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SPECIES PACKING IN TROPICAL FORESTS: DIEL FLIGHT ACTIVITY OF RAINFOREST DUNG-FEEDING BEETLES (COLEOPTERA: APHODIIDAE, SCARABAEIDAE, HYBOSORIDAE) IN BORNEO

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ABSTRACT. - I describe an activity study in which pitfall and flight intercept traps are used to collect rainforest dung beetles at Danum Valley Field Centre in northern Borneo over five 34 hour periods. Nine hundred and thirty two individuals of 47 species are recorded, from the families Scarabaeidae (subfamily Coprinae and Scarabaeinae), Aphodiidae (subfamily Aphodiinae) and Hybosoridae (subfamily Hybosorinae). There are two peaks in activity, one at mid-night and one at mid-day, with a very significant difference recorded between the two groups (one-way ANOVA, $F = 16.80$, df = 8, $P < 0.0001$), but no statistical difference within the tribes/subfamilies at each peak of flight activity. Results go against an expectation that species differentiation against any resource gradient in tropical rainforest should be complex and lead to multiple guild structures, although I suggest that the examination of more species-rich genera in any group of closely competing individuals may show greater differentiation through time. I conclude that the temporal overlap of many species at the same spatial scale in the rainforests at Danum Valley may be explained by the presence of several functional groups at each focus of activity, which allay inter-specific competition and allow the coexistence of species that show little differentiation from each other through time.

KEY WORDS. - Competition, Danum Valley, dung beetle, flight activity, resource utilization.

INTRODUCTION

Tropical forests are renowned for their great diversity of both plant and animal, and in particular insect, species (e.g. Erwin, 1988; Stork, 1991; Wilson, 1992). Rainforests offer a rich array of resources, habitats, and a high degree of spatial complexity, through which niches (sensu Hutchinson, 1957 and 1978) can diverge and speciation events occur. Within

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closely defined guilds, resource allocation can provide a means of differentiation through which potentially competing species can separate along resource gradients within their respective niche-hyperspaces. The richness of tropical forests can be seen as a reflection of the degree of species packing along each niche axis or resource gradient (Whitmore, 1984). Among resource that can be partitioned are: food (type, quality and size), space (vertical distribution, and distribution within and between habitat types), physical parameters (such as microclimate), and time (seasonal and diel).

Dung beetles utilize microhabitats that are ephemeral and patchily distributed, and competition within communities can be fierce (Hanski, 1991). Resource differentiation between species can be expected to play a major role in the co-existence of species within a community, along one or more resource gradient. In previous papers on the ecology and behaviour of rainforest dung beetle communities in Borneo myself and others have explored spatial patterns (Davis et al., 1997) and food specializations (Davis & Lantoh, 1996; Davis & Sutton, 1997). In this paper I examine the resource allocation of tropical rainforest dung beetles along one other resource gradient: time.

There have been few studies on the temporal distribution of insects in tropical forests (Wolda, 1978). Dung beetle flight activity has been examined in some communities, in some cases looking at seasonal and diel activity (Doube, 1991; Cambefort, 1991; Cambefort & Walter, 1991; Janzen, 1983), but few studies have looked at the diel flight activity of rainforest dung beetles (Fincher et al., 1971, Gill, 1991; Walter, 1985). In this paper I look at the diel flight activity of rainforest dung beetles from Malaysian Borneo, and compare data with other tropical rainforest sites.

Dung beetles of the family Scarabaeidae (after Balthasar, 1963), can be divided into discreet groups, or tribes (Hanski & Cambefort, 1991a), which reflect natural taxonomic divisions and are comprised of animals which display similar ecology and behaviour. Dung beetles can also be divided into four functional groups: tunnelers, rollers, dwellers, and kleptoparasites (Halffter & Matthews, 1966; Hammond, 1976; Klemperer, 1983). The ball rollers and tunnelers form the dominant functional groups in tropical latitudes, comprising the family Scarabaeidae. The Scarabaeidae is split into two subfamilies : the Scarabaeinae, which are ball rollers, and the Coprinae, which are tunnelers (Hanski & Cambefort, 1991b). Also within the closely competing group of dung and carrion feeders are the families Aphodiidae (subfamily Aphodiinae) and the carrion-feeding Hybosoridae (subfamily Hybosorinae), both of which are normally associated with the Scarabaeid dung beetles in the South-east Asian tropics (Hanski & Krikken, 1991). Below I discuss differences in flight activity of Bornean dung beetles between subfamilies (Aphodiinae and Hybosorinae) and tribes (within the subfamilies Scarabaeinae and Coprinae, family Scarabaeidae), and refer to the activity of different functional groups.

