

Abiotic influences on the behaviour of rodents, ants, and plants affect an ant-seed mutualism¹

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Abstract: Deserts are open environments characterized by striking shifts in temperature and light regimes. We hypothesized that the abiotic environment mediates the interaction between an ant-dispersed plant, *Datura wrightii* (Solanaceae), ant mutualists, and rodent seed predators in the Sonoran Desert. Field experiments contrasting diurnal and nocturnal seed collection rates in the presence of ants only, vertebrates only, and in the presence of both groups indicated that 85% of seed collection by mammalian seed predators occurred at night (between 1900 and 0700). Seed collection by ants, in contrast, was similar between day and night, although seed collection decreased during very hot days and very bright nights. The total number of seeds collected by both groups foraging separately exceeded the number removed when both groups shared access to seed depots, suggesting that ants and rodents compete for seeds. However, *D. wrightii* plants dehisced 86% of their fruits between 0700 and 1900, increasing the likelihood of seed collection by ant mutualists rather than rodent seed predators. Dehiscence was sensitive to environmental cues: greenhouse plants kept at constant temperature and humidity dehisced 47% of their fruits between 0700 and 1900. Additional field experiments demonstrated that seed-collecting ants transported seeds considerable distances to their nests, microsites that can be rich in nutrients. The mean (\pm SE) seed dispersal distance was 6.1 ± 0.5 m, the longest mean dispersal distance yet reported for an ant-dispersed seed.

Keywords: competition, desert, dispersal, foraging, harvester ant, moon, myrmecochory, seed predation, temperature.

Résumé : Les déserts sont des environnements ouverts caractérisés par des changements drastiques des régimes de température et de lumière. Nous avons émis l'hypothèse que l'environnement abiotique agit comme médiateur au niveau de l'interaction entre une plante dont les graines sont disséminées par les fourmis, le *Datura wrightii* (Solanaceae), des fourmis mutualistes et des rongeurs granivores dans le désert Sonoran. Les expériences menées sur le terrain et mettant en contraste des taux diurnes et nocturnes de prélèvement de graines en présence des fourmis seules, des vertébrés seuls et des deux groupes d'animaux indiquent que 85 % des prélèvements de graines par les mammifères se produisent pendant la nuit (entre 19 h et 7 h). Pour leur part, les prélèvements de graines par les fourmis ne diffèrent pas entre le jour et la nuit, bien qu'ils diminuent pendant les journées très chaudes et les nuits très lumineuses. Le nombre total de graines prélevées par les deux groupes lorsqu'ils recherchent leur nourriture séparément dépasse le nombre obtenu lorsque les deux groupes se partagent l'accès aux réserves de graines, ce qui suggère que les fourmis et les rongeurs entrent en compétition pour s'accaparer les graines. Les plants de *D. wrightii* ouvrent néanmoins 86 % de leurs fruits entre 7 h et 19 h, ce qui favorise les fourmis aux dépens des rongeurs. La déhiscence des fruits est toutefois sensible aux facteurs environnementaux : 47 % des fruits des plants conservés dans des serres à une température et un taux d'humidité constants s'ouvrent entre 7 h et 19 h. D'autres expériences menées sur le terrain montrent que les fourmis qui récoltent des graines les transportent à des distances considérables de leurs nids. La distance moyenne (\pm ÉT) de dissémination des graines est de $6,1 \pm 0,5$ m. Il s'agit de la plus longue distance moyenne de dissémination de graines rapportée pour des fourmis.

Mots-clés : compétition, désert, dissémination, fourmi, lune, myrmécochorie, prédation de graines, recherche de nourriture, température.

Nomenclature: Kearney & Peebles, 1960; Cole, 1968.

