Associations of scarab beetles (Insecta: Coleoptera: Scarabaeidae) with dung of four species of mammals in Khao Yai National Park, Thailand

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Abstract. To determine if dung from various species of native mammals are attractive to species of Scarabaeidae differentially in a seasonal evergreen forest in Thailand, we used pitfall traps baited with fresh dung of four species (barking deer, sambar deer, Asian elephant, pig-tailed macaque) and an unbaited control. The pitfalls were deployed in Khao Yai National Park for 24 hours in March 2010. All totaled, 9 genera and 23 species of scarab beetles were collected. Of these, *Loboparius schereri* (Petrovitz) represents a new country record with a known range to the northwest of Thailand. Overall scarab abundance and richness each differed significantly ($p < 0.001$) among bait types. From a multivariate perspective, discriminant function analysis computed four axes to distinguish the community of scarab beetles that was attracted to each dung type. The pigtailed macaque dung community was significantly different from that of all other baits ($p < 0.001$), whereas overlap existed among the other bait treatments; 83.3% of the pitfalls were re-classified to the correct bait type. Dung of the omnivorous macaques attracted a beetle community that was dramatically distinct from those of the other bait treatments and with the greatest abundance and richness of scarab species, whereas dung of the herbivorous species was far less attractive. This corroborates New World studies that have shown dung from the diet of omnivorous mammals attracts greater numbers and diversity of dung beetles. As such, conservation of omnivorous large animals in tropical forest systems is necessary for the conservation of rich dung beetle communities.

Key words. Scarabaeidae, pitfall, mammal dung, Thailand

INTRODUCTION

Among the many feeding strategies of the family Scarabaeidae, none have generated the interest nor are as environmentally necessary as those of dung beetles. Many insects exploit this resource, but it is dung beetles that have the greatest biomass and are the most speciose (Yasuda, 1996).

Although many species of dung beetles are widespread, non-specialist, and occur in a variety of habitats, other species are sensitive to certain environmental conditions such as vegetation cover, soil (Neails, 1977; Doube, 1983), shade (Gordon, 1983), and season, or specialise in exploiting the dung of particular host species. For example, certain species of Aphodiinae are attracted to deer dung during winter months in the eastern United States, whereas other related species are not so specialised in season, habitat, or food source (Gordon, 1983). Specialisation by components of the dung beetle community enables localised community differentiation, as was demonstrated in the Gauteng nature reserves in South Africa (Davis et al., 2005). Multivariate analyses revealed the six reserves to be locally unique such that faunal differences were greater among reserves than within each reserve. As such, each reserve harbored a unique community of dung beetles (Davis et al., 2005).

Many studies have reported the taxonomic composition of scarabs exploiting dung from different mammalian species. For example, 14 species of dung beetles were recorded from Japanese macaque faeces in Japan (Enari et al., 2011) and 19 species from woolly monkey faeces in Colombia (Castellanos et al., 1999). However, most studies associating the dung beetle fauna with host dung are in comparisons among species of hosts that generate the resource. Several of the studies have compared examples of herbivore, omnivore, and sometimes predator dung with their associated dung beetle communities (e.g., Fincher et al., 1970; Finn & Giller, 2002; Dormont et al., 2007; Filgueiras et al., 2009; Carpaneto et al., 2010; Davis et al., 2010). Other than a few recent studies in India (Sabu et al., 2006; Vinod & Sabu, 2007; Sabu et al., 2011), nearly all of these studies have been conducted in Africa, the Neotropics, or in temperate areas. Southeast Asia has been little studied, although the dung beetle fauna of the Indo-Australian archipelagoes was summarised by Hanski & Krikken (1991). Although the title indicates their treatment considered the Southeast Asian fauna, the only part of the mainland that was included was the Sundaland fauna of peninsular Malaysia; thus, the Indochinese fauna was not considered (Hanski & Krikken, 1991). In addition, various ecological aspects of dung beetle communities have been studied in Borneo (e.g., Davis et al., 2001; Slade et

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al., 2007). Earlier, Paulian (1945) discussed the scarab fauna of French Indochina and Balthasar (1963a, 1963b, 1964) presented detailed information on the Aphodiinae and Scarabaeinae in the Oriental and Palearctic, but these works are outdated taxonomically and do not present much ecological information for the species considered. In the past few decades, a number of taxonomic contributions on the scarab fauna of Thailand have been presented (e.g., Masumoto, 1989; Hanboonsong et al., 1999, 2003; Emberson & Stebnicka, 2001; Hanboonsong & Masumoto, 2001; Masumoto et al., 2002a, b, 2012).

