

Bait preferences of Australian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in tropical and subtropical Queensland forests

Kathryn M Ebert^{1*}, Geoff B Monteith², Rosa Menéndez³ and David J Merritt¹

¹*School of Biological Sciences, University of Queensland, St Lucia, QLD*

²*Queensland Museum, Brisbane, QLD*

³*Lancaster Environment Centre, Lancaster University, Lancaster, UK*

*k.ebert@uq.edu.au

Running title

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ABSTRACT

Dung beetles (Scarabaeidae: Scarabaeinae) are mainly coprophagous. Globally, many species co-exist with large mammalian fauna in grasslands and savannahs. However, tropical and subtropical rainforests, where large herbivorous mammals are scarce, support numerous dung beetle species. Many rainforest dung beetle species have been shown to be generalist saprophages or specialists on non-dung food resources. In Australian rainforests, observations of native dung beetles have indicated that some species are attracted to other resources such as fruit or fungi, although the extent to which this occurs is not known. To learn more about the diet breadth of Australian native rainforest dung beetle species, we assessed their attraction to a range of baits, including two types of dung, four types of carrion from both vertebrates and invertebrates, three types of rotting fruit and rotting mushrooms. We primarily surveyed rainforest sites but included two dry open-forest sites for comparisons. Of the two groups of Australian native dung beetles (Onthophagini and Australian Endemic Genera), the latter dominated the rainforest dung beetle fauna and were attracted to a greater variety of baits compared with Onthophagini. The Onthophagini were dominant in open-forest and were more likely to be attracted to a particular bait type, primarily dung. Our findings suggest that many of the species belonging to the 'Australian Endemic Genera' are generalist feeders and their ability to utilise a range of food resources contributes to their abundance and diversity in Australian rainforests.

Key words: Australian endemic genera, behaviour, pitfall trap, diversity, rainforest

INTRODUCTION

Dung beetles (Scarabaeinae) have a number of characteristics that make them useful as bioindicators. They are diverse and taxonomically well-characterised, have a rapid community turnover along environmental and habitat gradients, and are relatively easy to sample (Bicknell et al. 2014). Dung beetles are broadly distributed, yet individual species are stenotopic and sensitive to ecosystem changes (Nichols et al. 2007, Audino et al. 2014). Dung beetle assemblages show high habitat specificity according to factors such as vegetation cover and soil type (Davis et al. 2001, Hill 1996). They are especially reliant upon animal faeces, so their distribution can be sensitive to the presence of dung-producing vertebrates (Bicknell et al. 2014, Audino et al. 2014). In addition, dung beetles provide a number of key ecosystem functions such as nutrient cycling, soil bioturbation, secondary seed dispersal and parasite suppression (Doube 2018, Ridsdill-Smith & Edwards 2011). A great deal of dung beetle research has focused on their role in pastures, while their importance to tropical forest ecosystems has not been studied in as much depth (Nichols et al. 2008).

The majority of dung beetles are coprophagous, feeding on the dung of large herbivorous mammals (Scholtz et al. 2009). However, in tropical forests many species utilise a broader range of food resources (Scholtz et al. 2009, Salamao et al. 2014, Hanski & Cambefort 1991). It is thought that dung beetles originally derived from a saprophagous ancestor that evolved into a dung-feeding specialist to exploit the dung of large dinosaurs (Chin & Gill 1996). With the extinction of large vertebrates at the end of the Cretaceous, it is likely that the associated dung beetles also underwent extinctions (Gunter et al. 2016). Declines in large herbivore populations and increased competition for a limited resource may have led to evolution of less specialised species, which could utilise resources other than dung in their diet (Scholtz et al. 2009).

For dung beetles living in temperate or savannah regions, coprophagy has remained the dominant feeding strategy. In these habitats, a diverse herbivorous mammalian fauna is supported by grasslands and open woodlands. Temperate dung beetles tend to prefer open areas and are attracted to dung from a variety of species (Lumaret & Kirk 1991). The largest extent of savannah is found in Africa where this habitat supports a high diversity of dung beetle species, most of which feed on dung from a variety of herbivorous mammals. In African tropical forests, it is thought that the dung beetle fauna is derived from earlier savannah species as most specialise on the dung of either large herbivores, such as elephants, or small omnivores (Cambefort & Walter 1991).

Compared to African tropical forests, dung beetles in tropical forests in other parts of the world appear to utilise a broader range of food resources. In Southeast Asian tropical forests, dung beetles have been found to be attracted to dung, carrion, rotting fruits and fungi (Hanski & Cambefort 1991). In Borneo, the most abundant species have been found to be generalists, while rarer species are predominantly coprophagous (Hanski 1983). The Neotropical rainforests are the most extensive in the world and here the dung beetle inhabitants display a great diversity of feeding habits. Alternative food resources include toad dung, snake dung, bird droppings, bat guano, rotting fruits, fungus, vertebrate carrion and invertebrate carrion (Gill 1991, da Silva et al. 2012, Salamao et al. 2014, Estrada et al. 1993). The Neotropics have the highest recorded number of non-dung feeding species, greater than that of either African or Asian tropical regions (Halffter & Halffter 2009). In Australian rainforests, observations of native dung beetles show that some rainforest species are attracted to carrion, mushroom, rotting fruit and plant material in addition to dung (Monteith & Storey 1981, Dalglish & Elgar 2005, Storey & Weir 1988, Hill 1996, Doube et al. 1991, Matthews 1972, 1974, 1976).

In Australia, the higher classification of native dung beetles is currently in a state of flux. The fauna was fully revised by Matthews in the 1970s (Matthews 1972, 1974, 1976) who recognised three tribes, the Onthophagini (containing the cosmopolitan genus *Onthophagus* only), the Coprini (containing the Australian *Coptodactyla*, *Thyregeis* and *Demarziella*) and the Scarabaeini (containing 16 mostly Australian endemic genera). Each of these tribes was thought to be widespread globally, with the Australian taxa an integral component of each. Until recently, it was hypothesised that all these taxa probably populated Australia from the north via an “out of Africa” origin (Sole & Scholtz 2010). However, recent morphological (Tarasov & Genier 2015) and molecular (Tarasov & Dimitrov 2016) studies have shown that while the origin of *Onthophagus* accords with those ideas, the other Australian genera resolve into clades not associated with what were considered to be their relatives. For this reason, these studies allocated all the non-*Onthophagus* genera to an *incertae sedis* tribal status, with *Boletoscaper* consistently resolving as a separate clade from the other Australian endemic genera. Gunter et al. (2018) showed a high probability of a Mesozoic and Gondwanan origin for these Australian genera and, because *Boletoscaper* was clearly phylogenetically distinct from the other genera, used the term ‘Australian Endemic Genera’ (AuEG) as a convenient group name for the Australian non-*Onthophagus* taxa. In the present paper we follow this usage and use the term AuEG as a group name for all the Australian non-*Onthophagus* dung beetles.

Our aim in this study was to learn more about the behaviour and habits of Australian rainforest dung beetles. Testing the attraction to different types of bait gives us information about the diet breadth of these beetles which will help us to further define their role in rainforest ecology. It also provides behavioural information which complements phylogenetic studies and adds insight into the evolutionary origins of the Australian rainforest dung beetles.

