

# A comparison of the autecology of two seed-taking ant genera, *Rhytidoponera* and *Melophorus*

J. D. Majer · A. D. Gove · S. Sochacki ·  
P. Searle · C. Portlock

Received: 26 July 2010 / Revised: 15 September 2010 / Accepted: 28 September 2010 / Published online: 16 October 2010  
© International Union for the Study of Social Insects (IUSI) 2010

**Abstract** Members of the genus *Rhytidoponera* and, to a lesser extent, certain *Melophorus* spp. are keystone mutualists for the dispersal of seeds in the southwest of Western Australia, with important ramifications for the ecology and speciation of plants in this biodiversity hotspot. For this reason, it is important to understand the autecology of the relevant ant species and the way in which they interact with plant seeds. This paper addresses key aspects of the ecology of three such ant species, *Rhytidoponera violacea* (Forel), *R. inornata* Crawley and *Melophorus turneri perthensis* Wheeler. Data are presented on their geographic distribution, seasonality of foraging, diurnal activity, response to fire, nest site preference, nest structure, colony size, feeding habits, foraging response to seed availability, and seedling emergence from nests. The role of all three species as seed dispersers is confirmed, and all three species have ecologies that are well-suited for dispersal and survival of native plant seeds. Preservation of this interaction is important for the

conservation of plants, and it is fortuitous that all three species are able to survive disturbance and return to rehabilitated areas. However, the smaller *R. inornata*, and to a lesser extent, the larger *R. violacea*, are vulnerable to invasive ant [*Pheidole megacephala* (Fabricius)] incursions. *M. turneri perthensis* is able to coexist with the invasive ant unless this is at high densities, probably as a result of its ability to forage during high temperatures when the invasive species is inactive.

**Keywords** Myrmecochory · Seeds · Nests · Foraging · Fire

## Introduction

Although the advent of insect pollination of flowers is known to have been a driver of angiosperm diversification, seed dispersal by organisms such as ants has also been implicated, but not proven. Seed dispersal by ants (myrmecochory) may drive diversification by reducing extinction, hence providing selective advantages to plants, and by increasing speciation as a result of geographical isolation associated with extremely limited dispersal distances (Dunn et al., 2008). Lengyel et al. (2009a, b) tested the hypothesis that myrmecochory leads to higher diversification rates in angiosperm plants by comparing richness of plants in sister groups that were ant-dispersed or dispersed by other means. They found that ant-dispersed lineages contained on average more than twice as many species as did their non-myrmecochorous sister groups, suggesting that myrmecochory is a key evolutionary innovation and a globally important driver of plant diversity.

The Australasian ant genus *Rhytidoponera* is recognised as a keystone mutualist for dispersal of myrmecochorous

**Electronic supplementary material** The online version of this article (doi:10.1007/s00040-010-0124-z) contains supplementary material, which is available to authorized users.

J. D. Majer (✉) · A. D. Gove · S. Sochacki · P. Searle  
Curtin Institute for Biodiversity and Climate, Curtin University,  
PO Box U1987, Perth, WA 6845, Australia  
e-mail: J.Majer@curtin.edu.au

A. D. Gove  
e-mail: A.Gove@curtin.edu.au

J. D. Majer · A. D. Gove · S. Sochacki · P. Searle  
Department of Environment and Agriculture, Curtin University,  
PO Box U1987, Perth, WA 6845, Australia

C. Portlock  
Shire of Serpentine, Jarrahdale, WA 6124, Australia  
e-mail: cportlock@sjshire.wa.gov.au

plant species in Australia (Majer, 1982; Gove et al., 2007). Members of a second genus, *Melophorus*, are also important in this regard (Briese and Macauley, 1981; Majer, 1982). *Rhytidoponera* are common throughout Australia, occurring in all habitats. They are generalised foragers and tend to forage at night or during cooler parts of the day (Ward, 1981; Nielsen, 1997). The genus *Melophorus* is also found throughout Australia, and is most abundant and diverse in arid regions (Andersen, 2007). Members of the genus are capable of foraging at very high temperatures (Christian and Morton, 1992; Hoffmann, 1998).

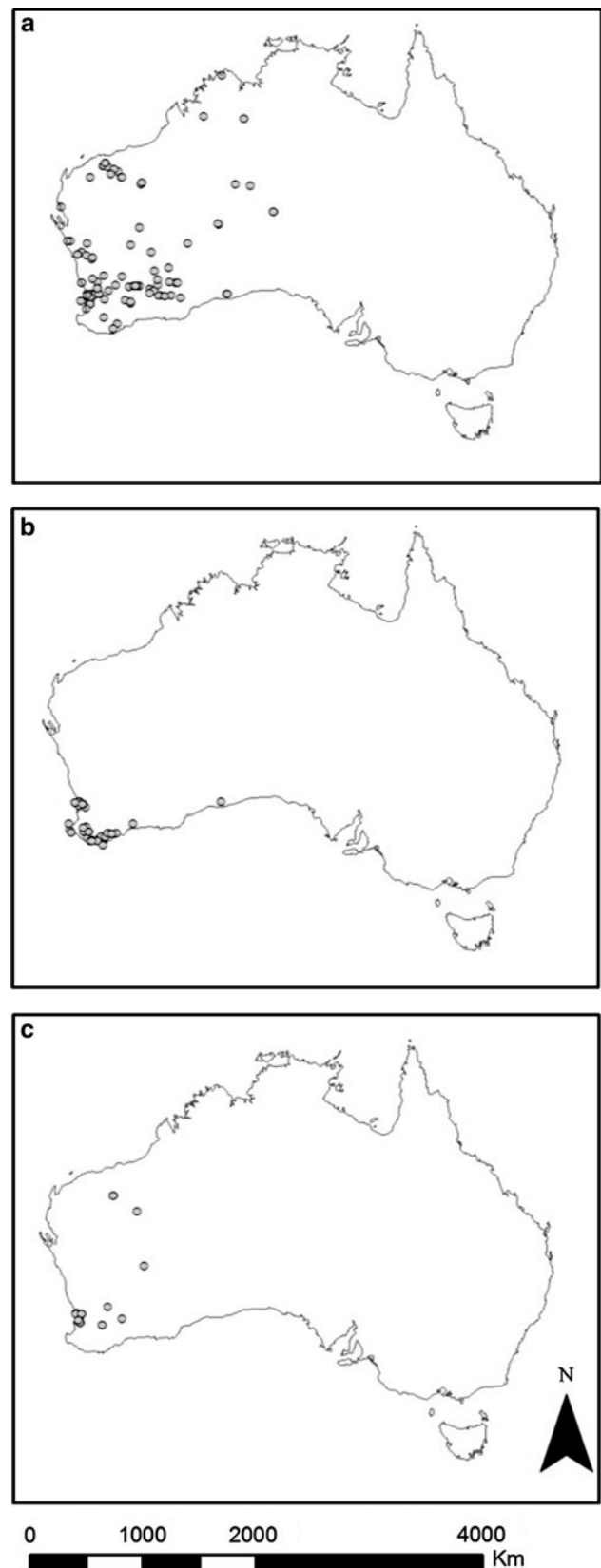
In view of their pivotal role in seed dynamics, and the fact that the southwest of Australia is a plant biodiversity hotspot (Myers et al., 2000; Hopper and Gioia, 2004), we revisit a dataset and compare the autecology and role in seed-taking of two southwest Australian species of *Rhytidoponera* with one species of *Melophorus*. The species concerned are *Rhytidoponera violacea* (Forel), *R. inornata* Crawley and *Melophorus turneri perthensis* Wheeler, which are the most prominent species involved in myrmecochorous relationships in southwestern Australia (Majer, 1982; Gove et al., 2007). *M. turneri perthensis* has been referred to as *Melophorus* spp. 1 (ANIC) in earlier papers.

