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Diel flight activity and habitat preference of dung beetles (Coleoptera: Scarabaeidae) in Peninsular Malaysia

Masahiro Niino[1], Tetsuro Hosaka[1, 2*], Masahiro Kon[3], Teruo Ochi[4], Toshihiro Yamada[1], Toshinori Okuda[1]

Abstract. Diel activity and habitat preferences are thought to be important for resource partitioning among species sharing food resources. Dung beetles in tropical forests provide a good example for testing this hypothesis, as they utilise a patchily distributed and ephemeral resource, i.e., mammalian dung, with strong inter- and intra-specific competition. However, information on diel activity patterns and habitat preferences of dung beetles remains limited in Southeast Asia. Our study demonstrates distinct diel activity and habitat preference of dung beetles in Peninsular Malaysia. Only a few small-sized diurnal species preferred open-land habitats, whereas the remainder favoured forest habitats. Large-sized species (>50 mg) were primarily nocturnal, while small-sized species (<50 mg) were diurnal. Therefore, although the numbers of individuals and species were higher during daytime, the biomass of dung beetles was 10 times higher at night than during the day in the forest, implying higher dung availability at night. Our review of diel activity in dung beetles in Southeast Asia suggests that activity patterns largely overlapped among species in the same genera or tribe; e.g., species in the Coprini tribe are almost all nocturnal, whereas those in Onthophagini, Oniticellini and Sisyphini are mostly diurnal. Therefore, diel flight activity might be largely determined by phylogenetic or physical constraints such as body size. Diel activity patterns may also facilitate the co-existence of dung beetles in different genera or tribes but may be less important for closely related species, except for some with diel activity patterns that differ from their congeners.

Key words. biomass, clear-cut, deforestation, diurnal, open land, nocturnal, Temengor

INTRODUCTION

The mechanisms of co-existence of highly diverse taxa have been a central issue of ecological studies in tropical forests (Ghazoul & Sheil, 2010). One plausible explanation is the niche assembly model (Ghazoul & Sheil, 2010). Differentiation in food, space and time is assumed to facilitate the co-existence of species within ecologically similar guilds (Whitmore, 1990).

Because dung beetles (Coleoptera: Scarabaeidae) exploit resources that are patchily distributed and ephemeral, strong competition between co-occurring species is highly probable and likely plays a major role in structuring communities (Hanski & Cambefort, 1991). Previous studies have demonstrated that dung beetles exhibit niche partitioning along several ecological axes, including dung food type, colonisation times, seasonality, macro- and micro-habitats, as well as foraging and nesting strategies such as tunneling or rolling (Hanski & Cambefort, 1991; Chao et al., 2013).

Differentiation in diel activity patterns among potentially competing species is another possible mechanism that facilitates co-existence (Whitmore, 1990). Such temporal differentiation appears particularly relevant in tropical forests where high rates of exploitation of carrion and dung occur (Feer & Pincebourde, 2005). Diel activity patterns may also be especially important among species that are closely related phylogenetically, as they often have similar competitive abilities and resource demands. Previous studies in other regions have demonstrated that most dung beetle species exhibit clear patterns in diel activity such as diurnal, nocturnal or crepuscular, but in most cases, diel activity is almost identical among closely related species (reviewed by Hanski & Cambefort, 1991). In Southeast Asia, information on the diel activity of dung beetles is limited (Hanski & Krikken, 1991), except for reports from Borneo (Davis, 1999; Slade et al., 2007) and peninsular Thailand (Boonrotpong et al., 2012). No studies have been conducted in Peninsular Malaysia, although the number of ecological studies on dung beetles has been increasing recently (e.g., Lee et al., 2009; Tregidgo et al., 2010; Qie et al., 2011, 2012; Kudavidanage et al., 2012).

Habitat specificity of dung beetles would also facilitate species co-existence at the landscape level. Clear responses of dung beetles to contrasting habitat types such as forest and open land have been well documented, mostly in the

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[1] The Department of Environmental Sciences, Graduate School of Integrated Arts and Sciences, Hiroshima University, Kagamiyama 1-7-1, Higashihiroshima, Hiroshima 739-8521, Japan; Email: tetsurau@yahoo.co.jp (*corresponding author)

[2] Department of Tourism Sciences, Graduate School of Urban Environmental Sciences, Tokyo Metropolitan University, 1-1 Minamiosawa, Hachioji, Tokyo 192-0397, Japan.

[3] 116-3, Nishida-cho, Jodoji, Sakyo, Kyoto 606-8417, Japan.

[4] 5-21-6, Toyono-cho, Toyono-gun, Osaka 563-0104, Japan.