Following on from the assumption that the diversity of insects in tropical forests reflect high levels of species packing along individual resource gradients (discussed above), it could be predicted that dung beetle species distributions along one resource gradient, time, should show complex patterns, and that there should be temporal separation of species both within and between ecologically similar groups (i.e. the tribes and subfamilies mentioned above). Complex patterns could be expected to be demonstrated by the separation of species into multiple guilds along the resource gradient. This paper examines these predictions by looking at the degree of complexity of temporal activity in Bornean rainforest assemblages at species, tribe and subfamily level.

METHODS

I carried out work at the Danum Valley Field Centre, which lies on the eastern edge of the Danum Valley Conservation Area (4° 58' N, 117° 48' E) : a 438 km^2 area of primary forest within the Ulu Segama Reserve in south-eastern Sabah (north-east Borneo). Much of the Conservation Area is lowland (< 760m), evergreen dipterocarp forest, where dipterocarps make up approximately 88% of the total volume of large trees (Newbery et al., 1992). I used dung baited pitfall traps and one flight intercept trap (see below). Each study was carried out over a 34 hour period, where traps were emptied at two hourly intervals during the day and four hourly intervals at night. One pitfall trap, baited with human faeces, was used for all activity studies, located on the Nature Trail by the Danum Valley Field Centre. I ran the trapping programme on five separated occasions between 14 September 1990 and 21 April 1992. The pitfall trap was made from a plastic container, 12.5cm in diameter and 13cm deep, covered by a plastic plate to protect the trap from rain. The pitfall was baited largely with human faeces : a proven attractant to dung beetles in rainforest habitats which is known to retain its attractiveness over three days (Howden & Nealis, 1975; Hanski, 1983). The bait was put in a plastic tube aerated with holes at the top, and suspended over the plastic container by a stick. Insects falling into the trap were killed by a solution of water, chloral hydrate and detergent. For the fifth and final activity study, I used a flight intercept trap (FIT) in addition to the pitfall traps (using the same sampling regime as the pitfalls). The FIT consists of a vertical wall of black terylene netting (with a mesh size of approximately 300 holes/cm^2) measuring 2.4 x 1.1 metres, over which a plastic rain-cover is suspended. The black net is believed to form an invisible barrier to insects flying through the dark forest interior; any that happen to fly against the cloth fall down into aluminium foil collecting trays (18 x 11cm internally and 4cm deep) on both sides of the vertical wall. A solution of water, detergent and chloral hydrate ensures that insects falling into the trays are killed quickly. FITs provide an unbiased sampling method of collecting beetles, unaffected by behavioural differences (e.g. resource specificity) within dung beetle communities (Hanski & Krikken, 1991; Davis, 1993), as they passively collect insects flying through the forest rather than using an attractant (see Hammond, 1990).

Species in this study are largely grouped according to tribe or subfamily. Where individual species show clear differences in flight activity from the rest of the tribe or subfamily (i.e. one species shows nocturnal activity whereas the rest of the group are diurnal), these species are separated off and examined independently. Such separation is therefore based on real, objective differences in flight activity.

RESULTS

A complete list of species collected during the study in contained in Table 1, with numbers of individuals captured at each sampling hour, in which a total of 932 individuals (47 species) are recorded. In Table 1 I have collated data from all five activity studies including both pitfall and flight intercept catches. Species are from the families Scarabaeidae (subfamily Coprinae and Scarabaeinae), Aphodiidae (subfamily Aphodiinae) and Hybosoridae (subfamily Hybosorinae). Species from the family Scarabaeidae are divided into tribes (following Hanski & Cambefort, 1991a). Table 2 summarizes the functional group and mean size or range of sizes for each group (from Davis, 1993).

Table 1. Complete list of species with flight activity over a 34 hour period, with samples taken by pitfall trap on five occasions and flight intercept tray on one occasion.

	Time of collection (hour)													
Subfamily Tribe *Species*	12	14	16	18	22	2	6	8	10	12	14	16	18	22
Coprinae														
Coprini														
Catharsius molossus					13	2	7							13
Copris doriae					2	3	1							3
C.ramosiceps					17									2
C.reflexus					5	4	1							14
C.sinicus						1								1
Synapsis cambeforti					1									2
Oniticellini														
Oniticellus tessellatus		1									3			
Onthophagini														
Onthophagus aereopictus					1									
O.aphodioides	1		2											
O.borneensis				1				16	3					
O.cervicapra complex	2	5	3	8					3	1	3	2		
O.incisus	1									2				
O.mulleri	1			2				3	3	2		1		
O.obscurior		2	2								1			
O.pacificus	1	1											1	
O.pavidus			2						1					
O.rorarius			2							2				
O.rudis	1	3		3				3	1	1				1
O.rugicollis	1	1		1					3	1			1	
O.semiaureus				1	1									
O.taeniatus			1											
O.vethi				1										
O.vulpes	1													
Onthophagus sp.1	3		1	9					2	3	2		3	
Onthophagus sp.3			1	1										
Onthophagus sp.6							1							
Onthophagus sp.8					5	4								
Onthophagus sp.15		1						1				1		
Onthophagus sp.24					1									
Onthophagus sp.29												1		
Anoctus sp.1								1						
Cyobius sp.1										1				
Proagoderus schwaneri									1	2		1	1	
Caccobius binodulus					1					1	1			
C.unicornis		4	3						1			3		
Scarabaeinae														
Canthonini														
P.dytiscoides							1	1						
Phacosoma sp.1					2									
Phacosoma sp.3			1				1							
Haroldius sp.1												1		

