

# Does the morphology of animal foraging pits influence secondary seed dispersal by ants?

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**Abstract** Secondary seed dispersal by ants (myrmecochory) is an important process in semi-arid environments where seeds are transported from the soil surface to an ant nest. Microsites from which ants often remove seeds are the small pits and depressions made by native and exotic animals that forage in the soil. Previous studies have demonstrated greater seed retention in the pits of native than exotic animals, but little is known about how biotic factors such as secondary seed dispersal by ants affect seed removal and therefore retention in these foraging pits. We used an experimental approach to examine how the morphology of burrowing bettong (*Bettongia lesueur*), greater bilby (*Macrotis lagotis*), short-beaked echidna (*Tachyglossus aculeatus*) and European rabbit (*Oryctolagus cuniculus*) foraging pits and ant body size influenced ant locomotion and seed removal from pits along an aridity gradient. Ants took 3.7-times longer to emerge from echidna pits (19.6 s) and six-times longer to emerge from bettong pits (30.5 s) than from rabbit pits (5.2 s), resulting in lower seed removal from bettong pits than other pit types. Fewer seeds were removed from pits when cages were used to exclude large body-sized (>2 mm) ants. Few seeds were removed from the pits or surface up to aridity values of 0.5 (humid and dry sub-humid), but removal increased rapidly in semi-arid and arid zones. Our study demonstrates that mammal foraging pit morphology significantly affects ant locomotion, the ability of ants to retrieve seeds, and therefore the likelihood that seeds will be retained within foraging pits.

**Key words:** ant–plant interaction, foraging pit, myrmecochory, seed dispersal, seed fate.

## INTRODUCTION

Secondary seed dispersal by ants (myrmecochory) is an important process in semi-arid environments. Myrmecochory represents the movement of a seed after it has arrived on the soil surface (van Oudtshoorn & van Rooyen 1999) and is classified as a non-symbiotic mutualistic interaction between ants and plants (Bas *et al.* 2009). Ants gain a food reward from this interaction because myrmecochorous plant seeds, such as *Acacias*, contain a lipid-rich external appendage (elaiosome), which is either consumed by ants after the seeds are transported back to the nest, or is fed to their larvae (Hanzawa *et al.* 1988; Lengyel *et al.* 2010). This relationship is thought to advantage the seeds, which are transported from the unpredictable soil matrix to nutrient-rich environments such as the ant nest (directed dispersal hypothesis; Salazar-Rojas *et al.* 2012; but see Rice & Westoby 1986). The seeds are then often discarded on refuse piles outside the ant nest (Pizo & Oliveira 2001) where they readily germinate, and some seeds may germinate within the nests. This process also reduces parent–offspring competition and seedling

competition (distance dispersal hypothesis; Giladi 2006).

Ants disperse seeds from a range of microsites such as dense vegetation, beneath leaf litter, from the soil surface, and soil surface depressions such as cracks, crevices and foraging pits. Foraging pits are small depressions in the soil constructed by animals such as the burrowing bettong (*Bettongia lesueur*), greater bilby (*Macrotis lagotis*) and short-beaked echidna (*Tachyglossus aculeatus*) while foraging for food (James & Eldridge 2007). Pits not only collect seeds, but become fertile patches because they trap leaf litter, and have greater soil moisture and lower temperatures than the surrounding exposed soil surfaces (Whitford & Kay 1999). Leaf litter captured in foraging pits is decomposed by microbes and macro-invertebrates, and results in enhanced nutrient pools compared with non-pit surface soils (Whitford 2002). Greater soil moisture in foraging pits is due to an increase in water infiltration in disturbed patches, and the presence of leaf litter which reduces soil temperature and evaporation (Eldridge & Mensinga 2007).