Introduction

Arid environments are characterized by striking changes in temperature, moisture, and light regimes. These changes influence the foraging of arthropods and vertebrates. For example, many ant species in arid environments respond to increases in temperature, moisture stress, and light intensity by increasing the proportion of nocturnal activity (Whitford & Ettershank, 1975; Briesse & Macauley, 1980) or by altering their daytime foraging (MacKay & Mackay, 1989; MacMahon, Mull & Crist, 2000). The foraging patterns of desert mammals and

arthropods can also change with the phase of the lunar cycle, perhaps indicating avoidance of visually-hunting predators during periods of greater illumination and hence vulnerability (Kotler, Ayal & Subach, 1994; Tigar & Osborne, 1999). It is well appreciated that ants and mammals compete for seeds in arid environments (Brown & Davidson, 1977; MacMahon, Mull & Crist, 2000) and that a seed's likelihood of being collected by either group differs among seasons (Pulliam & Brand, 1975). This study focuses on seed collection and competition during a shorter time scale, the 24-h cycle, and how the responses of ants, mammals, and maternal plants to the changes in the abiotic environment during that cycle influence seed fate.

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The seeds of *Datura wrightii* (Solanaceae), a Sonoran Desert native, are collected by both ants and mammals. They are adapted for dispersal by ants, a phenomenon known as myrmecochory. Myrmecochorous plants are rare in the arid regions of North America, representing but a small fraction of the flora (MacMahon, Mull & Crist, 2000). Ants are attracted to the seed's elaiosome, an attached food body that is typically ingested after seeds are transported to the colony's nest. Myrmecochorous plants can receive a variety of benefits from this interaction, including escape from mammalian seed predators foraging at the base of maternal plants (O'Dowd & Hay, 1980; Heithaus, 1981; Turnbull & Culver, 1983; Gibson, 1993; Fedriani *et al.*, 2004), colonization of habitats (Andersen, 1988), and dispersal to ant trash middens, sites that may be nutrient rich (Wagner, Brown & Gordon, 1997) and/or less vulnerable to natural enemies (O'Dowd & Hay, 1980; Hay & Fuller, 1981). As a result, a seed's interaction with ants and rodents has the potential to influence plant recruitment, resource acquisition, abundance, and distribution. Spatio-temporal heterogeneity in this interaction is common (O'Dowd and Hay, 1980; Heithaus, 1981; Gomez & Espadaler, 1998; Carney, Byerley & Holway, 2003; Fedriani *et al.*, 2004; Ness *et al.*, 2004). This heterogeneity may be partly attributable to external drivers, both biotic (*e.g.*, the presence of alternative food resources, abundance of predators and mutualists) and abiotic (*e.g.*, weather conditions) (Fedriani *et al.*, 2004).

In arid ecosystems such as the Sonoran Desert, the likelihood of seed collection by ant mutualists and mammalian seed predators is strongly influenced by the abiotic environment. If that environment influences foraging by ants and mammals differently, plants may benefit by making seeds available during portions of the day or within certain temperature ranges that increase the likelihood of collection by ants but not mammals. In such a scenario, competition between the two seed-collecting guilds could represent an opportunity for plants to replace a predator with a mutualist (rather than merely exchanging one natural enemy for another, as typically occurs where ants and rodents compete for the non-myrmecochorous seeds).

This study evaluates three hypotheses: 1) ant mutualists and mammalian seed predators compete for *D. wrightii* seeds; 2) although overlapping in space, seed collection by ants and small mammals frequently occurs in different temperature or diurnal environments; and 3) seed presentation (fruit dehiscence) is triggered by changes in the abiotic environment. We also describe the dispersal of *D. wrightii* seeds by ants.

STUDY ORGANISMS AND SITE

Datura wrightii is commonly found in Sonoran Desert river washes and other semi-disturbed sites. This perennial typically flowers and sets fruit from June to October. Individuals produce one to dozens of spiny fruits, each with 50-500 seeds. Fruits dehisce vertically, spilling a majority of the seeds directly beneath the parent plant at once. Each seed has an attached elaiosome. Photos and chemical analysis of the diaspores of a co-occurring sister species, *D. discolor*, can be found in O'Dowd and Hay (1980).

All fieldwork was performed on the riparian edges of the Canada del Oro river in Catalina State Park, at the base of the Catalina Mountains, 25 km north of Tucson, Arizona. This wash included mature, seed-producing *D. wrightii* plants along the riparian edge. Fieldwork in 2003 coincided with the Aspen Fires in forests at higher elevations in the Catalina Mountains (see Discussion below).

