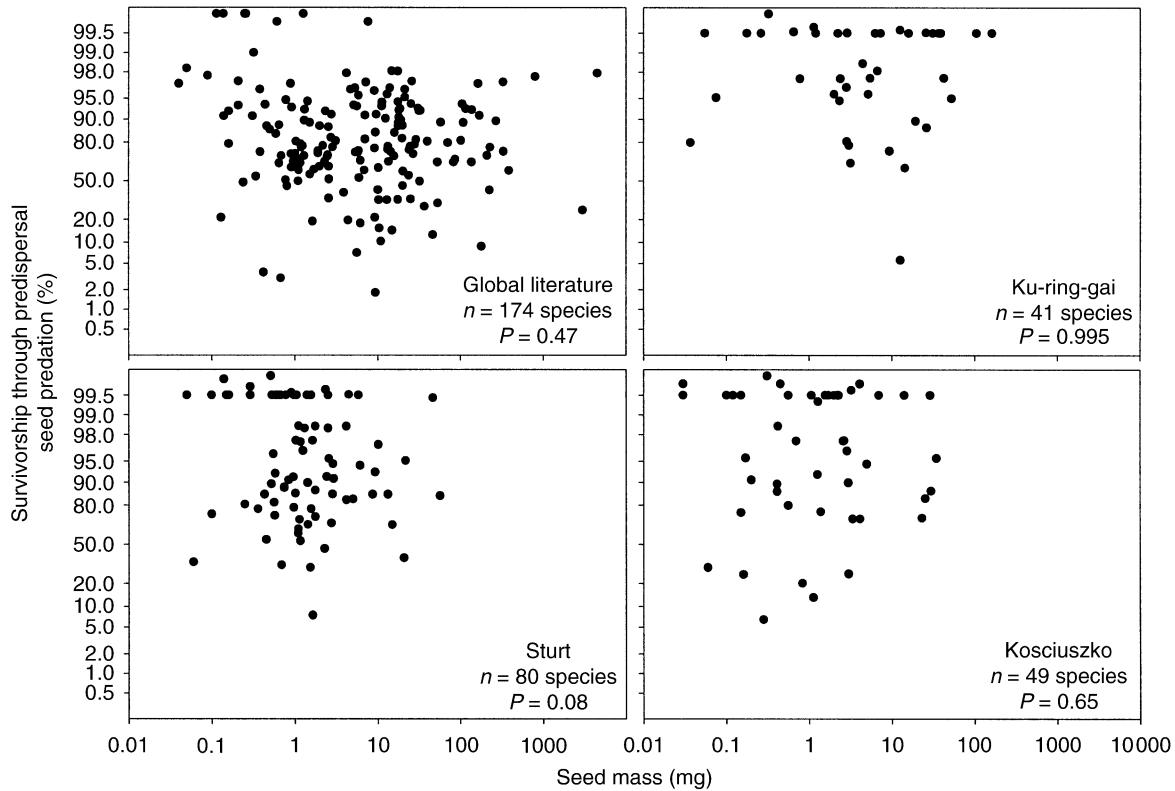


FIG. 2 Survivorship through predispersal seed predation (logit scale) vs. seed mass (log scale) from each of the three Australian habitats and from a compilation of data from previously published studies from the global literature. Kosciuszko species are from alpine and subalpine regions, Ku-ring-gai species are from dry sclerophyll vegetation, and Sturt species are from an arid environment. Each point represents the mean value for one species; P values indicate the results of random effects logistic regressions.

relationships between seed mass and survivorship in some habitats (see *Introduction*). In order to determine whether relationships between seed mass and pre- or postdispersal survivorship were different in some habitats, we analyzed data from the global literature using logistic regression models that included terms for habitat as well as for seed mass and species effects.