Table 1 (*contined*)

Subfamily Tribe *Species*	12	14	16	18	22	2	6	8	10	12	14	16	18	22
	Time of collection (hour)													
Gymnopleurini														
Paragymnopleurus maurus	1				2									
P.sparsus	10	7	7	3				5	4	6	6	2	2	
P.striatus								1						3
Sisyphini														
Sisyphus thoracicus	101	76	30	15	1	1		35	69	82	47	23	11	2
Aphodiinae														
Aphodius sp.1					53	25	13							
Hybosorinae														
Phaeochridius derasus					3		1							5
Phaeochroops gilleti					3									3
Phaeochroops silphoides					3									

Hours of darkess: 18-30 to 05-00

Table 2. Functional groups of dung beetle species (subfamilies Scarabaeidae and Aphodidae) collected from five activity studies by baited pitfall and flight intercept trap, including diurnal/ nocturnal activity and average size of beetles.

Subfamily or Tribe (from Figures 1-4)	Genus	Species, or no.species	Functional group	Size range (mm)+	Diurnal (D) / Nocturnal (N)
Coprini	*Copris*	3 spp.*	medium/large tunneler	13.0 - 18.0	N
	Copris	*C.reflexus*	small tunneler	9.0	N
	Catharsius	*C. molossus*	large tunneler	31.0	N
	Synapsis	*S. cambeforti*	large tunneler	25.0	N
Onthophagini	*Anoctus*	*Anoctus* sp.1	small tunneler	5.0	D
	Caccobius	2 spp.*	small tunneler	2.5	D
	Cyobius	*Cyobius* sp.1	small tunneler	3.5 - 5.0	D
	Haroldius	Haroldius sp.1	small tunneler	2.5	
	Onthophagus	23 spp.*	small/medium tunnelers	3.5 - 12.0	D (except *Micronthophagus* spp. : N)†
	Proagoderus	*P. schwaneri*	large tunneler	17.0	D
Oniticellini	*Oniticellini*	*O. tessellatus*	medium dweller	10.0	D
Canthonini	*Phacosoma*	3 spp.*	small roller	4.5 - 8.0	D
Gymnopleurini	*Paragymnopleurus*	3 spp.*	large roller	14.0 - 19.0	D
Sisyphini	*Sisyphus*	*S. thoracicus*	small roller	5.5	D
Aphodiinae	*Aphodius*	1 sp.	small dweller	2.0	N

* see Table 1 for list of individual species
+ from Davis (1993)
† See text

Figs. 1 - 4 present graphically diel activity data gathered by pitfall trapping from 10-00 to 22-00 over a 34 hour period. Samples are taken from one trap in one location replicated five times. These data do not include the flight intercept catches. Figures are grouped according to subfamily (i.e. Fig. 1: Coprinae; Fig. 2: Scarabaeinae; Fig. 3: Aphodiinae; and Fig. 4: Hybosorinae). Hours of darkness are from 18-30 until 05-00. In some cases the figures show only one species (i.e. Fig. 2.2, tribe Sisyphini, *Sisyphus thoracicus*; and Fig. 3, subfamily Aphodiinae, *Aphodius* sp.). In other instances, I have combined species within a tribe or subfamily to simplify the presentation, and to show overall trends within the tribe (i.e. in Fig. 1.1 the tribe Coprini has six species combined; in Fig. 1.2 all species of *Onthophagus* are combined, with the exception of one as yet undescribed species - *Onthophagus* sp.8 - which is objectively differentiated from the rest of the Onthophagini as this is the only species of *Onthophagus* which displays nocturnal behaviour (further discussed below); and in Fig. 4 the subfamily Hybosorinae is represented by three species, *Phaeochroops gilleti*, *Phaeochroops silphoides* and *Phaeochridius derasus*: in all these cases all individual species are listed in Table 1). In other cases two or more species are combined due to low numbers collected (i.e. in Fig. 2.1, tribe Gymnopleurini, *Paragynmopleurus maurus* and *P.striatus* are combined). Two tribes are not represented graphically due to low numbers of beetles collected (Oniticellini and Canthonini).

