SEED SIZE AND PLANT GROWTH FORM AS FACTORS IN DISPERSAL SPECTRA

MARK WESTOBY, BARBARA RICE, AND JOCelyn HOWELL
School of Biological Sciences, Macquarie University, New South Wales 2109, Australia

Abstract. All vascular plant species were listed on eight sites near Sydney, Australia. Four sites were on infertile and four on fertile soil. Each of the 335 species was classified according to seed mass (measured as fresh mass of embryo plus endosperm), morphological adaptations for dispersal by different vectors, and growth form. The infertile-soil sites had more species and more cover adapted for dispersal by ants, and the fertile-soil sites had more species and more cover with fleshy fruits adapted for dispersal by vertebrates. We tested the hypothesis that this difference could be interpreted as a secondary correlate of seed size or of growth form. Species with smaller seed mass or growing to <2 m tall were significantly more likely to be adapted for dispersal by ants relative to vertebrates. An indirect association via growth form was capable of accounting for up to 84% of the relationship between soil type and dispersal mode, an indirect association via seed mass for up to 23% of the relationship; the two together could account for a maximum of 85%. The indirect association via seed mass was relatively weaker because seed masses proved not to be very different between these soil types. There remained a significant residual tendency for species in any given seed size class and growth form to be more likely to be dispersed by vertebrates relative to ants on fertile soils than on infertile soils.

Key words: ants; Australia; dispersal; fruits; growth forms; nutrients; sclerophyll; seeds; soils; vegetation; vertebrates.

INTRODUCTION

Some plants are adapted to have their seeds dispersed by ants. Their diaspores include a food body. The diaspores are carried by ants to their nests, the food body is removed and eaten, and the discarded seed can subsequently germinate. This dispersal adaptation is much more important on infertile than on fertile soils. This is most apparent in Australia (Berg 1975, Rice and Westoby 1981, Westoby et al. 1982) and southern Africa (Milewski 1982, Milewski and Bond 1982), where the two largest known concentrations of ant-dispersed species are found. In these two areas ant dispersal is concentrated in sclerophyll species, which characteristically occur on low-nutrient soils. However, few ant-dispersed species have been reported in the sclerophyll vegetation of California (Berg 1966, Bullock 1974) or around the Mediterranean (Sernander 1906, Muller 1933), which indicates the association is with low soil nutrients rather than with sclerophyll as such.

Several hypotheses have been considered as to special adaptive advantages of being dispersed by ants (Westoby et al. 1982, Beattie 1983, 1985). Among these, the hypothesis that dispersal by ants serves to move seeds to nutrient-enriched microsites seemed likely at one time to explain the association of ant dispersal with low-nutrient soils. There is much evidence that ant nests can be chemically different from background soils (Davidson and Morton 1981, Beattie and Culver 1983, Culver and Beattie 1983, Beattie 1985), and some evidence that seedlings grow better in ant-nest soil, and in Australian sclerophyll vegetation where large percentages of species are ant dispersed, direct tests have not found that ant-dispersed seeds reach nutrient-enriched microsites (Majer 1982, Rice and Westoby 1986).

In view of this evidence against the nutrient-enriched microsite hypothesis, we hypothesized that the high incidence of dispersal by ants in sclerophyll vegetation might be a secondary correlate of diaspore size or plant growth form. For example, diaspore size in sclerophyll vegetation might be concentrated, for reasons presumably to do with seedling establishment, in a size range which coincidently is suited to dispersal by ants. Seeds' prospects of establishment are strongly influenced by the reserves of energy or mineral nutrient on which they can initially rely (Janzen 1969, Harper et al. 1970, Harper 1977, Grime 1979, Willson 1983, Foster 1986). Differences in mean seed mass between environments are thought to reflect the different problems posed for seedling establishment (Salisbury 1942, 1974, Harper et al. 1970, Baker 1972). Different seed sizes obviously tend to favor different seed dispersal methods. So it might be that lower-nutrient soils favor seed sizes in a range that in turn favors dispersal by ants. By an
argument of the same form, low-nutrient soils might favor plant growth forms that in turn favor seed dispersal by ants.

