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Seasonality, dung specificity and competition in dung beetle assemblages in the Australian Wet Tropics, north-eastern Australia

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Abstract: A trapping study of five mammal species in wet sclerophyll forest adjacent to rain forest in the Australian Wet Tropics was used to examine the seasonal diversity, abundance and dung-specificity of dung beetles associated with mammal dung. A total of 542 dung beetles from 11 species within three genera was recovered from beneath the traps of 1104 mammal captures. The diversity of beetles associated with the dung of the northern bettong (*Bettongia tropica*), a mycophagous marsupial, differed significantly from the diversity predicted by a null model. Numbers of beetles varied significantly with type of dung, indicating preference by beetles. Beetle numbers were related positively to a 1-mo lag in monthly mean minimum temperature and less strongly to maximum temperature and rainfall. Significantly more beetles per mammal capture were detected in the wet season than in the dry season. Dung beetles showed a strong preference for either the *Eucalyptus* woodland (six species) or the adjacent *Allocasuarina* forest (four species), with only one species occurring in both habitat types. Beetle species from the *Eucalyptus* woodland were typically only detected in the late wet and early dry seasons, while species in the wetter *Allocasuarina* forest were generally collected during the late dry and early wet seasons. A significant 'checkerboard' species effect was detected in both time and space in both habitat types, suggesting that competition for dung was strong.

Key Words: checkerboard species pairs, habitat selection, mammal, marsupial, resource specificity

INTRODUCTION

More than 480 native Australian dung beetle species have been described (Matthews 1972, 1974, 1976). Many of them are endemic and are probably adapted to use marsupial dung (Doube *et al.* 1991). The Wet Tropics of north-eastern Australia, with more than 100 species, probably has the greatest dung beetle diversity in Australia (Zborowski *et al.* 1995). Despite the diversity of species and habitats in tropical Australia, only a few studies have addressed aspects of their diversity, seasonality and bait specificity (Hill 1993, 1996; Wright 1997). Hill (1996) demonstrated that beetles in rain forest and adjacent open forest had strong habitat preferences, with assemblages changing over very short distances. Both Hill (1993) and Wright (1997) demonstrated that most species are found only in the wetter months.

Matthews (1972, 1974, 1976) caught most dung beetles in pit-fall traps using 'marsupial entrails'. She also used dung from domestic stock and humans, sometimes in conjunction with 'marsupial' dung. Although Hill (1996) compared a range of bait types to show some degree of specificity, only Wright (1997) compared dung from locally co-occurring marsupials. She demonstrated that significantly more dung beetle species were attracted to the dung of the rufous bettong (*Aepyprymnus rufescens*) compared with the dung of Sharman's rock wallaby (*Petrogale sharmani*), suggesting that there is a degree of specificity for different types of mammal dung. This is of particular relevance in Australia, where the native dung beetle fauna contains a number of species (genus *Onthophagus*) with morphological adaptations for attaching to the fur of native marsupials (Matthews 1972).

Matthews (1972) reviewed the ecology and distribution of species associated with kangaroos and wallabies (Family Macropodidae) and rat-kangaroos (Family

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Potoroidae), highlighting the strong mutualism between *Onthophagus peramelinus* and the rufous bettong (*Aepyprymnus rufescens*). Wright (1997) showed that *O. peramelinus* was associated exclusively with *A. rufescens* and did not occur where *A. rufescens* was absent. No species of *Onthophagus* have been shown to occur in conjunction with other potoroids.

Our study builds upon recent ecological work on tropical Australian dung beetles (Hill 1996, Wright 1997). We examined the occurrence of dung beetles on the fresh dung beneath cage-trapped native mammals in two adjacent habitat types in the Australian Wet Tropics. Our objectives were to elucidate seasonal activities of dung beetles, and their specificity with respect to dung origin. We tested the latter with presence–absence matrices of dung beetle species on dung types against the null model of random association (Gotelli 2000).