This study was undertaken to determine differences in the scarab fauna associated with dung of local mammal species in a protected, natural area in central Thailand. Further, we were interested in determining if any scarab species present were specialists on the dung of these mammals in a manner similar to the aphodiine specialists of the eastern United States (*sensu* Gordon, 1983).

MATERIALS AND METHODS

The field work was conducted in the Mo Singto Long Term Ecological Research plot, Khao Yai National Park, Nakhon Nayok Province, Thailand. The park is at the western extremity of the Phanom Dongrak mountain range which extends along the southern edge of Northeastern Thailand. Geographic coordinates of the plot are roughly 101°22″E, 14°26″N. The 30 ha plot is located in closed-canopy, seasonal evergreen forest habitat at elevations of 725 to 815 m. It lies within 500 m of the forest edge and park headquarters. The annual rainfall in the park based on records from 1994–2007 is approximately 2,200 mm (Brockelman et al., 2011). The rainy season is from May to October whereas the remaining months are relatively dry. Both April and October can be either dry (< 100 mm) or wet, making the length of the dry season quite variable. The mean monthly temperature varies between approximately 19° and 29°C, and mean annual temperature is 22–23°C. There is little evidence of human disturbance except for the presence of secondary forest about 25 years old on the north side of the plot. Approximately 0.32 ha of this regenerating forest overlaps the plot.

To determine if dung from different species of mammals are attractive to species of Scarabaeidae differentially, we used baited pitfall traps. Fresh dung was collected from four local species of mammals: pigtail macaque, *Macaca nemestrina* (Linnaeus); barking deer, *Muntiacus muntjak* (Zimmermann); sambar deer, *Cervus unicolor* Kerr; and Asian elephant, *Elephus maximus* Linnaeus. All samples were obtained in the morning of 23 March 2010 and were moist and warm.

Baited pitfall traps were set out in the afternoon of 23 March 2010 and left for 24 hours. Pitfalls contained water with a small amount of detergent as a wetting agent to facilitate submersion of small insects. Three sticks were fashioned as a tripod over the pitfall suspending approximately 8 cm^3 of mammalian dung (similar in size to that used by Peck & Howden [1984]) in black plastic netting. Unbaited control pitfalls included the black plastic netting without dung.

The sampling design was a 5 × 8 completely randomised design with the two deer species each represented by an additional pitfall, and 20 meters between each pitfall. Thus, 8–9 traps of each dung type were established along with 8 unbaited control traps. Specimens were identified using external morphological characters and genitalia. Taxonomic keys, illustrations, and comparisons with authoritatively identified museum material were used in addition to obtaining identifications and validations from systematic authorities (see Acknowledgements). Vouchers have been deposited as dry-pinned specimens in the Enns Entomology Museum, University of Missouri, and the Paul K. Lago Collection, University, Mississippi, USA.

To assess scarab species associations with mammal dung, overall univariate analyses of variance (ANOVA) for abundance and richness of scarab beetles among bait types were performed. More specific ANOVAs and *a posteriori* least significant difference (LSD) tests were performed on individual genera and Aphodiinae to determine differences in abundance for particular species. All univariate tests were performed using SPSS 17.0.

From the multivariate perspective, discriminant function analysis (DFA) was used to assess differences in the community of scarab species on each type of dung. DFA is a powerful technique that maximises intergroup differences while simultaneously minimising intragroup dispersion on each of several orthogonal axes. Abundances of all species of scarab were used as independent predictor variables to distinguish among types of mammalian dung. Subsequent pairwise F-tests identified which dung communities significantly differed from each of the other dung communities. The classification phase of DFA then assigned the content of each pitfall trap to a dung type based on the linear combination of variables from each discriminant function axis. Percent of correct assignments may be used as a separate measure of scarab community distinction among the types of mammalian dung. DFA was performed with SPSS 4.0.