We examine how *Rhytidoponera* and *Melophorus* behave in terms of their phenology, response to fire and interactions with myrmecochorous seed. Within this context, we examine nest structure, nest location, diurnal and seasonal variation in activity, the effect of fire and the species' associations with seed-fall and seed-collection. We also consider this in the context of habitat disturbance and subsequent restoration, and also in terms of invasive ant incursions. In doing this, we hope to obtain greater insight into the relationship between these three important seed takers, the seeds with which they interact, and how this important interaction might be impacted by human activity.

## Methods

### Geographic range of species

The distribution records of *R. violacea*, *R. inornata* and *M. turneri perthensis*, obtained by searching records of the CSIRO Entomology Biolink® database, are shown in Fig. 1 a, b, and c, respectively. These records are only for collections where specimens have been retained in the Curtin University or CSIRO–ANIC collections. As such, they are suggestive, rather than complete representations of the range of these three species. *Rhytidoponera inornata* occupies coastal areas of the southwest region of the state, and is also distributed along the south coast, at least as far as Esperance. By contrast, *R. violacea* is widely distributed throughout



**Fig. 1** Distribution maps of **a** *R. violacea*, **b** *R. inornata* and **c** *M. turneri perthensis* (data provided from Biolink, CSIRO)

most of the state, being present in most regions except for the northern part of the Kimberley. *M. turneri perthensis* is common in the southwest of WA and extends through the central Goldfields into the northern Pilbara region. It does not seem to extend into the arid interior of the State. The taxonomy of *Melophorus* is currently under review, so this distribution may ultimately represent more than one species.

#### Sites and general sampling techniques

Ant sampling was conducted between February 1976 and April 1979 at seven sites in the southwest of Western

Australia (Fig. 2; Supplemental Table S1). The Dwellingup, Karragullen and Manjimup sites are on the Darling Plateau, with laterite soils, while the Perth and Yalgorup sites are on the Swan Coastal Plain, which has sandy soil. Ant seasonality was assessed at six of the sites (not at Yalgorup) using a procedure described in detail in Koch and Majer (1980). At five of the sites, a  $6 \times 6$  grid of 18 mm internal diameter pitfall traps, 3 m apart, was left open for 1 week; while at Karragullen a  $5 \times 4$  grid of 54 mm internal diameter traps, 5 m apart, was used. Further details of the sites are given in Koch and Majer (1980) and Majer (1984). The six locations were repeatedly sampled on no less than a monthly basis for a year or more (see Supplemental Table S1 for period details). Additionally, a range of measurements and observations were performed on colonies and nests at the Karragullen and Dwellingup sites, and also at Yalgorup National Park.

#### Seasonality of foraging

We tested for a temporal correlation of *Rhytidoponera* and *Melophorus* activity in each of the six pitfall trap locations using Spearman's rank correlation. We then asked whether ant activity for each species varied seasonally. In order to create replicated samples, we matched up each month of sampling from the six locations (no matter in which year this month occurred). We then performed an ANOVA to determine whether ant activity varied significantly amongst months. We performed the tests separately for the three ant species.

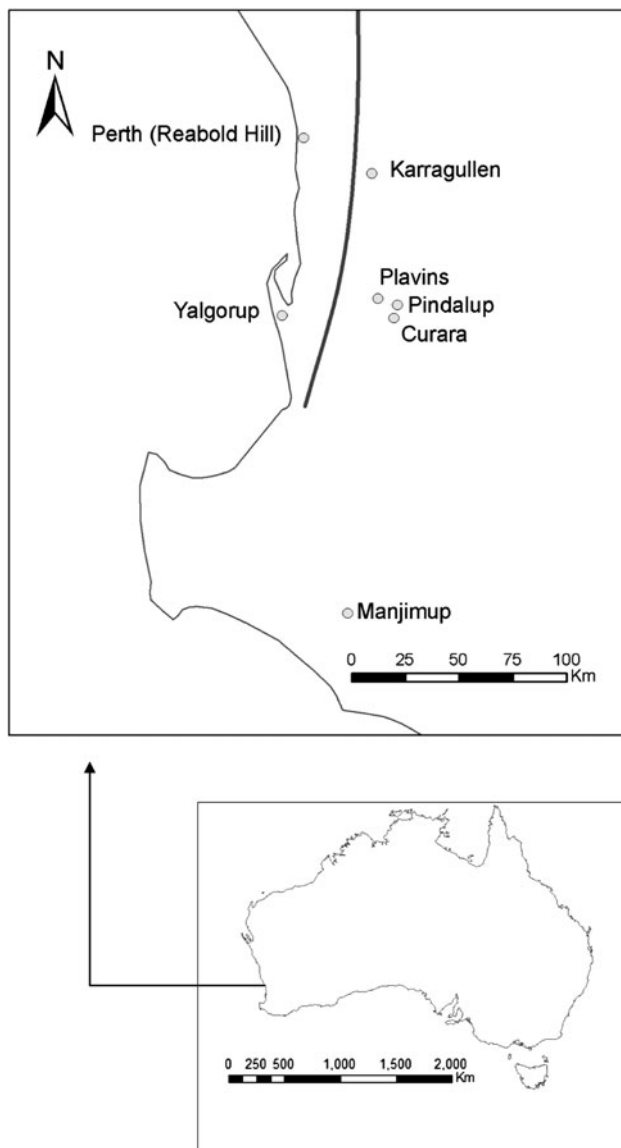
#### Diurnal activity

Notebook observations on diurnal activity were maintained at the Karragullen site over an 18-month period. In addition, in three seasons (summer, 22 Feb 1978; winter, 25 May 1978; spring, 31 Aug 1978), five nest entrances of each of the three species were observed for 3 min, every hour for 24 h and the number of individuals leaving the nest was quantified. The response of these species to daily environmental variation was compared.