The extent to which pits become safe sites for seeds and support plant germination depends on the capture and retention rate of seeds, the degree to which seeds avoid capture by ants, and whether the pit environment is conducive to plant germination,

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growth and survival. Pits of both native and exotic soil-disturbing animals have been shown to trap seeds from a range of plant species. In the Negev highlands Israel, pits constructed by the Nubian Ibex (*Capra nubiana*) supported a larger numbers of annual plants than similar-sized areas upslope of the pits (Gutterman 1997). Similarly, Cape porcupine (*Hystrix africae australis*) pits in South Africa have been shown to support a greater plant density and richness than the surrounding soil matrix (Bragg *et al.* 2005). However, previous research has shown that pits of different animals vary in their ability to capture and retain seeds, thereby enhancing the success of seed germination, influencing plant abundance and diversity. For example, in Australia, the pits of the burrowing bettong and greater bilby in South Australia contained 3.5 times more seedlings than the adjacent soil matrix and significantly greater seed species richness than pits of the introduced European rabbit (*Oryctolagus cuniculus*; James *et al.* 2010).

Pit shape and volume could also affect secondary dispersal by organisms, such as ants (Lipp *et al.* 2005), birds or small mammals by preventing access to seeds. In turn, this could affect seed retention rates in different shaped pits. For example, differences in pit morphologies could present a physical barrier to ants, preventing them from entering the pits, thus resulting in different seed abundance and diversity among different shaped pits. Additionally, the energy expended in removing seeds from pits will likely differ among different body sizes of ants. Therefore, steeply sided bettong and bilby pits might act as a filter on ant access by preventing small body-sized ants that may require relatively greater energy expenditure than large-bodied ants, from removing pit-resident seeds, effectively creating 'safe sites' for seeds (*sensu* Harper 1977). Finally, seed predation and thus retention in mammal pits may vary in relation to temperature and rainfall, which would influence food availability for ants. In Australia, myrmecochory is most frequent within dry heath and dry sclerophyll forest habitats where soils are nutrient poor (Davidson & Morton 1981). Therefore, seed removal would be expected to be greater in low productivity arid and semi-arid sites than more mesic sites with high soil fertility.

We used an experimental approach to examine how the morphology of mammal-constructed foraging pits affects ant locomotion and seed dispersal over an aridity gradient, and whether this accounts for differences in seed abundance between native and exotic animal pits. Pit morphology was based on three markedly different pit shapes that are created by the burrowing bettong, short-beaked echidna and the exotic European rabbit. We also examined whether ant body size influences seed removal within foraging pits by preventing large-bodied (>2 mm) ants from entering and removing seeds.

Specifically, we examined four research questions, with three underlying hypotheses: (i) Do mammal foraging pits physically restrict the movement of ants?, and, (ii) For those ants that are able to move freely in and out of pits, are they able to remove seeds, and if so, does seed removal vary across different pit morphologies? We expected that there would be fewer seeds removed from bettong pits because ants would take longer to emerge from these deep pits than from the shallower pits of rabbits or the flat soil surface. Emergence from echidna pits would be more difficult due to the more complex surface (Gibb & Parr 2010) created by the large clods of soil surrounding the pits. (iii) Does ant body size affect seed removal from foraging pits? Large ant species are more efficient at handling and transporting large seeds (Servigne & Detrain 2008) because of their larger head (and mandible) size (Rudolph & Loudon 1986). We therefore expected that fewer seeds would be removed from treatments where large ant species (>2 mm) are absent. (iv) Does seed removal from mammal pits vary along an aridity gradient? We expected that more seeds would be removed in areas of lower rainfall (arid and semi-arid environments) because plant cover is generally sparser, there are fewer resources for ants, and thus the pressure to removal all seeds would be greater as sites became more arid.

## METHODS

Our study comprised three separate experiments, which are described below.

### Ant emergence in relation to pit morphology

In November 2012, we constructed artificial foraging pits of bettongs, echidnas and rabbits at a site at Fowlers Gap Arid Zone Research Station (31°05'S, 142°42'E). Average rainfall at Fowlers Gap is 225 mm (BOM 2016), summer temperatures range from 20 to 31.4°C, and winter temperatures from 4.6 to 16.3°C. Soils are desert loams and calcareous earths, and the vegetation was dominated by arid shrub steppe with *Atriplex vesicaria*, *Maireana pyramidata* and *Maireana astrotricha*.

Bettong pits were constructed as steeply sided, cylindrical-shaped excavations (James *et al.* 2010) about 15 cm wide and 10–20 cm deep (Eldridge *et al.* 2012), with excavated soil concentrated on one side of the foraging pit. Echidna pits were basin-shaped depressions about 20 cm across and 15 cm deep (Eldridge *et al.* 2012), generally surrounded by large loose clods of soil (Eldridge & Mensinga 2007). Pits of the European rabbit are shallower than echidna pits, and were constructed to be 5 cm deep and 10 cm long with a ramp-like incline at the distal end (Eldridge & Kwok 2008). All pits were constructed to resemble naturally occurring pits.