Here we report a test of this hypothesis. We listed species on replicate fertile-soil and infertile-soil sites, and classified their diaspores according to dispersal morphology and according to size, and the plants themselves into growth form categories. (We dissected diaspores and weighed embryo plus endosperm, because this mass clearly represented part of the "problem" that had to be solved by a dispersal mode, while flesh, wings, hairs, etc. could be regarded as part of the dispersal "solution" adopted over evolutionary time.) The result was a four-dimensional contingency table, site type × diaspore mass × dispersal mode × growth form. If species in a given growth form and diaspore mass category proved equally likely to be ant dispersed, irrespective of whether they were on fertile or on infertile soils, this would have been consistent with the secondary correlate hypothesis.

**Methods**

We selected eight sites in national parks or state forests around the northern and southern suburbs of Sydney, Australia, ≈ 34° S, 151° E. Substantial areas of natural vegetation on infertile sandstone are conserved around Sydney, but most fertile soils were cleared quite early during European colonization. Only small patches of fertile-soil vegetation remain, usually within large areas of infertile Hawkesbury Sandstone. We were able to distribute our four fertile sites over three substrate types. Sites on infertile soil were then chosen to be interspersed with the fertile sites (Fig. 1), and to include both woodland and heathland vegetation, even though Rice and Westoby (1981) had found no evidence vegetation structure affected the incidence of dispersal by ants among infertile-soil vegetation types.

Within Australia sclerophyll and mesophyll vegetation types are often found close together, under the same climate but on different soils. It is well established that sclerophyll is a response to low soil nutrients (Beadle 1954, 1966). Thus fertile-soil sites could readily be distinguished from infertile-soil sites by the physiognomy of the vegetation, as well as by the geomorphology. Total soil phosphorus is typically used as the best single indicator of soil fertility (Bowen 1981, Williams and Raupach 1983), because it is a limiting macronutrient and is not very soluble, and atmospheric inputs are small. Samples of the top 20 cm of soil were collected from five random locations at each site, bulked, and analyzed for total soil phosphorus by standard methods (Lambert 1983).

For statistical power it was more important that each study site should include comparable numbers of species than that they should be of the same area. Our aim at each site was to sample a contiguous area including 50–100 species. We began with a sample area 50 × 20 m (0.1 ha), which as expected (Rice and Westoby 1983) proved sufficient to obtain >50 species at all the infertile sites, and also at sites 2 and 4. At site 1 we expanded the area to 0.2 ha. At site 3 we felt an expanded site would have been more heterogeneous than was desirable, so we left it at 0.1 ha and 42 species.

Each site was visited repeatedly from mid-1983 to late 1984, to make an initial list of species, to search for species that had been missed initially, and to collect ripe fruits of each species. In some instances fruit had to be collected from locations other than the study sites. For a few species we never acquired fruits. Between September and November of 1984 we estimated percentage canopy cover of different species at each site by means of ≥20 m of line intercept, distributed systematically over the site. This sampling was done during austral spring, but since the vegetation is overwhelmingly perennial and evergreen, season should make little difference.

The dispersal categories we used were defined on the basis of structures possessed by the propagules, not on the basis of direct field observation of dispersal, which was not practicable. The general types of structure associated with different dispersal syndromes are well known (van der Pijl 1982), and we made our initial
from clear that their small size has been shaped by their dispersal mechanisms. Many of these smaller species are quite small, and could be regarded as adapted for vertebrate rather than ant dispersal. We have inferred not to categorize them as adapted for wind dispersal in this sense. However, we have preferred to treat these species as having a combination of the two dispersal adaptations. In practice this decision was not important, since our conclusions would not be affected by it.

We have taken a conservative approach, assigning species to dispersal categories only when they have a definite structure serving some dispersal function, many species have remained in a category of having no particular dispersal morphology. Many of these are quite small, and could be regarded as adapted for wind dispersal in this sense. However, we have preferred not to categorize them as adapted for wind dispersal because we could find no objective basis for a size cutoff for such a category, and because it is far from clear that their small size has been shaped by natural selection acting on the dispersal process.

Where possible, we collected ripe diaspores from several plants at each site where a species occurred. At least five diaspores were weighed for each species, spread over plants and sites if possible. Fleshy fruits were weighed fresh promptly, after storing refrigerated for a few days, or after storing frozen in sealed containers for a longer period. They were subsequently dried at 80°C and weighed again. Another fresh diaspore was chosen from the midrange of sizes indicated by the weighings and was dissected into three components: embryo plus endosperm; “dispersal structure,” meaning any wing, food body, etc.; and the remainder, including the testa and other tissues surrounding embryo and endosperm. These three components were weighed both fresh and dry to estimate the percentage each contributed to a typical diaspore. In many cases >1 diaspore was dissected quantitatively, and in all cases further diaspores were cut apart to confirm that the one dissected quantitatively was not atypical internally. In the case of berries, aggregate fruits, and drupaceous fruits, with several seeds included within one body of flesh, the seeds in each of five diaspores were counted. The amount of flesh can therefore be expressed either on a per-diaspore or on a per-embryo basis. Measurements of mass were made using a Cahn microbalance to microgram precision. In the case of orchid seeds and fern spores it was not possible to weigh or dissect individuals, and an average mass for whole diaspores was obtained from weighing a group.