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Neotropics (reviewed by Nichols et al., 2007), although few studies have surveyed open lands in Southeast Asia (cf. Shahabuddin et al., 2005). Such studies also have important implications for possible changes in dung beetle communities after conversion of forests into agricultural lands or pastures.

The objectives of the present study were to reveal overall and species-specific patterns of diel activity and habitat preference of dung beetles by sequential trapping in open land and the surrounding forest in Peninsular Malaysia, and to examine whether diel activity is different or identical among closely related species by summarising the information from Southeast Asia.

MATERIAL AND METHODS

The study site was located in the Temengor Forest Reserve in Perak, Peninsular Malaysia (5°24'–5°34'N, 101°33'–101°39'E, 400–1000 m a.s.l.). The forest consists primarily of lowland and hill dipterocarp forests with some patches dominated by bamboo. The reserve is part of the 266,000 ha Belum–Temengor Forest Complex, the second largest contiguous rain forest in Peninsular Malaysia (Kaur et al., 2011). Of the 148,870 ha of the reserve, 9000 ha composed of 30 blocks have been managed by a state-owned company, and selective logging began in 2001 using Sustainable Forest Management (PITC, 2010).

Fieldwork was conducted at a logger camp and its surrounding forest in the reserve. The camp was a clear-cut (c. 1–2 ha) containing cabins and a log station. Some portions of the camp clearing were covered by grasses. Trees in the surrounding forest were selectively logged 10 years before our survey (PITC, 2010).

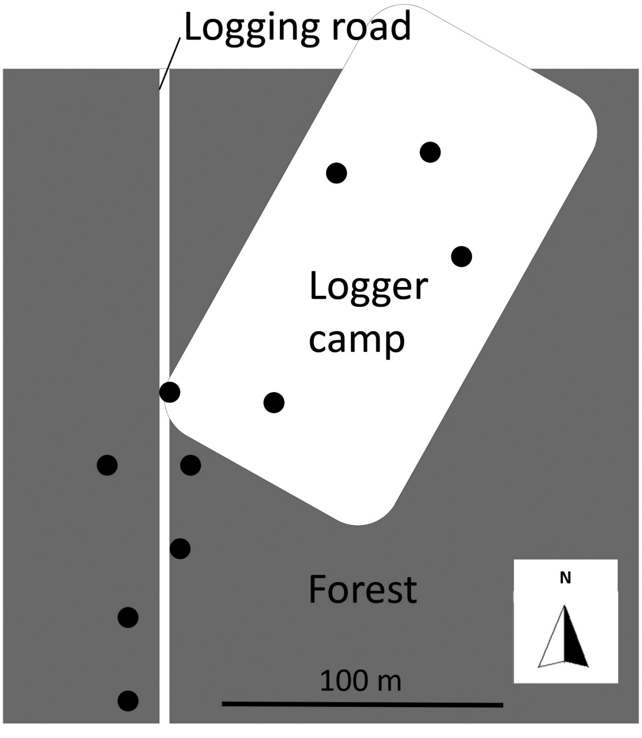

Fig. 1. Location of the pitfall traps (black circle) in the study site.

We set five baited-pitfall traps at both the logger camp (hereafter "open land") and the surrounding forests ("forest"). The pitfall traps were constructed of plastic containers buried flush with the ground. The containers (10 cm in diameter × 9 cm deep) contained 250 ml of a detergent solution; 150 g of fresh human dung wrapped with fine mesh net was hung on a wire over the middle of the trap. An umbrella (90 cm diameter) was placed 20 cm above the pitfall trap for protection from rain and direct sunlight. The distances of