The study was conducted within five blocks (4 m by 4 m) spaced approximately 10 m apart. Each block contained the three artificially constructed pit types. Within a

block, pits were randomly located about 0.5–1 m apart. Within the centre of each of the 15 pits (five blocks by three pit types), we placed an individual *Pheidole* sp. 1 ant, and recorded the time taken for it to emerge from the pit. We measured emergence times for each pit ten times, each time using a different ant.

### Effect of ant body size on seed removal from pits

This study was carried out at three sites within the State Forest at Cobar (31°30'S, 145°49'E) during January 2015. Average rainfall in Cobar over the past 10 years was 371.4 mm (BOM 2016). Summer temperatures range from 20 to 31.4°C, and winter temperatures 4.6–16.3°C. Soils are calcareous sands and red earths. Major vegetation groups include *Acacia* Shrublands and *Eucalypt* woodlands. Dominant trees include *Eucalyptus populnea* and *Callitris glaucophylla*, and dominant shrubs *Eremophila* spp., *Dodonaea viscosa*, *Senna* spp. and *Acacia* spp.

The three sites were separated by distances of about 200 m. Each site contained five randomly located and artificially constructed bettong, echidna and rabbit pits, and five non-pit soil surface control, which were all separated by distances of >1 m. Pits were constructed as in the emergence study. Each pit replicate was assigned to one of three cage treatments: (i) cage (a wire frame with 2 mm mesh), (ii) procedural cage control (a wire frame without mesh) and (iii) open control. The cages were 20 × 20 cm and 10 cm high. Half of the wire cages were covered with 2 mm insect-proof wire mesh and half served as procedural controls (i.e. frames without fly wire). Thus for this experiment, we had three sites × five blocks × four pit types (bettong, echidna, rabbit, surface) × three treatments (cage, cage control, open control). We placed a small cardboard dish containing 50 *Acacia longifolia* seeds in the centre of each pit and open control (soil surface). Seed removal was measured over 3 h, and ants interacting with seeds were collected for identification. Ants specimens were identified to genus (Shattuck 1999) and to species where possible using available identification keys. *Rhytidoponera* and *Camponotus* were the only ant genera >2 mm in body size that were excluded from the caged treatment. Smaller body-sized ants (<2 mm) that were able to interact with seeds in all cage treatments included *Iridomyrmex*, *Pheidole*, *Meranoplus*, *Monomorium* and *Tetramorium* spp.

### Seed removal over an aridity gradient

We tested the effect of pit morphology on seed removal at 16 sites along an aridity gradient between November and February from 2013 to early 2015. Sites were located at Scotia Sanctuary (33°13'S, 141°10'E), Fowlers Gap (31°05'S, 142°42'E), Hay (34°32'S, 144°51'E), Narranderra (34°45'S, 146°33'E), Yathong (32°37'S, 145°34'E), Borambola (35°11'S, 147°40'E), Cowra (33°51'S, 148°36'E), Goulburn (34°45'S, 149°45'E), Gundagai (34°59'S, 148°07'E), Canberra (35°10'S, 149°04'E), Yass (34°50'S, 149°01'E), Richmond (33°35'S, 150°43'E), Pagewood (33°56'S, 151°13'E), Bundanoon (34°40'S, 150°17'E), West Pennant Hills (33°46'S, 151°02'E) and

Katoomba (33°42'S, 150°19'E). Average rainfall over this gradient for the decade preceding the study ranged from 246.2 to 1471.5 mm (BOM 2016). Summer temperatures during the experiment ranged from 11.8 to 35.3°C and winter temperatures from 0.5 to 18.7°C (BOM 2016). The Aridity Index (AI) of sites was calculated using the annual mean aridity layer from the Atlas of Living Australia (ALA 2010). Because this index increases with increasing wetness, we calculated a more intuitive value as 'Aridity', where Aridity = 1 – Aridity Index such that increasing values corresponded to increased dryness, thus aiding the interpretation of our data. Our sites were therefore classified into different Aridity classes (Middleton & Thomas 1997): humid (Aridity <0.35: Bundanoon, Canberra, Gundagai, Katoomba, Pagewood, West Pennant Hills and Yass), dry sub-humid (Aridity 0.35–0.50: Borambola, Cowra, Goulburn and Richmond), semi-arid (Aridity 0.50–0.80: Hay, Narranderra and Yathong) and arid (Aridity 0.89–0.95: Fowlers Gap and Scotia Sanctuary).