#### Response to fire

Four of the six sites were subjected to controlled burns (see Supplemental Table S1). In each case a matched control (unburnt) plot of pitfall traps was sampled during the same period as the burnt plot, before and after the burn.

Analysis was performed separately for each species. We used a Before–After Control Impact (BACI) design, with each of the four sites representing a replicate. Within each site we calculated a mean value of ant abundance across sample periods for the BACI combination. After-fire



**Fig. 2** Map of southwest Western Australia, showing sites where detailed observations or samples were taken for *R. violacea*, *R. inornata* and *M. turneri perthensis*. The solid black line shows the position of the Darling Scarp, which separates sandy soil to the west, from lateritic soil to the east

activity was based on 12 months of post-fire data. We did not treat each sample period within each combination as a replicate, as in one case we only had one sample period prior to the burn. We tested for an effect of the burn on ant abundance by examining the interaction term.

### Nesting preference

Nest densities were quantified for *M. turneri perthensis* and *R. inornata* in 1 m grid cells of a 0.04 ha plot at Dwellin-gup; nests of *R. violacea* were not found in this plot. These densities were then compared to the frequency of ground cover and overstorey shade categories at the site. Nest location preference for each species was tested separately using a chi-square test.

### Nest structure and depth

The structure and depth of nests was assessed by lead casting. Lead was liquefied in a crucible and poured into nest entrances, then allowed to cool and solidify. The resulting caste was dug up, cleaned in water, photographed and measured, thus enabling structure and depth to be obtained. Five nests each of *R. inornata*, *R. violacea* and *M. turneri perthensis* were assessed from laterite at Karra-gullen or Dwellin-gup and a further five nests of *M. turneri perthensis* were assessed from sands at Yalgorup.

### Colony size

During the peak summer activity period, five nests each of *R. inornata* and *R. violacea* were excavated from the Karra-gullen site and the soil was passed through a stack of sieves of progressively decreasing mesh size. Ants were separated from the soil by floatation, and counted. We lacked comparable data for *M. turneri perthensis*, so five nests of this species were sampled from an equivalent area of sand plain in Perth during the summer of 2009. Our continuous observations on these species over the previous 30 years have not revealed any change in the ecology of these species, so the discrepancy in sampling time is not considered likely to influence these particular measurements.

### Feeding habits

At Karra-gullen, five nests of each species were observed for 30-min periods monthly between April 1978 and April 1979. All ants observed carrying food items were collected and the food was removed and identified to the best level possible.

Diet composition was further measured at Karra-gullen by scraping the soil middens from around nest entrances of the three species and separating the organic material from the soil

by floatation in saturated magnesium sulphate. The number of middens sampled was dictated by the number of suitable nests that could be found, consequently, the number varied from three (*R. inornata*), through five (*R. violacea*) to 10 (*M. turneri perthensis*). The seeds and arthropod fragments from this organic material were identified and counted.

### Foraging response to seed availability

During the period February 1978–April 1979, plant flowering phenology was monitored monthly at the Karra-gullen site. In each month, the species of flowering plants were recorded over a 1.2 ha area (see Majer, 1980a for further details). We divided the plant species into myrmecochores and non-myrmecochores and tested for correlations between ant activity and species richness of flowering myrmecochores in each month. As we were particularly interested in the correlation between ant activity and myrmecochore seed-rain, we tested for a correlation between the two with various lag periods (1, 2, 3 and 4 months). We tested for the correlation using data for the three ant species separately. We also tested for variation in flowering phenology of myrmecochore and non-myrmecochore plant species using the statistical technique described by Estabrook et al. (1982) (see also Guitián and Garrido, 2006).

### Seedling emergence from nests

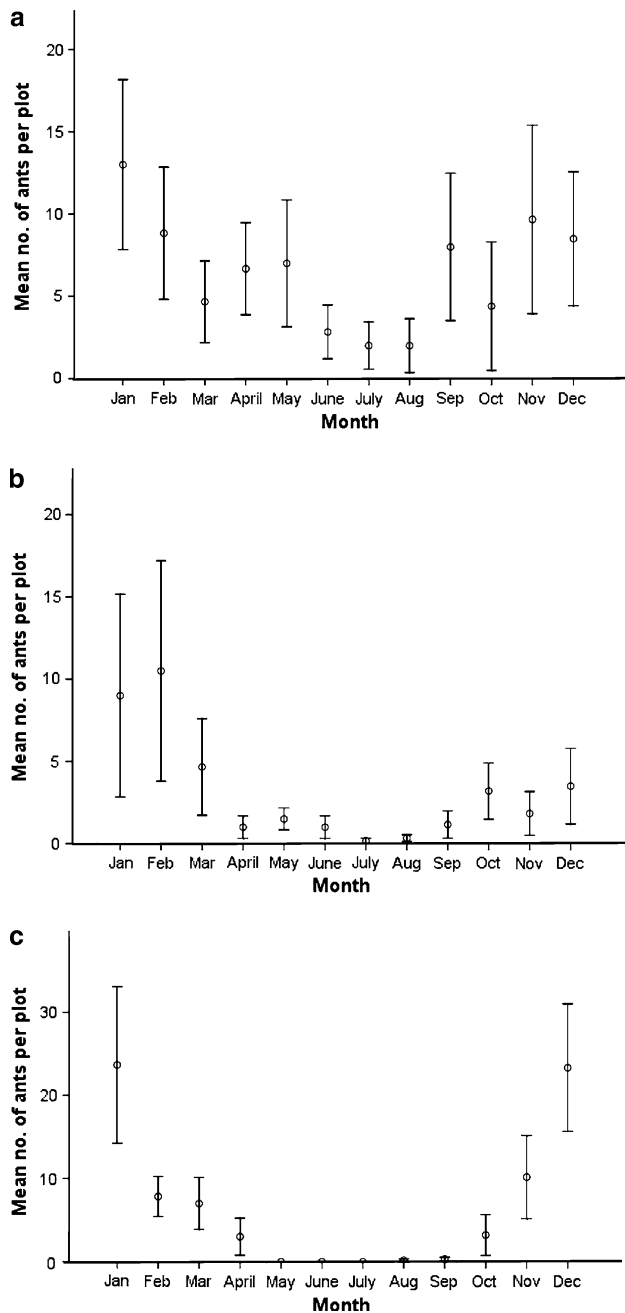
Since many local plant species require fire to stimulate germination, the effects of fire were simulated over 10 *R. inornata* and 15 *M. turneri perthensis* nests near Dwellin-gup, during winter, 1979. Fire was simulated by inverting a Pyrox Schwank® infra-red gas heater over the nest and heating the soil to 100°C at 2 cm depth for 30 min. An equivalent area of bare soil 1 m from the nest was also heated and a further set of unheated nests and nearby soil were also marked out. Seedling emergence was recorded in the marked out areas over the next 2 months.