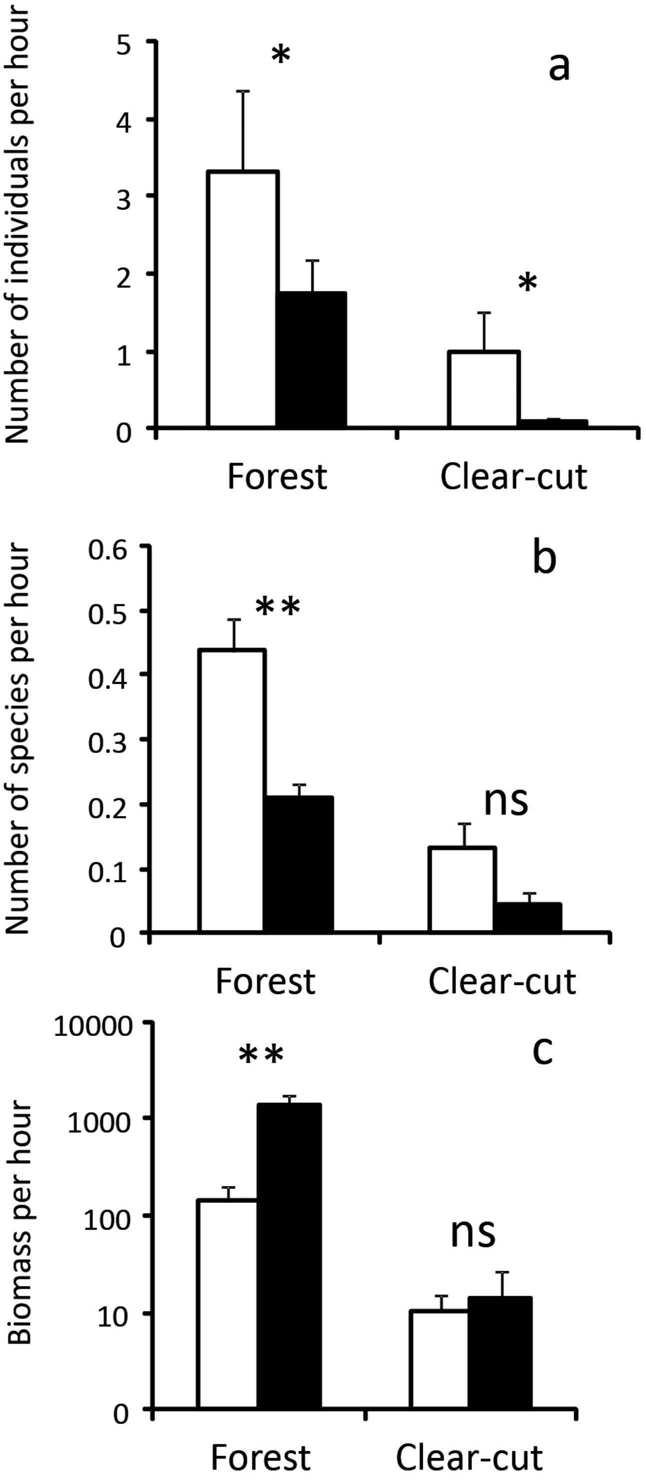

Fig. 2. Mean number of (a) individuals; (b) species; and (c) biomass of dung beetles collected per hour during daytime (blank bar) and at night (solid bar) in the forest and open land. Error bars indicate standard errors. $^{ns}P \geq 0.05$, $^{*}P<0.05$, $^{**}P<0.01$ (Kruskal-Wallis test).

traps from the nearest forest edge were 6–51 m for traps in the open land and 6–15 m for traps in the forest. The traps were located at least 30 m from each other. Dung beetles were collected according to the following schedule for 8 days without bait renewal: every 4 h (1200, 1600, 2000, 2400, 0400, 0800 and 1200 h) on the first day, every 6 h (1800, 2400, 0600 and 1200 h) on the second day, at 0800 h and 2000 h on the third day (Fig. 1) and every 24 h at 0800 h after the fourth day until the eighth day. With this sampling schedule, we also examined the response of dung beetles to different age of dung, i.e., days after dung placement, though we do not show the detailed results here; most species were attracted within 3 days after placement. Dung beetles in the traps were stored in 70% ethanol for later identification. After identification, the air-dried masses of 10 haphazardly selected individuals of each species were measured using an electronic balance to the nearest 0.1 mg (Sartorius CP224S). For species with fewer than 10 individuals, the masses of all individuals were measured. We assumed that the air-dried mass would well represent the dung beetle mass since all the specimens were air-dried for sufficiently long time (> 1 month) in the same condition. We followed Hanski & Cambefort (1991) and Davis (1999) for tribe classification.

To classify dung beetle species into guilds based on the pattern of diel flight activity and habitat type, we conducted cluster analysis using the proportion of forest samples (number of individuals collected in the forest / total number of individuals) and that of night time samples (number of individuals collected at night / total number of individuals) for each species. Because the timings of sunrise and sunset were around 0700 h and 1920 h, respectively, we regarded the traps set after 1800 h and collected before 0800 h as "nighttime traps", whereas those set after 0600 h and collected before 2000 h as "daytime traps" (Appendix 1). The cluster analysis was performed using Euclidian distance and the Ward method in R ver. 3.0.1 (R Core Development Team, 2013).