RESULTS

In total, 607 individuals from 11 genera and 23 species of Scarabaeidae were collected across all traps (Table 1). Overall scarab abundance and richness each differed significantly ($p< 0.001$) among bait types [abundance, F (4, 37) = 38.39; richness, F (4, 37) = 44.15]. *A posteriori* LSD contrasts resulted in identical significance levels: macaque > barking deer and sambar deer > elephant and unbaited control. Because abundance among bait types was significantly different, each of the taxa (subfamily and genera) was analysed separately. Based on nonparametric tests using the 'npmv' package in program R (Ellis et al., 2017), there was no significant effect of trap location on the abundance or richness of beetles detected (P > 0.5). Traps located on the edge of our trapping grid (hence fewer neighbors) collected a similar abundance and richness to those traps in the interior (surrounded by other traps) suggesting no significant effect of trap spacing on the overall abundance and richness.

Table 1. Total abundance of Scarabaeidae collected in mammal baited and unbaited pitfall traps in Khao Yai National Park, Thailand.

149	*Pleuraphodius lewisi* (Waterhouse)
126	*Onthophagus rutilans* Sharp
114	*Copris reflexus* (Fabricius)
60	*Onthophagus lindaai* Masumoto
51	*Sisyphus maniti* Masumoto
32	*Onthophagus gracilipes* Boucomont
15	*Copris carinicus* Gillet
12	*Oxyomus bremeri* Stebnicka
12	*Onthophagus taurinus* White
11	*Caccobius maruyamai* Masumoto, Ochi and Sakchoowong
7	*Loboparius schereri* (Petrovitz)
3	*Onthophagus doitungensis* Masumoto
3	*Onthophagus peninsularis* Boucomont
2	*Onthophagus falsivigilans* Masumoto
2	*Copris carniceps* Felsche
1	*Catharsius molossus* (Linnaeus)
1	*Phaeochroops lakhonicus* Kuijten
1	*Parascatonomus munetoshii* (Masumoto, Ochi and Sakchoowong)
1	*Sisyphus thoracicus chaiyaphumensis* Hanboonsong & Masumoto
1	*Parascatonomus penicillatus* (Harold)
1	*Onthophagus luridipennis* Boheman
1	*Onthophagus maesaensis* (Masumoto, Ochi and Hanboonsong)
1	*Plagiogonus krataay* (Masumoto)

Aphodiinae. The four species of aphodiines encountered during this study differed significantly in abundance among bait types. However, in individual analyses, only *Pleuraphodius lewisi* was significantly different. LSD contrasts revealed that it was more abundant in macaque, barking deer, and sambar deer dung than in elephant dung and the unbaited control. *Loboparius schereri*, *Oxyomus bremeri*, and *Plagiogonus krataay* abundances were not significantly different among bait types.

Caccobius. LSD contrasts indicated that the single species of this genus in our samples was more abundant in traps baited with macaque dung than with all other baits (i.e., barking deer, sambar deer, elephant, and the unbaited control).

Copris. The three species of *Copris* differed significantly in abundance among bait types. However, in individual analyses, only *C. reflexus* was significantly different in bait choice. LSD contrasts revealed that it was more abundant in macaque, barking deer, and sambar deer dung than in elephant dung and the unbaited control. *Copris carniceps* and *C. carinicus* abundances were not significantly different among bait types.