The interaction between habitat and seed mass was not significant for postdispersal survivorship ($P = 0.74$), but was significant for predispersal survivorship ($P = 0.001$). An additive model (no interaction) of seed mass and habitat showed significant effects of habitat on postdispersal survivorship ($P < 0.001$). Accordingly, data and regressions are presented separately for each habitat (postdispersal survivorship, Fig. 3; predispersal survivorship, Fig. 4). Bonferroni corrections (Sokal and Rohlf 1995) were applied to account for the large number of regressions performed. Of all the relationships tested, only the relationship between seed mass and postdispersal survivorship in subtropical and temperate rain forest proved significant after accounting for the number of regressions performed (Table 2), and it was positive rather than negative.

Differences between data from the literature and data from the field studies

Daily postdispersal survivorship was not significantly different ($P = 0.07$) between our field studies (mean = 83.2%; 95% CI = 79.1–87.6%) and the global literature (mean = 86.7%; 95% CI = 84.3–89.1%). However, a significantly ($P < 0.001$) lower percentage of seeds survived predispersal seed predation (throughout their entire development period) based on the literature (mean = 73.6%; 95% CI = 69.8–77.4%) than in data from our field studies (mean = 87.2%; 95% CI = 84.0–90.4%).

The percentage of species that suffered no predispersal seed predation (100% survivorship) was significantly higher in the field studies (66 of 170 species) than in the literature compilation (7 of 176 species; $\chi^2 = 63.8$, $df = 1$, $P < 0.001$; Fig. 5). This was also true for postdispersal survivorship (10 of 81 species in the field studies compared to 8 of 280 species in the literature compilation; $\chi^2 = 11.94$, $df = 1$, $P < 0.001$; Fig. 5). Thus, it seems that species experiencing 100% survivorship are considerably underrepresented in the literature. Consequently, for the remaining questions,

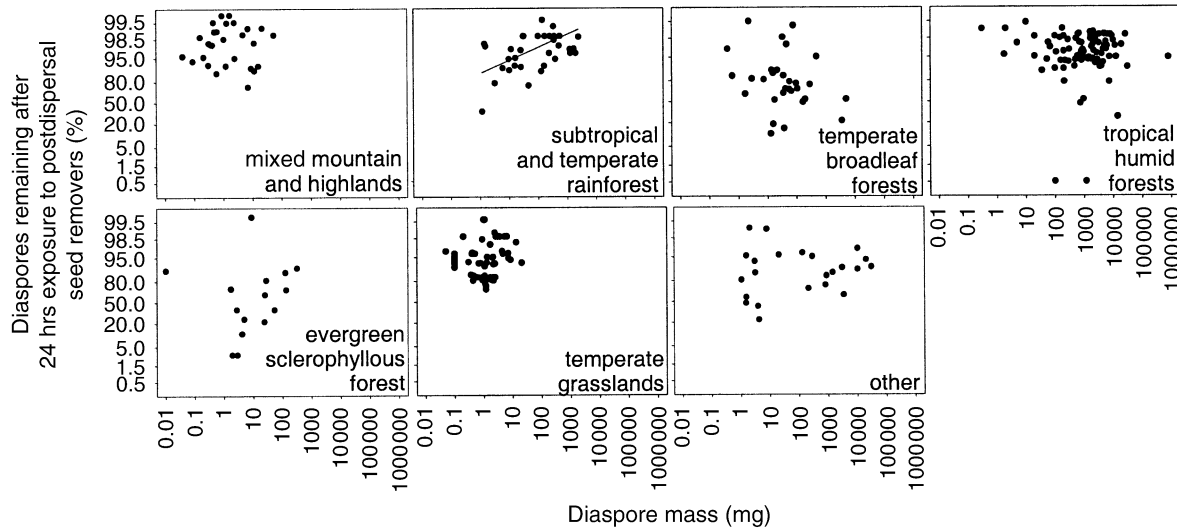


FIG. 3 Percentage of seeds remaining after 24 hours exposure to postdispersal seed predators (logit scale) vs. seed mass (log scale) from the global literature, analyzed by habitat type (habitat classifications are based on Udvardy [1975]). Each point represents the mean value for one species; *P* values indicate the results of random effects logistic regressions.

we have thought it best to consider only the fresh field data, where species were included without reference to any previous observations as to whether they suffered predation.