In Table 3 the mean time of activity, with standard error, has been calculated for species or tribes shown in Figs. 1 - 4 (plus the tribe Oniticellini, Table 1). In the tribe Gymnopleurini, I have only calculated the mean activity of *Paragymnopleurus sparsus*, where a clear pattern of flight activity was shown, and have not included data from the other two species (*P.striatus* and *P. maurus*) because of low numbers sampled. Calculations use data from one complete activity cycle, where both the start and end of activity can be seen (i.e. incomplete cycles are not used). Data are taken from total samples collected (i.e. both trapping methods - Table 1). Means and standard errors have not been calculated for species which were only represented by a few species, due to low numbers. Calculations of mean flight activity follow suggestions by Southwood (1987), although the nomenclature used here is my own. The start of flight activity (h_0) is taken to be one hour before the first recorded specimen (h_1), and the time of each collection (hour) is converted into amount of time (number of hours) elapsed after h_0 (h_n, where n = sample number). At each sampling period, the number of beetles is multiplied by h_n, giving a value X for each time period of activity, from which mean period of activity ($\bar{X}$) and S.E. are calculated. To convert the values of $\bar{X}$ and S.E. into units of time (hours), I have multiplied these values by N_1/N_2, where N_1 = number of time periods where activity is recorded, and N_2 = total number of beetles in all samples used in calculations. The value of $\bar{X}$ obtained in this way ($\bar{X}_1$) gives the mean number of hours following commencement of flight activity, and the mean hour of activity ($\bar{X}_2$), given in Table 3, is calculated by adding $\bar{X}_1$ to the value to the time (hour) at which flight activity started, h_0 (i.e. if h_0 = 05-00, mean time of flight activity = 05-00 + $\bar{X}_1$).

When the mean flight times of all groups are analysed, a very significant difference between the groups is found (one-way ANOVA, $F = 16.80$, df = 8, $P < 0.0001$), due to the difference in flight times of night-flying versus day-flying groups. No significant differences are found between the mean flight times of diurnal groups of dung beetle ($F = 0.29$, df = 4, $P = 0.8$), and similarly no significant differences are found between the mean flight times of nocturnal groups ($F = 0.50$, df = 4, $P = 0.70$).

Differences in flight activity are clearly shown in Figs. 1-4, with groups divided into day-flying and night-flying activity. Nocturnal groups include the tribe Coprini, and the