Soil groups over the aridity gradient included calcareous sands, desert loams, red earths, alluvial soils, red, brown and yellow podzolics and siliceous sands, supporting a large range of vegetation. The aridity gradient included major vegetative groups; Mallee woodland, Chenopod shrubland, *Eucalyptus* open forest and woodland. Trees over the aridity gradient included *Eucalyptus* spp. and *C. glaucophylla*. Dominant shrubs over the aridity gradient included; *Acacia aneura*, *Senna* spp., *D. viscosa*, *Eremophila* spp., *A. vesicaria*, *M. astrotricha* and *M. pyramidata*. Although the study was carried out over 2.5 years, it was always carried out in summer, with relatively constant temperatures. Sites were sampled widely across the gradient in any 1 year in order to avoid potential confounding effects in relation to slight differences rainfall across years.

At each of the 16 sites, we established five (4 m by 4 m) blocks, spaced 20 m apart. Each block contained one randomly located, artificial bettong pit, echidna pit, rabbit pit and a soil surface control, separated by distances of >1 m. In the centre of each pit and non-pit control, we placed a small cardboard dish containing 40 *A. longifolia* seeds. Seed removal was measured over a 3 h between 9.00 and 12.00 hours and ants interacting with seeds were collected for identification. All seeds were removed from the plots after the experiments.

### Seed species used in all studies

We used coastal wattle (*A. longifolia* subsp. *sophorae* (Labill.) Court) seeds in the body size and aridity studies because *Acacia* seeds are highly adapted for ant dispersal. *Acacia longifolia* subsp. *sophorae* is a prostrate or decumbent shrub approximately 0.5–3 m tall occurring in heath and sclerophyll forests along the eastern and southern coast of Australia and around the Tasmanian coast on sand dunes and adjacent alluvial flats. Seed pods are approximately 40–150 mm long and 3–10 mm wide containing up to 10 seeds and are coiled and twisted on opening. Seeds are black with a smooth and shiny surface approximately 5–6 mm long and 3–4 mm wide and contain a large yellow or orange cup-shaped elaiosome. Many species of *Acacia* occurred over our gradient, with different sized seeds and different types, size and shapes of

elaiosomes. We therefore used the seed of one species in order to ensure that size and shape did not differ across the gradient, thus maintaining a similar attractiveness to ants. This minimized any potential bias related to differential seed attractiveness across the gradient.

### Statistical analysis

To test whether pit morphology affected ant emergence (Study 1), we used a linear mixed model (LMM) with the *lme4* package (Bates *et al.* 2015) in *R* (R Core Team 2015). Prior to modelling, emergence time was  $\log_{10}$ -transformed to meet assumptions of normality. The model tested emergence time against pit type (fixed effect) using block as a random effect. Tukeys's *post hoc* tests were used to determine differences in emergence times between the three pit types, using the function *glht* in package *multcomp* (Hothorn *et al.* 2008). To test the effect of body size on seed removal (Study 2), we used generalized linear mixed models (GLMM) with the *lme4* package and a binomial distribution. The model included pit type (bettong, echidna, rabbit, surface) and treatment (Cage, Procedural Cage control, Open) and their interactions.

To test aridity effects on seed removal (Study 3), we used GLMMs with pit treatment, aridity and their interaction as fixed effects, and site and block as random effects. This model was used to predict seed removal over the aridity gradient. We also developed a second-order polynomial using the *poly* function in *R* (R Core Team 2015) on the fixed factor 'aridity' to test for a potential unimodal relationship between seed removal across the gradient. To test for the effects of fixed factors, we added a single fixed factor to the model until we reached the full model and tested it against the previous reduced model using bootstrapping with the function *pbcomp* in package *pbkrtest* (Halekoh & Højsgaard 2014) with 1200 iterations. To test the effect of aridity class and body size on seed removal, we replaced 'aridity' with aridity class and cage treatment in two separate models. Tukeys's *post hoc* tests were used to determine differences within fixed factors pit treatment, aridity class and cage treatment and their interactions.