Species were classed into four growth form categories working from Beadle et al. (1972), supplemented by personal knowledge. The four categories into which it was possible to divide species were: herbaceous species plus low or scrambling shrubs <50 cm tall; shrubs from 50 to 200 cm tall; tall shrubs >200 cm, small trees, and trees; climbers, vines, and twiners. The herbaceous species were predominantly perennial, sclerophyllous monocots.

**Results**

Total soil phosphorus concentration was in the range 69–115 mg/kg for sites chosen as infertile, and 216–786 mg/kg for sites chosen as relatively fertile (Table 1).

The common categories of morphological adaptation for dispersal were flesh for vertebrates, food bodies for ants, wings or hairs to increase air resistance, and no particular morphological adaptation (Table 1). Species with other types of adaptation, or with combinations of adaptations, contributed only small percentages.

We consider first the interaction between dispersal mode and site fertility. We isolate the main effect in that interaction, and then consider the role of growth form and offspring mass in relation to that main effect.

Consider first the cross-classification of dispersal type...
### Table 1. Number of species with different dispersal morphologies at each of the eight sites (Fig. 1). Sites 1–4 were on fertile soil, 5–8 on infertile soil, as indicated by the total soil phosphorus levels.

| Dispersal morphologies          | Site 1 | Site 2 | Site 3 | Site 4 | Site 5 | Site 6 | Site 7 | Site 8 |
|--------------------------------|--------|--------|--------|--------|--------|--------|--------|--------|
| No special adaptation          | 40     | 28     | 15     | 27     | 34     | 25     | 44     | 33     |
| Air resistance                 | 10     | 10     | 5      | 11     | 8      | 8      | 12     | 9      |
| Flesh for vertebrates          | 12     | 19     | 18     | 31     | 4      | 3      | 8      | 5      |
| Food body for ants             | 21     | 12     | 2      | 5      | 37     | 38     | 45     | 38     |
| Ballistic + ants               | 2      | 1      | 0      | 1      | 2      | 7      | 4      | 3      |
| Ballistic                      | 1      | 1      | 1      | 1      | 1      | 0      | 0      | 0      |
| Uncertain                      | 2      | 0      | 0      | 1      | 2      | 2      | 1      | 1      |
| Exozoochores                   | 2      | 0      | 0      | 1      | 0      | 0      | 0      | 0      |
| Vertebrates + ants             | 2      | 2      | 1      | 3      | 0      | 0      | 1      | 0      |
| Total soil P (mg/kg)           | 786    | 216    | 650    | 677    | 103    | 115    | 110    | 69     |

### Table 2. Contingency analysis of numbers of plant species using different dispersal morphologies in different sites (Table 1). Rows 5–9 of dispersal morphologies in Table 1 aggregated into one "miscellaneous" row, resulting in a 5 x 8 table.

| Comparison/contrast          | df | G²     | P   | % of total heterogeneity |
|------------------------------|----|--------|-----|-------------------------|
| Dispersal × site             |    | 141.8  | <.001 | 100                     |
| ([Vertebrate + ant] vs. others*) × site | 7  | 4.7    | >.5  | 3                       |
| (Among others) × site        |    | 7.1    | >.5  | 5                       |
| (Vert vs. ant) × site        |    | 130.1  | <.001 | 92                     |
| (Vert vs. ant) × (fert vs. infert) | 1  | 102.4  | <.001 | 72                     |
| (Vert vs. ant) × (among fert) | 3  | 26.1   | <.001 | 18                     |
| (Vert vs. ant) × (among infert) | 3  | 1.5    | >.5  | 1                       |

* Others = no special adaptation, air resistance, and miscellaneous.

by site (Table 1 with rows 5–9 aggregated into a single category; contingency analysis summarized in Table 2). The two classifying variables interacted strongly (G² = 141.8, df = 28, P < .001). However, most of the between-site differences resided in rows 3 and 4, flesh for vertebrates and food bodies for ants (G² = 130.1, df = 7, P < .001). Within rows 3 and 4, the heterogeneity resided principally between the fertile-soil sites 1–4 and the infertile sites 5–8 (G² = 102.4, df = 1, P < .0001). There was significant heterogeneity among the fertile sites (G² = 26.1, df = 3, P < .0001), but not among the infertile sites (G² = 1.53, df = 3, P = .67).