MATERIALS AND METHODS

Sampling sites

Trapping sites were located in southeast Queensland (SEQ) on the Springbrook plateau and in northeast Queensland (NEQ) on the Atherton Tableland. One of the SEQ sites was located at the Australian Rainforest Conservation Society property *Ankida* in wet sclerophyll forest along the north western edge of the plateau. The other site was in Springbrook National Park at the southern end of the plateau, in high altitude temperate rainforest southwest of the Repeater Station at the end of Repeater Station Road approximately 6.5 km south of *Ankida*. These sites were sampled four times at monthly intervals from November 2016 through to February 2017. The NEQ sites were sampled once during February 2017. Four rainforest sites were sampled within or adjacent to the Wet Tropics World Heritage Area. Two sites (Thiaki1 & Thiaki2) were sampled at the privately owned Thiaki Creek Nature Reserve where previous dung beetle surveys have been conducted (Kenyon et al. 2016). In Danbulla National Park, we surveyed at the following two sites: one at Robson Creek adjacent to the CSIRO Terrestrial Ecosystem Research Network long-term monitoring area, and the other at Mt Haig about 4.5 km northwest of the Robson Creek site. Two dry, open-forest locations on the Atherton Tableland were also sampled at Granite Gorge Nature Park located about nine km southwest of Mareeba, and Tinaroo Waters, a small forested area on the western side of Lake Tinaroo at the end of Black Gully Road. Detailed descriptions of the eight sites are given in Table S4. This strategy resulted in 28 transects in total, 23 in rainforest, one in wet sclerophyll and four in open-forest. Sites were chosen where repeated dung beetle sampling had been undertaken in the past by GBM and/or RM, and thus, the dung beetle fauna occurring at the sites was well-known and could be reliably identified.

Transect design

Two linear transects running roughly parallel to each other were established at each location approximately 25 m apart. Eleven traps (ten baited and one control) were placed every 20–25 m along each transect. Baits were placed at random. Each trap consisted of a 450 ml plastic cup set into the ground with the top level with the surface. The cups were covered with a wire grid to reduce trap interference and had angled roof pieces to protect them from rain. Baits were wrapped in porous cloth and suspended from the grid into the cup. Cups contained approximately 100 ml of water with some detergent added. Traps were set in the early afternoon and collected after 24 hours to capture both nocturnal and diurnal species. Dung beetles were strained from the trap fluid and preserved in 75% ethanol.

Baits used

Ten baits were used, including two types of dung, one type of vertebrate carrion, three types of invertebrate carrion, three types of decaying fruit and decaying mushroom (see Table 1). Eastern grey kangaroo dung (*Macropus giganteus*) was used to represent a mammalian herbivore dung source that has been shown to effectively attract dung beetles (Hill 1996, Kenyon et al. 2016). Bird dung has been shown to be attractive to native dung beetles in New Zealand (Stavert et al. 2014) so free-ranging fowl dung was used to represent an avian omnivore dung source. Liver and entrails have been used as a carrion source to attract dung beetles (Hill 1996, Matthews 1972, 1974), however, it was decided that dead mice would represent a more typical source of vertebrate carrion found in the rainforest. Some dung beetles are known to decapitate *Atta* ant alates to use as a larval food source (Hertel & Colli 1998), while others are known to predate upon millipedes (Larsen et al. 2009). Many dung beetles have been trapped at insect carrion and some even subsist on snail mucus (Vaz-de-Mello 2007) so crickets, mealworms, earthworms and snails were chosen as invertebrate carrion sources. A number of Australian studies have found fruit to be attractive to some species (Hill 1996, Monteith & Storey 1981, Storey & Weir 1988) so decaying banana, cucumber and pineapple baits were chosen to present a range of olfactory stimulants. Several Australian native dung beetles have been found to utilise mushroom as a food source and some use it for larval provisioning (Matthews 1972, 1974, Bornemissza 1971, Monteith & Rossini 2017). The efficacy of decayed mushroom as a bait for dung beetle species that may be poorly attracted to dung baits has led to its widespread use, in conjunction with dung, in survey trapping in Australia over the last decade. This includes large scale trapping at Lamington, Atherton Tableland and elsewhere (Monteith & Menéndez unpubl., Derhe et al. 2016) and smaller local surveys (Monteith & Kenyon 2011, Monteith & Ebert 2016).

Identification

Specimens were identified to species level and grouped phylogenetically either within the AuEG or *Onthophagus* (Table S1). Undescribed species were recorded according to the nomenclature coding system devised by Geoff Monteith (QM) and Tom Weir (ANIC) for Australian museum collections. Voucher specimens were pinned, labelled and stored at the Queensland Museum.

Data analysis

The Simpson index (D) was used to calculate a diet diversity measure for each species for which we collected more than 20 specimens. Diet diversity (breadth) was expressed as the reciprocal $1/D$, so that the value of diet breadth increased with diet evenness (Magurran 2004). Measures of diet breadth were compared between AuEG and *Onthophagus* using a Wilcoxon rank sum test (Gardener 2012). Correlation between diet breadth in this study and percent occurrence at mushroom baits in past studies was tested using Spearman's rank correlation.

To assess which species had a higher occurrence at certain types of bait we used the IndVal method (Dufrene & Legendre 1997). Tshikae et al. (2008) considered that if a species has an IndVal greater than 50 for a particular bait, it is considered to have a preference. If the IndVal is greater than 70, it is considered to be a specialist, whereas a value less than 50 is considered to be generalist. IndVals were only calculated for species for which more than 20 specimens (greater than 0.5% abundance) were collected (Table S3).

Beetle associations with different baits were tested using chi-square residuals. A chi-square test of independence was used to analyse each species and its occurrence at each bait. To test the dependence between species and bait, the Pearson (standardised) residuals were calculated using $r = (o - e) / \sqrt{e}$ (where o represents the observed values and e represents expected values). Positive residuals indicate a positive association or overrepresentation at a particular bait, whereas a negative residual indicates a negative association or underrepresentation at a particular bait. Residuals greater than two are considered significant (Gardener 2012). Statistical analyses were performed using RStudio v1.1.442 (R Core Team 2017).

RESULTS

Overall, 74 species of dung beetles (Scarabaeidae: Scarabaeinae) were collected (Table S1). Fifty-one species were collected at the rainforest/wet sclerophyll sites and 23 species were collected at the dry, open-forest sites. While some of the sites had species in common, all had different species compositions. No species were shared between rainforest and open-forest sites. Throughout the study, only five specimens were collected in control traps.

A total of 3733 dung beetle specimens were collected from the rainforest/wet sclerophyll sites. Of these, 92.7% of specimens were AuEG species and 7.3% were *Onthophagus* species. Of the 129 specimens collected from the two dry, open-forest sites, 48% were AuEG species and 52% were *Onthophagus* species (Table 2).

Bait preferences at SEQ and NEQ rainforest sites

At the SEQ sites, the most abundant species were AuEG species, which were attracted to eight to ten types of baits. The *Onthophagus* species were predominantly attracted to dung or mushroom, in the case of *Onthophagus kumbaingeri*. At the NEQ-RF sites, the most abundant species was *Temnoplectron politulum* (AuEG) which was collected at all ten baits. Several other abundant AuEG species were also attracted to multiple baits, whereas the *Onthophagus* species were collected only at dung baits (Table S2).

Bait preference at NEQ dry, open-forest sites

Fewer beetle specimens were collected per site at open-forest sites compared to rainforest sites (Table 2). Even though 23 species were collected from the two sites, only 129 individuals were collected and most species were represented by fewer than 5 individuals. At Granite Gorge, the three most abundant species were all *Onthophagus* which were attracted to as many as four baits. Only one individual from each of three AuEG species were collected. At Tinaroo, the most abundant species was *Coptodactyla nitida* (AuEG) which was collected mainly at dung baits, but was also attracted to three other baits in small numbers. *Onthophagus semimetallicus*, the second most abundant beetle species, was collected mainly at dung baits. (Table S2).

Bait attraction analysis for more common species

The diversity of baits allows a comparison of attractiveness among those species where more than 20 individuals were collected. Across all sampling sites, 26 such ‘abundant’ species were identified, representing 35% of the species collected. The relative abundance of these 26

species at the ten different baits is shown in Figure 1. The most notable outcome was that AuEG species were attracted to a more diverse array of baits than *Onthophagus* species: AuEG species were all attracted to three or more baits with ten species being attracted to eight or more baits. On the other hand, *Onthophagus* species were attracted to only three or fewer baits (Fig. 1). *Onthophagus kumbaingeri* stands out among the *Onthophagus* species because it was rarely collected at dung traps, but frequently collected at mushroom and snail baits.