Methods

SEED COLLECTION BY ANTS AND RODENTS

Seeds were added to three types of depots: rodent-exclusion (ant accessible), ant-exclusion (rodent accessible), and shared access (simultaneously accessible to rodents and ants). Each depot consisted of 10 seeds in a Petri dish surrounded by a mesh cage (dimensions: 15 × 15 × 5 cm, mesh size: 2 × 2 cm). At the ant-exclusion depots, the Petri dish exterior was painted with Insect-a-Slip® (BioQuip Products, Rancho Dominguez, California), a slippery substance that ants cannot climb. The tops of these cages were removed to permit access by small mammals. Petri dishes in the rodent-exclusion depots lacked Insect-a-slip® and were surrounded by an intact cage. Shared-access depots lacked both Insect-a-slip® and cage lids. Three depots (one of each type) were placed under 10-14 *D. wrightii* canopies at either 0700 or 1900. Depots were inspected 12 h later, and seeds were counted and replenished at that time for a second 12-h experiment. We chose these two 12-h periods to be consistent with the time periods in the fruit dehiscence study (see below). Hereafter, we refer to activity during the 1900-0700 experiments as nocturnal, although that period also includes crepuscular foraging at dawn and dusk (approximately 0500 and 2000, respectively). Foraging between 0700 and 1900 occurred in full daylight. This 24-h procedure was repeated nine times from June 21 to July 14, 2003. Air temperatures at 1300 and 0100 (the midpoint of the diurnal and nocturnal experiments) were measured at a weather station within 5 km of our study site, at a similar elevation on the same side of the Catalina Mountains. We hypothesized that temperature (and perhaps other correlated variables such as aridity and surface soil temperature) could influence foraging by ants and rodents.

To evaluate the effects of the abiotic environment on seed collection rates, we used three analysis of variance (ANOVA) models, each including temperature, diel period (day *versus* night, a categorical variable), and an interaction term (temperature × diel period) as independent variables. Dependent variables included seed collection at the three depot types. The means from each of the 12-h experiments ($n = 17$) were used as replicates (total number of depots = 612, or three types × 10-14 depots per type × 17 12-h experiments). To test for competition, we used sign tests to compare the total number of seeds collected by ants and rodents foraging separately with the number of seeds collected at depots accessible to both groups. Each 12-h period was used as a replicate, and separate tests were performed for the diurnal and nocturnal experiments.

FRUIT DEHISCENCE

The timing of fruit dehiscence was monitored in autumn 2002. Sixteen potted plants were kept outdoors, and the fruits were censused in the morning and evening (approximately 0700 and 1900, respectively). To evaluate whether timing of fruit dehiscence varied with ambient conditions, a similar survey was performed in a climate-controlled greenhouse at the University of Arizona exposed to ambient sunlight. Fruits on 66 plants were censused in the morning and evening (approximately 0700 and 1900, respectively) from September 25 to October 10, 2002. The outdoor and greenhouse plants were derived from the same seed pool and grown in identical soils. The null hypotheses that diurnal and nocturnal fruit dehiscence would occur with similar frequency was evaluated with two-sided paired *t*-tests, using individual plants as replicates.

ANT-GENERATED SEED DISPERSAL CURVES

Individual seeds were placed at 1-m intervals along a transect less than 1 m from the wash's riparian edge. We followed each ant that collected a seed, recording ant identity, the distance seeds were displaced from their original position, and seed deposition site. Observations were performed between 0700 and 1100 on June 27, July 6, and July 24, 2003. We observed ants during the morning because foraging intensity decreased dramatically as mid-day temperatures increased. The species composition of the seed-collecting ant guild did not change throughout the day (J. H. Ness, pers. observ.). We did not monitor seed collection at night, because it was difficult to follow the ants and we were concerned that our lights would alter the ant behaviours. We followed 101 seeds.