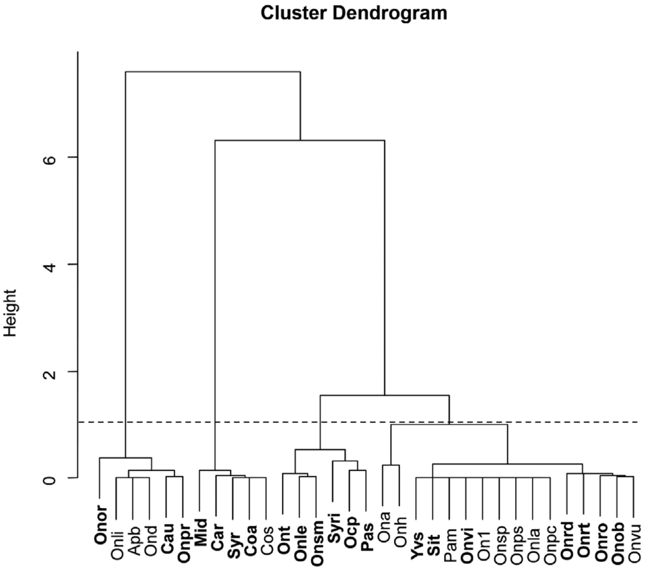

Fig. 3. Cluster analysis groupings of dung beetle species based on the level of specificity to forest habitat and nocturnal activity patterns. Four groups were identified at a dissimilarity of 1.0 (broken line). See Table 1 for species codes. Species with more than five individuals are shown in boldface.

RESULTS

In total, 1093 individuals of dung beetles belonging to 34 species in 11 genera of Scarabaeinae and one individual of Aphodiinae were collected (Table 1). The number of individuals per trap was significantly higher in the forest (mean ± SE: 141.8 ± 28.2) than in the open land (42.6 ± 19.8; $P<0.05$, Kruskal-Wallis test). Similarly, the number of species per trap was significantly higher in the forest (17.8 ± 2.8) than in the open land (5.8 ± 3.9; $P<0.01$). The total biomass of dung beetles per trap was 40 times higher in the forest (56,500 ± 14,700 mg) than in the open land (1420 ± 747 mg; $P<0.01$).

The numbers of individuals and species were significantly higher during the daytime than at nighttime in both the forest and open land (Fig. 1a, b). In contrast, the biomass of dung beetles was 10 times higher at night than during the day in the forest (Fig. 1c). Dung beetle biomass did not significantly differ between night time and daytime in the open land. However, after excluding the biomass of two individuals of *Catharsius renaudpauliani*, the largest species in the present study, biomass became significantly lower at night than during the day (mean ± SE: 1.6 ± 0.9 mg vs. 10.4 ± 4.7 mg; $P<0.05$, Kruskal-Wallis test). Since *C. renaudpauliani* is a forest-dwelling species as shown below, these individuals were likely to have flown from the surrounding forest to the open land.

At the species level, most species showed clear specificity to habitat type (forest or open land) and diel fight activity (nocturnal or diurnal; Appendix 1). The cluster analysis classified the species into four guilds: diurnal open-land group, nocturnal forest group, diurnal and nocturnal forest group and diurnal forest group (Fig. 2).

The diurnal open-land group mainly consisted of species in the tribe Onthophagini, including *Onthophagus orientalis*, *Onthophagus proletarius* and *Caccobius unicornis*, which were all small-sized species (<50 mg), with only 0–9% and 6–25% of individuals collected in the forest and at night, respectively (Table 1). No nocturnal species were found in the open land.

The nocturnal forest group primarily consisted of species in the tribe Coprini, including *C. renaudpauliani*, *Copris agnus* and *Microcopris doriae*, with 90–100% and 95–100% of individuals collected in the forest and at night, respectively. These species were all large-sized (>50 mg).

The nocturnal and diurnal forest group consisted of species in various tribes with 100% of individuals collected in the forest and 42–63% collected at night. These species would be diurnal or nocturnal species with crepuscular flight activity, as they were also collected during periods including evening (1600–2000 h) or early morning (0400–0800 h) rather than evenly throughout the day (Appendix 1). Species

Table 1. Code names, air-dried body masses (mean ± SE) and numbers of individuals of dung beetle species collected.