## Results

### Seasonality of foraging

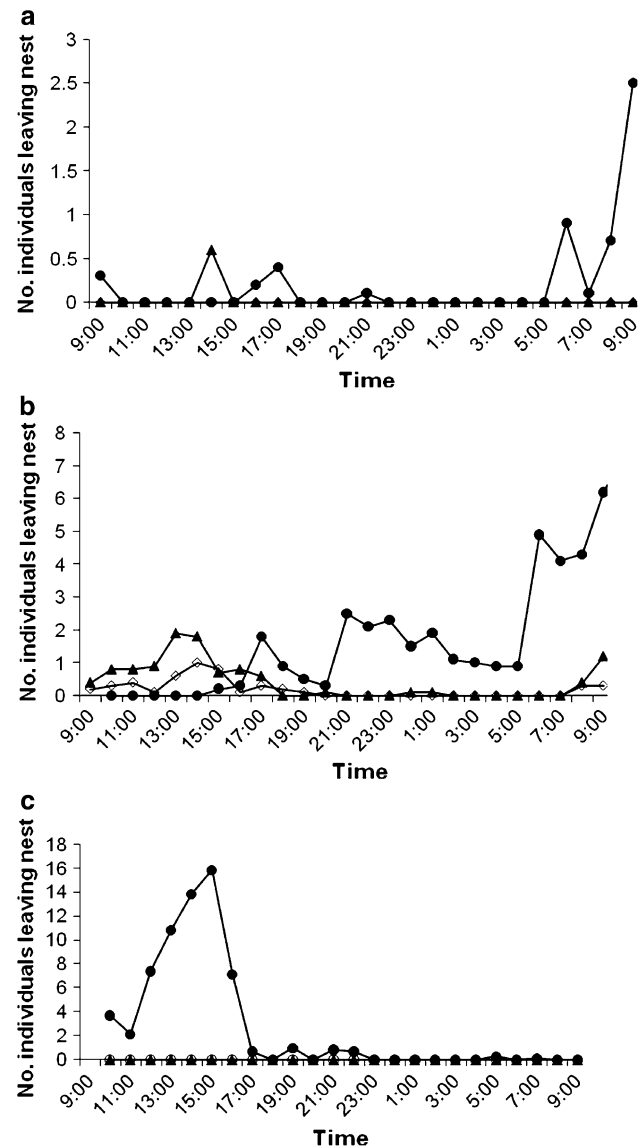
Across the periods sampled, *Rhytidoponera* spp. and *Melophorus* monthly activities were positively correlated with each other in only two of the six locations, Karra-gullen and Reabold Hill ( $P = 0.025$ ,  $P < 0.001$ ,  $Rho = 0.576$  and  $0.868$ , respectively).

*Melophorus turneri perthensis* showed significant seasonal variation in activity ( $F_{11,70} = 4.462$ ,  $P < 0.001$ ; Fig. 3c). Both *Rhytidoponera* spp. followed a similar seasonal pattern in activity (Fig. 3a, b), but this was not



**Fig. 3** Seasonal variation in activity of **a** *R. violacea*, **b** *R. inornata* and **c** *M. turneri perthensis* at six sites. Error bars represent 1 standard error; vertical axes scales differ in the three graphs

significant for *R. violacea* ( $F_{11,59} = 1.306$ ,  $P = 0.244$ ) or *R. inornata* ( $F_{11,59} = 0.846$ ,  $P = 0.596$ ). *M. turneri perthensis* exhibited a more pronounced increase in activity during the spring–summer months (November to February). *Rhytidoponera* also demonstrated a peak in activity during January to February, but not to the same extent. *M. turneri perthensis* exhibited a complete lack of activity during winter months, while both *Rhytidoponera* spp. maintained low-level activity during this period.



**Fig. 4** Diurnal activity of **a** *R. violacea*, **b** *R. inornata* and **c** *M. turneri perthensis* over three seasons. Activity was quantified as the number of individuals leaving a nest over a 3-min period, recorded each hour; vertical axes scales differ in the three graphs. Filled circle summer, filled triangle winter, empty diamond spring

On average, across all locations and all sampling periods, *Rhytidoponera* spp. was 1.4 times more active than *Melophorus*.

#### Diurnal activity

All ant species were most active in the summer months (Fig. 4a–c). While *Rhytidoponera* spp. activity peaked in the morning (Fig. 4a, b), approximately after sunrise, *Melophorus* activity peaked during early afternoon (Fig. 4c); generally the warmest part of the day. No *Melophorus* activity outside of nests was recorded during the winter and spring observation periods. During winter,



*Rhytidoponera* (*inornata* especially) activity peaked during the early afternoon, again in the warmest part of the day.

### Response to fire

*Rhytidoponera violacea* and *R. inornata* demonstrated no clear response to fire. *R. violacea* maintained activity after the burns (Fig. 5a,  $F_{1,12} = 0.399$ ,  $P = 0.54$ ). *R. inornata* may have declined in activity after the burns, but so did activity in the unburnt plot (Fig. 5b,  $F_{1,12} = 0.117$ ,  $P = 0.738$ ). The effect of burning on *Rhytidoponera* spp. activity was therefore inconsequential.