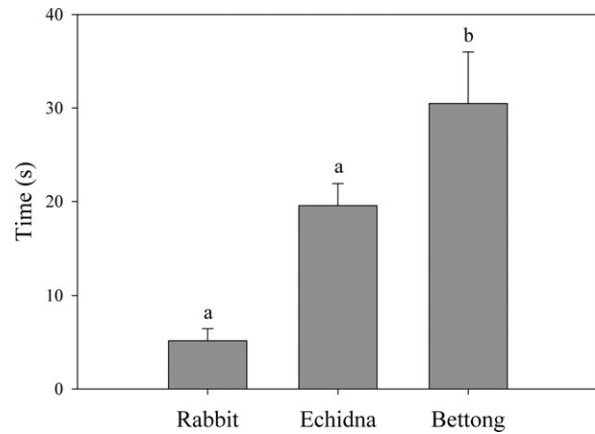
## RESULTS

### Ant emergence in relation to pit morphology

*Pheidole* sp. 1 workers took six-times longer to emerge from bettong pits (30.5 s) and 3.7 times longer to emerge from echidna pits (19.6 s) than from rabbit pits (5.2 s,  $P < 0.001$ , Fig. 1), supporting our first hypothesis.

### Effect of ant body size on seed removal from pits

Fourteen ant species from seven genera were recorded in the second study. Ants located and

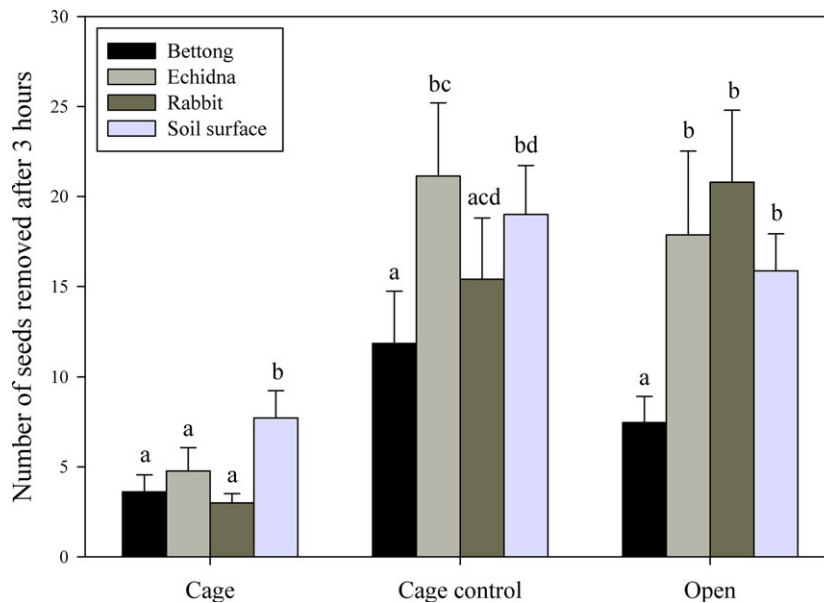


**Fig. 1.** Mean (+SE) time (seconds) taken for ants to emerge from mammal pits. Different superscripts indicate significant differences among treatments at  $P < 0.05$ .