What is the magnitude of seed loss to pre- and postdispersal seed predators?

In Sturt, Ku-ring-gai, and Kosciuszko, postdispersal survivorship (through 24 hours of exposure to seed predators) was $83.3 \pm 2.14\%$, mean ± 1 SE. By comparison, $87.2 \pm 1.62\%$ of seeds survived destruction by predispersal seed predators through to the time when they completed development. In addition, almost all seeds will spend more than 24 hours on the ground before germination or incorporation into the soil pro-

file. Thus, postdispersal seed removal seemed to have a stronger effect on survivorship than predispersal predation. This was also the conclusion reached by Hulme (2002) from a 28-species data set compiled from the literature.

We also tested whether high predispersal survivorship was associated with high postdispersal survivorship (as was found across 23 species by Hulme [2002]). For those species for which we had gathered both pre- and postdispersal survivorship data, there were no significant correlations between logit-transformed pre- and postdispersal survivorship for species at Ku-ring-gai Chase National Park ($n = 21$, $P = 0.31$, $R^2 = 0.055$), Kosciuszko National Park ($n = 13$, $P = 0.74$, $R^2 = 0.01$), or across all sites combined ($n = 78$, $P =$

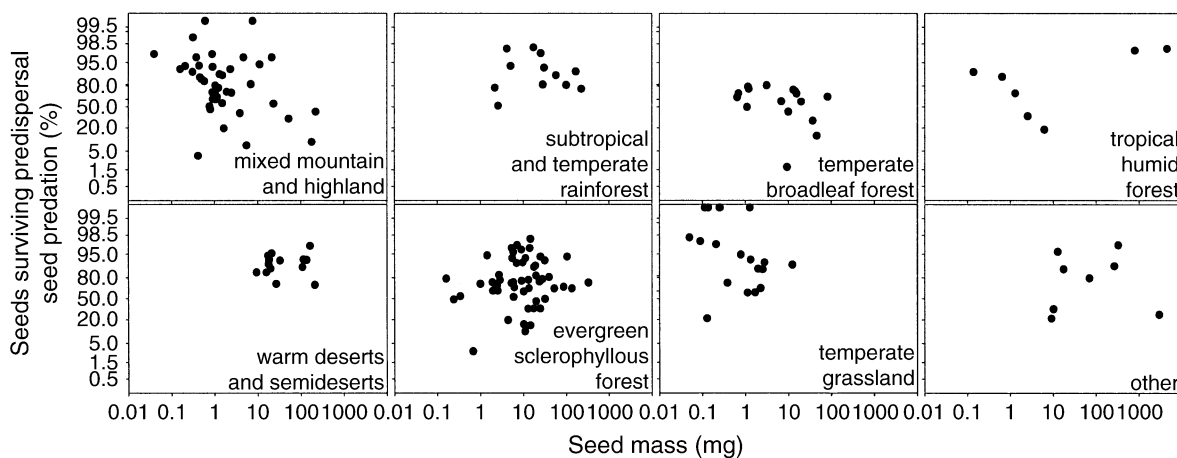


FIG. 4 Survivorship through predispersal seed predation (logit scale) vs. seed mass (log scale) from the global literature analyzed by habitat type (habitat classifications are based on Udvardy [1975]). Each point represents the mean value for one species. *P* values indicate the results of random effects logistic regressions.