Onthophagus. Overall abundance of the 11 species of *Onthophagus* (including *Parascatonomus*) differed significantly among bait types. However, in individual analyses, only six (*O. doitungensis*, *O. gracipiles*, *O. lindaae*,
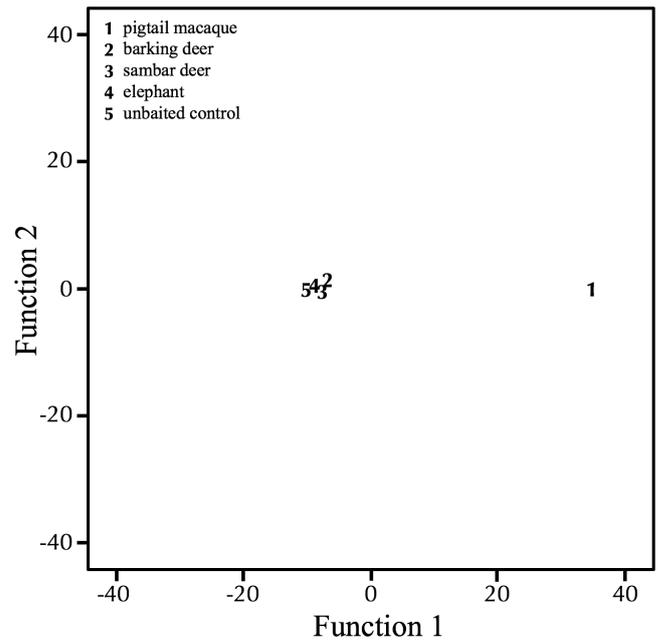

Fig. 1. Two-dimensional discriminant function plot depicting centroids of dung beetle pitfall trap observations for each of four types of dung and an unbaited control. Pigtail macaque traps were distant from the other traps to the extent that individual trap positions are not depicted here. For finer resolution of trap distribution of treatments 2–5, see Fig. 2.

O. peninsularis, *O. rutilans*, and *O. taurinus*) exhibited significance in bait choice. LSD contrasts for each of the six species revealed that all were more abundant in traps baited with macaque dung than with all other types of bait (i.e., barking deer, sambar deer, elephant, and the unbaited control).

Sisyphus. The two species of *Sisyphus* differed significantly in abundance among bait types. However, in individual analyses, only *S. manti* was significantly different in bait choice. LSD contrasts revealed that it was more abundant in traps baited with macaque dung than with all other types of bait (i.e., barking deer, sambar deer, elephant, and the unbaited control). *Sisyphus thoracicus chaiyaphumensis* abundance was not significantly different among bait types.

Catharsius, Phaeochroops. Only one specimen of each of these genera was collected. Thus, there was no significant difference in abundance among bait types for *Catharsius molossus* and *Phaeochroops lakhonicus*.

Discriminant function analysis distinguished among the five types of baits using four canonical axes (Figs. 1, 2). The first function alone accounted for 99.5% of the variation among groups and was represented predominantly by 12 species of scarabs (Table 2). In pairwise F-tests associated with DFA, the scarab community of pigtail macaque dung was highly significantly different from that of all other baits ($p < 0.001$); barking deer differed only from pigtail macaque; sambar deer differed from pigtail macaque, elephant, and the unbaited control; and elephant differed from only pigtail macaque and sambar deer (Table 3). In the classification phase of DFA, 83.3% of the pitfalls were re-classified to the correct bait type.

Table 2. Factor loadings (correlations) on each of four axes of the discriminant function analysis performed for Scarabaeidae collected in mammal baited and unbaited pitfall traps in Khao Yai National Park, Thailand.