Data from two published surveys (Derhe et al. 2016, Kenyon et al. 2016) and one unpublished survey (Monteith & Menéndez, unpubl.) of attractiveness of paired dung- and mushroom-baited traps can be compared to the bait attractiveness outcome shown in Figure 1. For background information, several dung beetle surveys have been conducted during the last decade at Lamington and Beechmont in southeast Queensland, and at Thiaki and Robson Creek in northeast Queensland at sites close to those of the current study (Monteith & Menéndez, unpubl., Derhe et al. 2016, Kenyon et al. 2016). These surveys demonstrated that a more complete picture of dung beetle diversity could be obtained using both dung and mushroom as baits. Combined, the three studies produced 32,301 specimen records for the 26 listed ‘abundant’ species of this current study. To compare with the present study, past survey records for these 26 species (with the exception of *Aptenocanthon monteithi*) were graphed according to relative abundance at dung and mushroom baits (Fig. 2). It is apparent that there is an approximate accord between the results of the current multi-bait study and the two-bait surveys. In general, a high dietary breadth in the ten-bait study accords with a higher attraction to mushroom in the two-bait surveys. Overall, members of *Onthophagus* have a high dung preference in the two-bait surveys (Fig. 2), as well as a high dung preference in the multi-bait study (Fig. 1). However, *O. kumbaingeri* is distinguished from other *Onthophagus* species by its mushroom preference under both bait-choice scenarios. A comparison between the diet breadth measures (Table 3) and the relative abundance at mushroom-baited traps (Fig. 2) for each species showed a positive correlation (Spearman’s rank correlation, $S=589$, $\rho=0.744$, $p<0.001$).

The AuEG species collectively showed a significantly greater diet breadth than the *Onthophagus* species (Table 3). Plots of chi-square residuals showed that the AuEG had significant positive associations with non-dung baits and an underrepresentation at dung baits (Fig. 3). In contrast, the abundant *Onthophagus* species had significant positive associations with dung baits, with the exception of the mushroom specialist, *O. kumbaingeri* (Fig. 4).

Six of the abundant species (*Amphistomus* NQ3, *Coptodactyla nitida*, *Onthophagus arrilla*, *O. dicranocerus*, *O. sydneyensis* and *O. waminda*) showed a preference (>50) for kangaroo dung using IndVals (Table S3). Three other species, *Onthophagus wagamen*, *O. millamilla* and *O. rubicundulus*, did not have IndVals greater than 50, yet they occurred exclusively at dung baits. This is a reflection of the fact that IndVals are calculated to include frequency of occurrence at each trap. Calculations for each species only take into account the sites from which the species was collected and because we only sampled two traps per bait at each NEQ site, presence or absence in one trap has a greater influence on the calculations. More trap numbers would most likely give more accurate results.

Overall, dung was the most attractive type of bait, attracting the greatest numbers of individuals and the greatest number of species. The two types of dung (kangaroo and fowl) attracted similar numbers of specimens (35% and 29% of specimens respectively); however, most *Onthophagus* species were collected more often at kangaroo dung and showed a positive association with dung (Fig. 1, 4). Eleven percent of specimens were collected at mouse baits. The three types of invertebrate carrion (cricket/mealworm, snail, earthworm) together attracted 13% of the specimens. Rotting mushrooms attracted 9% of specimens, while rotting fruits (banana, cucumber and pineapple), collectively, attracted 2.5% of specimens (Table S2).

While decaying fruit attracted the fewest beetle specimens across all locations, in some species more than 5% of specimens were collected at this bait type. At the SEQ sites, 14% of *Cephalodesmius laticollis* and 7% of *Amphistomus trispiculatus* were trapped at the three different rotting fruit baits (Fig. 1). At the NEQ rainforest sites, *Aptenocanthion monteithi*, *Coptodactyla depressa* and *Lepanus dichrous* were collected at rotting fruit baits (Fig. 1). *Aptenocanthion monteithi* and *L. dichrous* were collected at cucumber, 6.7% and 5.9% respectively, while 14% of *C. depressa* specimens were collected at all three types of rotting fruit (Fig. 1, Table S2). All of these species showed a positive association with fruit baits (Fig. 3).

DISCUSSION

General trends

An emerging pattern at all of the rainforest sites was that the most abundant species were attracted to multiple types of bait. At each site, three or four species made up 75-90% of the sample and were attracted to at least four different baits. Similar results were found in a southeast Asian rainforest study, where the most abundant species were attracted to a range of baits (dung, carrion, rotting fruits and mushrooms), while rarer species were exclusively coprophagous (Hanksi & Krikken 1991). A study in the Queensland Wet Tropics also found that the most abundant species came to multiple baits (Hill 1996). While our results suggest that these highly abundant beetles may be generalist feeders, it is important to note that attractiveness to a particular type of bait or odour may not necessarily mean that the beetles feed on the bait or utilise it for larval provisioning. The detailed behaviour of many of these species remains unknown.

Another pattern that emerged from this study was that the abundant species at the rainforest sites belonged to the AuEG. Each of the rainforest study sites had a unique species assemblage, which was always dominated by AuEG species. Of the 51 species collected at rainforest sites, 30 were AuEG and 21 were *Onthophagus* species. Even though overall species richness between the two phylogenetic groups was not markedly different in the rainforest sites, the species abundance differed greatly with 93% of individuals belonging to AuEG. Several species of *Onthophagus* were collected at each rainforest site, but they were always less numerous. Species lists from other rainforest studies show a similar pattern of AuEG dominating rainforest sites (Hill 1996, Derhe et al. 2016, Kenyon et al. 2016). The opposite was true at the two NEQ dry open-forest sites, where *Onthophagus* were the most abundant. Our results reflect the distributions compiled by Matthews (1972,1974) who found that canthonines (currently the main constituents of the AuEG) are mainly forest-dwellers and onthophagines are mainly found in more open habitats. A possible explanation might be that the AuEG species have a long evolutionary history of living in Australian rainforests and, perhaps due to a paucity of high-volume dung sources and the availability of diverse saprophagic resources, they diversified into more generalist feeders. As Australia became increasingly arid, the range of the AuEG species was limited to the wetter, more stable environments. *Onthophagus* species arriving from the north were perhaps better adapted to the extensive drier, open-forest habitats and could diversify in such environments. Further research is needed to test this possibility.

Limited behavioural data have been recorded for AuEG dung beetles, with the exception of *Cephalodesmius armiger*. *Cephalodesmius* are unique in that they culture plant material to make synthesised brood material (Monteith & Storey 1981). *Cephalodesmius laticollis* was the most abundant beetle collected at Springbrook (SEQ) and also showed the highest level of diet breadth. Behavioural observations confirm that, like *C. armiger*, this species makes brood material from a range of resources, and has been observed feeding on dung, rotting fruit and dead millipedes (Monteith & Storey 1981, K. Ebert, pers. obs.). Based on the fact that *Cephalodesmius* utilise alternative food resources it would seem plausible to expect that other AuEG species might also use a variety of resources for brood production. Field observations of nesting behaviour in other AuEG species are needed to test this hypothesis.

Three flightless AuEG species accounted for 91% of the specimens collected at Springbrook (1000 m elevation). These three, flightless species (*Cephalodesmius laticollis*, *Amphistomus trispiculatus* and *Monteithocanthion glaber*) showed a high level of diet breadth and were collected at eight to ten different baits. The Mt Haig site was the highest elevation site sampled in NEQ (over 1000 m). Here, another flightless species, *Aptenocanthion monteithi*, was common in the samples taken at a wide range of baits. Flightlessness in dung beetles has been linked to stable and persistent microhabitats and possibly to energy conservation in cooler areas (Scholtz et al. 2009). Subtropical rainforests and high-altitude temperate forests in Australia tend to have a higher incidence of flightless species than corresponding forest areas in other parts of the world (Scholtz et al. 2009). Our results indicate that flightless species are attracted to a wide range of baits, which suggests that they have a generalised diet. Being flightless would limit foraging ability so a more generalised diet would be advantageous. This also highlights the fact that transect design should be taken into consideration in areas where flightless dung beetles occur. Distance between traps should take into account the size and mobility of the dung beetle species.