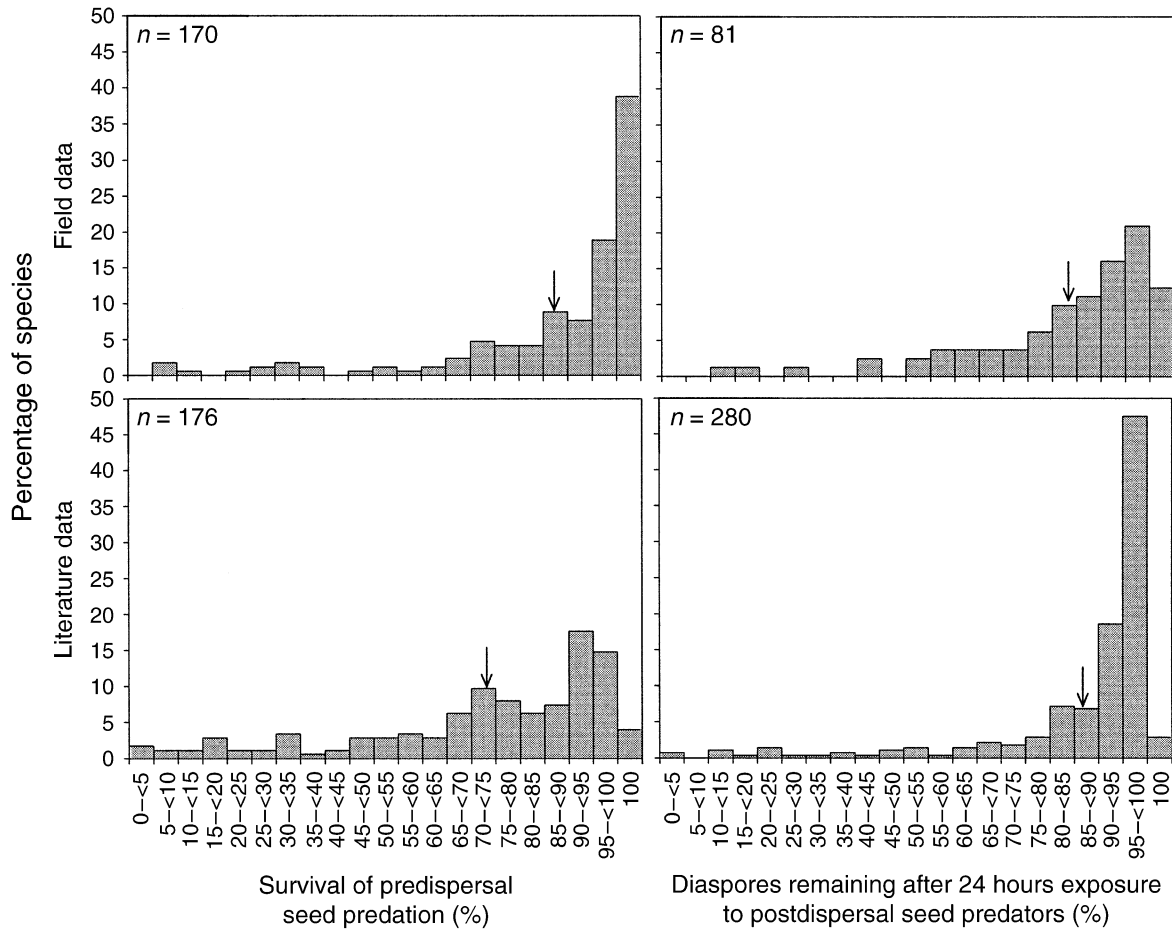


FIG. 5 Frequency distributions of survivorship through predispersal seed predation and postdispersal seed removal for the field studies and the global literature. Note the much lower frequency of species recorded with 100% survivorship in the literature. Arrows indicate means.

TABLE 2. Results of cross-species logistic regressions on the relationship between \log_{10} seed mass and the percentage of seeds remaining after predispersal seed predation and postdispersal seed removal.