Species	DF 1	DF 2	DF 3	DF 4
C. molossus	0.09831*	0.01591	0.03820	0.01333
O. lindaai	0.09776*	0.04400	0.02591	−0.01269
O. penicillatus	−0.07386*	−0.01143	−0.02786	−0.01176
S. maniti	0.03211*	0.00588	0.01357	0.00206
O. doitungensis	0.02506*	0.00459	0.01059	0.00161
O. peninsularis	0.02506*	0.00459	0.01059	0.00161
O. falsivigilans	0.01868*	0.00342	0.00789	0.00120
P. krataay	0.01223*	0.00224	0.00517	0.00078
P. lakhonicus	0.01223*	0.00224	0.00517	0.00078
S. thoracicus	0.01223*	0.00224	0.00517	0.00078
O. maesaensis	0.01223*	0.00224	0.00517	0.00078
P. munetoshii	0.01223*	0.00224	0.00517	0.00078
C. reflexus	0.01473	0.53420*	−0.14197	−0.21907
P. lewisi	0.01655	0.30326*	−0.21225	0.04824
O. luridipennis	−0.00278	0.06092	−0.37339*	0.07692
L. schereri	−0.00356	0.14596	0.30660*	−0.24980
C. indicus	0.00697	0.14482	−0.28884*	0.18793
C. carniceps	−0.04253	−0.12402	−0.26357*	−0.04248
O. taurinus	0.05633	0.06422	0.13709*	−0.08815
O. gracilipes	0.04097	0.06198	0.06913*	−0.06740
O. bremeri	0.00284	0.14340	0.04140	0.40248*
C. maruyamai	−0.06149	−0.05526	0.19113	0.23940*
O. rutilans	0.03209	0.08448	0.10429	0.15837*
Eigenvalue	773.45	3.15	0.57	0.07
Variance explained	99.51	0.41	0.07	0.01

Asterisks indicate the axis with which a scarab species has its greatest correlation.

Table 3. Results of pairwise F-tests associated with discriminant function analysis to assess differences in scarab communities associated with mammal dung-baited pitfall traps in Khao Yai National Park, Thailand. *F*-statistic appears above *p*-value for each pairwise contrast.

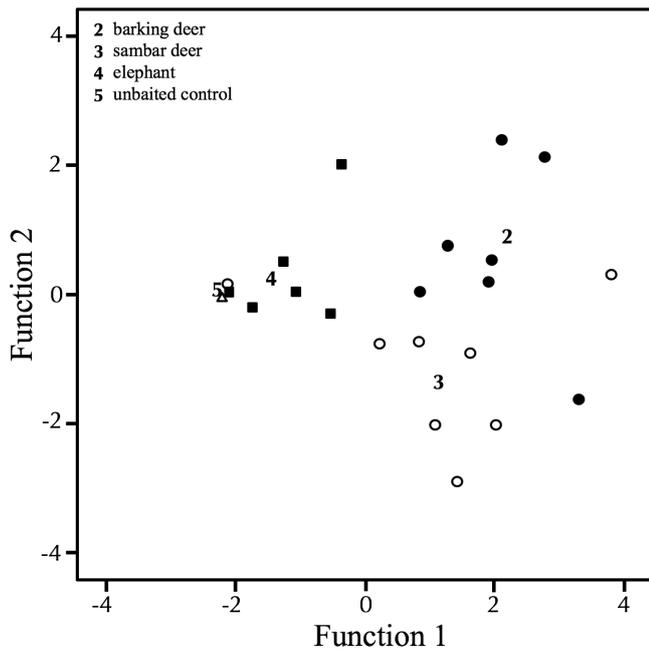|	Pigtail Macaque	Barking Deer	Sambar Deer	Elephant
Barking Deer	689.22 <0.0001			
Sambar Deer	712.45 <0.0001	1.1489 0.3744		
Elephant	655.11 <0.0001	1.5081 0.1831	2.4417 0.0265	
Unbaited control	649.31 <0.0001	2.0917 0.0543	3.5696 0.0032	0.21145 0.9988

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Fig. 2. Two-dimensional discriminant function plot depicting individual dung beetle pitfall traps for each of three types of dung and an unbaited control. Each symbol represents a trap with its position based on the composition of that trap. Instances where traps overlapped on the plot are not indicated. Numbers indicate centroid of each trap type.

Fig. 3. *Loboparius schereri* (Petrovitz) (Scarabaeidae: Aphodiinae), a new country record for Thailand.

DISCUSSION

Our sampling regimen provided a snapshot of dung beetle activity in late March in the Mo Singto research plot within Khao Yai National Park. A single new country record was recorded: *Loboparius schereri* (Petrovitz) (Fig. 3) was known previously from Nepal, India, and Pakistan (Stebnicka, 1986). Two of the species we encountered (*Caccobius maruyamai* and *Parascatonomus munetoshii*) were described after the completion of our field work and analyses (Masumoto et al., 2012).