Overall, 72% of the total heterogeneity resided in the interaction between fleshy fruit vs. ant food body and fertile vs. infertile sites. The only other significant heterogeneity (18% of the total) was among fertile sites, still with respect to fleshy fruit vs. ant food body. The relative proportion with fleshy fruit was not correlated with the actual fertility level of the four fertile sites (r = −0.04, df = 3, NS).

As expected, substantially more species on infertile sites were ant dispersed than on fertile sites (Fig. 2). The first new conclusion was that the high incidence of dispersal by ants on these infertile soils comes about at the expense of dispersal by vertebrates, not at the expense of dispersal by wind or by no special morphological adaptation (Fig. 2). The other means of dispersal were about equally common.

Percentage of cover in each category varied among sites more than did the percentage of species. However, fertile sites had significantly more cover of species with fleshy fruits (Fig. 3; t test, P < .05), and infertile sites had almost significantly more cover of species with
food bodies for ants (t test, .10 > P > .05). Cover by species with other dispersal adaptations was not significantly different between fertile and infertile sites.

In light of the above analysis, we consider the role of offspring mass and plant growth form only in relation to the trade-off between dispersal by ants and by vertebrates, comparing fertile with infertile sites. For this purpose we accumulated into two dispersal mode × two site fertility categories all species that occurred in at least one of the fertile sites or at least one of the infertile sites, and that possessed either a food body for ants or fleshy fruit for vertebrates. Thus row 9 of Table 1 was added to row 3, and rows 4 and 5 to row 4. The cases in the resulting tables are not species, but instances of a species using a dispersal mode in a site type. Any species that occurred in both a fertile and an infertile site, or that had both fleshy fruit and a food body, contributed two cases to the contingency tables. The cross-classification of two dispersal modes × two site fertilities × four offspring mass classes × four plant growth forms is given in Table 3.

We used fresh mass of embryo plus endosperm to measure offspring mass on the basis that this mass is the "problem" that must be "solved" by natural selection adapting the fruit for a particular dispersal vector. However, it could also be argued that tissues grouped under "other" should be included as part of the "problem," on the grounds that their mass might be shaped by selection acting on parts of the life history other than dispersal, so that whatever dispersal vector is adopted has to move their mass. To check the generality of conclusions based on embryo-plus-endosperm fresh mass, we also constructed contingency tables based on other measures. We used fresh mass of embryo plus endosperm, plus "other" expressed on a per-seed basis when there was more than one seed in a diaspore; fresh mass of whole diaspore, including dispersal structures, and including multiple seeds in some cases; and oven-dry masses corresponding to the three fresh masses. Analysis using the other five measures of mass produced qualitatively the same answers as will be presented below, using fresh mass of embryo plus endosperm.

The question can now be phrased, informally: for offspring in a given mass class or plants in a given growth form category, was the probability that they lived on fertile or on infertile soil? There was a strong effect of offspring size, with larger propagules (embryo plus endosperm, plus other) more likely to be ant dispersed than tall shrubs, trees, or climbers (Fig. 5). There was also a strong effect of plant growth form, with herbaceous perennials and shrubs <2 m tall much more likely to be ant dispersed than tall shrubs, trees, or climbers (Fig. 5). In both cases, however, there was also a difference between site types, with species on

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**Table 3. Four-way classification of cases of species having adaptations to use vertebrates or ants for dispersal, occurring on fertile-soil or infertile-soil sites, belonging to one of four growth forms and having embryo-plus-endosperm fresh mass in various classes. Figs. 4–6 and Table 4 are derived from various aggregations of this table.**

| Embryo-plus-endosperm fresh mass (mg) | Plant growth form* | Vertebrate sites | Ant sites |
|--------------------------------------|-------------------|-----------------|----------|
| <1                                   | Plant growth form | Vertebrate      | Ant      |
| 1–10                                 | Plant growth form | Vertebrate      | Ant      |
| 10–100                               | Plant growth form | Vertebrate      | Ant      |
| Unknown                              | Plant growth form | Vertebrate      | Ant      |

*Herbs and shrubs <50 cm tall, shrubs 50–200 cm tall, shrubs >200 cm tall and trees, and climbers and twiners.
fertile soils more likely to be vertebrate dispersed, even within a given range of offspring masses or within a given plant growth form (Figs. 4 and 5).