METHODS

Study area

The study was conducted at Davies Creek (17°01′S, 145°35′E, altitude 550 m asl) on the Lamb Range, at the western edge of the Wet Tropics World Heritage Area in north-eastern Australia. Vegetation on the Lamb Range grades from upland tropical rain forest on the eastern and upper western slopes through a variety of wet sclerophyll forest types (defined by Harrington & Sanderson 1994) and eventually into dry sclerophyll woodland to the west. The study area was located in wet sclerophyll forest types 4 (mixed forest with a continuous grassy ground layer; hereafter '*Allocasuarina* forest') and 7 (medium forest with a grassy ground layer; hereafter '*Eucalyptus* woodland'; Harrington & Sanderson 1994) on the western side of the range.

The climate of the area is tropical, with a distinct wet season from January to April. Annual rainfall is probably about 1200–1400 mm, based on the nearby weather stations of Kuranda (2090 mm; in wet rain forest) and Kairi (1260 mm; in drier *Eucalyptus* woodland). Based on regional rainfall patterns, we defined seasons as: early wet (November–January), late wet (February–April), early dry (May–July) and late dry (August–October).

Collection of samples

Mammals were trapped in collapsible platform cat traps (Mascot Wire Works Pty. Ltd., Sydney, Australia). Nine trapping grids were used; the primary site was an 8 × 6-trap grid (48 traps in total) in *Eucalyptus* woodland where eight traps were spaced at 50-m intervals along each line, with the six lines spaced at 100-m intervals. Eight smaller 'satellite' grids, each consisting of 12 traps (three lines of four traps), were distributed evenly between *Eucalyptus* and *Allocasuarina* habitats (Figure 1). At these sites, traps were spaced at 50-m intervals along each line, with lines spaced at 100-m intervals. The arrangement of these grids was related to other aspects of our research that dealt with population ecology of marsupials, and there was no influence of grid size on faunal diversity and abundance that we could detect. Trapping was undertaken as a series of ten field trips between February 1995 and January 1997. During each trapping period, each site was typically trapped for 3–5 consecutive nights. Traps were baited late each afternoon with a mixture of rolled oats, peanut butter, honey and vanilla essence rolled into small (30 mm diameter) balls. Traps were cleared of mammals during the night, usually beginning at around 22h00 (approximately 4 h after sunset) and finishing 2–5 h later. When a mammal was captured it was identified to species and a range of data collected as part of a broader study. All dung beneath the trap was collected for dietary analyses (see Vernes *et al.* 2001) and all dung beetles associated with the dung were collected and immediately preserved in 70% ethanol for later identification.

Statistical analysis

The distribution of beetle species was examined for non-random patterns of species co-occurrence in a presence–absence matrix. Diamond (1975) coined 'checkerboard distribution' to describe a pattern where only one taxon of a pair of species occurs on a given island or resource unit. Such a pattern suggests competitive exclusion. We tested the co-occurrence of beetle species on individual dung resources (i.e. each trap containing a mammal where beetles were collected) with 'EcoSim' Version 7 (Gotelli & Entsminger 2002). We used the C-score index of co-occurrence (Stone & Roberts 1990), which measures the average number of 'checkerboard units' between all possible pairs of species. In a competitively structured community, the C-score should be significantly larger than expected by chance. Row sums were fixed (number of occurrence of each species is maintained), but column sums were assigned equal probability (the occurrence of a species at a resource site in the null communities is not influenced by a previous occurrence at another resource site).

To determine whether number of beetles captured per mammal differed significantly among the three most commonly captured mammals, we used a permutation test (Good 1994). As a test statistic, we used the sum-squared deviations between observed and expected values (H_0: number of beetles randomly assigned to mammal species). The same approach was used to test whether beetle