The primary dung beetle guilds (rollers, dwellers, tunnelers) are represented by the species collected in this study. Specifically, two species are rollers (*Sisyphus*), four are dwellers (*Loboparius*, *Oxyomus*, *Plagiogonus*, and *Pleuraphodius*), and 16 are tunnelers (*Caccobius*, *Catharsius*, *Copris*, *Onthophagus*, *Parascatonomus*). The collection of a single specimen of *Phaeochroops* was adventitious as members of the genus are presumably carrion specialists (Kuijten, 1981), but it is not unusual to capture carrion beetles in traps baited with primate faeces.

From a biodiversity standpoint, the Scarabaeinae and Aphodiinae fauna of Thailand is fairly extensive (e.g., Balthasar 1963a, 1963b, 1964; Stebnicka, 1992; Hanboonsong et al., 1999; Ek-Amnuay, 2008). Because of this, one might wonder why so many species that should have been present within our study area were absent from our traps, including entire genera such as *Onitis*, *Paragymnopleurus*, and *Trichaphodius*. Undoubtedly, the limited diversity indicated

in this study is related directly to our sampling strategy, particularly the duration of our sampling and the size of the baits we used. Landin (1961) and Lumaret & Kirk (1987) discussed variability in reproductive performance based on dung pat size, and size is important when beetles select breeding sites, particularly among species in the dwellers guild. Overall, it is likely that some larger beetles would be less prone to be attracted to the relatively small baits we used in this study (Peck & Howden, 1984). Our short trapping duration may also explain the absence of some species; however, in one of the few studies that examined study duration, Aruchunnan et al. (2015) found that of the 29 species captured during their 5-day sampling period, 26 (89.7%) of the species were captured during the first 24 hours, with only two species added after three days and one additional after five days. In the same study, 84.6% of the individuals were captured during the first 24 hours.

Studies directly examining variation in attractiveness of different sized dung baits within pitfall surveys are scarce, but some interesting patterns have been observed within various studies that relate directly to our project. Peck & Howden (1984) clearly demonstrated that different sized baits attract different cohorts of dung beetles. Smaller baits tended to be less attractive to larger species, but large baits remained fairly attractive to smaller species. This explains the absence of relatively common larger species of dung beetles from our samples. Similar results were reported by Errouissi et al. (2004), who observed different small bait and large bait assemblages of dung beetles in southern France and other Mediterranean locations. Based on the findings of these two studies, we apparently sampled a "small bait assemblage" during our project. In a study comparing human faeces and elephant dung, at least 10 times as much (2,500 g) of the latter was needed per trap in order to attract a similar number of dung beetles as 200 g of human faeces (Cambefort & Walter, 1991). This at least partly explains the relative lack of specimens in our traps baited with elephant dung. Siddall & Hoevenaars (2016) examined edge effects and dung preference among dung beetles in Kibale Forest National Park in Uganda. Using primate and elephant dung baits of

approximately twice the size used in our study (15–20 cc), they discovered that primate faeces greatly outperformed elephant dung in attracting dung beetles. Clearly, our data are in accord with that observation. In terms of edge effects, diversity and biomass of beetles attracted to primate faeces are greater at their "core" (heavily forested sites) (Siddall & Hoevenaars, 2016). For those species attracted to elephant dung, the pattern was the opposite, although not statistically significant, showing little difference in diversity and biomass on the edges of forested areas compared to core areas. They suggested that dung beetles specialising on elephant dung might be better adapted to edge habitats since elephants themselves are more likely to be found at edges. Since our trapping efforts occurred within heavily forested habitat, this might have contributed to the lower level of attraction to elephant dung than to primate faeces. Sabu et al. (2006) reported that elephant dung was most attractive to beetles after three to five days in the moist Western Ghats forests (see also Vinod & Sabu [2007] for further consideration of the dung beetle fauna associated with elephant dung in India). Thus, the combination of small bait size, trap placement and bait that was too fresh apparently minimised the trapping effectiveness of our elephant dung pitfalls, although dung samples from all species in our study were chosen for their consistent age to minimise this as a source of error.