To test the secondary correlate hypothesis formally by fitting loglinear models to the four-dimensional contingency table, it was necessary to collapse offspring masses and plant growth forms from four down to two categories each. Otherwise expected counts in the cells of the table would have been unacceptably low.

The association between soil and dispersal mode can be quantified by the marginal association $SD$ (or vice versa) before any opportunity has been given for indirect effects via seed mass $M$ or growth form $F$ to explain any of the relationship between $D$ and $S$. All six marginal associations among pairs of the four variables were significant (Table 4). Table 4.

| Model | $G^2$ | $P$ |
|-------|-------|-----|
| 1. SM, SD, SF, MD, FD, FM | 8.03 | .1545 |
| 2. SD, SF, MD, FD, FM | 8.08 | .2322 |
| 3. SM, SF, MD, FD, FM | 14.04 | .0029 |
| 4. SM, SD, MD, FD, FM | 24.76 | .0004 |
| 5. SM, SD, SF, FD, FM | 14.78 | .0220 |
| 6. SM, SD, SF, FD, MD | 39.56 | .0001 |
| 7. SM, SF, MD, FD | 11.15 | .0838 |
| 8. SM, MD, SD, F | 104.39 | .0001 |
| 9. SF, FD, SD, M | 38.31 | .0001 |
| 10. SM, MD, F | 135.58 | .0001 |
| 11. SF, FD, M | 44.88 | .0001 |
| 12. SD, M, D | 161.96 | .0001 |
| 13. SD, M, F | 131.55 | .0001 |
| 14. SF, D, M | 120.67 | .0001 |
| 15. MD, S, F | 145.54 | .0001 |
| 16. FD, M, S | 96.15 | .0001 |
| 17. FM, D, S | 149.01 | .0001 |
| 18. S, F, M, D | 171.93 | .0001 |

*Models with combinations such as DM use higher order marginal totals as well as the marginal totals of the individual variables. Likelihood-ratio contingency table tests ($G^2$) measure the amount of heterogeneity left unexplained when a given model is fitted; $P$ measures the significance of that heterogeneity. Marginal and partial associations (Brown 1985) are obtained by subtracting models as shown.

Was the hypothesis adequate that soil $S$ determined offspring mass $M$ or plant growth form $F$, which in turn determined dispersal mode $D$? Consider the partial association $SD$, which is the reduction in $G^2$ when an SD term is added to the model last, after every opportunity has been given for all other two-way associations to explain the relationship between $S$ and $D$ (Brown 1985). The partial association $SD$ was only 15% as large as the marginal association, but still significant ($G^2 = 6.01, P < .025$, Table 4). Thus indirect effects involving $M$ and $F$ could explain as much as 85% of the relationship between $S$ and $D$, but not all of it.

All three of the variables soil fertility, growth form, and seed mass were significantly associated with dispersal mode even after all possible cross-correlations
had been accounted for (Fig. 6; partial associations SD, FD and MD in Table 4). No three-variable associations were necessary to explain the data (model with all six two-variable associations had $P > .05$, Table 4). Thus, slopes of the lines in Fig. 6 can be regarded as parallel. The line for tall plants on infertile soil appears different, but its position represents only a very approximate estimate, because the data points are percentages from out of only five and four cases, respectively.

What was the maximum percentage of the SD relationship that could be explainable in terms of each of the indirect effects? This can be assessed by taking the reduction in $G^2$ when SD was added to the model after the indirect effect, and comparing this to the marginal association SD. The effect of SD added after SF, FD was to reduce $G^2$ by 6.57 (Table 4), 16% as much as when SD was added first. Thus an indirect relationship via growth form might account for as much as 84% of the SD association. The effect of SD added after SM, MD was to reduce $G^2$ by 31.19, 77% as much as when SD was added first. Thus, an indirect relationship via seed mass might account for as much as 23% of the SD association. The indirect relationship via seed mass was comparatively weak, even though dispersal mode was strongly related to seed mass (Fig. 4), because seed mass proved not to be strongly differentiated between these soil types (marginal association SM, $G^2 = 9.97$, partial association SM, $G^2 = 0.05$; Table 4). Thus seed mass was predominantly associated with variation in dispersal mode within, rather than between, these soil types.

