Diel flight activity and ecological segregation within an assemblage of tropical forest dung and carrion beetles

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Abstract: Temporal variation in activity of dung and carrion beetles in tropical forest is considered as a mechanism of ecological segregation between potentially competing species. We describe the diel flight activity of Scarabaeidae collected with baited pitfall traps at Les Nouragues field station in French Guiana. A total of 2663 individuals of 63 species was recorded, from the subfamilies Coprinae, Scarabaeinae and Aphodinae. Temporal guilds of diurnal, nocturnal and crepuscular species were identified. Diurnal species were about twice as numerous and abundant as either nocturnal or crepuscular species. Two main activity patterns characterize the diurnal species while nocturnal and crepuscular species show overlapping activity. The association of activity rhythm with the other niche variables, food selection, functional group, body size and relative abundance, was analysed using multiple correspondence analysis. Small diurnal coprophagous species were opposed to large crepuscular necrophagous species. Species packing is suggested but further analysis showed that the variables were independent of one another. The temporal differentiation of species combined with separation along multiple niche dimensions and resource gradients may facilitate the coexistence of species assumed to be strongly affected by interspecific competition.

Key Words: Competition, dung beetle, flight activity, French Guiana, niche segregation, Scarabaeidae

INTRODUCTION

Insects are particularly representative of richness of tropical forest animal communities (May 1988, Stork 1993, Wilson 1992). They provide a good example of narrow ecological segregation along several resource gradients between potentially competing species. Fine partitioning of resources such as food, space, microclimate and time is assumed to facilitate coexistence of species within ecologically similar guilds (Tokeshi 1999). Because dung beetles exploit resources that are patchily distributed and ephemeral, strong competition between co-occurring species is most probable and must play a major role in structuring communities (Hanski & Cambefort 1991a). Although no study has provided clear evidence of competition in this group, observations on behavioural interference competition and appraisal of exploitation competition in tropical forests strongly suggest that it is a current process (reviewed in Hanski 1989).

Dung beetles have been divided into three main functional groups: rollers, tunnellers and dwellers. Their food relocation techniques suggest different abilities for resource provisioning that facilitate coexistence of species between groups (Hanski & Cambefort 1991b). Ecological diversification through food preference, seasonality and habitat choice has been considered as a means of resource partitioning among dung beetles (Cambefort & Walter 1991, Davis *et al.* 1997, Doube 1991, Hanski 1983, Howden & Young 1981, Peck & Forsyth 1982). But divergence in diel activity patterns between syntopic, potentially competing species is another important mechanism making coexistence easier. Temporal differentiation appears particularly relevant in tropical forests where high rates of exploitation of carrion and dung occur especially because the resource is presumably limited (Feer 1999, Klein 1989, Peck & Forsyth 1982). They make crucial the priority effect and enhance the transience of the microhabitat (Hanski & Koskela 1977).

Studies on the temporal distribution of insects in tropical forests are scarce (Wolda 1978). Seasonal and diel activity of dung beetles have been examined in

some communities (Cambefort 1991, Cambefort & Walter 1991, Doube 1991, Janzen 1983). Diel flight activity of rain-forest dung beetles was studied by Davis (1999), Fincher *et al.* (1971), Gill (1991) and Walter (1985). These studies commonly distinguished two major groups of species forming a nocturnal and a diurnal guild. In Borneo, Davis (1999) found a strong overlap between the mean flight activity within both groups but he admitted that it may mask more complex temporal variations within the more species-rich groups. In other tropical forests, patterns along the time-of-day axis show more variation. In Africa, Walter (1985) distinguished various temporal patterns among diurnal and nocturnal species. In Panama, diurnal species display several distinctive patterns of flight activity and some species are possibly auroral/crepuscular (Gill 1991) or active both by night and day (Howden & Young 1981). A similar grouping of species by temporal activity seems to prevail also in French Guiana (Feer 2000).

This paper examines new data on the temporal flight activity of the species, genera or tribes in the Guianan rain forest. The aim is to show how variation in activity among and within guilds is related to divergences on other niche axes. We considered food selection, membership of the different functional groups, body size and abundance as dimensions affecting interference and pre-emptive competition for food. We analysed the association of activity rhythm with other variables of the niche in our species assemblage using a multivariate analysis. We tested for species packing by examining deviations from expectation in the distribution of the species and we proposed other types of ecological segregation.