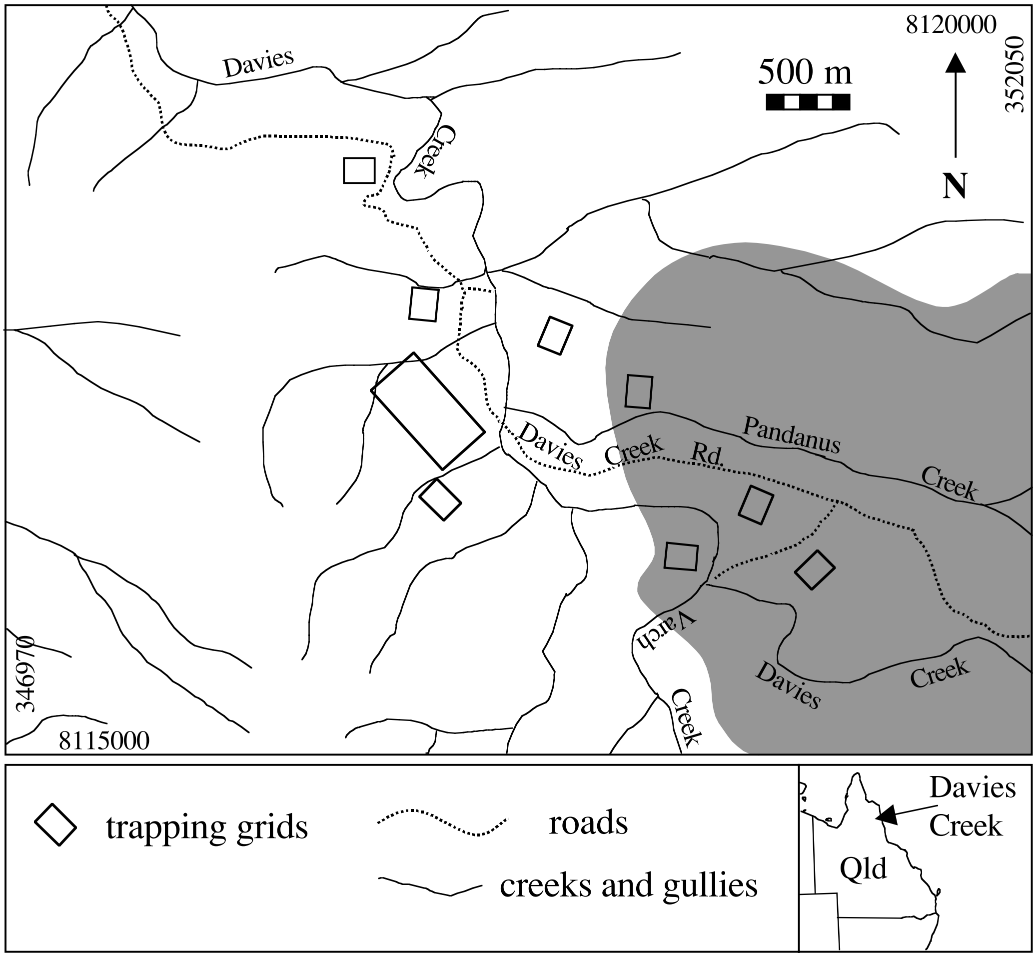

Figure 1. Study area at Davies Creek, on the Lamb Range, Queensland (Qld), north-eastern Australia, showing location of trapping grids and major site features. The shaded region indicates *Allocasuarina* forest; the unshaded region is *Eucalyptus* woodland.

diversity differed significantly among the five mammal species.

Potential correlations between beetle numbers collected per trip and climatic variables were tested by linear correlation, using actual data as well as 1–3-mo time lags. Mean maximum and minimum temperatures and monthly rainfall were collected on site during each field trip and between field trips using a standard rain gauge and maximum/minimum thermometer.

RESULTS

Mammal captures

Five species of mammal were captured from a total of 4531 trap nights (Table 1). The most commonly captured mammal was the northern brown bandicoot (*Isoodon macrourus*; 511 captures), followed by the northern bettong (*Bettongia tropica*; 403 captures), giant

Table 1. Summary of the captures made per season of five native mammals on the Lamb Range, north-eastern Australia, between January 1995 and January1997.