Nevertheless, the data we gathered represent a baseline study of dung beetles and their food preferences in an area where very little is known of this fauna. In a similar study also conducted in Thailand, species composition of scarabaeine dung beetle populations in primary and secondary forests in Ton Nga Chang Wildlife Sanctuary in the southernmost tip of the country was studied (Boonrotpong et al., 2004). The authors used 400 g of pig dung as bait in pitfalls, with the traps set 50 m apart along three 2-kilometer transects. The traps were run for three days every two months from April 1999 through May 2000. In total, 20 species of Scarabaeidae (Scarabaeinae [2 rollers] and Coprinae [18 tunnellers]) were represented in their samples. Their community composition was similar to that of our study, although our trapping was conducted for only 24 hours. Species common to the two sites included *Copris carinicus*, *C. reflexus*, *P. munetoshii*, and *O. rutilans*. Although the presence of a larger roller, *Paragymnopleurus maurus* (Sharp), in Ton Nga Chang samples might reflect the use of larger baits, the taxonomic composition of their study suggests a "small bait assemblage" similar to that of our study. Rollers are well known to be more diverse in open habitats such as grasslands or savannah than in forests (Halffter & Matthews, 1966); thus, the relative lack of rollers in these studies reflects that both studies in Thailand were conducted in forest habitats.

Our dung preference study included three distinctly different groups of mammals: an omnivore (primate), two relatively small herbivores (deer - compact pellets) and a large herbivore. Interestingly, all specimens of rollers (*Sisyphus* sp.) were captured at macaque faeces (Table 3). Only *S. manti* Masumoto was captured in sufficient numbers to suggest it is a true primate dung specialist. The four species of dwellers in the subfamily Aphodiinae are varied in their preferences, with two (*Pleuraphodius lewesi* and *Oxyomus bremeri*) clearly being generalists. In contrast, *Loboparius schereri* was represented by seven specimens and appears to be a deer specialist, whereas *Plagiogonus krataay* was too poorly represented in our samples to generalise about its preferences.

Tunnelers was the most common guild in our samples. The single specimen of *Catharsius molossus* (L.) we captured was the largest dung beetle in our samples. Although Ong et al. (2013) considered this species a specialist on herbivore dung in Singapore, our specimen was attracted to macaque faeces; congeners are known to be attracted to pitfall traps baited with human faeces (Slade et al., 2011). Interestingly, the majority of the specimens collected in Singapore (49 of 52) were attracted to cow dung rather than pig dung. The authors suggested that "unattractiveness" of pig dung in their study was due to a "well balanced omnivorous diet" the domestic pigs were fed. *Copris carinicus* and *C. reflexus* appear to be generalists with specimens of each species collected in each of the four dung types. A third species, *C. cariniceps*, was attracted only to barking deer dung during our study, but too few specimens were collected (two) to generalise about its food preferences.

Eleven species of *Onthophagus* (including *Parascatonomus*) were represented in our samples, of which only seven exhibited significant differences in abundance among bait types. Of these, six were captured only at macaque dung and another only at barking deer dung (Table 3), but numbers were too small to make meaningful generalisations. One species, *O. rutilans*, appears to be a generalist because specimens were attracted to four bait types. The majority of specimens of the other three, *O. lindaai*, *O. gracilipes*, and *O. taurinus*, were collected from traps baited with macaque faeces; thus, they appear to specialise on the protein-rich dung of omnivores. These results are similar to findings reported by Cambefort & Walter (1991) for Taï National Park in the Ivory Coast, in which 16 species were found to be specialists on elephant dung and 11 species on omnivore dung. All of the latter were members of the genus *Onthophagus*, and only one member of that genus was a specialist on elephant dung.