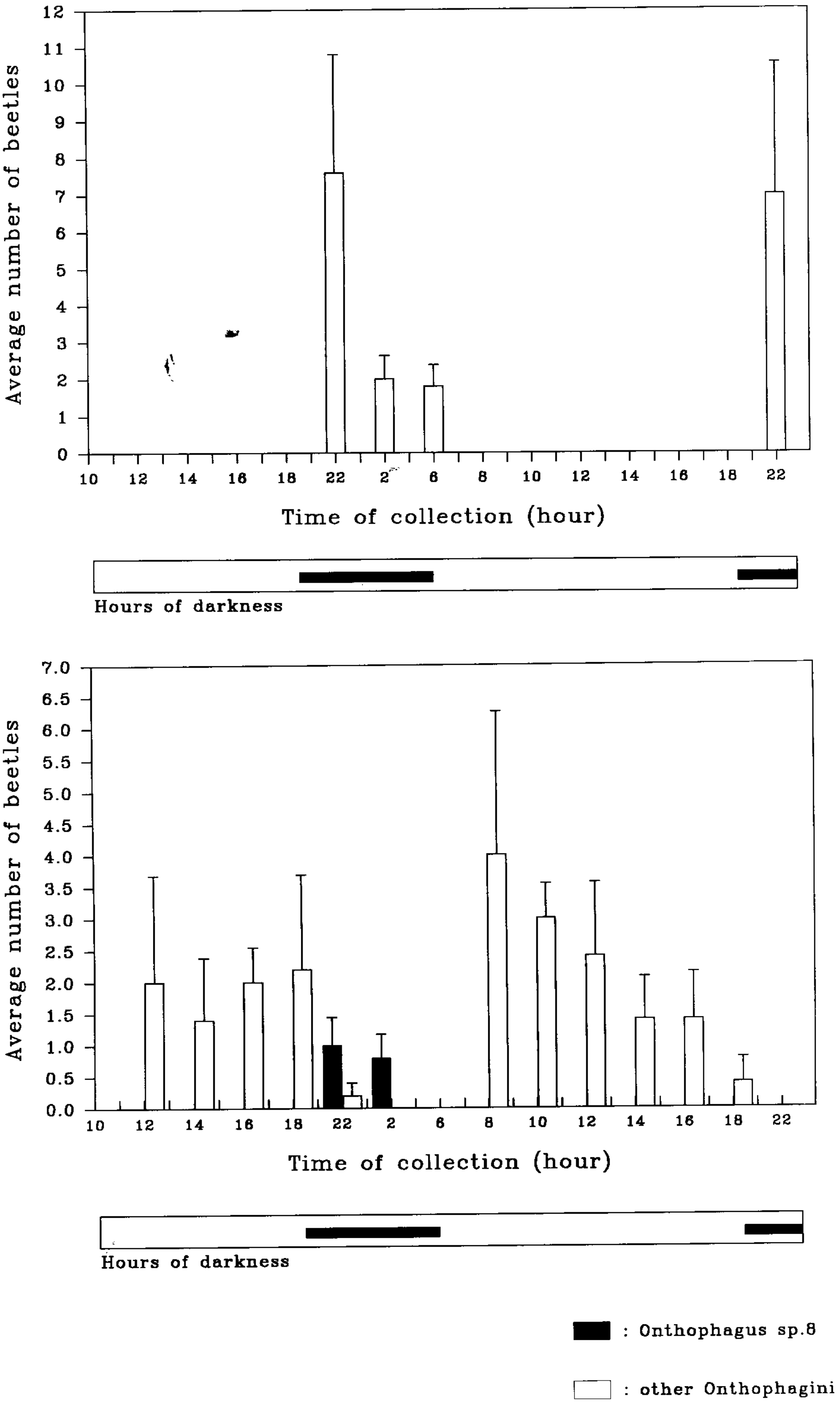

Fig. 1. Flight activity of species within the subfamily Coprinae. 1.1 (top) Tribe Coprini and 1.2 (bottom) Tribe Onthophagini. Bars show mean numbers of beetles captured at each hour (± S.E) by pitfall trap.