	Season			
Total number of captures of each mammal species	Early wet (Nov–Jan)	Late wet (Feb–Apr)	Early dry (May–Jul)	Late dry (Aug–Oct)
Bettongia tropica Wakefield	98	71	134	100
Isoodon macrourus Gould	63	143	189	116
Perameles nasuta Geoffroy	1	–	2	2
Uromys caudimaculatus Krefft	13	22	47	36
Dasyurus hallucatus Gould	9	15	40	3
Total trap nights	1116	1060	1486	869

Table 2. The number of times encountered and number of individuals (parentheses) of each dung beetle species collected from the dung of five native mammals trapped on the Lamb Range, north-eastern Australia, between January 1995 and January 1997.

	Mammal species				
Beetle species	*Bettongia tropica*	*Isoodon macrourus*	*Perameles nasuta*	*Uromys caudimaculatus*	*Dasyurus hallucatus*
Coptodactyla glabricollis (Hope)	7 (13)	18 (33)	–	–	–
Coptodactyla monstrosa Felsche	1 (1)	1 (1)	–	–	–
Coptodactyla onitoides Gillet	1 (1)	–	–	–	–
Coptodactyla subaenea Harold	32 (108)	44 (262)	–	13 (35)	3 (4)
Onthophagus bicornis Macleay	11 (21)	–	–	–	–
Onthophagus bornemisszanus Matthews	10 (23)	5 (5)	–	1 (1)	–
Onthophagus jangga Matthews	1 (2)	–	–	–	–
Onthophagus muticus Macleay	–	2 (2)	–	–	–
Onthophagus tricavicollis Lea	1 (1)	–	–	–	–
Temnoplectron politulum Macleay	3 (8)	1 (1)	2 (12)	1 (1)	–
Temnoplectron rotundum Westwood	1 (1)	4 (5)	–	–	–
Total	68 (179)	75 (309)	2 (12)	15 (37)	3 (4)

white-tailed rat (*Uromys caudimaculatus*; 118 captures), northern quoll (*Dasyurus hallucatus*; 67 captures) and long-nosed bandicoot (*Perameles nasuta*; 5 captures). Bandicoots, bettongs and quolls belong to separate marsupial families the white-tailed rat is a murid rodent.

Perameles nasuta, was captured infrequently (Table 1) in *Allocasuarina* forest, and *D. hallucatus* was captured almost exclusively in *Eucalyptus* woodland. The three most commonly captured mammals, from which most dung beetles were collected, were trapped in both forest types in approximately similar proportions (see Vernes 2003).

Beetles associated with mammal dung

Eleven species of dung beetle from three genera were found associated with the dung of captured mammals (Table 2). The most common beetle species was *Coptodactyla subaenea* (409 beetles), being found with the dung of the four most commonly captured mammals (Table 2). Five other species (*Onthophagus bicornis*, *O. jangga*, *O. tricavicollis*, *C. onitoides O. muticus*) were found on only one type of dung.

Of the 149 collections made of dung beetles beneath trapped mammals, 137 (92%) contained a single species, 10 (7%) comprised two species, and two collections (1%) were made of three species. Analysis of the co-occurrence of beetle species on individual dung resources (i.e. each trap containing a mammal where beetles were collected) with 'EcoSim' Version 7 (Gotelli & Entsminger 2002) revealed a significant deviation from the null model in both the *Eucalyptus* woodland (C-score = 16, $P < 0.01$) and the *Allocasuarina* forest (C-score = 60.9, $P < 0.0001$). When analyses were performed for individual field trips (3–5 d duration) the 'checkerboard effect' remained significant in the *Eucalyptus* woodland (C-score range: 6–10, $P < 0.03$), but was non-significant in the *Allocasuarina* forest (C-score = 0, $P > 0.35$).

Patterns in beetle abundance and diversity

We collected 489 beetles from the three most commonly captured mammals at an overall rate of 0.51 beetles per mammal capture. Based upon this rate expected under H_0 and the data in Table 1, we constructed the distribution of the test statistic (several runs of 10 000 permutations) and determined the probability that the original data would be at least as extreme as actually observed assuming random permutations. We found a significant P value of 0.0001; more beetles than expected were associated with *I. macrourus* dung (0.60 beetles per capture) and fewer than expected were associated with *U. caudimaculatus* dung (0.31 beetles per capture).