Species	Code	Biomass (mg)	N
Aphodiinae			
Aphodius brahminus	Apb	1.5	1
Scarabaeinae			
Canthonini			
Ochicanthon peninsularis	Ocp	9.9 ± 5.1	13
Coprini			
Catharsius renaudpauliani	Car	1157.8 ± 122.2	225
Copris agnus	Coa	182.0 ± 16.5	9
C. spinator	Cos	111.4	1
Microcopris doriae	Mid	65.3 ± 6.5	21
Synapsis ritsemae	Syri	511.8 ± 31.8	8
S. roslihashimi	Syro	412.3 ± 92.0	2
Oniticellini			
Yvescambefortius sarawacus	Yvs	110.8 ± 50.5	20
Onthophagini			
Caccobius unicornis	Cau	2.0 ± 0.1	15
Onthophagus aphodioides	Ona	2.1 ± 0.7	2
O. dayacus	Ond	5.0	1
O. hidakai	Onh	2.9 ± 0.9	4
O. kawaharai	Onk	2.9	1
O. laevis	Onla	2.6	1
O. leusermontis	Onle	13.5 ± 0.8	105
O. liliputanus	Onli	3.0	1
O. obscurior	Onob	16.5 ± 0.6	230
O. orientalis	Onor	30.9 ± 4.6	22
O. penicillatus	Onpc	25.1 ± 17.4	2
O. peninsulomerus	Onps	19.0	1
O. proletarius	Onpr	9.0 ± 0.5	161
O. rorarius	Onro	48.4 ± 10.1	33
O. rudis	Onrd	11.4 ± 0.9	22
O. rutilans	Onrt	39.5 ± 4.3	11
O. semifex	Onsm	33.3 ± 6.4	6
O. sepilokensis	Onsp	8.6 ± 2.2	2
O. sp. 1	On1	Not measured	1
O. taeniatus	Ont	13.0 ± 1.2	105
O. viridicervicapra	Onvi	40.2 ± 24.1	3
O. vulpes	Onvu	17.4 ± 2.6	29
Gymnopleurini			
Paragymnopleurus maurus	Pam	140.2	1
P. striatus	Pas	250.0 ± 30.3	26
Sisyphini			
Sisyphus thoracicus	Sit	11.4 ± 1.6	8
Total			**1093**

in Canthonini and Onthophagini, such as *Ochicanthon peninsularis*, *Onthophagus taeniatus*, *Onthophagus leusermontis* and *Onthophagus semifex*, might be diurnal-crepuscular species, as they were active during daytime including early morning and evening but were inactive at midnight. In contrast, *Paragymnopleurus striatus* (tribe Gymnopleurini) and *Synapsis ritsemae* (tribe Coprini) might be nocturnal-crespucular species because they were active at night including evening but inactive at noon. However, their crepuscularity could not be confirmed in the present study since our trap collection was not frequent enough to detect their activity peak.

The diurnal forest group was the largest group in terms of number of species, mainly consisting of species in Oniticellini, Onthophagini and Sisyphini (Scarabaeidae), including *Onthophagus obscurior*, *Onthophagus rorarius*, *Onthophagus rudis*, *Onthophagus vulpes*, *Sisyphus thoracicus* and *Cambefortius sarawacus*, with 92–100% and 0–30% of individuals collected in the forest and at night, respectively.

DISCUSSION

Diel activity and habitat preference. The present study demonstrated distinct diel activity patterns and habitat preference of dung beetles in Peninsular Malaysia. Many species avoided camp clearings but concentrated in the forest habitats. The response of each dung beetle species to habitat types was distinct even though some traps were located less than 10 m from forest edge. Previous studies also reported rapid alternation of dung beetle communities at the edge between forests and open lands such as savanna

(Feer, 2008; Spector & Ayzama, 2003) or open forest (Hill, 1996). Only a few small-sized diurnal species, such as *O. orientalis*, *C. unicornis* and *O. proletarius*, were abundant in the open land. These species were rarely collected in the surrounding forests. Similar patterns have also been reported at clear-cuts embedded in tropical rain forests, which are dominated by small numbers of the small-sized non-forest species (Vulinec, 2002; Scheffer, 2005; Nichols et al., 2007).

Generally, dung beetles in tropical forests are unable to exploit modified habitats (e.g., clear-cuts) that experience high temperatures (Navarrete & Halffter, 2008; Peyras et al., 2013), likely because the increase in daytime temperature can exceed the maximum temperature (c. 42°C) tolerated by dung beetles (Chown & Klok, 2011). The body temperature of small-sized species is often lower than that of large-sized species during flying and walking (Barthromew & Heinrich, 1978; Chown & Klok, 2011), which may be advantageous for activity under high-temperature conditions. Those species dominating the open land may be originally adapted to forest gaps and/or riparian forests, with the ability to tolerate hot and dry conditions (Davis et al., 2001; Scheffer, 2005). Notably, the three species that dominated the open land are all widespread throughout Southeast Asia and other seasonal regions such as India, Myanmar, China and Japan (Balthasar, 1963; Obata, 2006).