**DISCUSSION**

The observation of the high incidence of dispersal by ants on infertile soils prompted this study. Our first finding was that the shift between soil fertility levels consisted of species adapted for dispersal by ants on infertile soils replacing species adapted for dispersal by vertebrates on more fertile soils. Species having structures giving air resistance, or with no special morphological adaptations at all, were about equally common in relation to soil fertility. Thus any adaptive interpretation as to why dispersal by ants should be particularly favored on infertile soils needs to compare dispersal by ants with dispersal by vertebrates. This finding was possible because we obtained complete dispersal spectra instead of focusing on the incidence of a single dispersal type, as has usually been done in previous work (e.g., Rice and Westoby 1981, Sorensen 1986, Willson 1986).

This study cross-classified dispersal spectra by seed mass and plant growth form for the first time, and also obtained the components of mass for a large number of diaspores. By this means we have shown that quite a large proportion of the difference between the two vegetation types in dispersal mode used could be understood as an indirect association via plant stature or (to a lesser extent) via embryo-plus-endosperm mass. However, there remained a significant direct association between soil fertility and dispersal mode, which could not be accounted for by these indirect relationships.

In which directions might causal influences run? The differences in soil fertility between the two groups of sites can be traced to geomorphology, so associations between soil fertility and the other three variables must surely represent effects of soil fertility on the frequencies of different dispersal modes, growth forms, and seed masses, rather than vice versa. As to relationships among dispersal modes, growth forms, and seed masses, it is a matter of judgement which ways causation might run.

The indirect association of soil fertility with dispersal mode via seed mass was relatively weak in this comparison because these fertile and infertile soils turned out to have quite similar ranges of seed size. The strong association of seed mass with dispersal mode could represent either embryo-plus-endosperm mass predisposing diaspores to particular dispersal adaptations, or dispersal biology shaping embryo-plus-endosperm mass. In this comparison the association between seed mass and dispersal mode mainly explained variation within rather than between vegetation types. However, seed mass is known to vary among some vegetation types. Shaping of dispersal mode by embryo-plus-endosperm mass might be responsible for quite a large proportion of the variation in dispersal spectra among different vegetation types around the world. For example, the large percentage of woody plants in tropical moist forests that have vertebrate-dispersed fruits (Gentry 1982, Tanner 1982) could result from strong selection for large embryo plus endosperms, rather than from the distances and placement achieved by vertebrate dispersers. Generally, it will be helpful to account for embryo-plus-endosperm size when considering the
adaptive merits of different dispersal modes in different environments.

The indirect association of soil fertility with dispersal mode via growth form was strong in this study. Partly this was because the mix of growth forms was strongly affected by soil fertility, a well-known effect (e.g., Beadle 1966, Kruger et al. 1983), and partly it was because dispersal mode was strongly related to plant growth form, with plants growing to <2 m tall much more likely to be dispersed by ants. Seeds taken by ants rarely travel >2 m in these vegetation types (Mossop 1989, L. A. Hughes, unpublished manuscript). A possible interpretation of this association between growth form and dispersal mode is that dispersal distances of <2 m are rarely satisfactory for parent plants growing to more than ~2 m tall, but more often satisfactory for plants <2 m tall.

What might explain the residual association between soil fertility and dispersal mode, after possible indirect effects via seed mass and plant growth form have been accounted for? We would like to suggest two hypotheses that have not yet been tested, but could be.

The first is that the food bodies needed to induce ants to disperse a seed are cheap in mineral nutrients, and for that reason ant dispersal is economical on low-nutrient soils, where mineral nutrients are more likely to be the limiting currency for seed production. Food bodies accounted for only 1–2% of the P in propagules adapted for dispersal by ants, while they accounted for 8–10% of the energy (Westoby et al. 1982). However, wings and hairs for air resistance were equally economical in P, and on those grounds we rejected the cheap-food-body hypothesis. The work reported here shows that we should have been comparing ant-dispersed seeds with fleshy fruit, not with wind-dispersed propagules.

The second hypothesis is that the dispersing assemblages are different between fertile and infertile sites, relevant ants being more abundant on infertile soils, or relevant vertebrates on fertile, or both. The hypothesis that ant-adapted seeds are removed faster by ants at infertile-soil sites than at fertile-soil sites has already been tested and rejected (Mossop 1989). However, it remains possible that the ants doing the removing are less beneficial at fertile than at infertile-soil sites, or that vertebrate-adapted fruits are removed more quickly by vertebrates at fertile than at infertile-soil sites.

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