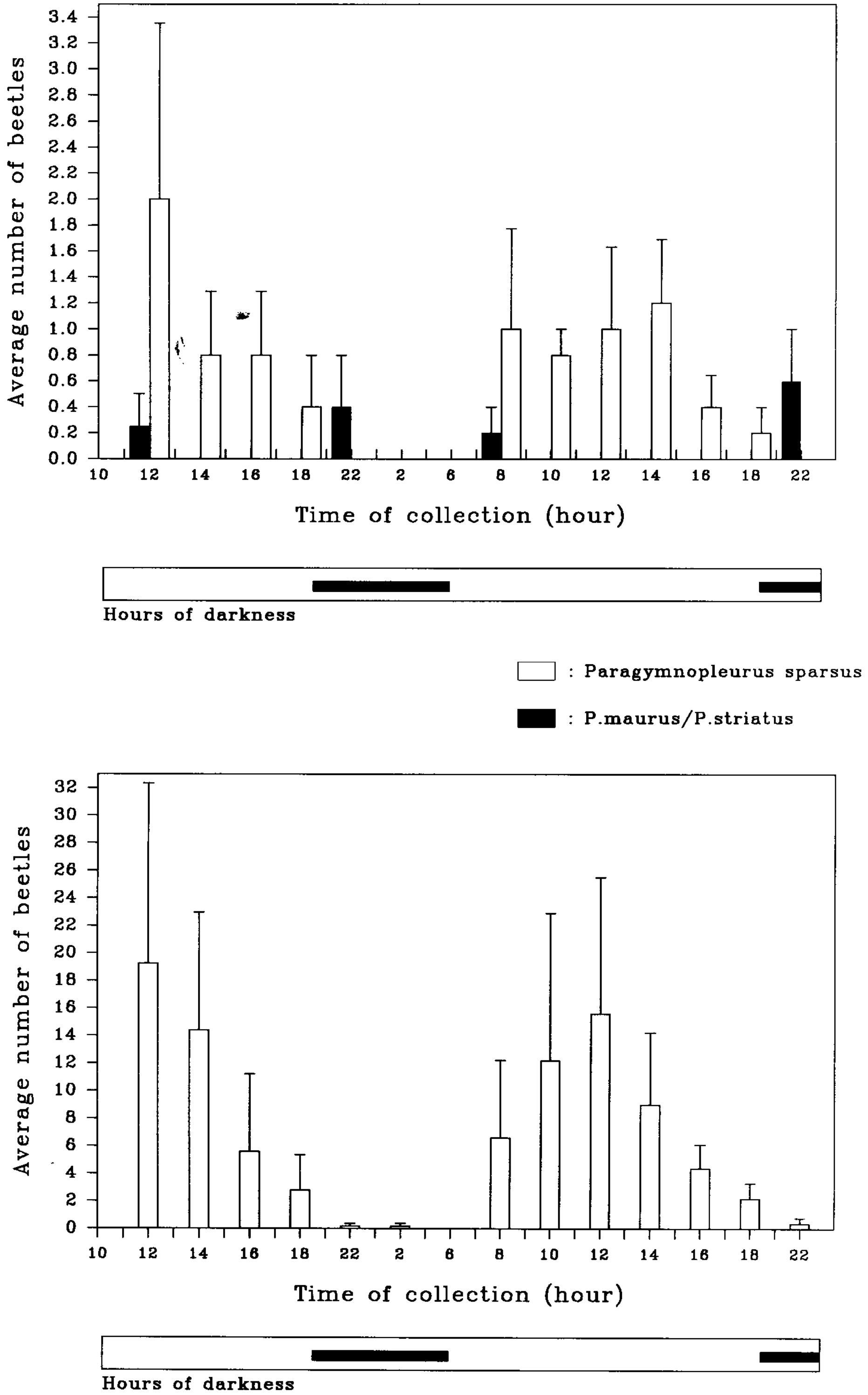

Fig. 2. Flight activity of species within the subfamily Scarabaeinae. 2.1 (top) Tribe Gymnopleurini and 2.2 (bottom) Tribe Sisyphini. Bars show mean numbers of beetles captured at each hour (± S.E) by pitfall trap.

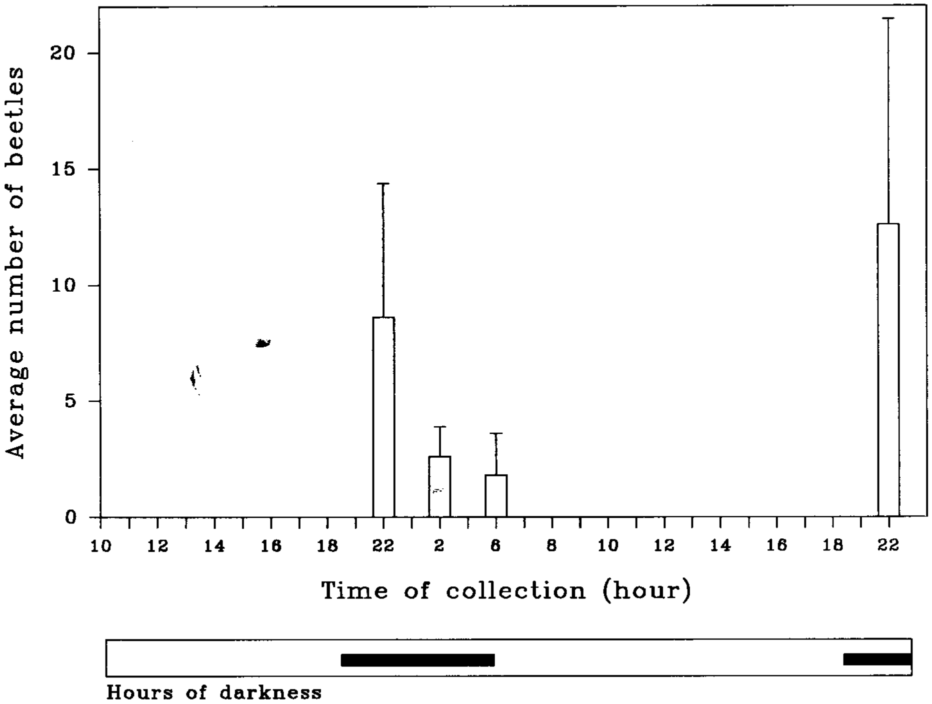

Fig. 3. Flight activity of species within the subfamily Aphodiinae. Bars show mean numbers of beetles captured at each hour (± S.E) by pitfall trap.