Of the 11 species of beetle collected, ten were associated with the dung of *B. tropica*, seven with the dung of *I. macrourus*, three with the dung of *U. caudimaculatus*, and one with each of *P. nasuta* and *D. hallucatus* (Table 2). We ran permutation tests to determine whether beetle diversity varied among *B. tropica*, *I. macrourus* and *U. caudimaculatus* (three mammals with the highest beetle numbers). When corrected for unequal numbers of beetles encountered, no significant difference was found, though P did approach significance ($P = 0.067$; test statistic = sum of squared deviations from average number of beetle species per mammal). When adjusted for unequal capture rates of the three mammals, beetle diversity differed significantly ($P < 0.0001$), with *B. tropica* having more species associated with its dung than predicted.

Seasonal effects on beetle occurrence

Total numbers of beetles collected beneath traps were strongly related to a 1-mo lag in monthly mean

Table 3. The number of collections made, distribution between sexes, seasonal distributions of individuals and the habitat associations of each dung beetle species collected from the dung of five native mammals trapped on the Lamb Range, north-eastern Australia, between January 1995 and January 1997.

		Numbers of individuals							
Beetle species	Number of collections	Females	Males	Early wet	Late wet	Early dry	Late dry	Habitat association
Coptodactyla glabricollis	22	25	21	–	32	14	–	*Eucalyptus*
Coptodactyla monstrosa	2	2	–	–	1	1	–	*Eucalyptus*
Coptodactyla onitoides	1	–	1	–	–	1	–	*Allocasuarina*
Coptodactyla subaenea	70	232	177	3	255	150	1	Both habitats*
Onthophagus bicornis	9	9	12	–	21	–	–	*Eucalyptus*
Onthophagus bornemisszanus	18	15	14	18	4	1	6	*Allocasuarina*
Onthophagus jangga	2	2	1	2	–	–	1	*Allocasuarina*
Onthophagus muticus	2	1	1	–	1	–	1	*Eucalyptus*
Onthophagus tricavicollis	1	1	–	–	–	1	–	*Eucalyptus*
Temnoplectron politulum	4	12	10	–	–	2	20	*Allocasuarina*
Temnoplectron rotundum	5	1	5	–	5	1	–	*Eucalyptus*

* 301 beetles collected in *Eucalyptus*, 108 beetles collected in *Allocasuarina*.

minimum temperature ($r^2 = 0.91$; $P = 0.0002$), with weaker relationships detected between beetle numbers and a 2-mo lag in monthly mean maximum temperature ($r^2 = 0.62$; $P = 0.02$) and a 1-mo lag in total monthly rainfall ($r^2 = 0.51$; $P = 0.04$). The number of species collected per season was highest in the late wet (seven species) and early dry (eight species) seasons (Table 3). Five species were collected in the late dry season and three species in the early wet season (Table 3). Corrected for the numbers of mammal captures in each season, beetle numbers were significantly higher than expected in the late wet season and significantly lower than expected for all other seasons (Figure 2). These changes relate to fewer individuals collected per beetle species in the early wet season, and significantly more individuals collected per beetle species (principally *C. subaenea*) in the late wet season (Table 3; Figure 3).