Habitat type	Predispersal seed predation			Postdispersal seed removal		
	<i>n</i>	<i>P</i>	Slope	<i>n</i>	<i>P</i>	Slope
Evergreen sclerophyllous forest	54	0.28	0.27	15	0.31	0.66
Mixed mountain and highland ecosystems	42	0.02	-0.92	29	0.93	0.03
Subtropical and temperate rainforest	12	0.91	-0.07	35	0.003	0.86
Temperate broadleaf forest	16	0.01	-0.79	31	0.17	-0.31
Warm deserts and semideserts	15	0.33	0.36
Tropical humid forests	7	0.17	0.66	89	0.93	-0.02
Temperate grasslands	19	0.02	-1.91	58	0.27	0.27
Other	8	0.59	0.27	23	0.23	0.25

Notes: These analyses were performed using the global literature data analyzed by habitat type (based on Udvardy [1975]); *n* is the number of species. To account for the large number of regressions performed here, Bonferroni corrections were applied; thus, we did not consider a relationship to be significant unless its *P* value was <0.006 (0.05/8) for predispersal seed predation or 0.007 (0.05/7) for postdispersal seed predation.

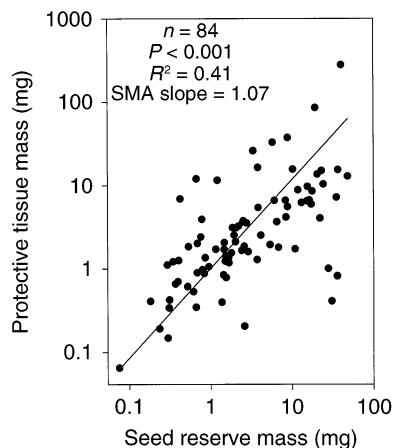


FIG. 6 The relationship between protective tissue mass and seed reserve mass, both on log scales, for 84 species from Australia. Plant species allocate approximately equal amounts of biomass to seed reserves and protective structures.

0.61, $R^2 = 0.003$), although there was a weak positive relationship across the 44 species from Sturt National Park ($P = 0.03$, $R^2 = 0.10$).

Protective tissue mass as a predictor of survivorship

Protective tissue mass was positively related to seed reserve mass across 84 species ($P < 0.001$, $R^2 = 0.41$; Fig. 6). The SMA slope of this relationship was not significantly different from one (1.07 with a 95% confidence interval of 0.90 to 1.26). There was a range of 0.013–18 g defensive tissue per gram of seed reserve, and protective tissue was not correlated with postdispersal survivorship ($n = 65$ species, $P = 0.38$; Fig. 7).

DISCUSSION

Seed mass and survivorship

The most important finding of this work was that large seeds do not have lower pre- or postdispersal survivorship than small seeds. In fact, there is some suggestion in our data of weak *positive* relationships between diaspore mass and survivorship. There are ways in which the data reported here might still be consistent with lower survivorship of large seeds, but they require fairly complicated assumptions.

We measured the percentage of seeds remaining after 24 hours of exposure to postdispersal seed predators, but what is ultimately important for plants is the percentage of seeds that survive the entire period of exposure to seed predators following dispersal. If larger seeds tended to spend longer on the soil surface than small seeds, and were thus exposed to seed predators for a longer period of time (Bekker et al. 1998), then this effect might outweigh the weak positive correlation between the percentage of diaspores remaining after a given time and diaspore mass. Second, large and small diaspores may be removed by different taxa (Brown

and Davidson 1976). There is some suggestion that those taxa removing large diaspores may be more likely to be predators, and less likely to be secondary dispersers, than the taxa that remove smaller diaspores (Hulme 1997). At least in some ecosystems, ants tend to remove smaller diaspores, whereas rodents tend to have a heavier impact on larger diaspores (Mittelbach and Gross 1984, Abbott and Van Heurk 1985, Samson et al. 1992). In Australia, ants are the major seed-harvesting guild, and are responsible for both dispersal and predation (Andersen 1991). The fate of diaspores removed by ants depends largely on the identity of the ant species involved, but seed mortality rates can be >60% (Hughes and Westoby 1992). The sizes of diaspores removed by ants and rodents can overlap substantially (Brown and Davidson 1976), and ants were observed removing some of the largest diaspores available in the Australian studies (A. Moles, *personal observation*). It is thus unclear how significantly the measurement of diaspore removal rather than predation per se may have affected our results.