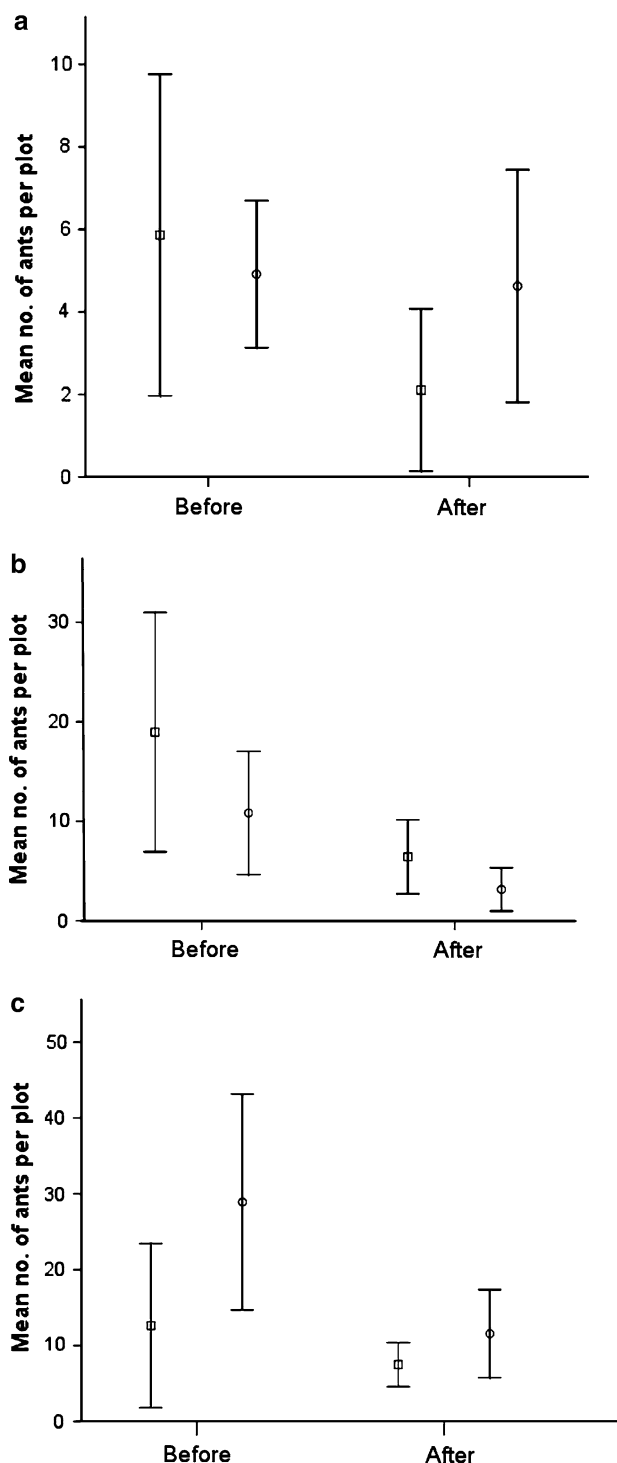
In the control plots there were as many *M. turneri perthensis* individuals active after the burns as there were before the burns (Fig. 5c). In the burnt plots, however, activity decreased, with 1.7 times as many individuals active before the burns as compared to after the burn. This direction of change was only apparent in three of four sites (in the fourth site, activity increased by >100% after the burn) and there was not a significant treatment  $\times$  time effect ( $F_{1,12} = 0.518$ ,  $P = 0.485$ ). Therefore, although fire may decrease *Melophorus* activity, this pattern is not uniform.

### Nesting preference

We located 27 nests each of *R. inornata* and *M. turneri perthensis*, representing nest densities of 675/ha for each species. We were unable to locate sufficient nests of *R. violacea* to examine densities or nest–habitat relationships, although unpublished observations elsewhere suggest that similar nest densities to *R. inornata* can be achieved. *R. inornata* did not demonstrate a significant nest site preference (ground cover,  $\chi^2 = 0.73$ ; top cover,  $\chi^2 = 3.67$ ; Supplemental Table S2). In contrast, *M. turneri perthensis* had a significant nest site preference for sites with a low ground cover ( $\chi^2 = 10.13$ ,  $P < 0.01$ ) and low overstorey shade ( $\chi^2 = 7.35$ ,  $P < 0.05$ , Supplemental Table S2).

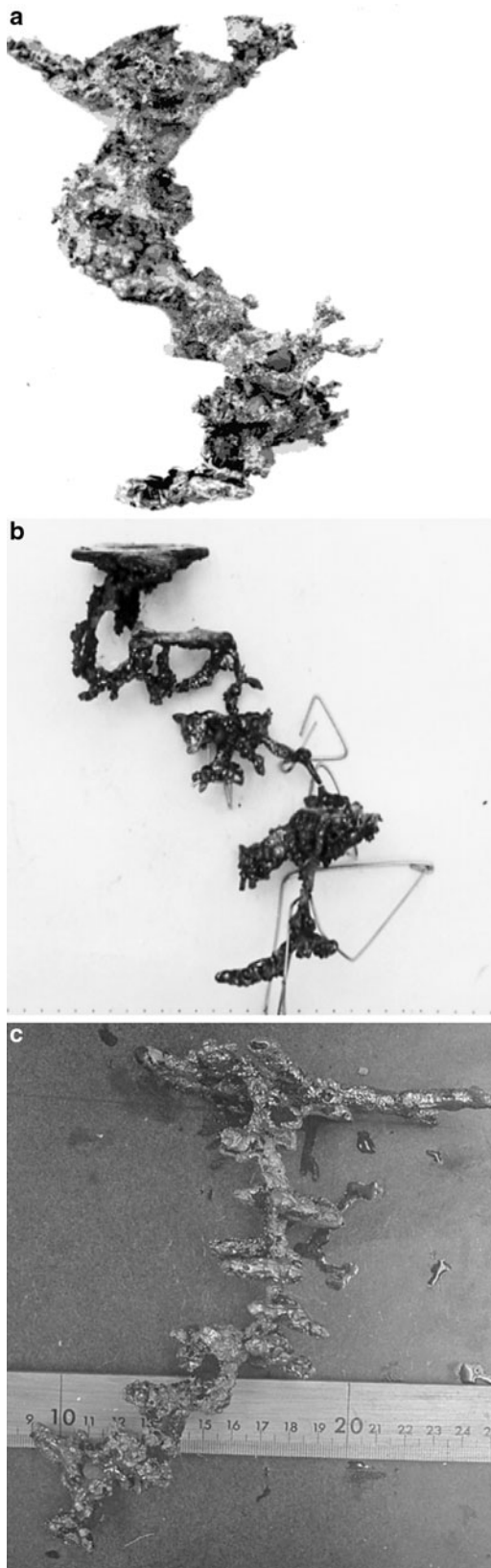
### Nest structure and depth

*Rhytidoponera violacea* nests were, on average, 22.2 cm deep (Supplemental Table S3) and were often associated with buried woody material. Structurally, nests tended to comprise a broad vertical channel, which often spiralled around a live or dead woody taproot (Fig. 6a). *R. inornata* nests were of a similar depth (mean = 25.2 cm) but the channels of the nest were much finer than those of the other *Rhytidoponera* spp., and led off into smaller side branches (Fig. 6b). *M. turneri perthensis* nests were of a rather different structure, comprising a vertical channel with a series of side galleries at reasonably regular intervals (Fig. 6c). Seeds were frequently observed embedded in the lead from



**Fig. 5** Effects of burning on activity of **a** *R. violacea*, **b** *R. inornata* and **c** *M. turneri perthensis* in four sites. Empty square control plots, empty circle burnt plots. Error bars represent 1 standard error; vertical axes scales differ in the three graphs

these galleries. *M. turneri perthensis* nests from the laterite were significantly more shallow (mean = 12.7 cm) than nests in the sandy soil at Yalgorup (mean = 21.7 cm) ( $F_{3,34} = 5.37$ ,  $P = 0.004$ ) (Supplemental Table S3).