Bait-specific observations

Overall, dung attracted the greatest numbers of individuals and the greatest number of species. Both dung types (kangaroo and fowl) attracted similar numbers of specimens; however, *Onthophagus* species were collected more often at kangaroo dung. In a north Queensland study Vernes et al. (1999) found that AuEG species were commonly collected at four types of mammal dung, whereas *Onthophagus* species usually preferred one type of dung. Frank et al. (2017) analysed the nutrient quality of various types of vertebrate dung (carnivore, omnivore, herbivore) collected from farms and zoos in Germany to look for

correlations between nutritional composition and dung volatiles. While the most nutritious dung was expected to be most attractive to dung beetles, this was not the case. The study found that different dung beetles showed specific preferences for different types of dung irrespective of nutritional content, indicating that there must be other factors driving dung beetle preferences.

The different types of carrion baits, collectively attracted 24% of specimens. Attraction to carrion has been found in other dung beetle species that are mainly generalist feeders in rainforests (Gill 1991, Hanski & Krikken 1991, Halffter & Matthews 1966). There are a few cases of carrion specialists in Africa (Tshikae et al. 2008) and the Neotropics (Gill 1991) but it is not common, and it is not known if these species actually use carrion in larval provisioning. Some dung beetles are known to feed exclusively on invertebrate carrion or predate upon invertebrates. These include some *Canthon* species in Brazil that utilise the alate queens of leafcutter ants (*Atta*) for brood provision (Hertel & Colli 1998), the millipede-feeding specialist, *Sceliages*, in South Africa (Forgie et al. 2002) and the millipede predator, *Deltochilum valgum*, in Peru (Larsen et al. 2009). In our study, more than 15% of specimens collected at invertebrate carrion belonged to several of the abundant AuEG species (*Lepanus* NQ9, *Aptenocanthon monteithi*, *L. dichrous*) and showed a greater association with invertebrate baits than other species. A few other species (listed as follows) were collected exclusively at invertebrate or vertebrate carrion, but in small numbers: *Lepanus pisoniae* (8), *L. pygmaeus* (10) and the rare *L. storeyi* (2). *L. storeyi* is limited to high-altitude rainforests in SEQ and is rarely collected. *L. storeyi* is usually only collected in litter samples and only once has it been collected at a fungus-baited pitfall (Weir & Monteith 2010). This study collected two specimens at snail-baited traps. While there is a South American dung beetle (*Zonocopris*) that is phoretic on land snails and feeds on snail mucus (Vaz-de-Mello 2007), there is no evidence that *Lepanus storeyi* has a similar relationship with snails. Its attraction to snails may be more likely related to the fungal diet of snails (Parkyn et al. 2015). *Lepanus pygmaeus* was only collected at cricket/mealworm bait at the Tinaroo site (NEQ-OF). This was of interest because this species had not been collected at this site during significant earlier trapping efforts with dung and mushroom baits (Monteith & Menéndez, unpubl.). Our results suggest that *Lepanus* species are generalist feeders that often feed on alternatives to dung. Comparisons with data collected from dung beetle surveys in the past decade using paired dung-mushroom baited traps (Monteith & Menéndez, unpubl., Derhe, et al. 2016) have shown that more than 50% of *Lepanus dichrous*, *L. globulus*, *L. NQ9* and *L. NSW2* specimens have been collected from mushroom-baited traps. Hill (1996) also found that three

Lepanus species (*L. pisoniae*, *L. palumensis*, and *L. latheticus*) were predominantly attracted to carrion (liver).

Rotting fruits are attractive to a number of dung beetle species especially in the Neotropics and southeast Asian tropical forests (Halffter & Halffter 2009, Gill 1991, Salamao et al. 2014). Most of these are considered to be generalist feeders and very few are thought to utilise fruit for brood provision with the exception of a fig-feeding specialist, *Onthophagus rouyeri*, in Borneo (Davis & Sutton 1997). In our study, several AuEG species were attracted to rotting fruit baits but in addition to other baits, so are likely to be generalist feeders. Two of the open-forest mushroom specialist *Onthophagus* species (*O. walteri* and *O. latro*) were also collected at fruit baits, but only in small numbers.

Onthophagus species collected at rainforest sites were attracted mainly to dung-baited traps, with a few individuals attracted to carrion. The only abundant rainforest *Onthophagus* species found at baits other than dung was *O. kumbaingeri*, a specialist mushroom feeder (Matthews 1972). In contrast, *Onthophagus* species in open-forest sites were attracted to a wider variety of baits than the rainforest *Onthophagus*. At Granite Gorge, *Onthophagus fabricii* and *O. asper* were both collected at earthworm baits as often as dung baits; however, the numbers of specimens collected at these open-forest sites were too few to draw conclusions about specialisation. A higher proportion of mycetophagy occurs among the Australian *Onthophagus* compared to *Onthophagus* elsewhere in the world (Matthews 1972) and several open-forest dwelling *Onthophagus* species groups (*dunningi* and *erichsoni*) are known, specialist mycophages (Matthews 1972, Bornemissza 1971, Monteith & Rossini 2017). Studies in Borneo (Hanski 1983) and Central America (Gill 1991) found that some *Onthophagus* species are attracted to other baits such as carrion and fruit. In northern Cape York (QLD), the rare *Onthophagus vilis* has been found feeding on fallen fruits from *Syzygium suborbiculare* and *Siphonodon pendulus* (Storey & Weir 1988). Further studies on bait attraction and behaviour would help to determine if, perhaps, *Onthophagus* fill the niche of a more generalist feeder in the drier, open-forest areas where AuEG species are not as abundant.

Leaf litter collected from the Mt Haig site during this study contained five *Pseudignambia* specimens (AuEG) but none were collected in the baited pitfalls. *Pseudignambia* is a very small (2.5-2.8 mm), flightless genus, with thick setae covering the dorsal body surface and the dorsal portion of its eyes greatly reduced. Matthews (1974) has suggested that these modifications may indicate myrmecophily, but nothing is known of

Pseudignambia's reproductive behaviour. The fact that no *Pseudignambia* were trapped in the baited pitfalls highlights the importance of using different methods in a survey.

CONCLUSIONS

Results from this study concurred with Hill's (1996) study that found a distinct rainforest and open-forest dung beetle fauna, and that the rainforest fauna is richer in species. Our results show that the abundant rainforest dung beetles are attracted to a range of food resources. Each area surveyed had unique dung beetle assemblages that included both generalist and specialist species. While dung was attractive to most dung beetles, many species were attracted to a variety of other decomposing microbe-rich sources. The most abundant rainforest dung beetles were those attracted to a wide range of baits (generalists), whereas those with strong dung preferences (specialists) were less abundant. The abundance of AuEG species at multiple types of bait suggests that they, as generalist feeders, may have a broader role in rainforest decomposition. More studies on the behaviour and habits of the native Australian dung beetles will help to define that role. Furthermore, very little is known about the larval provisioning behaviours for many of the native species. We do not know if dung beetles feeding on a broad range of food resources are utilising the same alternative food resources for provisioning brood. Detailed studies of beetles in natural situations are needed to answer these questions and increase our understanding of resource use in Australian dung beetles.

This study has also allowed us to re-examine previous survey outcomes that were based on dual-baited traps allowing us to conclude that, in general, species that are attracted to mushrooms are also attracted to non-dung baits. Thus, our results can be interpreted as implying that attraction to mushroom can be an effective indicator of attraction to dung alternatives. Using mushroom baits in conjunction with dung baits appears to be an effective means of sampling generalist-feeders in rainforest dung beetle assemblages. However, using a wider variety of baits may provide additional measures of species abundance and add information about their behaviours.

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Table 1. Bait descriptions. The baits used, their sources and details of preparation in a study of bait preferences of Australian dung beetles. Bait letter codes and colour codes are used throughout the figures and tables. All baits were prepared in 25-30 g aliquots, wrapped in porous cloth and suspended over a 450 ml pitfall trap.