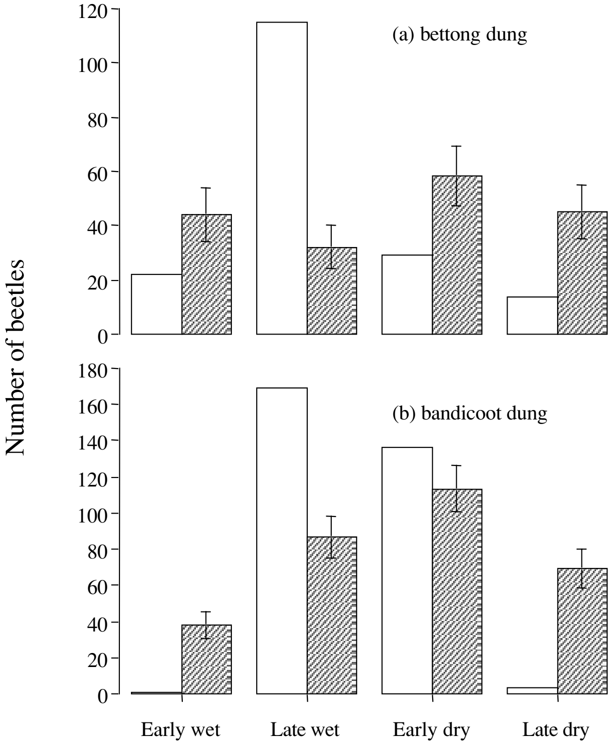

Figure 2. Number of beetles observed (open bars) and predicted to occur (hatched bars) ± SE with the dung of (a) northern bettongs (*Bettongia tropica*) and (b) northern brown bandicoots (*Isoodon macrourus*) at each season. The predicted values were generated from 10 000 random iterations of the data to correct for unequal capture success of each mammal species in each season.

Habitat associations of beetles

Most species displayed strong habitat associations with either the *Eucalyptus* woodland (six species) or the *Allocasuarina* forest (four species; Table 3). Only *C. subaenea* was found on dung in both habitats, but was three times more abundant in the *Eucalyptus* woodland than it was in the *Allocasuarina* forest (Table 3). Of the six most commonly occurring beetle species, three occurred in the *Eucalyptus* woodland and were found only on dung in the late wet season, and to a lesser degree, the early dry season (Figure 3). In contrast, two species that were found only in the *Allocasuarina* forest (*O. bornemisszanus* and *T. politulum*) were present on dung in the highest proportions in the late dry and early wet seasons, but were also present during the late wet and early dry seasons (Figure 3). *Coptodactyla subaenea* was found at all times of the year, but most commonly in the late wet season (Figure 3).