**Fig. 6** Nest castings of **a** *R. violacea*, **b** *R. inornata* and **c** *M. turneri perthensis*. The two *Rhytidoponera* spp. were from laterite soil, and the nest of *M. turneri perthensis* was from sandy soil

### Colony size

The number of workers per nest of *R. violacea* and *R. inornata* was small and fairly similar (mean = 173.2 and 197.6 workers, respectively), and sizeable numbers of alates were found to be present (Table 1). Numbers of workers in the *M. turneri perthensis* nest were also fairly small (mean = 230.4) and no alates were found (Table 1).

### Feeding habits

*Rhytidoponera inornata* workers were not observed carrying food frequently enough to make any generalisations about food preferences. *R. violacea* was observed carrying invertebrate prey or carrion throughout the year and seeds were present in their forage during March and April, comprising 6.3% of dietary observations from the entire observation period (Table 2). *M. turneri perthensis* ceased foraging during the cooler months, but was observed carrying seed from November through to May, with this component comprising 29.1% of forage. The rest comprised miscellaneous plant fragments (25.3%) and invertebrates (54.6%) (Table 2). Taking account of the full observation period, *M. turneri perthensis* carried 4.6 times as many seeds as *R. violacea*.

We were able to obtain data from middens for all three species and all exhibited an omnivorous diet of arthropods and seeds, although we cannot discount the possibility that they might also feed on nectar. The latter is most unlikely, as none of these species ascend trees or shrubs. Based on nest middens, *M. turneri perthensis* was the most reliant on seeds (49.3%), followed by *R. violacea* (37.6%), and *R. inornata* (8.0%) (see Supplemental Table S4 for details).

### Foraging response to seed availability

Flowering phenologies of myrmecochorous and non-myrmecochorous plant species were very similar ( $D_{\text{observed}} = 0.216$ ,  $D_p = 0.05 = 0.309$ ), with peaks in September–October. The best regression models relating ant activity to myrmecochore flowering were found after a 4-month lag for both *M. turneri perthensis* ( $R^2 = 0.572$ ; Fig. 7c) and *R. violacea* ( $R^2 = 0.692$ ; Fig. 7a). In none of the lag periods was the activity of *R. inornata* positively correlated with myrmecochore flowering, with only a negative correlation being found after a 1-month lag ( $R^2 = 0.232$ ; Fig. 7b).

### Seedling emergence from nests

Some seedlings emerged from the directly heated rectangle surrounding the nest opening of both *R. inornata* and *M. turneri perthensis*. However, many seedlings emerged

**Table 1** Numbers of worker and alate ants in five *R. violacea* and five *R. inornata* nests measured at Karragullen and five *M. turneri perthensis* nests measured at Perth

	<i>Rhytidoponera violacea</i>						<i>Rhytidoponera inornata</i>						<i>Melophorus turneri perthensis</i>					
	1	2	3	4	5	Mean	1	2	3	4	5	Mean	1	2	3	4	5	Mean
Workers	46	359	176	150	135	173.2	37	194	403	290	64	197.6	257	241	256	247	151	230.4
Alate males	8	0	101	295	75	95.8	147	1	27	6	46	45.4	0	0	0	0	0	0
Alate females	0	0	0	0	0	0	0	57	0	91	0	29.6	0	0	0	0	0	0

All nests were collected during the peak summer foraging period

**Table 2** Quantities of food items carried to *R. violacea* ( $n = 5$ ) and *M. turneri perthensis* ( $n = 10$ ) nests at Karragullen

	Mar	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mar	Apr	%
<i>R. violacea</i>												
Seeds	3	2	0	0	0	0	0	0	0	0	0	6.3
Plant fragments	1	0	0	0	1	0	0	0	0	0	0	2.5
Invertebrates	7	13	3	7	6	6	6	6	3	8	8	91.2
<i>M. turneri perthensis</i>												
Seeds	4	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	3	9	2	5	29.1
Plant fragments	2	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	8	2	3	5	25.3
Invertebrates	11	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	4	5	8	8	45.6

Measurements made in most months between March 1978 and April 1979 for 30-min periods per nest

n.f. not foraging

from a 3 cm boundary outside of the rectangle, presumably because the lateral conduction of heat provided conditions that were optimal for these plant species (Fig. 8). For both ant species, the number of seedlings emerging was much higher around ant nests, it being almost non-existent elsewhere (Supplemental Table S5). Furthermore, the number of seedlings emerging was much higher around the heated nests than the unheated counterparts. *M. turneri perthensis* demonstrated a significant species  $\times$  treatment interaction, with *Trymalium ledifolium* emerging in higher densities from heated nests than other treatments ( $F_{3,112} = 3.9$ ,  $P = 0.011$ ). *Acacia pulchella* was not affected by treatments. A similar pattern was evident in *R. inornata* nests ( $F_{3,72} = 2.3$ ,  $P = 0.082$ ).

## Discussion

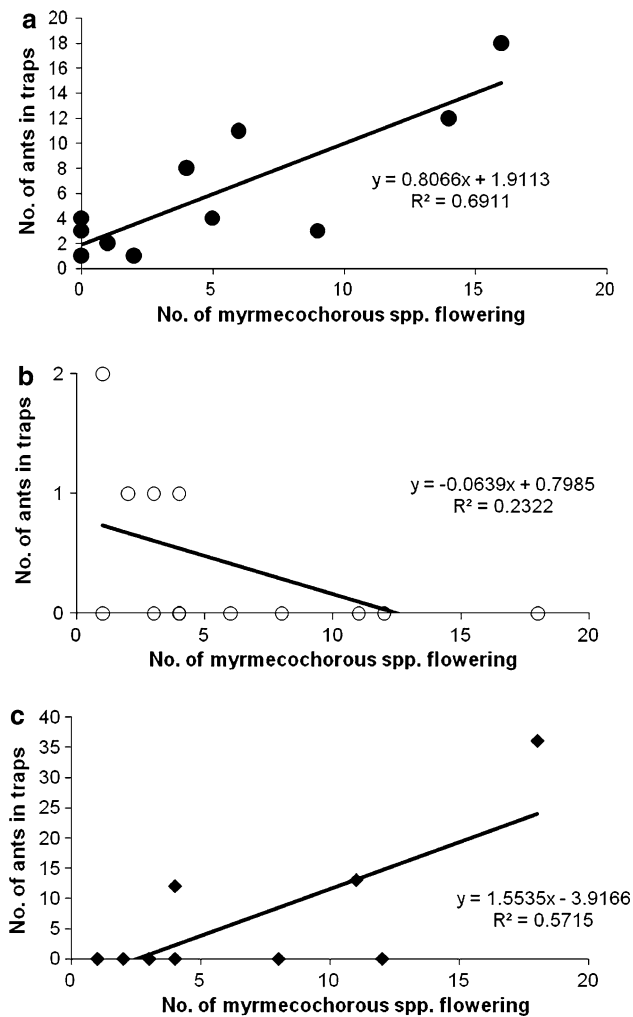
The findings presented here, along with those from an earlier paper which examined the fate of seeds taken by these three ant species (Majer, 1982), indicate a close association between the biology of these ant species and their potential to disperse angiosperm seeds. All three species are distributed throughout the Southwest Botanical Province of Western Australia, albeit with *R. inornata* being more confined to the extreme south of this region. They are thus well situated to disperse seeds of many families found

within this exceptionally biodiverse (Hopper and Gioia, 2004) region. It should be stressed that there are other species from both ant genera which are involved in myrmecochorous relationships, and members of other ant genera as well.