MATERIAL AND METHODS

Study site

The work was carried out at the Nouragues Biological Field Station (4°5′N, 52°40′W) which lies at 100 km south of Cayenne, French Guiana. The station is located in the centre of the Nouragues Natural Reserve (1000 km²) covered by undisturbed evergreen forest (Bongers *et al.* 2001). The climate is characterized by a long wet season lasting from December to August, often interrupted by a short, drier period around March. The average annual rainfall is 2990 mm and the mean temperature is 26.3 °C (Grimaldi & Riéra 2001). Dominant canopy plant families include Leguminosae, Sapotaceae, Burseraceae, Chrysobalanaceae, Lecythidaceae, Rubiaceae, Vochysiaceae and Nyctaginaceae (Poncy *et al.* 2001). A total of 127 mammal species were recorded at the site including 67 non-flying species (Bongers *et al.* 2001).

Sampling method

We used baited pitfall traps made of plastic pots, 10 cm in diameter and 15 cm deep, protected from rain. The bait was put in a small plastic pipe covered on two sides by mosquito net and suspended over the pot. Insects falling into the traps were killed by a solution of water with detergent and sodium chloride. Ten traps were spaced 20 m apart along a linear transect. They were baited with human faeces, dung of howler monkey (*Alouatta seniculus*) or carrion (rotten meat or fish). Each study was carried out over a 24-h period with faeces and a 48-h period with carrion. First traps were emptied at 4-h intervals. Then, during the year 2002, they were checked every hour during dusk and dawn periods and every second hour during the day. We ran the trapping programme with 40% carrion (n = 150 trap days), 30% human faeces and 30% howler dung in February, April, May and October between 1995 and 2002. Most of the data were recorded during the wet period. We think that they are not biased because no changes in activity rhythm were observed between the periods and the proportions of the species in the rhythm categories in a larger sample (see after) showed no significant variation between wet and dry season (F. Feer unpublished data). Additional data were obtained from field observations made on carrion, human faeces and howler dung and occasional captures in bat or bird nets. Some small diurnal species can be found perching on leaves in the undergrowth (Gill 1991) presumably to relocate food sources. Data on perching dung beetles were used as a complement because they correlate with diel activity for most species (F. Feer, *pers. obs*). The feeding habits of species were determined in a sample composed of the above-described trapping data added to other data obtained with the same method since 1995 [total individuals n = 18 077, trapped with dung (679 trap-days) and carrion (204 trap-days), see Feer 2000]. Species were classified as specialists if 90% or more of the individuals were captured with only one bait type. Food generalists are species which showed no strong preference for dung or carrion. The weighted abundance used as an indicator of population biomass, is the product of the abundance with the mean body size of the species.

Data analysis

Data (number of species in modalities of species variables) were subjected to multiple correspondance analysis (MCA), a multivariate method permitting the study of a population of I individuals described by K qualitative variables (Greenacre 1984). One individual may be represented as a point of the vectorial space with K dimensions and each variable is represented as a vector of the vectorial space with I dimensions. MCA provides
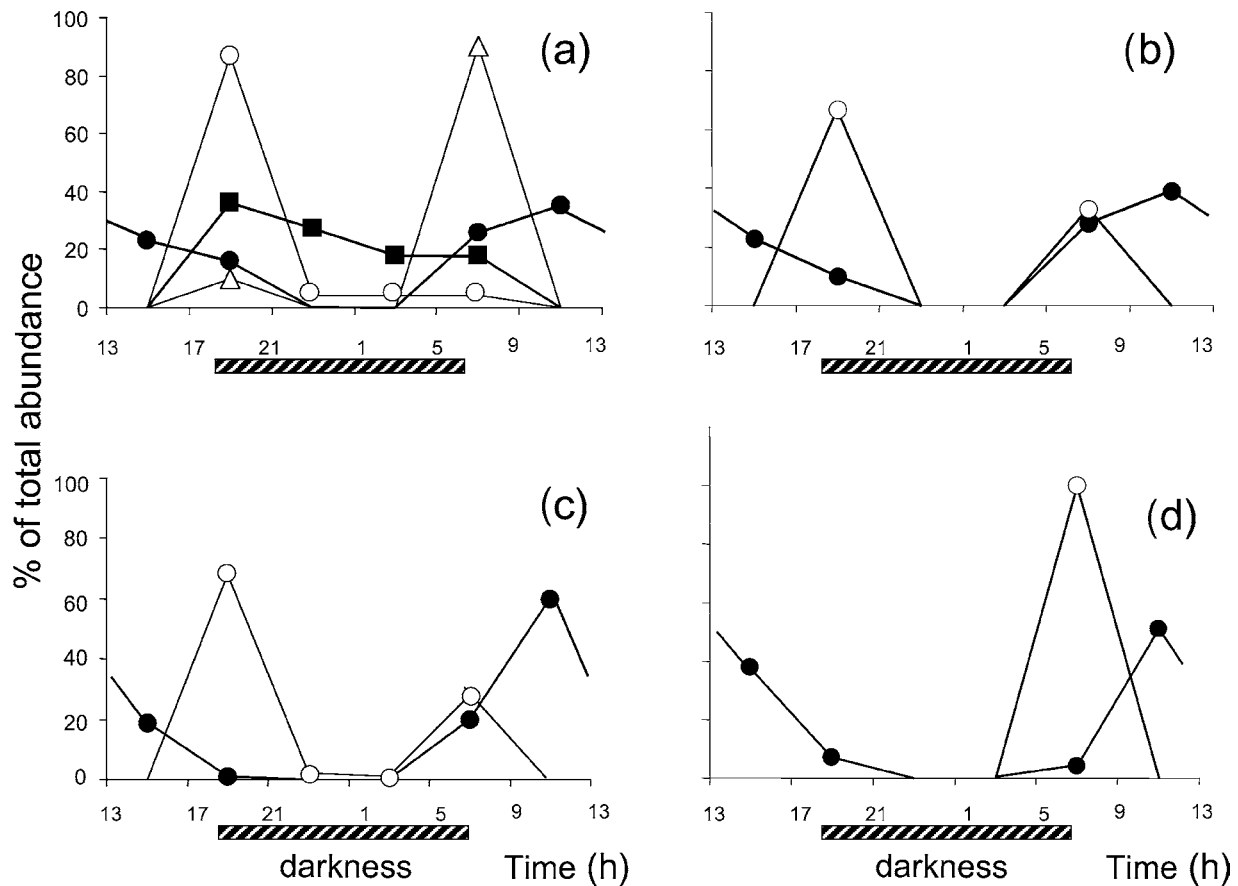
Figure 1. Flight activity of (a) *Canthidium bicolor, C. chrysis, C. onitoides, C. gestaeckeri, C. aurichalceum, C. dohrni, Canthidium* sp. 1 plotted together (●), *Canthidium* sp. 2 (■), *C. aterrimum* (○) and *C. derollei* (△); (b) *Oxysternon durantoni, O. festivum, Phanaeus chalcomelas, P. cambeforti* plotted together (●) and *Coprophanaeus parvulus, c. jasius, c. dardanus, c. christophorowi, c. lancifer* plotted together (○); (c) *Canthon (Glaphyrocanthon) semiopacus, C. (G.) quadriguttatus, Hansreia affinis, Trichocanthon sordidus* plotted together (●) and *Deltochilum guyanense, D. septemstriatum, D. submetallicum* plotted together (○); (d) *Eurysternus hirtellus, E. confusus, E. cayennensis, E. balachowskii, E. caribaeus* plotted together (●) and *E. velutinus* (○).