Irrespective of any of these complications, it remains the case that large-seeded species did not show the higher percentage of diaspores remaining after 24 hours' exposure to seed predators predicted by the optimal foraging or apparency arguments outlined in the *Introduction*. The simplest explanation for this would be if different types of predator specialize in different ranges of seed mass, and the abundance of each predator builds up when a particular size category of seed is underexploited. Thus, if large seeds were initially subject to higher rates of seed predation than small seeds, an increase in the number of predators utilizing the abundant small seed resource might be expected, as well as a relative decrease in the number of seed predators using the scarcer large seeds. These changes in abundance would be expected to result from improved reproductive success or survivorship among species using the initially less utilized, smaller seed part of the resource spectrum. As a supplementary mechanism, plant species that are heavily preyed upon might undergo selection for stronger defenses (such as hard seed coats or toxins) until their survivorships were approximately equal to those of other species.

Our results support the hypothesis that the relative increase in the establishment of large-seeded species following the addition of predator-proof cages (Brown and Heske 1990, Reader 1993) results from increases in interspecific competition following the removal of predators, rather than from a relative increase in the number of large seeds (Brown and Heske 1990). One might expect large-seeded species to do better than small seeds in a highly competitive environment (Turnbull et al. 1999).

Differences between data from the literature and data from the field studies

There were significant differences between data from the literature and data from the field studies. Postdis-

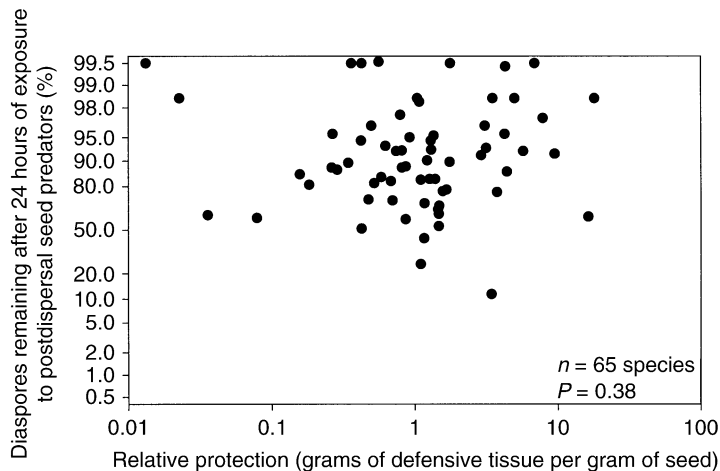


FIG. 7. Survivorship through 24 hours of exposure to postdispersal seed predators (logit scale) vs. seed protection (log scale) for Australian species. Each data point represents a mean value for one species.

persal survivorship was slightly (but not significantly) higher in the field studies than across the global literature, and predispersal survivorship was much higher in the field studies than in the global literature. We have also presented evidence that species reported as having 100% survivorship are heavily underrepresented in the literature compared to the field studies. The difference in postdispersal survivorship might be an artifact, because our field studies were of shorter duration and smaller magnitude than many of the studies in reported in the literature. That is, our smaller sample sizes make it more likely that no seed removal will be observed (especially in cases where levels of survivorship are very high). This hypothesis is supported by the higher percentage of species in the literature recorded as having 95–100% postdispersal survivorship. However, it seems unlikely that this hypothesis can account for the enormous difference between predispersal survivorship data from the field studies and the literature (66 out of 170 species showing 100% survivorship in field studies compared to seven out of 176 species in the literature), as both field and literature studies report lifetime predispersal survivorship, and the percentage of species showing nearly 100% survivorship in the literature is actually lower in the literature than in the field studies. Thus, it seems highly likely that publication bias is present in the predispersal survivorship literature. This publication bias could arise from researchers choosing not to study species that have nil or low levels of seed predation, especially when they are studying only one or a few species.