Results

SEED COLLECTION BY ANTS AND RODENTS

Seed removal rates from the rodent exclosures (ant-accessible depots) were influenced by temperature but not diel period (Table I). The temperature × diel period interaction was nearly significant (*P* = 0.06), perhaps because temperature was a particularly accurate predictor of seed collection by ants during the day (mean number of seeds collected per depot = -0.57(Temp) + 24.2; *r*² = 0.86; Figure 1a). For example, a 10 °C increase induced a six-fold decrease in the rate of seed collection by ants. The effect of lunar illumination on seed collection by ants was marginally significant (simple linear regression, *F* = 4.83, *df* = 7, *P* = 0.06; *r*² = 0.41); fewer seeds were collected on nights with full moons (2.5 ± 0.2 seeds per depot;

mean ± SD; *n* = 2 nights), than on those with half moons (3.8 ± 2.0; *n* = 5) or new moons (5.0 ± 1.5; *n* = 2).

Seed removal from the ant exclosures (where rodents had access) was 15 times greater at night relative to daytime removal (Figure 1b). Diel period was a significant predictor of seed collection rate, although temperature and temperature × diel period interactions were non-significant (Table I). Rodents collected similar numbers of seeds on nights with full moons (mean ± SD = 6.2 ± 1.5; *n* = 2 nights), half moons (5.2 ± 1.6; *n* = 5), and new moons (6.1 ± 0.7; *n* = 2) (simple linear regression, *F* = 0.17, *df* = 8, *P* = 0.69).

The total number of seeds taken from rodent and ant exclosures exceeded the number taken from the depots accessible to both taxa during 15 of the 17 12-h experiments. The difference was significant for depots at night (9 of 9, *P* = 0.004) but not for depots during the day (6 of 8, *P* = 0.29; Figure 1c). Temperature was a significant predictor of seed removal rates at the depots accessible to both ants and rodents, and the temperature × diel period interaction was also significant (Table I).

FRUIT DEHISCENCE

Diurnal dehiscence was more common than nocturnal dehiscence for 13 of the 16 outdoor plants (*t* = 4.89, *df* = 15, *P* < 0.001); 86% of the outdoor fruits dehisced during the day. In contrast, greenhouse plants exhibited diurnal and nocturnal fruit dehiscence with similar frequency (47% versus 53% of all fruits, respectively; *t* = 0.51, *df* = 65, *P* = 0.61).

ANT-GENERATED SEED DISPERSAL CURVES

Seeds were collected exclusively by *Pogonomyrmex californicus* and *Aphaenogaster cockerelli* (58% and 42% of the seeds, respectively). The diaspore (seed and attached elaiosome) was always returned to the nest. *Aphaenogaster cockerelli* dispersed seeds shorter distances (mean ± SE = 3.94 ± 0.39, range: 0.61-15.1 m) than did *P. californicus* (mean ± SE = 9.05 ± 0.99, range: 0.85-25.2 m; Figure 2). Mean ± SE dispersal distance for all seeds was 6.06 ± 0.53 m.

Discussion

Dispersal can provide multiple benefits to seeds and plants, including escape from natural enemies, colonization of habitats, and directed dispersal to microsites particularly suitable for germination (Howe & Smallwood, 1982). All of these benefits may be conferred to *D.*

TABLE I. Analysis of variance models evaluating the main effects of temperature, diel period (day versus night), and interactions between temperature and diel period on seed collection by ants, small mammals, and collection by both groups foraging together.

Dependent variable	Source	df	SS	F	P
Collection by ants alone	Temperature	1	11.45	8.58	0.012
	Diel period	1	2.88	2.16	0.166
	Temperature × Diel period	1	5.51	4.13	0.063
Collection by mammals alone	Temperature	1	0.25	0.22	0.649
	Diel period	1	24.41	20.96	0.001
	Temperature × Diel period	1	1.61	1.38	0.262