As suggested by Hanski & Krikken (1991) and Davis (1999), the numbers of individuals and species were higher during the day than at night, mainly because of the species-rich diurnal *Onthophagus* species. However, the biomass of dung beetles was much higher at night than during the day in the forest due to the aggregation of large nocturnal species of the tribe Coprini. Because large-sized species utilise disproportionately larger amounts of dung compared to small-sized species (Larsen et al., 2005; Slade et al., 2007), amount of dung removed by beetles would be much greater at night than during the day. Slade et al. (2007) estimated that about 75% of dung removal was caused by such large-sized nocturnal Coprini species, particularly *Catharsius dayacus*, in Borneo.

Diel flight activity and resource partitioning. If segregation in diel flight activity patterns plays an important role in resource partitioning among dung beetle species, it is likely to be more distinct among congeneric or closely related species, as they often have similar body sizes and demands for resources. However, our summarised data on diel flight activity of dung beetles in Southeast Asia (Appendix 2) do not support this assumption but instead suggest that diel activity is quite similar among species within the same genus or tribe. For example, species in *Catharsius*, *Copris* and *Microcopris* (tribe Coprini) are almost all nocturnal, whereas those in *Onthophagus* and *Caccobius* (Onthophagini), *Yvescambefortius sarawacus* (Oniticellini) and *S. thoracicus* (tribe Sisyphini), are mostly diurnal. Therefore, diel flight activity might be largely determined by phylogenetic or physical constraints such as body size. Thus, diel flight activity may facilitate the co-existence of dung beetles in different genera or tribes but would not be as important for closely related species, with the exception of some with diel activity patterns that differ from those of their congeners. One plausible factor accounting for the differences in diel flight activity is the body size of beetles. The members of Coprini are large-sized beetles (usually >50 mg in body mass and >10 mm in body length), whereas those of Onthophagini and Canthonini are small- to medium-sized beetles (usually <50 mg and ≤10 mm). Small beetles generally have a small superposition/apposition eye that is unlikely to gather enough light for reliable vision at night (Byrne & Dacke, 2011). Moreover, large-sized species would overwhelm small-sized species under cooler conditions (i.e., at night) with their higher ability to elevate thoracic temperatures above ambient during foraging and dung processing (Bartholomew & Heinrich, 1978; Chown & Klok, 2011).

Species with diel activity patterns that differed from other congeneric members were only found in *Paragymnopleurus* (Gymnopleurini), *Onthophagus* (Onthophagini) and probably *Synapsis* (Coprini) (Appendix 2). *Paragymnopleurus striatus* was rather nocturnal, although *P. maurus* and *P. sparsus* were relatively diurnal. Some *Onthophagus* species are crepuscular or nocturnal, although the majority of members are diurnal (Davis, 1999; Boonrotpong et al., 2012). We also observed an unidentified *Synapsis* species rolling a ball of dung around noon (M. Nino & T. Hosaka, unpublished data), even though the other members of Coprini are all nocturnal (however, this tribe may possibly be polyphyletic; Philips, 2011). These exceptional species that exhibit different diel activity patterns may have an advantage in occupying dung and nesting sites when congeners are absent.

However, segregation in diel activity patterns may occur at a finer timescale among nocturnal or diurnal species (Davis, 1999). More detailed studies using frequent trap collection (e.g., once every hour) may be needed to reveal such fine-scale segregation among closely related species. More frequent trap collection is particularly needed to demonstrate the activity peak of crepuscular species (Feer & Princebourde, 2005), which was not clear in our study. In addition, ecological axes other than diel flight activity such as dung type, dung age and foraging and nesting strategies may be more important in terms of resource partitioning among these species (Hanski & Cambefort, 1991; Davis, 1999; Chao et al., 2013).

Diel activity may reflect the primary dung fauna on which dung beetles rely. In the Temengor Forest Reserve, large mammals such as the elephant, tiger, wild pig, tapir, deer, bear, monkeys and macaques are likely to be major dung producers. *Onthophagus* species and *S. thoracicus* apparently have an advantage in utilising fresh dung of diurnal animals such as monkeys and macaques (Whitmore, 1990), whereas Coprini species were often dominant within elephant dung defecated at night (T. Hosaka, personal observation). Diel differences in dung defecation by mammals may affect the diel activity of dung beetles (Hanski & Cambefort, 1991, Feer & Princebourde, 2005). The larger biomass of dung beetles at night may imply larger amount of available dung at night than during daytime at the study site.

Finally, most studies of diel activity of tropical dung beetles have only focused on the timing of foraging (arrival on dung). However, as revealed in African dung beetle communities (Chao et al., 2013), the duration of colonisation on a dung pile would be equally important for understanding inter- and intra-specific competition and resource partitioning among dung beetles in Southeast Asia.