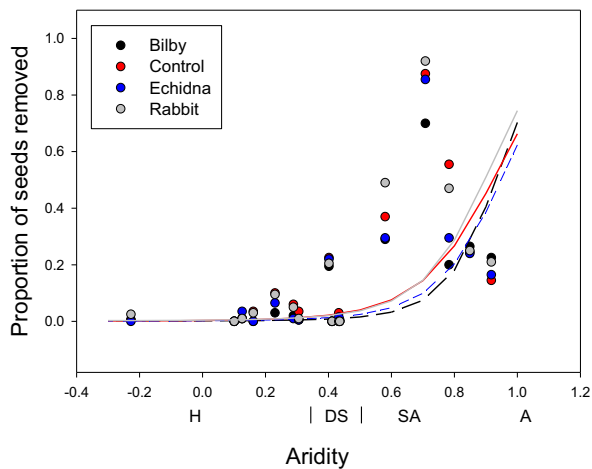
removed some or all seeds from 94% of all pits. As predicted, fewer seeds were removed from the caged treatment that excluded ants  $>2$  mm in body size (Fig. 2). Seed removal was 3.4-times greater in the procedural control (Cage control) and 3.1-times greater in the Open treatment than the Cage treatment. The significant pit by treatment interaction ( $P < 0.001$ ) indicated no difference in removal among the three pit types when large ants were prevented from removing seeds (Cage), but substantial variation in removal among pit types in the Open treatment. Within the procedural control, fewer seeds were removed from bettong pits (Mean  $\pm$  SE;  $11.9 \pm 2.87$ ) than echidna pits ( $21.1 \pm 4.07$ ) and the soil surface ( $19 \pm 2.72$ ). There was however, no significant difference in seed removal between bettong and rabbit pits within the procedural control. For the open treatment, however, there were fewer seeds removed from the bettong pits than the other three microsites.

### Seed removal over the aridity gradient

We recorded a total of 52 ant species from 10 genera over the aridity gradient. *Pheidole* and *Iridomyrmex* were the most speciose genera ( $n = 16$  each). Ants located and removed some or all seeds from 48% of the total number pits in our study. Fewer seeds were removed after 3 h from bettong ( $4.9 \pm 0.97$  seeds; mean  $\pm$  SE) than echidna ( $5.5 \pm 1.08$ ) pits, the soil surface ( $6.7 \pm 1.16$ ) or rabbit pits ( $6.9 \pm 1.22$ ). Seed removal in the pit treatments was very low in humid and dry sub-humid zones, but increased markedly in the semi-arid and arid zones (Fig. 3). We found a significant pit by aridity class interaction ( $P < 0.001$ ). Within semi-arid sites, there was significantly greater seed



**Fig. 2.** Effects of cage treatments on the number of seeds removed the three treatments after 3 h (+SE). For each of the three treatments, different superscripts indicate significant differences among the four pit types at  $P < 0.05$ . [Colour figure can be viewed at [wileyonlinelibrary.com](#)]



**Fig. 3.** Modeled relationship showing the proportion of seeds removed in pits and the surface (control) after 3 h in relation to increasing aridity (increasing dryness). Both observed values (symbols) and the fitted model (lines) are shown. A, arid; DS, dry sub-humid; H, humid; SA, semi-arid. [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

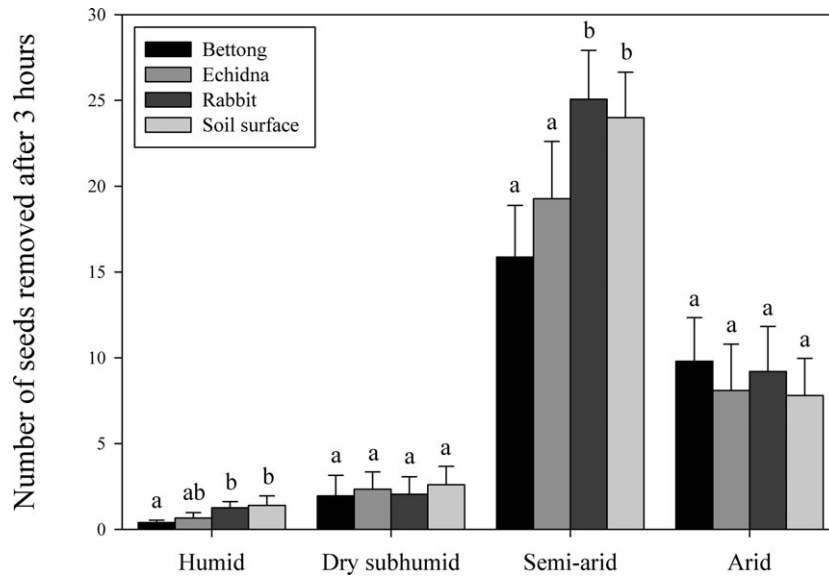
removal from rabbit pits and the soil surface than pits constructed by native mammals. Similarly, within the humid sites, seed removal was significantly higher in rabbit pits and the soil surface than bettong pits, but overall differences in seed removal was small compared with semi-arid sites. In arid and dry sub-humid sites, there was little difference in seed removal between pit treatments (Fig. 4) Seed removal from pit treatments was also more variable at semi-arid sites than sites in other aridity classes.