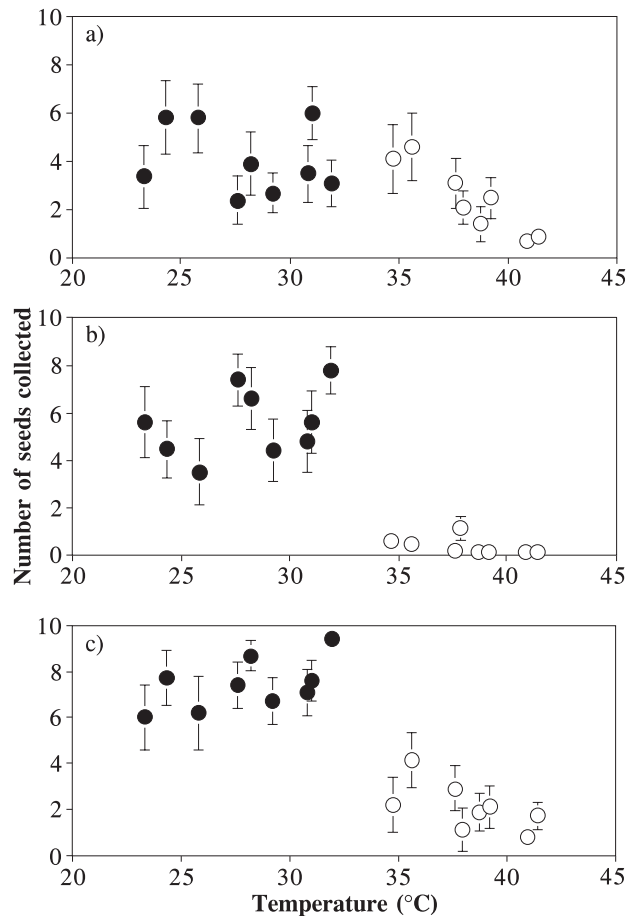


FIGURE 1. The relationship between temperature and the mean number of seeds collected in 12 h at depots that excluded rodents but not ants (a), excluded ants but not rodents (b), and were accessible to both groups (c). Each point indicates the mean (\pm SE) from 11-14 seed depots. Filled circles indicate depots exposed to seed collectors at night (1900-0700), and empty circles indicate depots exposed during the day (0700-1900). Temperature values indicate the temperatures at the midpoint of these experiments (0100 and 1300, respectively).

wrightii by the seed-collecting ant community. Below, we discuss differences in seed collection by ants and rodents, the evidence for competition between those two groups, how the timing of seed presentation may favour collection by ant mutualists, and the fate of seeds subsequent to their collection by ants.

In our study, the total number of seeds removed from depots where ants and rodents foraged separately exceeded the number taken from depots where they shared access. This difference indicates that seed removal by one group may deprive the other of access to seeds (Heithaus, 1981). Competition among ants and rodents for seeds has been well documented in the deserts of the southwestern United States (Brown & Davidson, 1977; MacMahon, Mull & Crist, 2000), although in that setting both groups typically act as seed predators. Because ants collect *Datura* seeds to consume the elaiosome rather than the seed itself (O'Dowd & Hay, 1980), this inter-guild competition may rescue seeds from predation by small mammals. Competition was greatest at night, as rodents foraged most intensively during that period. The difference in the foraging schedules of ants and rodents has been noted by

other researchers (rodents and ants: Heithaus, 1981; Turnbull & Culver, 1983; Gibson, 1993; rodents: Hay & Fuller, 1981). Indeed, the prevalence of nocturnal rather than diurnal seed collection led us to conclude that mammals were the most common vertebrate seed predators, rather than birds (see also Mares & Rosenzweig, 1978; Fedriani *et al.*, 2004). In such cases, diurnal fruit dehiscence decreases the vulnerability of seeds to small mammal seed predators.

The prevalence of diurnal rather than nocturnal seed presentation may be an adaptation to decrease seed predation by small mammals. This pattern in seed presentation has been reported for ant-dispersed plants in three families: Violaceae (*Viola nuttalli*; Turnbull & Culver, 1983), Scrophulariaceae (*Melampyrum lineare* and *M. silvaticum*; Gibson, 1993), and Solanaceae (*D. wrightii*; this study). This is the first study to demonstrate the phenotypic plasticity of that pattern in dehiscence. Plants in an environment with consistent temperatures and humidity (a greenhouse) dehisced fruits at equal frequencies during the night and day. Temperature and humidity change predictably during day and night in the Sonoran Desert and the temperate deciduous forest occupied by the other aforementioned species. Whether similar patterns of seed presentation for myrmecochorous plants are observed in biomes with more consistent temperature and humidity, such as the humid tropics, is an interesting, and unexplored, question.