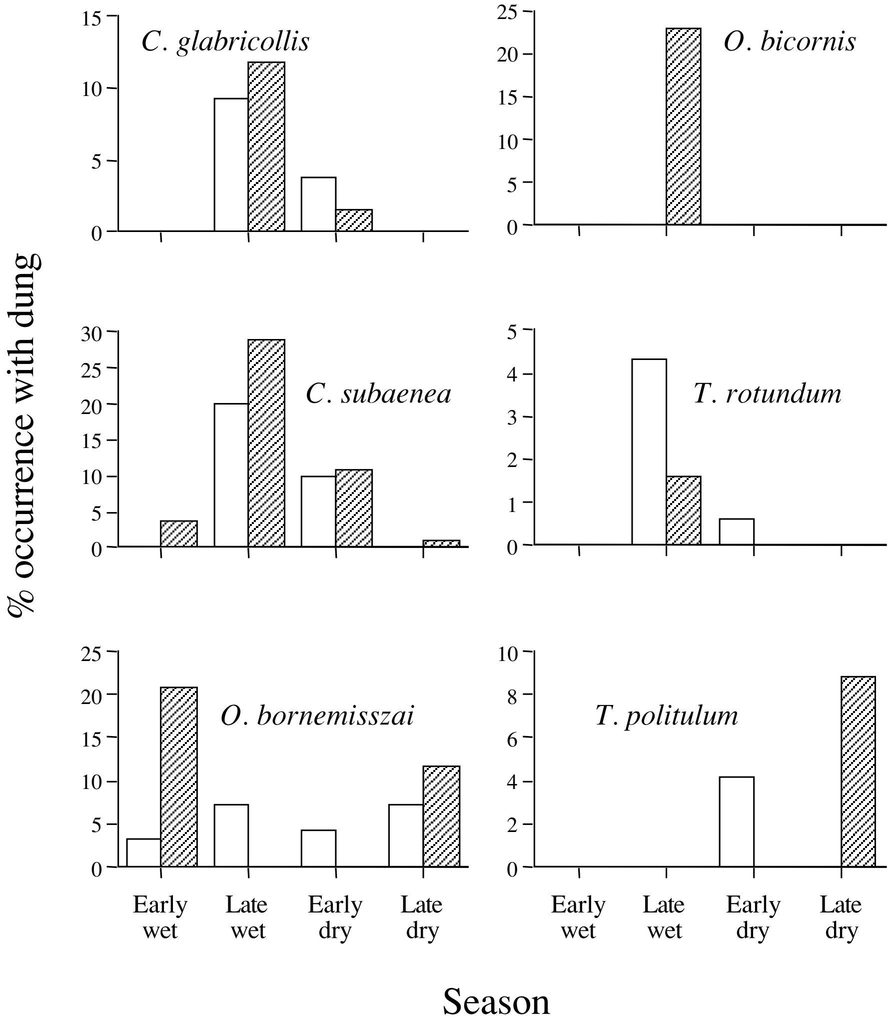

Figure 3. Seasonal occurrence of the six most commonly encountered dung beetle species expressed as a percentage of mammal scats that had beetle associates in each season, for northern bettong (*Bettongia tropica*; hatched bars) and northern brown bandicoot (*Isoodon macrourus*; open bars) dung. *Coptodactyla glabricollis, Onthophagus bicornis* and *Temnoplectron rotundum* occurred exclusively in the *Eucalyptus* woodland, *O. bornemisszanus* and *T. politulum* occurred exclusively in the *Allocasuarina* forest, and *C. subaenea* occurred in both habitat types.

DISCUSSION

Most studies of dung beetle seasonality suggest that activity is greatest during moist and minimal during dry periods (Doube *et al.* 1991). Wright (1997) reported that *Onthophagus peramelinus* activity was influenced by rainfall rather than soil moisture and temperature, and Maelzer (1961) and Tyndale-Biscoe *et al.* (1981) also report rainfall as the dominant influence for the few taxa they studied. Hill (1993) reported simple seasonal patterns in the Australian Wet Tropics, similar to other tropical regions with distinct wet and dry seasons (Anderson & Coe 1974, Janzen 1983). Our results show the expected seasonality, but indicated that a 1-mo lag in mean minimum temperature (and to a lesser extent, mean maximum temperature), rather than rainfall, most strongly predicted beetle numbers. Rainfall was still a significant predictor though, and moisture to some degree appeared to influence activity in the two habitat types. Dung beetles in the *Allocasuarina* forest, which is a wetter type than the *Eucalyptus* woodland, showed a greater range of seasonal activity, for example, being found in high numbers in the late dry season. *Eucalyptus* woodland has less leaf litter, less ground cover and a more open canopy than *Allocasuarina* forest; and beetles in this habitat type did not become active until well into the wet season.

Our analyses indicated that northern bettong dung attracted more dung beetle species than expected from a null model. Of the three species of *Onthophagus* collected exclusively with *B. tropica*, *O. bicornis* was recorded sufficiently often (11 collections of 21 beetles) to indicate specificity for bettong dung at our site. Matthews (1972) noted that *O. bicornis* was apparently rare, and that its ecology was unknown. Given that we collected this species frequently, and only on northern bettong dung, we suggest that it may be a macropodoid specialist. A second species, *O. bornemisszanus*, was collected twice as often from bettong dung compared with bandicoot dung, despite bettongs being captured less often than bandicoots. Matthews (1972) described *Onthophagus bornemisszanus* from two locations in northern Queensland within the current range of the northern bettong, suggesting that bettong dung may be a favoured resource.

Of the other dung beetle species that were reasonably common, no preference for dung was apparent. Surprisingly, *O. muticus*, believed to be a macropod specialist (Matthews 1972), was collected twice on the dung of bandicoots. Conversely, *Coptodactyla subaenea* and *Temnoplectron politulum* appeared to be generalists, each being collected from dung of four of the five mammals sampled, and *C. subaenea* was the only beetle species collected from the dung of the predatory northern quoll (*Dasyurus hallucatus*) in our study. Hill (1996) collected both of these species from all four bait types (banana, mushroom, liver and dung) that he employed, indicating omnivory.