Bait name	Bait code	Bait colour code	Bait description
Kangaroo dung	KROO		grey kangaroo dung - gathered fresh from native population then frozen until use
Fowl dung	FOWL		domestic fowl dung - gathered fresh from free range domestic chickens, then frozen until use
Mouse	MOUSE		dead mice - commercially available, frozen; broken in half and allowed to thaw and decompose for several hours prior to use
Cricket/mealworm	CRMW		a mixture of dead crickets and mealworms - commercially available; purchased live, then frozen until use; thawed and decomposed for several hours prior to use
Snail	SNAIL		crushed dead snails - commercially available or wild caught; frozen until use; thawed and decomposed for several hours prior to use
Earthworm	EWRM		dead earthworms - commercially available; purchased live, then frozen until use; thawed and decomposed for several hours prior to use
Banana	BAN		rotting banana; decomposed 24 hours at 25-30°C in humid environment
Cucumber	CUC		rotting cucumber: decomposed 24 hours at 25-30°C in humid environment
Pineapple	PIN		rotting pineapple: decomposed 24 hours at 25-30°C in humid environment
Mushroom	MSHRM		rotting mushroom: decomposed 24 hours at 25-30°C in humid environment

Table 2. Comparison of dung beetle species abundance and richness between the two phylogenetic groups at each site in a study of bait preferences of Australian dung beetles. The total number of species (richness) and the total number of specimens (abundance) collected at each location are shown. The two SEQ-RF sites were each sampled four times. The NEQ-RF and NEQ-OF sites were each sampled once.

		<i>Onthophagus</i>			AuEG	
Site description		sampling events	# of species	# of specimens	# of species	# of specimens
SEQ-RF	Ankida	4	7	98	7	510
	Springbrook	4	2	7	6	299
NEQ-RF	Thiaki 1	1	8	78	8	723
	Thiaki 2	1	7	45	11	395
	Robson Creek	1	6	23	13	1267
	Mt Haig	1	7	24	9	267
NEQ-OF	Granite Gorge	1	10	38	3	3
	Tinaroo	1	7	29	4	59

Table 3. Diet breadth for abundant species of Australian dung beetles in a study of bait preferences. Diet breadth is determined by using the Simpson index (D) to calculate a diversity measure of bait choices. A higher number indicates a greater number of baits were chosen (calculated by 1/D). The average diet breadth for AuEG = 3.96 and for *Onthophagus* = 1.55. Differences in AuEG and *Onthophagus* values are significant (Wilcoxon rank sum test, W=5, p<0.001). + indicates flightlessness.

Species - AuEG	Diet Breadth	Species - AuEG	Diet Breadth	Species - <i>Onthophagus</i>	Diet Breadth
+ <i>Cephalodesmus laticollis</i>	7.08	<i>Amphistomus</i> NQ5	3.93	<i>Onthophagus kumbaingeri</i>	2.30
<i>Lepanus dichrous</i>	5.97	<i>Coptodactyla depressa</i>	3.43	<i>Onthophagus millamilla</i>	2.06
+ <i>Aptenocanthon monteithi</i>	5.41	<i>Lepanus globulus</i>	3.26	<i>Onthophagus wagamen</i>	1.92
<i>Lepanus</i> NQ9	5.25	<i>Coptodactyla nitida</i>	3.02	<i>Onthophagus rubicundulus</i>	1.56
+ <i>Amphistomus trispiculatus</i>	5.11	<i>Demarziella scarpensis</i>	2.68	<i>Onthophagus sydneyensis</i>	1.15
+ <i>Monteithocanthon glaber</i>	5.07	<i>Temnoplectron subvolitans</i>	2.54	<i>Onthophagus arrilla</i>	1.13
<i>Diorygopyx tibialis</i>	4.50	<i>Amphistomus</i> NSW1	2.14	<i>Onthophagus dicranocerus</i>	1.10
<i>Lepanus</i> NSW2	4.12	<i>Amphistomus complanatus</i>	2.13	<i>Onthophagus waminda</i>	1.08
<i>Temnoplectron politulum</i>	4.04	<i>Amphistomus</i> NQ3	1.77		

Fig. 1. Relative abundance of the twenty-six most abundant species of Australian dung beetles at ten different baits from a study of bait preferences in Australian dung beetles.

Horizontal bars show the percentage of specimens collected in this study at each of the different baits. Different baits correspond with different colours. Numbers of specimens collected for each species are in parentheses. Blue box highlights the AuEG species. Yellow box highlights the *Onthophagus* species. + indicates flightlessness.

Fig. 2. Comparison of relative abundance at dung and mushroom baits of twenty-six species of Australian dung beetles from past surveys. Horizontal bars show the percentage of specimens collected in paired dung and mushroom survey traps at Lamington, Springbrook and Beechmont in southeast Queensland, Thiaki and Robson Creek in northeast Queensland (see text for reference to studies). Data from 25 of the 26 species analysed in this paper are incorporated into the bar charts. Numbers of specimens collected for each species are in parentheses. Blue box highlights the AuEG species. Yellow box highlights the *Onthophagus* species. + indicates flightlessness.

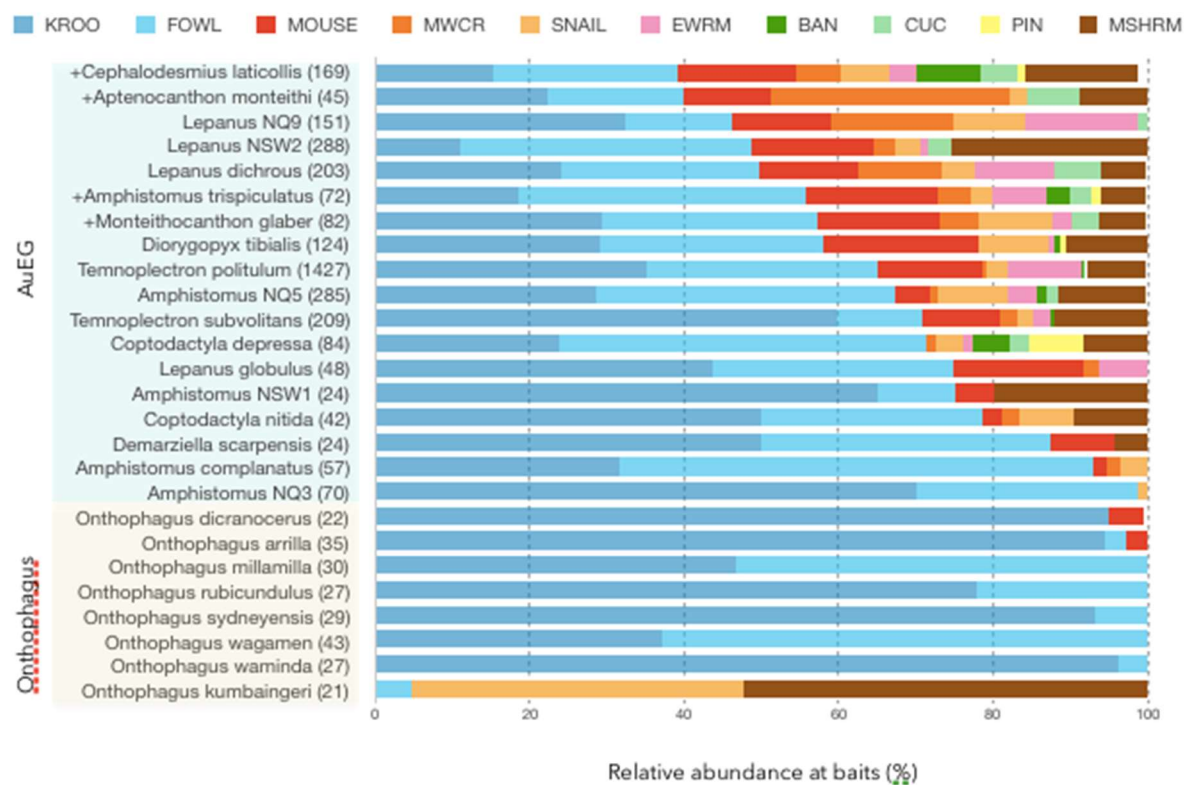
Fig. 3. Chi-squared residuals for eight representative AuEG species with the highest diet breadth in a study of bait preferences in Australian dung beetles. Positive residuals indicate a positive association with the particular bait; negative residuals indicate that the species is underrepresented at that bait. * indicates flightlessness.