graphical representation of the relationships between the variables and their modalities. Two or more modalities are close to each other on a graph or are associated all the more that they are present or absent simultaneously in a large number of individuals. The different variables and their modalities (Appendix 1) were body size (s1: 3.4–7.9 mm; s2: 8–13.9 mm; s3: 14–45 mm), activity rhythm (crepuscular, diurnal, nocturnal), food preference (coprophagous, necrophagous, generalist), functional group (roller, tunneller, dweller) and relative abundance (low: 0.01–0.19%; medium: 0.2–1.9%; high: 2–15% of total). The diurnal-nocturnal species were not included in the data. The MCA was performed with the StatBoxPro programme.

For analysing the relationships among variables we test a series of hierarchical models based on the log-linear model (Sokal & Rohlf 1997). We proceed sequentially until reaching the simplest model that adequately fitted the data (i.e. with a non-significant likelihood-ratio chi-square). The goodness-of-fit tests provide an overall indication of how close the expected values are to actual data. The Freeman–Tukey deviates help to identify the most divergent cases.

RESULTS

Activity rhythm

A total of 2663 individuals (63 species) were trapped at the different sampling hours (Appendix 1). Species from the family Scarabaeidae were divided into tribes following Hanski & Cambefort (1991a).

Within the genus *Ateuchus* two species (*A. simplex, A. murrayi*) were active during night and day with maximum flying activity in the early hours of the night and in the early hours of the day. Other species are either diurnal (*A.* sp. 1, *A. aeneomicans* according to perching data) or nocturnal (*A.* sp. 2). Most *Canthidium* species were diurnal (Figure 1a) and only *C.* sp. 2 showed clear nocturnal activity. *Canthidium aterrimum* flew preferentially during dusk with a reduced nocturnal

activity. *Canthidium derollei* also flew at dusk but it was mainly active at dawn and in the early hours of the day. Within the genus *Uroxys* one species (*U.* sp. 1) flew during both day and night and another (*U.* sp. 2) was nocturnal.

All species of the genus *Dichotomius* were truly nocturnal. Three of the most abundant species (*D. subaeneus, D. lucasi, D. boreus*) showed a high flight activity in the early hours of the night. *Dichotomius lucasi* was most active during hours immediately after dusk, before the peak activity of the two other species. Other *Dichotomius* species did not contain sufficient numbers of individuals for clear patterns to emerge.