All three species exhibit a diurnal and seasonal activity that coincides with periods of seed production, which ranges from around 1–4 months after the main September–October flowering period (Majer, 1980a), with seeds tending to fall during daytime, when hot conditions cause certain fruits to desiccate and shed seeds (B. Lamont, pers. comm.). Nevertheless, as flowering of myrmecochore and non-myrmecochore plant species were closely correlated, it does not appear that phenologies have evolved to take advantage of, for instance, the increased activity level of ants in the spring–summer months. It therefore appears that ant activity levels fortuitously correlate with seed production (i.e., a lag of approximately 3–4 months after flowering). By contrast, Guitián and Garrido (2006), working in Spain, have found that myrmecochores flower approximately 4 weeks before non-myrmecochores, possibly as an adaptation to produce seed at a time of maximal ant activity.

On the whole, *Rhytidoponera* activity is less seasonal and coincides less with seed-fall than does *Melophorus* activity. Inspection of the food carrying data for *R. violacea* and *M. turneri perthensis*, and also the midden analysis of all three species, indicates that *Melophorus* appears to be more





**Fig. 7** Relationships between activity of **a** *R. violacea*, **b** *R. inornata* and **c** *M. turneri perthensis* and the species density of flowering myrmecochores at Karragullen, WA. The relationships for *R. violacea* and *M. turneri perthensis* incorporate a 4-month time lag since flowering, while that for *R. inornata* incorporates a 1-month time lag; vertical axes scales differ in the three graphs

dependent on seeds than *Rhytidoponera*. This suggests that, throughout the year, *Rhytidoponera* probably switches to other food sources, such as winter-active invertebrates. We suspect that *Rhytidoponera* does not store seeds for long periods of time, as evidenced by nest diggings reported in Majer (1982) and the fact that seeds taken to the nest are often returned to the surface in less than 12 h (A. Gove, pers. obs.). Therefore, *Rhytidoponera* is likely to be relying upon other food sources throughout much of the year, rather than storing seed for long periods.

All three species have relatively shallow nests, although at least for *Melophorus*, nests tend to be deeper in the sandplain than in the lateritic soils. Colony sizes are relatively low and, in the case of *Melophorus*, are much lower than for the larger nests of *Melophorus bagoti* Lubbock.



**Fig. 8** Photos of seedling emergence from heated nests of *R. inornata*. The inner rectangles show the heated area and the outer rectangles delimit areas affected by lateral conduction of heat

from more arid parts of Australia (Conway, 1992). The dependence upon seeds, rather than carbohydrates in nectar form, may account for the small nests, unlike the situation with high nest abundance species that are dependent upon liquid carbohydrates (Davidson et al., 2004). Despite this, nest densities were relatively high, averaging 675 nests per hectare for both *R. inornata* and *M. turneri perthensis*, and probably similarly high for *R. violacea* in areas where it is present. Combining the data on density of nests with the quantity of seeds found in forage and on middens indicates the high importance of these species in the dynamics of seed dispersal.

The structure of the nests also has a bearing on the survival of seeds and germination of the resulting seedlings. Many of the plant species dispersed by these ants are obligate seeders (Bell, 2001) which often rely on fire to germinate the seeds. Nest sievings reported in Majer (1982) indicate that seed tends to be buried in nests or under middens at a depth which is likely to be protected from the extreme effects of fire, but heated sufficiently for seed to germinate (Portlock et al., 1990). The nest heating experiment demonstrates this effect quite clearly. The preference of *M. turneri perthensis* for open conditions might have

positive feedback effects on the plant community, with seedlings being encouraged to germinate in open areas where plants have died and opened up the canopy.

All three ant species have been found to survive fire, although, surprisingly for a thermophilic species (Hoffmann, 1998), *Melophorus* may be more impacted than *Rhytidoponera*. At this stage, we are unsure about the reason for this difference, although its greater dependence on seeds in its diet when compared with *Rhytidoponera* might leave it less equipped to switch to other food sources when fire depletes the supply of plants which produce seeds. Some of the colonies used for assessment of food collection were subject to a cool autumn burn during the course of the study (see Majer, 1984 for details), and foraging continued after the burn, with seed in the diet often being replaced with burnt plant fragments (J. Majer, unpubl. data).

In our recent study of the importance of *Rhytidoponera*, seed removal rate was closely related to the presence of *Rhytidoponera* (Gove et al., 2007). However, in examining this data set further, seed removal rate was not associated with *Melophorus* presence ( $F_{1,16} = 0.996$ ,  $P = 0.335$ ), even though Majer (1982) demonstrated that it was also an important seed-taking agent. Trials in Gove et al. began at approximately 0800 h and, although they often continued during times when temperatures were in the high 30s, they were biased towards the cooler part of the day when *Rhytidoponera* was more active than *Melophorus*. Had the trials been focussed on the hotter part of the day, the undoubtedly important role of *Melophorus* would probably have become more evident.

The pivotal role that these ant species play in the dispersal, survival and therefore conservation of native plants, many of which are highly endemic and possibly threatened (Hopper and Gioia, 2004), highlights the need to understand and preserve this important plant–insect interaction. How well do these three species cope with habitat disturbance then? The extensive studies which J. Majer has undertaken in the southwest of Western Australia indicate that all three species can tolerate a high degree of habitat disturbance. Furthermore, when totally disturbed areas such as mine sites are rehabilitated, all three species are early colonizers of the area (Majer and Nichols, 1998). Seed removal trials in the maturing vegetation indicate that the myrmecochorous relationship is also rapidly restored (Majer, 1980b). The situation is less optimistic when invasive ants are involved. Callan and Majer (2009) quantified the impact of progressively increasing densities of the invasive ant, *Pheidole megacephala* (Fabricius) intruding into Perth native woodland on the Swan Coastal Plain. The smaller *R. inornata* and, to a lesser extent, the larger *R. violacea*, were vulnerable to incursions of this ant, with the former being eliminated when *Pheidole* was present at the lowest density, and the latter disappearing when *Pheidole* densities reached

100 per pitfall trap. By contrast, close relatives of *M. turneri perthensis* were able to coexist with all but very high densities of the invasive ant (>1,000 ants per pitfall trap), probably as a result of the ability to forage during high temperatures when the invasive species is inactive. The impact of these changes in composition of myrmecochorous ants was not investigated, but it is assumed that this will result in changes in the dynamics of the relationship.