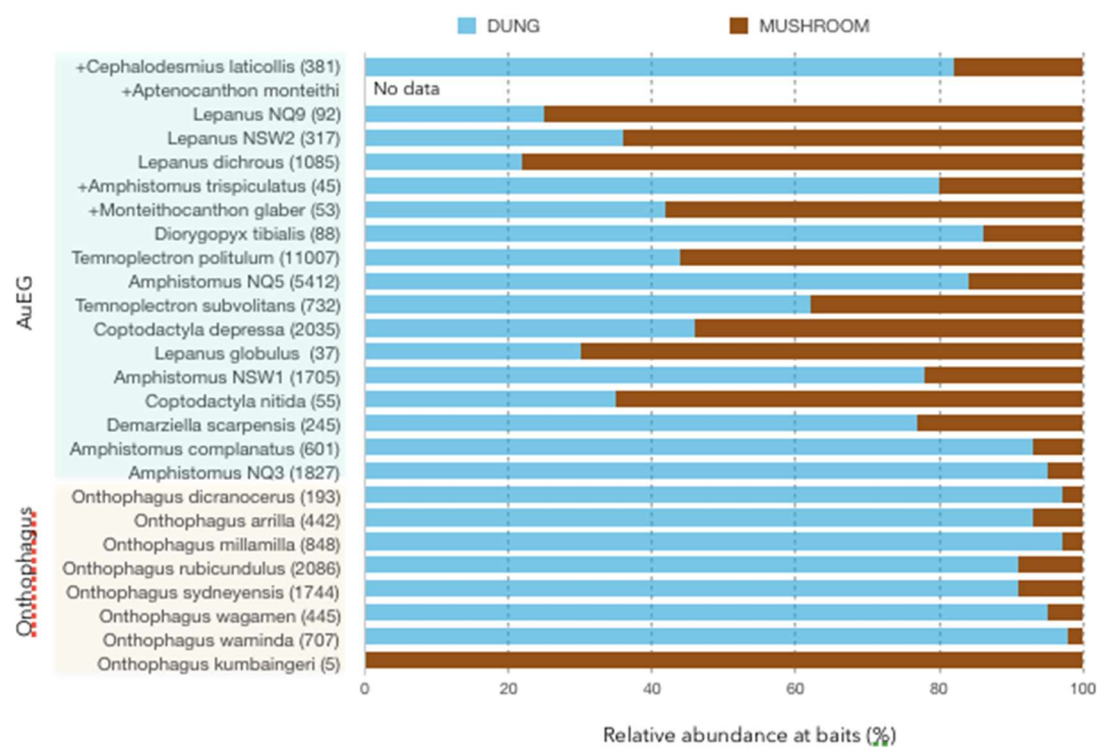
Fig. 4. Chi-squared residuals for eight of the most abundant *Onthophagus* species in a study of bait preferences in Australian dung beetles. Positive residuals indicate a positive association with the particular bait; negative residuals indicate that the species is underrepresented at that bait.

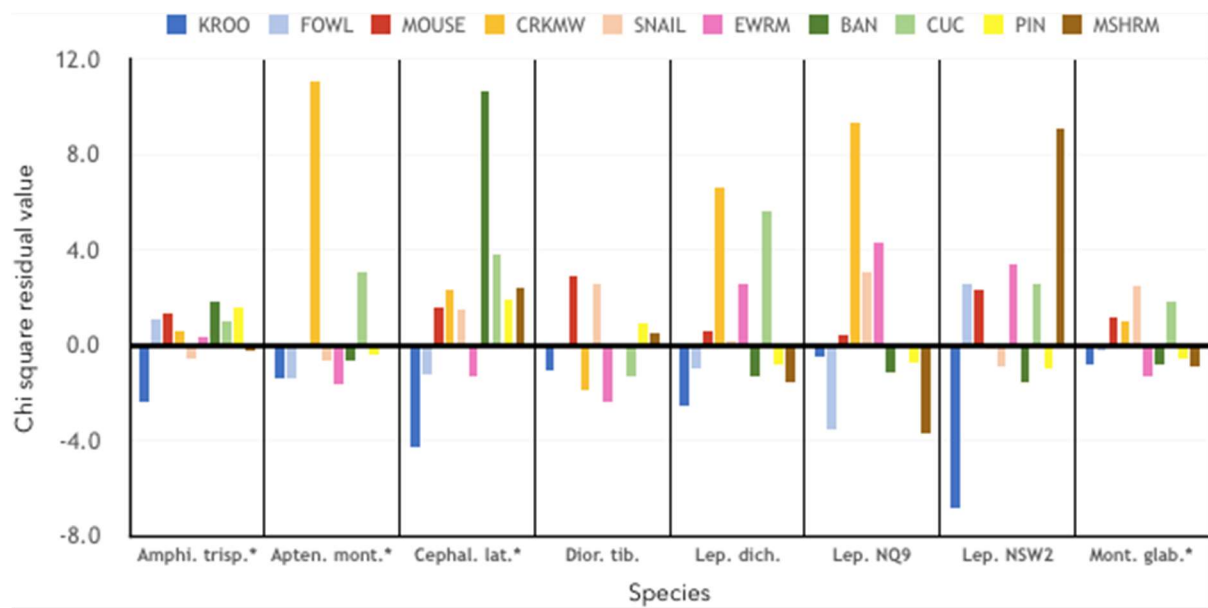
Figure S1. Relative abundance of representative species of Australian dung beetles at different baits in southeast Queensland rainforest sites (SEQ-RF) from a study of bait preferences in Australian dung beetles. Bar graphs show the relative abundance of the four to six most abundant species at different baits. Numbers in parentheses indicate total number of specimens collected. Blue background box highlights the AuEG species. **A**=*Ankida*, **B**=Springbrook. The bottom graphs show the change in species numbers for each of the four sampling periods and the changes in bait attraction over the four sampling events. **C**=*Ankida*, **D**=Springbrook.

Figure S2. Relative abundance of representative species of Australian dung beetles at different baits in northeast Queensland rainforest sites (NEQ-RF) from a study of bait preferences in Australian dung beetles. Bar graphs show the relative abundance of the six most abundant species at different baits. Blue background box indicates the AuEG species. Numbers in parentheses indicate the total number of specimens collected. **A**: Thiaki1, **B**: Thiaki2, **C**: Robson Creek, **D**: Mt Haig.

Figure S3. Relative abundance of representative species of Australian dung beetles at different baits in northeast Queensland open-forest sites (NEQ-OF) from a study of bait preferences in Australian dung beetles. Bar graphs show the relative abundance of the five most abundant species at different baits. Blue background box indicates the AuEG species. Numbers in parentheses indicate the total number of specimens collected. **A**: Granite Gorge, **B**: Tinaroo.