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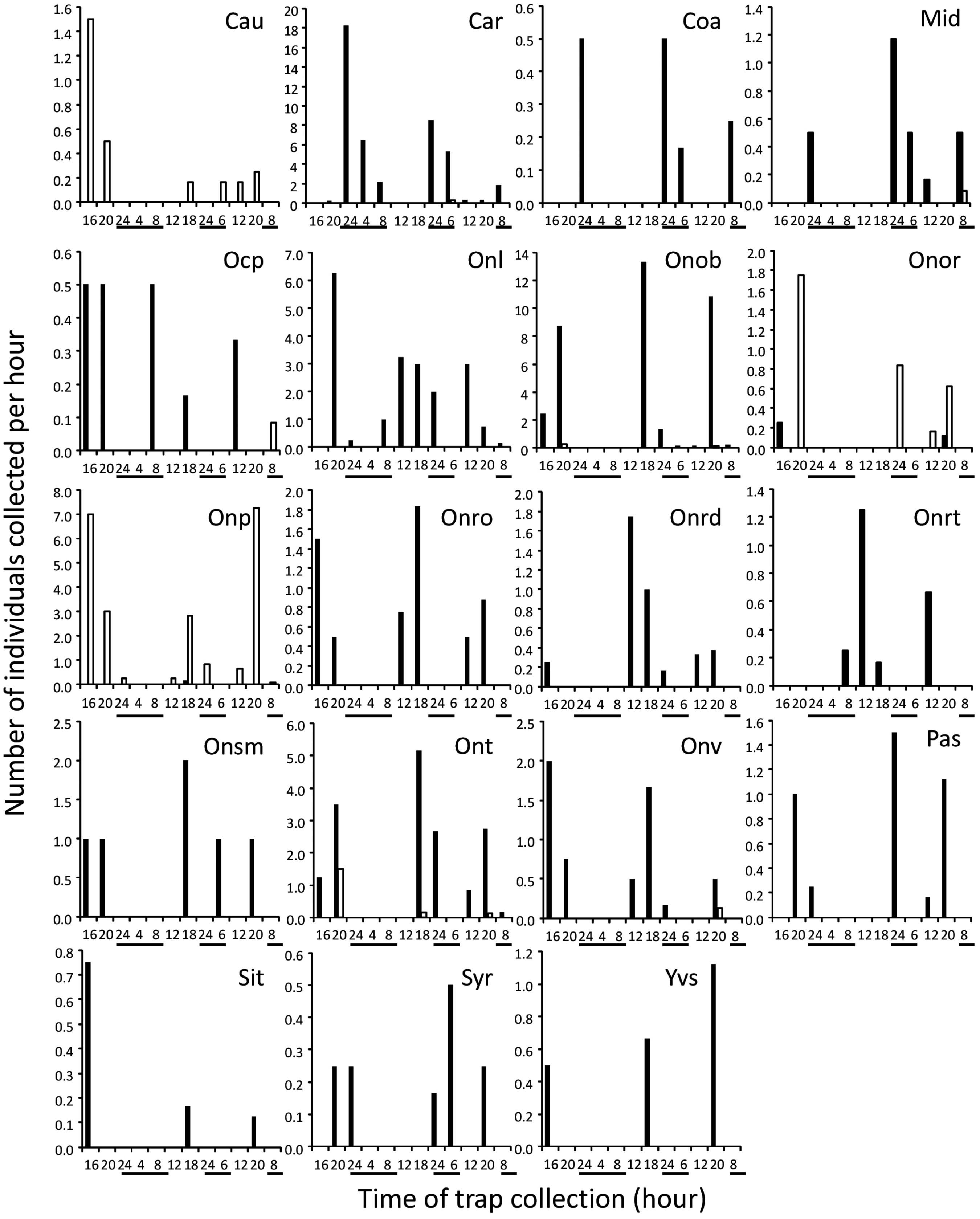
APPENDICES

Appendix 1. The number of dung beetles collected per hour within each of five pitfall traps in the forest (black bars) and the camp clearing (white bars) at different trap collection times. Horizontal lines under the time of collection indicate "nighttime traps". Species with ≤ 5 individuals collected are not shown. See Table 1 for species codes.



Appendix 2. Summary of the diel activity patterns of dung beetles in Peninsular Malaysia (P: present study), peninsular Thailand (B: Boonrotpong et al., 2012) and Borneo (D: Davis, 1999, S: Slade et al., 2007). Undescribed *Onthophagus* species are not shown. Diel activity patterns based on less than five individuals are noted in the parentheses.