Seed mass, survivorship, and seed defenses

Our results showed that plants allocate a large amount of biomass to seed protection. Seed reserve masses are, on average, approximately equal to the mass of protective structures. Plants could make, on average, twice as many seeds as they do at present if they did not allocate dry mass to defensive structures. Thus the cost of seed defense is not trivial, and should

be taken into account when reproductive output of different species is being compared. At first glance, one might expect that species allocating more to protection have greater postdispersal survivorship. On the other hand, it could equally be argued that species whose ancestors had particularly low survivorship would be selected to increase their allocation to protection, resulting in a negative correlation between protection and survivorship. Thus, there is a negative feedback loop: protection increases survivorship in ecological time, but predation increases protection in evolutionary time, and the net consequence could be that no particular correlation between the two is expected, which is what we observed in this study. Indirect support for this hypothesis can be found in Grubb et al. (1998), who demonstrated that high nitrogen content and high levels of seed defense were correlated across 194 species from Australian rain forest.

Where to next?

An important feature of this study is that it quantifies the relative chances of large and small seeds surviving a crucial step in the life history of plants. Logically, individuals of both large- and small-seeded species must produce an average of one surviving offspring per lifetime. Small-seeded species produce more seeds per square meter of space occupied (Jakobsson and Eriksson 2000, Henery and Westoby 2001). Therefore, large-seeded species must have a greater percentage of individuals surviving through the whole life cycle from seed production to seed production. Our results suggest that this advantage is not gained at the stages of pre- or postdispersal seed predation, because the slight advantage of large-seeded species under postdispersal seed removal is not sufficient to counter the one-to-one trade-off between seed mass and seed number for a given amount of reproductive effort (Henery and Westoby 2001). Present evidence suggests that large-seed advantage is likely to be strongest during seedling establishment (Leishman et al. 2000). Thus, future work

might attempt a similar synthesis on the percentage of seedlings surviving seedling establishment across a wide range of seed sizes.

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APPENDIX A

A detailed description of field sites is available in ESA's Electronic Data Archive: *Ecological Archives* E084-083-A1.

APPENDIX B

Data on seed mass and survivorship through predispersal seed predation of plant species in Sturt National Park, New South Wales, Australia, are available in ESA's Electronic Data Archive: *Ecological Archives* E084-083-A2.

APPENDIX C

Data on seed mass and survivorship through predispersal seed predation of plant species in Ku-ring-gai Chase National Park, New South Wales, Australia, are available in ESA's Electronic Data Archive: *Ecological Archives* E084-083-A3.

APPENDIX D

Data on seed mass and survivorship through predispersal seed predation of plant species in Kosciuszko National Park, New South Wales, Australia, are available in ESA's Electronic Data Archive: *Ecological Archives* E084-083-A4.

APPENDIX E

Data on seed mass and survivorship through postdispersal seed removal in Sturt National Park, New South Wales, Australia, are available in ESA's Electronic Data Archive: *Ecological Archives* E084-083-A5.

APPENDIX F

Data on seed mass and survivorship through postdispersal seed removal in Ku-ring-gai Chase National Park, New South Wales, Australia, are available in ESA's Electronic Data Archive: *Ecological Archives* E084-083-A6.

APPENDIX G

Data on seed mass and survivorship through postdispersal seed removal in Kosciuszko National Park, New South Wales, Australia, are available in ESA's Electronic Data Archive: *Ecological Archives* E084-083-A7.

APPENDIX H

Data on seed mass and survivorship through predispersal seed predation from the global literature are available in ESA's Electronic Data Archive: *Ecological Archives* E084-083-A8.

APPENDIX I

Data on seed mass and survivorship through postdispersal seed removal from the global literature are available in ESA's Electronic Data Archives: *Ecological Archives* E084-083-A9.