## DISCUSSION

Our study demonstrated that mammal foraging pit morphology significantly affects ant movement, the ability of ants to retrieve and remove seeds, and therefore the likelihood that seeds will be retained within the pits. Ants took longer to emerge from the foraging pits constructed by the native vertebrates, bettongs and echidnas, than from the soil surface or pits constructed by the exotic rabbit. Furthermore, because of these longer emergence times, seed removal rates were significantly lower for bettong and echidna pits than rabbit pits and the surface. Seed removal followed a unimodal relationship over the aridity gradient, with maximum rates in semi-arid landscapes and lower rates in arid and dry sub-humid–humid sites. Furthermore, large body-sized ants  $>2$  mm (including *Camponotus* and *Rhytidoponera* species) were more efficient at removing seeds from mammal pits than smaller ant genera. Our study indicates that native mammal pits may provide effective safe sites (*sensu* Fowler 1988) for seeds and therefore potentially assist plant recruitment.

### Pit morphology influences ant locomotion

Consistent with our first hypothesis, bettong and echidna pits hindered the movement of ants more than those of the exotic European rabbit. As predicted, ants took six-times longer to emerge from bettong pits and 3.7-times longer to emerge from



**Fig. 4.** Effects of aridity on the average number of seeds removed from pits after 3 h (+SE). Within an aridity class, different superscripts indicate significant differences among treatments at  $P < 0.05$ .

echidna pits than from rabbit pits. Bettong pits are typically deep, vertically faced and cylindrical (Eldridge *et al.* 2012), and likely to present a more energetically demanding obstacle to emerge from than shallower, wedge-shaped pits of the European rabbit. It is likely, therefore, that morphological differences in foraging pit shape and depth were largely responsible for our observations. Longer emergence times from bettong pits likely reflect the increased energetic cost of locomotion when ascending pits with steeply sided walls, preventing the egress of ants carrying large seeds or increasing the time taken for them to transport a relatively heavy load. Previous studies have shown that ants moderate their speed with inclination, with steeper inclinations resulting in slower ant locomotion (Holt & Askew 2012; Khuong *et al.* 2013), consistent with our findings.

Ant foraging costs include travel from the food source to the nest, transporting food sources (either internally or externally) back to the nest, handling costs and positioning food in the mandibles to maintain stability during locomotion (Schilman & Roces 2005). We found that fewer seeds were removed from bettong pits after 3 h than from echidna pits, rabbit pits or soil surface, partially supporting our second hypothesis that removal should be lower in bettong and echidna pits. Our findings may account for the observation of greater seedling abundance in bettong pits (11.2 seedlings  $m^{-2}$ ) than similar-sized rabbit pits (6.2 seedlings  $m^{-2}$ ) from studies in arid shrublands in South Australia (James *et al.* 2011). Higher seed retention in bettong pits

may reflect an increased energetic cost of removing seeds up steep-sided walls. A study of the grass-cutting ant (*Atta vollenweideri*) showed greater  $CO_2$  respiration by laden than unladen workers (Moll *et al.* 2012). Furthermore, leaf tissue transport by the leaf-cutter ant *Atta cephalotes* has been shown to decline sharply on uphill slopes compared to downhill and horizontal trails (Lewis *et al.* 2008) as ants have to expend extra energy to overcome the forces of gravity.

Carrying seeds up steep slopes such as those on the walls of bettong pits may have a larger effect on ant stability during locomotion than the shallower, and steady ramp-like sides of rabbit pits. Ants tend to reduce their mean stride length, mean speed and mean stride frequency to maintain stability while carrying loads (Zollikofer 1994). Leaf-cutter species *Acromyrmex heyeri* also exhibit shorter handling and transport time for lighter fragments of grass than larger fragments (Bollazzi & Roces 2011). Additionally, bettong pits and goanna pits capture more leaf litter compared to rabbit pits, due to the size of the pit opening (James *et al.* 2009). High litter retention in bettong pits likely increases the environment complexity of the pit and may affect ant visual and olfactory cues in seed detection, resulting in lower seed removal.