The dung beetle community associated with pigtail macaque dung was significantly different from that of all other dung types (Fig. 1, Table 3) to the extent that 100% of the samples from macaque dung were reclassified to this dung type. As such, no overlap in beetle community attributes occurred with those of the other dung types. The first discriminant function comprised 12 species of greatest importance (Table 2) in accounting for 99.5 percent of the variation among dung type communities. This suite of species is not characterised by a predominant life history strategy, but is represented by an eclectic group of taxa. The other three dung types and unbaited control had similar community attributes such that they were distributed in four-dimensional DFA space with overlap among groups. More specifically, 78% of the barking deer dung samples were distinct, but overlap and incorrect classification occurred with sambar deer and elephant dung communities. Sambar deer dung communities were more

Table 4. Species of dung beetles collected in pitfall traps within Mo Singto research plot, Khao Yai National Park, Thailand, March 2010. Numbers refer to individuals captured in traps baited with specific types of dung.

Species	Macaque	Barking Deer	Sambar Deer	Elephant	Control	Total
Catharsius molossus (L.)	1	0	0	0	0	1
Copris cariniceps Felsche	0	2	0	0	0	2
Copris carinicus Gillet	5	6	3	1	0	15
Copris reflexus (Fabricius)	35	35	41	3	0	114
Loboparius schereri (Petrovitz) *†	0	0	7	0	0	7
Onthophagus doitungensis Masumoto	3	0	0	0	0	3
Caccobius maruyamai Masumoto, Ochi & Sakchoowong	7	0	2	2	0	11
Onthophagus falsivigilans Masumoto	2	0	0	0	0	2
Onthophagus gracilipes Boucomont	28	1	3	0	0	32
Onthophagus lindaai Masumoto	58	1	1	0	0	60
Onthophagus luridipennis Boheman	0	1	0	0	0	1
Onthophagus maesaensis Masumoto, Ochi & Hanboon	1	0	0	0	0	1
Onthophagus penicillatus Harold	1	0	0	0	0	1
Onthophagus peninsularis Boucomont	3	0	0	0	0	3
Parascatonomus munetoshii Masumoto, Ochi & Sakchoowong	1	0	0	0	0	1
Onthophagus rutilans Sharp	89	9	20	8	0	126
Onthophagus taurinus White	11	0	1	0	0	12
Oxyomus bremeri Stebnicka *	3	3	4	2	0	12
Phaeochroops lakhonicus Kuijten	1	0	0	0	0	1
Plagiogonus krataay Masumoto *†	1	0	0	0	0	1
Pleuraphodius lewesi (Waterhouse) *†	55	45	41	7	1	149
Sisyphus manti Masumoto	51	0	0	0	0	51
Sisyphus thoracicus chaiyaphumensis Hanboonsong & Masumoto	1	0	0	0	0	1
Total individuals	357	103	123	23	1	607
Dung beetle species/dung type	20	9	10	6	1	23

* Aphodiinae
† formerly held in genus *Aphodius*

distinct and only one sample classified with barking deer. Elephant dung samples were the least distinct and only 50% classified correctly, with the other half classifying as the unbaited control. Thus, in addition to the dramatically higher abundance of dung beetles on pigtail macaque dung, community composition on pigtail macaque dung also is distinct.

In summary, six of the 23 species in our samples were generalists in dung preference; three were attracted to deer dung only (two were represented by one or two specimens) and 14 were attracted totally or in high percentage to macaque dung (10 represented by three or fewer specimens). In this forested habitat, omnivore faeces attracted more scarab individuals than did all other baits combined, with the two deer species attracting far fewer. Elephant dung was not attractive in this study for the various reasons discussed above.

The dung of the omnivorous macaques with higher protein and a greater variety of food items was far more attractive to scarabs than was the low protein dung of the herbivore species. This corroborates New World studies that have shown omnivore dung to be more attractive to dung beetles than herbivore and carnivore dung (Filgueiras et al., 2009; Marsh et al., 2013; Bogoni & Hernández, 2014). The addition of a carnivore dung source in a study such as this would provide a wider array of protein levels, although it has not been shown to be more attractive to dung beetles (Filgueiras et al., 2009; Marsh et al., 2013; Bogoni & Hernández, 2014). Tropical forests with a robust community of omnivores are more likely to provide the organic resources necessary to support the conservation of a rich and diverse dung beetle community. As such, the loss of omnivores from the system portends a concomitant dramatic loss in biodiversity of the dung beetle community that is dependent on this resource.

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