The lunar cycle had no discernable effect on the number of seeds collected by small mammals. We attribute this similarity to the *D. wrightii* canopy above the experimental depots. This cover may decrease the vulnerability of small mammals to predation during bright nights, such as those with full moons (Kotler, Ayal & Subach, 1994). Intriguingly, if moonlight constrains the foraging by ants more than rodents, *Datura* seeds may be more vulnerable during brightly lit nights.

The mean dispersal distance reported here (> 6 m) well exceeds those included in a recent world survey of myrmecochorous dispersal distances (Gomez & Espadaler, 1998), and the maximum dispersal distance (26 m) is much farther than reported in most studies. This difference may be attributable to the large size of seed-collecting harvester ants in this community (*P. californicus* mean body length \pm SD = 7.7 ± 0.4 mm, $n = 14$; *A. cockerelli* = 7.4 ± 0.2 , $n = 10$; Ness *et al.*, 2004). We did not monitor seed dispersal distances at night, however, and the composition of the ant assemblage collecting seeds during that period could differ. For example, Whitford and Ettershank (1975) distinguish *P. californicus* and *A. cockerelli* as strictly diurnal and facultatively nocturnal, respectively. Thus, the true dispersal curve of *D. wrightii* may include proportionately more dispersal by the latter species than does the purely "diurnal" curve shown in Figure 2 (although diurnal dehiscence would lessen this difference). Is the great dispersal distance of *D. wrightii* relative to ant-dispersed plants in other communities important to the plant? Even short-range dispersal by ants (< 2 m) can decrease competition with the maternal plant and/or natural-enemy-inflicted mortality for seedlings (Kjellsson, 1991; Boyd, 2001). The rarer long-distance dispersal events may help seeds colonize distant sites, transport that is perhaps also facilitated by