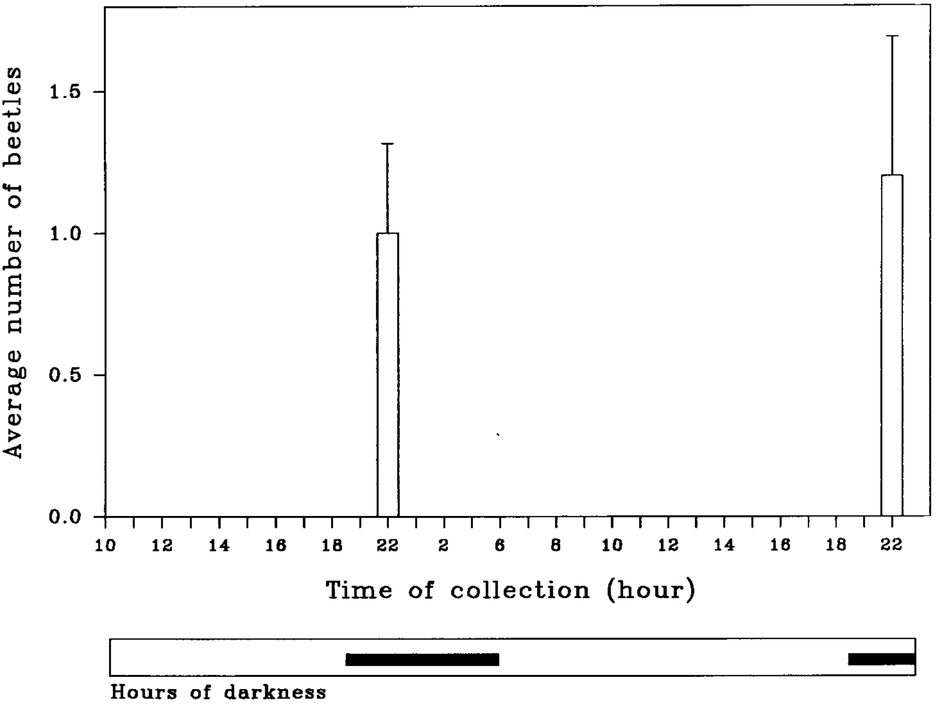

Fig. 4. Flight activity of species within the subfamily Hybosoridae. Bars show mean numbers of beetles captured at each hour (± S.E) by pitfall trap.

Table 3. Mean time of activity for each subfamily or tribe, ± SE.

Subfamily or Tribe⁺ (from Figures 1-4)	species, or no.species	Mean time of activity (± S.E)
Coprini	6 spp.*	23.97 (0.68)
Onthophagini (excl. *Micro-onthophagus*)	27 spp.*	11.56 (1.22)
Onthophagini (*Micro-onthophagus* only)	*Onthophagus* sp.8	23.78 (1.67)
Oniticellini	*Oniticellus tessellatus*	14.00 (0.50)
Gymnopleurini	*Paragymnopleurus sparsus*	12.16 (1.29)
Sisyphini	*Sisyphus thoracicus*	11.97 (1.41)
Aphodiinae	*Aphodius* sp.1	24.24 (0.75)
Hybosoridae	3 spp.*	22.80 (0.90)

* see Table 1 for list of individual species
⁺ tribe Canthonini not included due to insufficient data (see text)
Figures to two decimal places

subfamilies Aphodiidae and Hybosoridae; diurnal groups include the tribes Sisyphini, Gymnopleurini, and Oniticellini. The tribe Onthophagini has both nocturnal and diurnal elements, with most species of the tribe showing diurnal activity (mainly comprised of the genus *Onthophagus* - Table 1), and one species showing nocturnal activity (*Onthophagus* sp.8: as shown in Fig. 1.2).

Table 1 includes details of the flight activity of individual species. Within the Coprini, *Copris ramosiceps* was only active between 18-00 and 22-00, suggesting that this species only flies in the early hours of the night. Within the tribe Onthophagini (Fig. 1.2), some species may be crepuscular, although only one species, *O.borneensis*, shows clear early morning activity: other species do not contain sufficient numbers of individuals for clear patterns to emerge. Specimens collected in the trap emptied at 22-00 may well be crepuscular, as this trapping period covers the period from dusk (18-00), although activity of species after 22-00 suggests true nocturnal activity. I carried out observations of activity in the field at Danum Valley to clarify whether species were crepuscular or nocturnal: these showed that species of the tribes Coprini and subfamilies Aphodiidae and Hybosoridae are truly nocturnal, with other species from other tribes or subfamilies either crepuscular or diurnal (with the exception of *Onthophagus* sp.8 - see below) (Davis, 1993).

Of the species within the tribe Onthophagini, it is interesting to note that only *Onthophagus* sp.8 is nocturnal. Within the genus *Onthophagus*, the majority of species have eyes that are narrowly exposed, being either bean shaped or luniform (Krikken & Huijbregts, 1987). A small number of species, however, have broad eyes, and are united in the artificial subgenus *'Micronthophagus'*, which are presumed to have arisen independently from the usual *Onthophagus* condition (Krikken & Huijbregts, 1987). *Onthophagus* sp.8 shows the large-eyed condition, and belongs to the *Micronthophagus* grouping. The genus is described on the basis of large eyes only (J.Huijbregts and J.Krikken pers.comm, also Krikken & Huijbregts, 1987). Its large eyes may well be an adaptation that allows nocturnal activity (pers. obs.).

Of the diurnal species, two - *Paragymnopleurus sparsus* and *Sisyphus thoracicus* - show a clear increase in activity towards mid-day (Figs 2.1 and 2.2; and Table 3). I only collected *Oniticellus tessellatus* between 12-00 and 14-00 (Table 1), and although it is represented by a few specimens it would also seem to peak at around mid-day.

DISCUSSION

Flight activity in dung beetles is known to be regulated by such factors as temperature, light and humidity (Walter, 1985), and peak activity during the hottest part of the day implies a degree of resistance to higher temperatures and reduced humidity. In a detailed, wide-ranging study on the ecology and behaviour of rainforest dung beetles in Sabah, I noted that species more active activity towards mid-day are in general more abundant in riverine forest (Davis, 1993), where conditions are generally lighter and less humid, and this may reflect their resilience to higher temperatures and lower humidity. Both *Paragymnopleurus sparsus* and *Sisyphus thoracicus* - the two species which clearly show increased activity towards mid-day (this study) - also show increased abundance in riverine forest (Davis, 1993).