Bandicoots had more individual beetles associated with their dung than predicted from a null model, whereas the giant white-tailed rat (*Uromys caudimaculatus*) had fewer than predicted. Bettongs showed no deviation. These three mammals have different diets in our study area; bettongs eat considerably more fungus than the other two, whereas bandicoots eat more vegetation and white-tailed rats eat a range of food types including fruit, seeds and fungi (Gordon & Comport 1998, McIlwee & Johnson 1998, Vernes *et al.* 2001). Confounding factors, however, include the size of the resource and their aromatic qualities. Bandicoot faecal pellets are typically much larger and smell more strongly than pellets from the other two mammals (pers. obs.).

The 11 species of dung beetle collected in our study represent moderate diversity compared with other recent studies in the region. At a rain forest/open forest ecotone site in north-eastern Queensland, Hill (1996) detected 27 species using a range of bait types and capture methods; Wright (1997), working in open woodland, collected 40 species on two types of marsupial dung; and Howden *et al.* (1991) collected 22 species in rain forest using flight intercept, light and baited pitfall traps. Locations in other tropical regions show similar results. Davis *et al.* (2000) collected 40 species in Borneo using human excrement while Estrada *et al.* (1999) collected 30 species in a range of forest fragments in Mexico using a dung homogenate from a range of domestic and wild mammals. Our methods may have precluded capture of several generalist species, and probably would not have detected non-native species attracted to larger resources, or species attracted to non-mammal bait such as fungi, vegetable matter or carrion (Matthews 1972). Furthermore, some species are rarely attracted to dung and are generally only captured using flight intercept or light traps (Matthews 1972).

In our study area, the ecotone between *Eucalyptus* woodland and *Allocasuarina* forest was abrupt and these two habitats each had a unique beetle assemblage with the exception of the ubiquitous resource-generalist *C. subaenea*. Hill (1996) showed that dung beetle assemblages across a rain forest/open forest ecotone in north-eastern Queensland changed dramatically over shorter distances, in the order of tens of metres. Competition between dung beetles for patchy, ephemeral dung resources is intense (Doube *et al.* 1988, Trumbo 1994) and coarse habitat partitioning may be one way for beetles to avoid competition. We captured our three most abundant mammals (northern brown bandicoots, northern bettongs and giant white-tailed rats) in broadly similar proportions in both habitats, so availability of the dung resource is unlikely to have caused such a sharp change in beetle assemblages.

The frequency of co-occurrence of species on individual islands (or resource patches) may be regulated by competition at a finer scale (Diamond 1975). Statistical analysis of such data, particularly the choice of an appropriate null hypothesis and test statistic, has been hugely controversial. Based on tests with real and simulated data, Gotelli (2000) recommends using the C-score for a preliminary analysis of co-occurrence patterns. Applying this test to absence/presence data of dung beetle species on the 'islands' of dung beneath trapped mammals showed a strong 'checkerboard effect' (Diamond 1975) in both habitats. The C-score consistently exceeded the value expected from random species distribution, a pattern indicating strong competitive avoidance (Gotelli & Entsminger 2002). This pattern may have been driven by the ubiquitous *C. subaenea*, which accounted for 60% of our collections and 75% of individual beetles. Furthermore, *C. subaenea* occurred in both habitats, during all seasons and on most types of dung, and the average numbers of *C. subaenea* at a single dung resource exceeded that of any other species. A simple strategy by other dung beetle species for optimizing reproductive success at our study site may simply be to locate a dung resource not yet discovered by *C. subaenea*.

Competition between species can be reduced by minimizing spatial and temporal overlap (Giller & Doube 1989). The dung beetles in our study appeared to partition resources to some degree by selective use of dung by different mammals, and strongly by differentiating between adjacent habitat types.

Comparisons of species assemblages from the few studies published from the Australian Wet Tropics (Hill 1993, 1996; Howden *et al.* 1991, Wright 1997) typically reveal more unique species than species in common, suggesting that communities are variable in time and/or space within a broad geographical area. Further research on dung beetle assemblages throughout the wet tropics region should prove fruitful in understanding regional patterns of biodiversity and community organization in this diverse group.

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