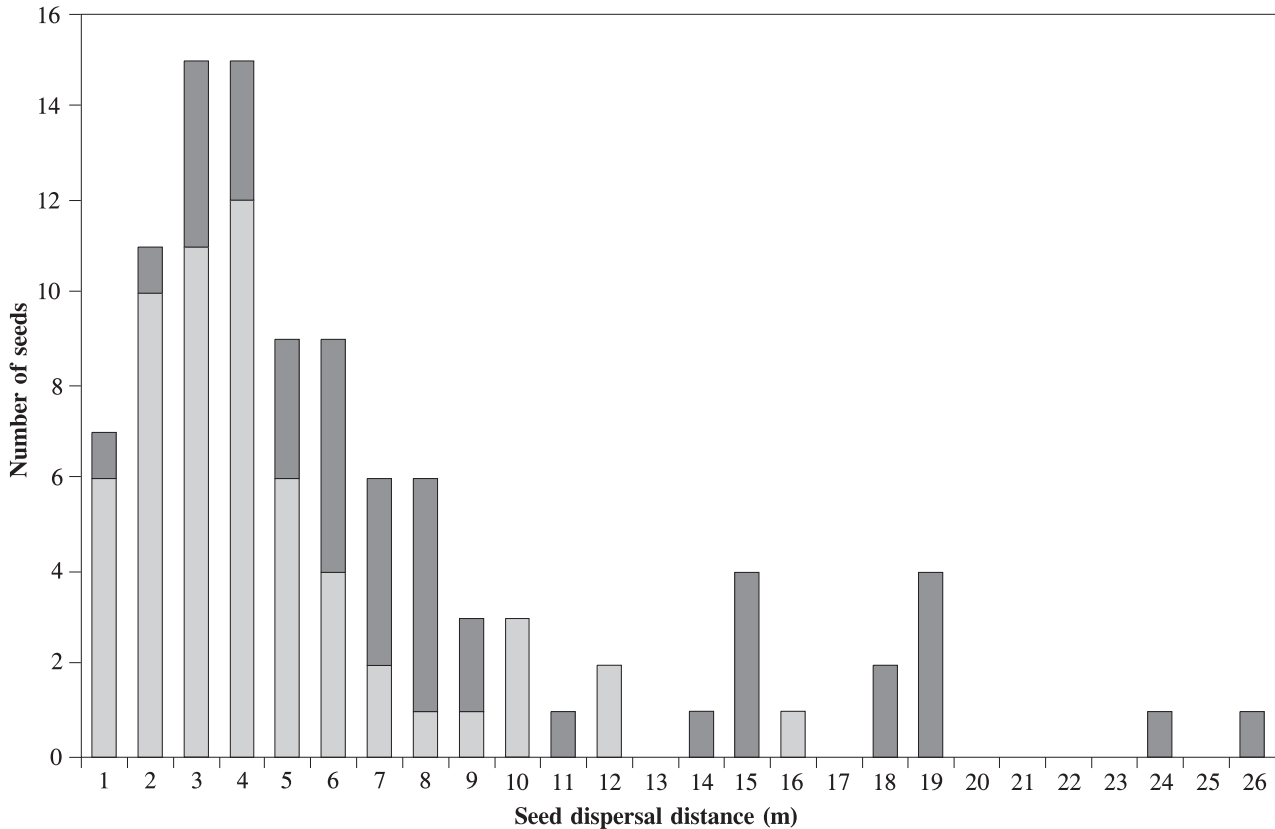


FIGURE 2. The dispersal curve for *Datura wrightii* seeds transported by ants in a Sonoran Desert dry river wash. One hundred and one seed dispersal events were observed, and all seeds were collected by either *Aphaenogaster cockerelli* or *Pogonomyrmex californicus* (shown in pale grey and dark grey, respectively). All seeds were transported to ant nests.

secondary dispersal by wind or water. Unlike these passive flows, however, ant transport can also move seeds upstream or between washes (O’Dowd & Hay, 1980).

Ant-collected seeds arrive at the ant nest. After the elaiosome is detached and eaten, *Datura* seeds collected by harvester ants (*P. californicus* and *Veromessor pergandei*) are expelled from the nest undamaged onto the external colony midden, or trash heap (O’Dowd & Hay, 1980). Should the seeds remain on these sites, they may benefit from a greater concentration of nutrients on those middens, as the concentrations of ammonium, nitrate, phosphorous, and potassium are elevated in harvester ant mounds, relative to adjacent soils (*P. barbatus*: Wagner, Brown & Gordon, 1997). Seeds are also less vulnerable to small mammal predation in these exposed sites, relative to those underneath the maternal plant canopy (O’Dowd & Hay, 1980; Hay & Fuller, 1981).

Several limitations of this study warrant comment. First, the number of seeds included in each depot in this study represents a fraction of the seeds in a typical *Datura* fruit. We used 10 seeds per depot, following earlier studies of *Datura* (O’Dowd & Hay, 1980; Hay & Fuller, 1981). O’Dowd and Hay (1980) found that the collection of *Datura* seeds by rodents is distant-responsive (increasing with proximity to the canopy of the maternal plant), rather than dependent on the density of seeds. Those researchers also noted that rodents typically consumed all the seeds at the depots they discovered; seed predation rate was influenced more by the likelihood of

depot discovery than by the number of seeds at those depots (see also Heithaus, 1981). Thus, we considered an experimental design that favoured greater replication (more depots with fewer seeds per depot) to be most appropriate for this study. We note, however, that our ability to detect competition between rodents and ants for seeds could be influenced by the densities of seeds placed in the experimental arrays. Second, our attempt to follow the fates of seeds and seedlings over time was thwarted by the Aspen Fires in the Catalina Mountains. The storm that ultimately extinguished this fire filled the wash with a layer of silt runoff approximately 75 cm deep. This deposition wholly buried *D. wrightii* plants and ant nests in the area. As a result, whether the ants’ documented effects in protecting and moving seeds influences an individual plant’s reproductive success or population-scale measures remains speculative. Last, the effects of granivores on seeds are not wholly antagonistic in all cases (Chambers & MacMahon, 1994; Longland *et al.*, 2001), and seed-collecting ants may themselves act as seed predators. Indeed, the harvester ants we and others (Bullock, 1974; O’Dowd & Hay, 1980; Carney, Byerley & Holway, 2003) identify as mutualists act as seed predators of other plant species. Clearly, the benefits conferred to plants differ among ant and plant species.

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