To summarise, this paper confirms the important role that these three ants have in the dispersal and survival of seeds in the southwest of Western Australia. All three species have foraging and feeding strategies which maximise the collecting and dispersal of seeds and placing them in positions which are ideally suited for subsequent germination and survival. This aspect of the relationship is explored further in the case of *R. violacea* in Lubertazzi et al. (2010) and in an, as yet unpublished, MSc thesis (McCoy, 2008).

**Acknowledgments** This work was funded by a grant from the discontinued, Reserve Bank Rural Credits Development Fund. Chris Portlock's contribution was funded by his previous employer, the now defunct Forests Department of Western Australia. Prof. Andy Beattie, Dr Rob Dunn, Dr Brian Heterick, Dr Ben Hoffmann and Dr David Lubertazzi are thanked for their comments on an earlier draft of this manuscript.

## References

- Andersen A.N. 2007. Ant diversity in arid Australia: a systematic overview. In: *Advances in Ant Systematics (Hymenoptera: Formicidae): Homage to E.O. Wilson - 50 Years of Contributions* (Snelling R.R., Fisher B.L. and Ward P.S., Eds). *Mem. Am. Entomol. Inst.* **80**: 19–51
- Bell D.T. 2001. Ecological response syndromes in the flora of southwestern Australia: fire resprouters versus reseeder. *Bot. Rev.* **67**: 17–40
- Briese D.T. and Macauley B.J. 1981. Physical structure of an ant community in semi-arid Australia. *Austral. J. Bot.* **2**: 107–120
- Callan S.K. and Majer J.D. 2009. Impacts of an incursion of African Big-headed ants, *Pheidole megacephala* (Fabricius), in urban bushland in Perth, Western Australia. *Pacific Cons. Biol.* **15**: 102–115
- Christian K.A. and Morton S.R. 1992. Extreme thermophilia in a central Australian ant, *Melophorus bagoti*. *Physiol. Zool.* **65**: 885–905
- Conway J.R. 1992. Notes on the excavation of a nest of *Melophorus bagoti* Lubbock in the Northern Territory, Australia (Hymenoptera: Formicidae). *J. Austral. Entomol. Soc.* **31**: 247–248
- Davidson D.W., Cook S.C. and Snelling R.R. 2004. Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. *Oecologia* **139**: 255–266
- Dunn R., Gove A. and Majer J.D. 2008. Seed dispersal mutualisms with ants and patterns of plant diversity in western Australia. In: *Fronteiras do Conhecimento em Insetos Sociais* (Vilela E.F., Santos I.A., Schoereder J.H., Campos L.A.O. and Serrão J.E., Eds). Editora Universidade Federal de Viçosa, MG, pp 325–347
- Estabrook G.F., Winsor J.A., Stephenson A.G. and Howe H.F. 1982. When are two phenological patterns different? *Bot. Gaz.* **143**: 374–378

- Gove A.D., Dunn R.R. and Majer J.D. 2007. A keystone ant species promotes seed dispersal in a “diffuse” mutualism. *Oecologia* **153**: 687-657
- Gutián J. and Garrido J.L. 2006. Is early flowering in myrmecochorous plants an adaptation for ant dispersal? *Plant Species Biol.* **21**: 165-171
- Hoffmann B.D. 1998. Thermophilia in a tropical Australian ant of the *Melophorus aenovirens* (Lowne) species-group (Hymenoptera: Formicidae) *Austral. J. Entomol.* **37**: 162-167
- Hopper S.D. and Gioia P. 2004. The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **35**: 623-650
- Koch L.E. and Majer J.D. 1980. A phenological investigation of various invertebrates in forest and woodland areas in the southwest of Western Australia. *J. R. Soc. West. Austral.* **63**: 21-28
- Lengyel S., Gove A.D., Latimer A.M., Majer J.D. and Dunn R.R. 2009a. Ants sow the seeds of global diversification in flowering plants. *PLoS ONE* **4**: e5480
- Lengyel S., Gove A.D., Latimer A.M., Majer J.D. and Dunn R.R. 2009b. Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: A global survey. *Persp. Plant Ecol. Evol. Syst.* **12**: 43-55
- Lubertazzi D., Aliberti-Lubertazzi M., McCoy N., Gove A.D., Majer J.D. and Dunn R.R. 2010. The ecology of a keystone seed disperser, *Rhytidoponera violacea*, with implications for the evolution of myrmecochory. *J. Insect Science* (in press)
- Majer J.D. 1980a. A flowering calendar for Karragullen, a northern Jarrah forest locality. *W.A. Herbarium Research Notes* **5**: 19-28
- Majer J.D. 1980b. The influence of ants on broadcast and naturally spread seeds in rehabilitated bauxite mines. *Reclam. Rev.* **3**: 3-9
- Majer J.D. 1982. Ant-plant interactions in the Darling Botanical District of Western Australia. In: *Ant-Plant Interactions in Australia* (Buckley R., Ed). Dr W. Junk, Dordrecht. pp 45-61
- Majer J.D. 1984. Short-term responses of soil and litter invertebrates to a cool autumn burn in jarrah (*Eucalyptus marginata*) forest in Western Australia. *Pedobiol.* **26**: 229-247
- Majer J.D. and Nichols O.G. 1998. Long-term recolonization patterns of ants in Western Australian rehabilitated bauxite mines with reference to their use as indicators of restoration success. *J. Appl. Ecol.* **35**: 161-182
- McCoy N. 2008. The geographic mosaic of myrmecochory in a global biodiversity hotspot and the fate of seeds dispersed by a keystone seed disperser. MSc thesis, North Carolina State University.
- Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. and Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853-858
- Nielsen M.G. 1997. Foraging strategy and energetic cost of food transport in the ant *Rhytidoponera aurata* (Roger) in tropical Australia. *Proc. Int. Coll. Social Insects* (Kipyatkov V.E., Ed). IUSSI, St Petersburg, vol. 3, pp 247-252
- Portlock C.C., Shea S.R., Majer J.D. and Bell D.T. 1990. Stimulation of germination of *Acacia pulchella*: laboratory basis for forest management options. *J. Appl. Ecol.* **27**: 319-324
- Ward P.S. 1981. Ecology and life history of the *Rhytidoponera impressa* group (Hymenoptera: Formicidae). 1. Habitats, nest sites and foraging behavior. *Psyche* **88**: 89-108