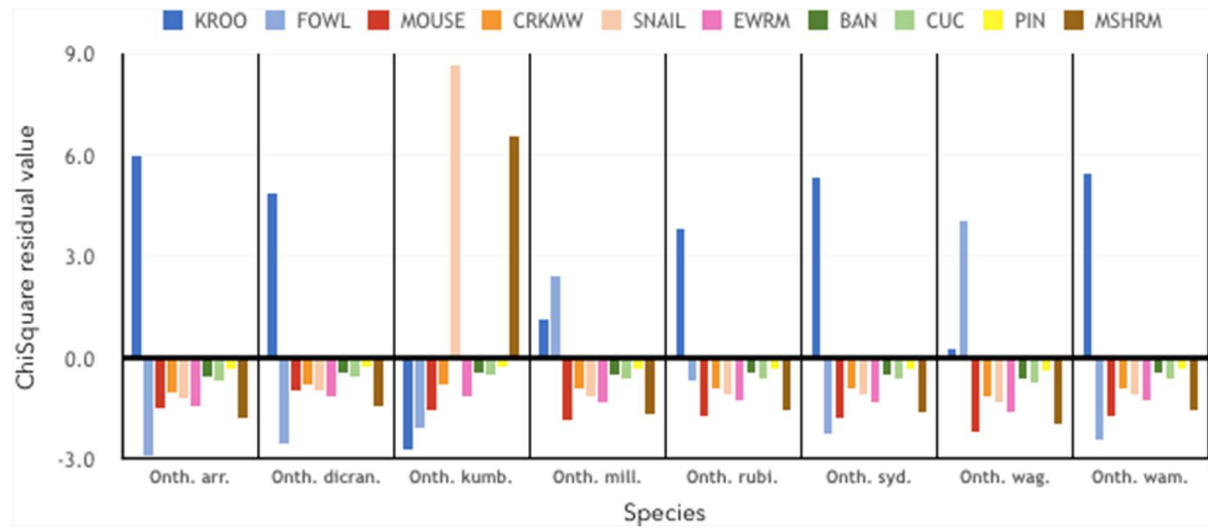


Table S1. Dung beetle species abundance at each site from a study of bait preferences of Australian dung beetles. The site abbreviations are as follows: ANK = *Ankida*, SPR = Springbrook, TH1 = Thiaki1, TH2 = Thiaki2, ROB = Robson Creek, MtH = Mt Haig, GRG = Granite Gorge, and TIN = Tinaroo. The Australian Endemic Genera are listed alphabetically first, followed by *Onthophagus* species.

[illegible]

<i>Onthophagus pupureicollis</i>							1		1
<i>Onthophagus quadripustulatus</i>							1		1
<i>Onthophagus rubicundulus</i>			19	8					27
<i>Onthophagus rubrimaculatus</i>								3	3
<i>Onthophagus semimetallicus</i>								13	13
<i>Onthophagus</i> SEQ2	1								1
<i>Onthophagus sydneyensis</i>	29								29
<i>Onthophagus tabellicornis</i>							1		1
<i>Onthophagus thoreyi</i>								2	2
<i>Onthophagus wagamen</i>			26	16		1			43
<i>Onthophagus walteri</i>								3	3
<i>Onthophagus waminda</i>			1	12	13	1			27
<i>Onthophagus wilgi</i>				1					1
<i>Onthophagus yeyeko</i>							7		7
<i>Onthophagus yungaburra</i>						1			1
total numbers of <i>Onthophagus</i>	98	7	78	45	23	24	38	29	342
total beetle numbers	608	308	801	440	1290	291	41	88	3867
total number of species	14	10	16	18	19	16	13	11	
	ANK	SPR	TH1	TH2	ROB	MtH	GRG	TIN	

Table S2. Dung beetle species abundance at each bait from a study of bait preferences of Australian dung beetles. Bait codes are as follows: KROO = kangaroo dung, FOWL = fowl dung, MOUSE = mouse carrion, CRMW = cricket/mealworm carrion, SNAIL = snail carrion, EWRM = earthworm carrion, BAN = rotting banana, CUC = rotting cucumber, PIN = rotting pineapple, MSHRM = rotting mushroom. The Australian Endemic Genera are listed alphabetically first, followed by *Onthophagus* species.

[illegible]

<i>Onthophagus capelliformis</i>	2	2										
<i>Onthophagus consentaneus</i>	2		1								1	
<i>Onthophagus cuniculus</i>	4	1				2					1	
<i>Onthophagus darlingtoni</i>	4	4										
<i>Onthophagus dicranocerus</i>	22	21		1								
<i>Onthophagus dunningi</i>	1					1						
<i>Onthophagus fabricii</i>	11		5			1	5					
<i>Onthophagus fuliginosus</i>	5	5										
<i>Onthophagus kumbaingeri</i>	21		1			9					11	
<i>Onthophagus laminatus</i>	1	1										
<i>Onthophagus latro</i>	4									1	3	
<i>Onthophagus macrocephalus</i>	1		1									
<i>Onthophagus mamillatus</i>	9	5	3	1								
<i>Onthophagus millamilla</i>	30	14	16									
<i>Onthophagus minusculus</i>	3		2				1					
<i>Onthophagus mundill</i>	10	8	2									
<i>Onthophagus NQ8</i>	1	1										
<i>Onthophagus parallelicornis</i>	1	1										
<i>Onthophagus pupureicollis</i>	1	1										
<i>Onthophagus quadripustulatus</i>	1						1					
<i>Onthophagus rubicundulus</i>	27	21	6									
<i>Onthophagus rubrimaculatus</i>	3						3					
<i>Onthophagus semimetallicus</i>	13	5	6	1		1						
<i>Onthophagus SEQ2</i>	1		1									
<i>Onthophagus sydneyensis</i>	29	27	2									
<i>Onthophagus tabellicornis</i>	1			1								
<i>Onthophagus thoreyi</i>	2	2										
<i>Onthophagus wagamen</i>	43	16	27									
<i>Onthophagus walteri</i>	3								1		2	
<i>Onthophagus waminda</i>	27	26	1									
<i>Onthophagus wilgi</i>	1	1										
<i>Onthophagus yeyeko</i>	7	7										
<i>Onthophagus yungaburra</i>	1	1										
total for Onthophagus	342	209	80	5	0	14	13	0	1	1	19	0
Overall totals at each bait	3867	1351	1120	429	120	162	237	31	52	14	346	5

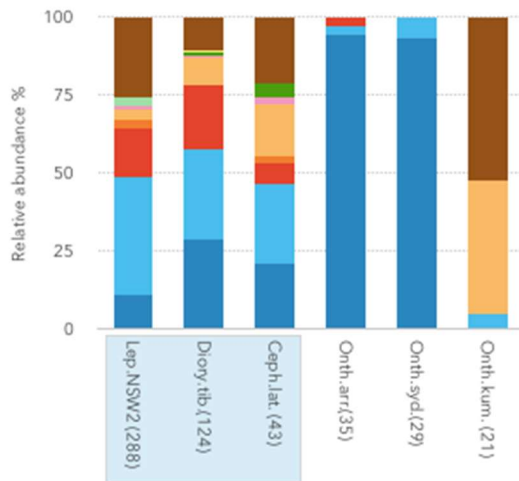
Table S3. Percentage indicator value (IndVal) of dung beetle species at each bait from a study of bait preferences in Australian dung beetles. Bold, coloured IndVal blocks indicate a preference value (>50) or specialist value (>70). Values less than 50 reflect a generalist diet. Bait codes are as follows: KROO = kangaroo dung, FOWL = fowl dung, MOUSE = mouse carrion, CRMW = cricket/mealworm carrion, SNAIL = snail carrion, EWRM = earthworm carrion, BAN = rotting banana, CUC = rotting cucumber, PIN = rotting pineapple, MSHRM = rotting mushroom. The Australian Endemic Genera are listed alphabetically first, followed by *Onthophagus* species.

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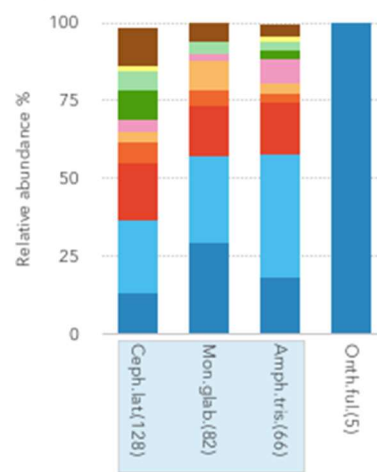
Table S4. Site descriptions in a study of bait preferences of Australian dung beetles. Site descriptions for each location where beetles were sampled. Site names and codes are used throughout the figures and tables. Descriptions include a vegetation description which was determined using Queensland Globe (<https://qldglobe.information.qld.gov.au>) overlaid with information accessed from the Queensland Government Regional Ecosystems classification database (Queensland Government Regional Ecosystem Description Database: Science, Information Technology and Innovation, Queensland Government, [Regional ecosystem descriptions](#) API, licensed under [Creative Commons Attribution 4.0](#) sourced on 10 January 2018 from <https://data.qld.gov.au/dataset/regional-ecosystem-description-database/resource/adb569fd-c660-40ad-a4ed-2b9c3eda7023>).