Species	Diel activity pattern	Literature
Aphodiinae		
Aphodius brahminus Harold	(Diurnal)	P
A. sp. 1	Nocturnal	D
Scarabaeinae		
Coprini		
Catharsius dayacus Lansberge	Nocturnal	S
C. renaudpauliani Ochi et Kon	Nocturnal	P, D, S
Copris agnus Sharp	Nocturnal	P, S
C. sinicus Hope	Nocturnal	D, S
C. spinator Harold	(Nocturnal)	P
Microcopris doriae (Harold)	Nocturnal	P, D, S
M. hidakai Ochi et Kon	Nocturnal	S
M. reflexus (Fabricius)	Nocturnal	D
Paracopris ramosiceps (Gillet)	Nocturnal	D, S
Synapsis ritsemae (= *cambeforti*) Lansberge	Nocturnal-Crepuscular?	P, D
S. roslihashimi Ochi et Kon	(Nocturnal)	P
Oniticellini		
Oniticellus tessellatus (Harold)	(Diurnal)	D
Yvescambefortius sarawacus (Gillet)	Diurnal	P
Onthophagini		
Anoctus sp. 1	(Crepuscular)	D
Caccobius unicornis (Fabricius)	Diurnal	P, D
C. binodulus Harold	(Diurnal)	D
Cyobius sp. 1	(Diurnal)	D
Onthophagus aereopictus Boucomont	(Diurnal)	D
O. angustatus Boucomont	(Diurnal)	S
O. aphodioides Lansberge	(Diurnal)	P, D, S
O. babirussoides Krikken et Huijbregts	Diurnal	B
O. borneensis Harold	Diurnal	D, S, B
O. carinensis Boucomont	Diurnal	B
O. dayacus Boucomont	(Diurnal)	P
O. deflexicollis Lansberge	Crepuscular	B
O. hidakai Ochi et Kon	(Diurnal)	P
O. incisus Harold	Diurnal	D, S, B
O. laevis Harold	Diurnal	P, S
O. leusermontis Huijbregts et Krikken	Diurnal-Crepuscular?	P
O. liliputanus Lansberge	(Diurnal)	P
O. mulleri Lansberge	Diurnal	D, S, B
O. obscurior Boucomont	Diurnal	P, D
O. ochromerus Harold	Diurnal	S
O. orientalis Harold	Diurnal-Crepuscular	P, B
O. pacificus Harold	Diurnal	D, S, B
O. pavidus Harold	Diurnal	D, S
O. penicillatus Harold	(Diurnal)	P
O. peninsulomerus Huijbregts et Krikken	(Diurnal)	P
O. proletarius Harold	Diurnal	P
O. rorarius Harold	Diurnal	P, D, S
O. rudis Sharp	Diurnal-Crepuscular	P, D, B
O. rugicollis Harold	Diurnal	D, S, B
O. rutilans Sharp	Diurnal	P
O. sarawacus Harold	Diurnal	S
O. semiaureus Lansberge	Diurnal	D
O. semifex Krikken et Huijbregts	Diurnal-Crepuscular?	P
O. seniculus (Fabricius)	Diurnal	B
O. sepilokensis Ochi et Kon	(Diurnal)	P
O. sobrius Balthasar	Diurnal	B
O. taeniatus Boucomont	Diurnal-Crepuscular	P, D, S, B
O. vethi Krikken	(Diurnal)	D
O. ventralis Lansberge	Diurnal	B
O. viridicervicapra Ochi, Kon et Tsubaki	(Diurnal)	P

Appendix 2. Cont'd.

Species	Diel activity pattern	Literature
O. vulpes Harold	Diurnal	P, D, S, B
O. waterstradti Boucomont	(Diurnal)	S
Proagoderus schwaneri (Vollenhoven)	(Diurnal)	D
P. watanabei (Ochi et Kon)	Diurnal	S
Canthonini		
Haroldius sp. 1	(Diurnal)	D
Ochicanthon peninsularis	Diurnal-Crepuscular?	P
O. dytiscoides (Boucomont)	(Crepuscular)	D
O. sp. 1	(Crepuscular)	D
O. sp. 3	(Crepuscular)	D
Gymnopleurini		
Paragymnopleurus maurus (Sharp)	Diurnal	P, D, S
P. sparsus (Sharp)	Diurnal	D, S
P. striatus (Sharp)	Nocturnal-Crepuscular?	P, D, S
Sisyphini		
Sisyphus thoracicus Sharp	Diurnal	P, D, S