As predicted, fewer seeds were removed from the caged treatments that excluded ants larger than 2 mm in body size, consistent with our second hypothesis. Larger ant species may be more efficient at removing seeds up steep slopes as they need fewer steps and therefore less energy to cover

a certain distance compared to small ant species (Lipp *et al.* 2005). Additionally, the mean dispersal distance of seeds is known to be highly positively correlated with mean ant body mass (Ness *et al.* 2004), and the capacity of ants to move material is known to be a function of head size (Rudolph & Loudon 1986), which is directly related to mandible size (Sudd 1969). Small ants generally carry small seeds while larger ants prefer larger seeds (Kaspari 1996). This occurs as large ants are better at handling and dispersing larger seeds (Servigne & Detrain 2008) due to their large mandible size (Gómez *et al.* 2005). Our results imply that large ant genera such as *Rhytidoponera* have a greater impact on seed fate than smaller ant genera such as *Iridomyrmex* and *Pheidole*, as they are more efficient at manipulating and removing *Acacia* seeds from mammal foraging pits regardless of pit morphology. Taken together, our results suggest that the physical structure of bettong pits means that they act as safe sites for seeds, at least for foraging by ants. However, they may still be consumed by rodents and other seed predators that are less affected by the structure of the pits.

#### Seed removal changes over an aridity gradient

We found that seed removal displayed a unimodal response over the aridity gradient, with larger variation in seed removal within arid and semi-arid ecosystems than in dry sub-humid and humid sites. Higher seed removal would be expected in nutrient-poor environments such as arid and semi-arid systems given the strong selection pressure for seeds to be transported from unpredictable, resource-poor environments to resource-rich microsites such as ant nests (Beattie 1985; Salazar-Rojas *et al.* 2012; though see Rice & Westoby 1986). However, we found that fewer seeds were removed from arid (Aridity 0.8–1.0) than semi-arid (Aridity 0.6–0.8) sites, which is inconsistent with the hypothesis of a greater removal with increasing aridity. Lower seed removal from arid sites may occur due to reduced above- and below-ground biomass compared with semi-arid sites (Jiao *et al.* 2016), which can alter the abiotic environment such as increasing soil temperatures, thereby affecting the foraging behaviour of thermophobic ant species. The total biomass of ants has been shown to be uncorrelated or weakly negatively correlated with increased precipitation (Dunn *et al.* 2009) in the Southern Hemisphere. Therefore, arid and semi-arid environments may support a greater diversity of seed harvesting ants of different body sizes which are more efficient at locating and removing seeds. However, previous studies have shown that mean annual precipitation has no effect

on Australia ant richness (Morton & Davidson 1988). We recorded those ants removing seeds across the gradient and found that species of *Iridomyrmex* and *Rhytidoponera* occurred over all climate classes whilst species of *Pheidole* occurred over all climate classes except semi-arid sites. It does not seem likely therefore, that differences in ant composition or body size distribution is responsible for our observed seed predation rates.

#### CONCLUDING REMARKS

Overall, our study showed that the foraging pits constructed by bettongs had the greatest effect on ant movement and seed retention, and we attribute this to the morphology of the pits (steep-walled, deep, unstable) and hence the need for a greater expenditure of energy by the ants to retrieve seeds from the pits. Seed retention was greater in the pits of native vertebrates than those of the European rabbit or the soil surface. Our work highlights the ecological importance of foraging pits as safe sites for seeds as it prevents secondary dispersal by ants. This greater seed retention in animal foraging pits highlights the potential for using native bioengineers for restoring degraded semi-arid and arid environments (*sensu* Byers *et al.* 2006). Our study illustrates how pit morphology significantly affects ant foraging by restricting both ant movement and food extraction. This knowledge improves our understanding of the factors influencing seed germination within foraging pits of different animals and our results account for the lower number of seeds found in rabbit pits. This information can be used to help assess the potential impacts of exotic herbivores (such as the European rabbit) on ecosystem functions such as germination and the acquired knowledge can assist in restoring degraded semi-arid and arid environments. Additionally, our study illustrates that the body size of ants significantly affects seed fate as larger ant genera such as *Rhytidoponera* are more efficient at manipulating and removing seeds from mammal foraging pits regardless of pit morphology.

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