Diurnal species tend to be smaller than nocturnal species (Cambefort, 1991), which may relate to thermoregulatory constraints prohibiting large black beetles, which tend to make up the majority of nocturnal species, from flying during the day (Bartholomew & Heinrich, 1978). At Danum Valley, nocturnal species tend to be larger than diurnal species (i.e. the dominant nocturnal group, tribe Coprini, range in size from 9 - 31 mm, whereas the commonest diurnal group, tribe Onthophagini, range from 3.5 - 12 mm, with the smallest diurnal species at 2.5 mm - see Table 2), and are generally black or dark in colouration (diurnal species can have patterning or colour, and some species are metallic - pers. obs.). Species of roller are diurnal only, and can be both large or small (Table 2). In this study, diurnal species are more numerous than nocturnal species: 36 diurnal species compared to 11 nocturnal (see also Walter 1985), whereas work on rainforest communities in other areas has shown a dominance of nocturnal species over those active during the day (Halffter & Matthews, 1966; Howden et al., 1991). These differences may reflect variances in resource supply between different areas. Dung beetles in the Australian tropics show greater numbers of species active at night rather than during the day (Howden et al., 1991), presumably reflecting the increase in mammal activity, and therefore of dung production, at night (C. Hill, pers. comm). In Borneo the activity of diurnal mammals, and a greater production of suitable resources during the day, may play a more important role in contributing to the higher diversity of day-flying than night-flying species (Davis et al., 1997). It is possible, however, that the larger size of nocturnal species may lead to an overall reduction in species numbers (i.e. fewer individuals are needed to consume any unit area of resource), and the much lower diversity of nocturnal species may not necessarily reflect a similar reduction in resource production.

As I have already established, dung beetle species tend to be either diurnal or nocturnal, as very different adaptations (morphological and behavioural) are required for day and night activity (Hanski & Cambefort, 1991b). The temporal separation between day-flying and night-flying species means that potential competitors with similar ecology and behaviour (i.e. from the same functional group) never meet, and this allows for the co-existence of species at the same spatial scale. In this paper, activity studies have shown a clear dichotomy between diurnal species and those active at night, with two peaks of activity, one at around mid-day (12-00) and the other around mid-night (24-00) (Table 3). There is strong overlap in mean activity between diurnal species, and similarly between nocturnal species. Dung beetles are therefore separated into only two clear guilds based on temporal resource dynamics, rather than the multiple guilds initially predicted. It is possible that the strong overlap between the mean flight activity of both groups masks more complex temporal variation within the more species rich groups (such as the tribe Onthophagini), although most of the groups shown in Figs. 1-4, in the same temporal guild, are made up of one or few species all of which show similar peaks in flight activity. However, the peaks in activity include species from several functional groups, and it seems likely that differentiation between these animals along resource gradients other than time are equally, if not more, important. Competition between dung beetles tends to be strong (Hanski, 1991), but variation between functional groups leads to increased intra-specific competition and reduced inter-specific competition (as discussed above). Overlapping peak mean activities tend to be made up of species from different functional groups (Figs. 1-4), which utilize the resource in different ways. The mid-day peak in activity consists of one small ball-roller (*Sisyphus thoracicus*), one large ball-roller (*Paragymnopleurus sparsus*) and one 'dweller' (i.e. animals that live within the dung mass) species (*Oniticellus tessellatus*). The mid-night peak in activity consists of large and medium tunnelers (tribe Coprini), a small tunneler (the species *Onthophagus* sp.8), and small dwellers (subfamily Aphodiinae). Differences in feeding specializations can also provide an additional resource gradient other than time: the subfamily Hybosorinae, which has overlapping mean activity with the other nocturnal groups (Table 3), is a group of carrion specialists (Hanski & Krikken, 1991), and so is functionally different from the other nocturnal species, which are dung feeders. It is also known that species in the tribe Onthophagini show feeding specializations that play an important role in niche differentiation (Davis, 1993; Davis & Sutton, 1997).

Although this study shows that temporal resource utilization may not be as complex as may be expected, at least on a macro-scale, species from different functional groups that overlap both temporally and spatially at the mid-night and mid-day foci of flight activity will utlilize the resource in very different ways, and the species packing displayed by Bornean dung beetles may well depend largely on such ecological differences. It is always possible, however, that fine-scale examination of the temporal dynamics of more species rich genera will show greater differentiation through time, where physical, ecological and behavioural similarities between species can not allay inter-specific competition, and time may form the only axis through which species can differentiate and achieve spatial coexistence.

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