Site name	Code	location	coordinates	altitude	Vegetation description - Regional Ecosystem
Springbrook	SEQ-RF	Springbrook National Park at southern end of Springbrook plateau	-28.241Sx153.267E	1010 m	complex notophyll vine forest (RE12.8.6) on basalt soils
Ankida	SEQ-RF	Ankida Nature Refuge, northwestern end of the Springbrook plateau	-28.182Sx153.251E	630 m	wet sclerophyll forest (<i>Eucalyptus saligna</i> or <i>Eucalyptus grandis</i> tall open forest with vine forest understory (RE12.8.8)
Thiaki 1	NEQ-RF	Thiaki Creek Nature Reserve	-17.428Sx145.422E	960 m	complex notophyll vine rainforest on basaltic soils (RE7.8.4a)
Thiaki 2	NEQ-RF	Thiaki Creek Nature Reserve	-17.435Sx145.511E	985 m	complex notophyll vine rainforest on basaltic soils (RE7.8.4a)
Robson Creek	NEQ-RF	Danbulla National Park	-17.117Sx145.631E	720 m	complex mesophyll vine rainforest (7.3.36a) on alluvial soils
Mt Haig	NEQ-RF	Danbulla National Park	-17.098Sx145.601E	1194 m	simple microphyll vine-fern forest with granite soils (7.12.19)
Granite Gorge	NEQ-OF	Granite Gorge Nature Park, 9 km SW of Mareeba	-17.047Sx145.350E	510 m	open forest dominated by <i>Corymbia clarksoniana</i> and/or <i>Eucalyptus leptophleba</i> and/or <i>E. platyphylla</i> on sandy soils (RE9.5.9)
Tinaroo	NEQ-OF	west side of Lake Tinaroo at end of Black Gully Road	-17.184Sx145.552E	680 m	<i>Eucalyptus tereticornis</i> (forest red gum) open forest with sandy soil (RE7.11.44)

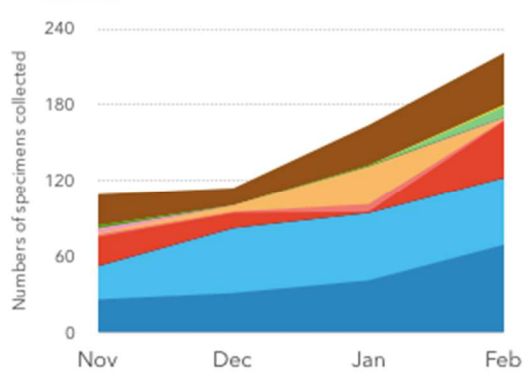
A. Ankida



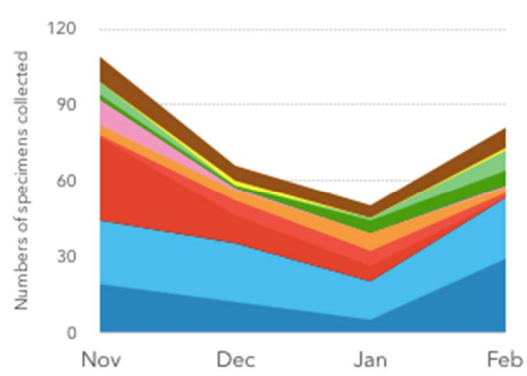
B. Springbrook



C. Ankida

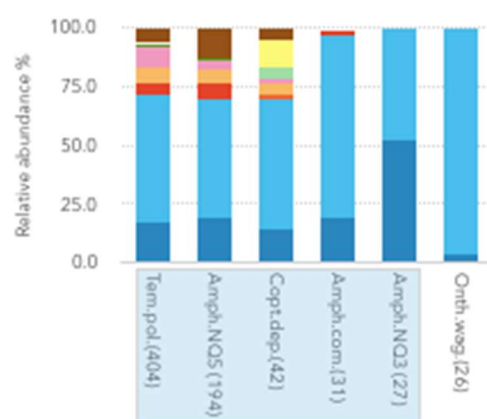


D. Springbrook

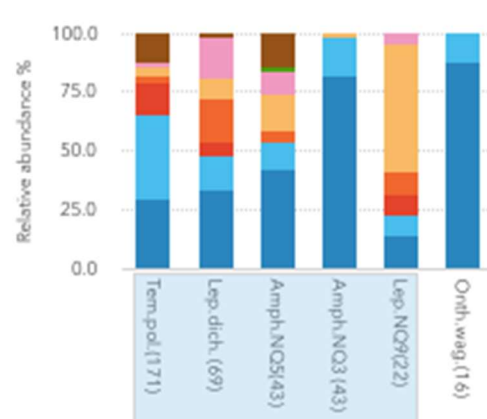


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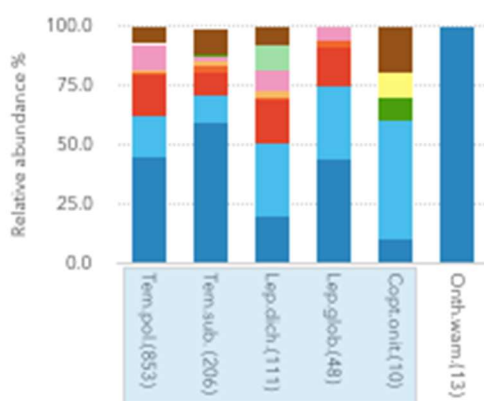
A. Thiaki1



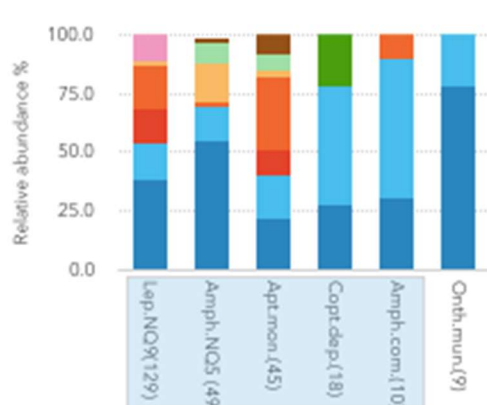
B. Thiaki2



C. Robson Creek

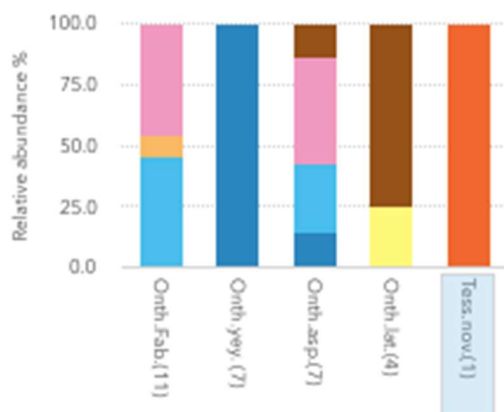


D. Mt Haig

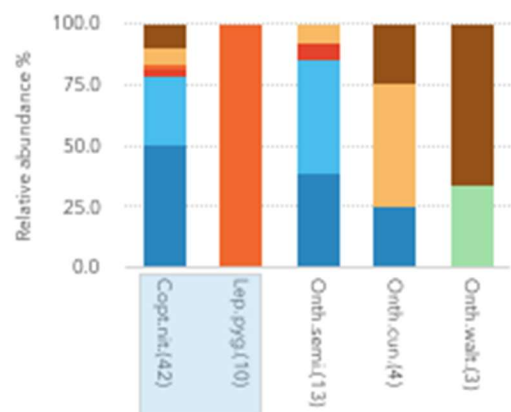


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A: Granite Gorge



B: Tinaroo



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