Within the genus *Onthophagus, O. rubrescens* was diurnal with a maximum flight activity between 9h00 and 11h00, and *O. haematopus* flew only between 7h00 and 9h00 and between 17h00 and 19h00.

Within the Phanaeini (Figure 1b), the genera *Oxysternon* and *Phanaeus* were truly diurnal. Both *Oxysternon* species had maximum flight activity between 9h00 and 13h00. The two *Phanaeus* species were also mainly active in the morning but there was a time lag between their maximum flight hours: 70% (n = 10) of *P. chalcomelas* were captured between 9h00 and 13h00 and 75% (n = 12) of *P. cambeforti* between 6h00 and 7h00. Direct observations and captures in flight of *Sulcophanaeus faunus* were mostly made (90%, n = 20) between 7h00 and 9h00. *Coprophanaeus* species are all dusk and/or dawn active. *Coprophanaeus parvulus, C. jasius* and *C. dardanus* flew between 6h00 and 7h00 and between 18h00 and 19h00. The rare captures of *C. christophorowi* were all made within these intervals. Direct observations or captures of *C. lancifer* were mostly made (74%, n = 19) between 18h00 and 19h00.

Within the Canthonini (Figure 1c) seven species are diurnal. Overall they flew preferentially between 9h00 and 13h00. However, two abundant species may be differentiated: 80% (n = 51) of *Hansreia affinis* were captured between 5h00 and 9h00 whereas 46% (n = 222) of *Trichocanthon sordidus* were captured between 11h00 and 13h00. But according to data on perching these species are more similar with a bimodal diurnal activity. The three *Glaphyrocanthon* species had similar preferential morning activity according to direct observations and perching data.

The nocturnal *Deltochilum carinatum* was most active between 21h00 and 1h00. *Deltochilum* species such as *D. submetallicum, D. guyanense* and *D. septemstriatum* flew mainly at dusk and dawn although some individuals were captured during the night and early hours of the day. Direct observations and captures of *D. icarus* and *D. orbiculare* suggest an activity limited to dusk and dawn.

Within the genus *Eurysternus* (Figure 1d) five species were diurnal. One among them, *E. caribeus*, showed a bimodal pattern with a maximum flight activity at early and late hours of the day. *Eurysternus velutinus* flew at dawn (73%, n = 26) and in the early hours of the day. Although much rarely trapped, *E. hamaticollis* may have the same activity pattern.

The Aphodinae, *Aphodius* sp. 1, flew mainly during the night although some observations were carried out during the day.

Structure of the species assemblage

In summary, three main temporal guilds are distinguished that structure the community (Table 1). Diurnal species are about twice as numerous and abundant as either nocturnal or crepuscular species. Diurnal species also have the largest relative weighted abundance. Despite comprising a small number of species, a fourth guild of diurnal–nocturnal species have a large relative abundance because one species, *A. simplex*, is the most abundant in the total sample (23.5%).

Two diel activity patterns emerge within the dominant diurnal guild. Small Canthonini species (< 10.2 mm in length), one *Onthophagus* and small Phanaeini fly preferentially during the first half of the day whereas *Canthidium* and some *Eurysternus* species fly throughout the day. The more homogeneous nocturnal guild comprises species flying preferentially during the first half of the night. Most of the species with a reduced period of activity fly at dawn and dusk but some species such as *C. lancifer* and, possibly, *C. dardanus* and *D. orbiculare*, are mostly active at dusk.

In our assemblage, 79% of nocturnal species are black (i.e. *Dichotomius* spp.) while the remaining species are dark brown. Fifty-two per cent of diurnal species have bright colours (red, yellow, green, often bicoloured), sometimes with a metallic sheen. Other diurnal species are dark or have dull brown cryptic colours (i.e. *Eurysternus* spp.). Within the tribe Phanaeini, diurnal *Oxysternon* species are iridescent bright green or red but the two *Phanaeus* species are bronze. Dawn–dusk-active *Coprophanaeus* species are iridescent blue or black and dark green.

The first two axes of the correspondance analysis explained 18% and 16% of the total variance, respectively. Modalities or classes of the variables were projected in

Table 1. Partitioning of time among 63 dung beetle species by species richness, abundance and weighted abundance, i.e. product of abundance and mean body size (percentage of the total in parentheses).

Diel activity[a]	Number of species	Abundance	Weighted abundance
Diurnal	27 (42.9)	901 (33.8)	8111 (35.2)
Nocturnal	13 (20.6)	431 (16.2)	4876 (21.2)
Dawn and dusk active	14 (22.2)	367 (13.8)	3988 (17.3)
Nocturnal–diurnal	3 (4.8)	934 (35.1)	5981 (26.0)

[a] The total percentage is not 100 because 6 species out of 63 were not categorized.
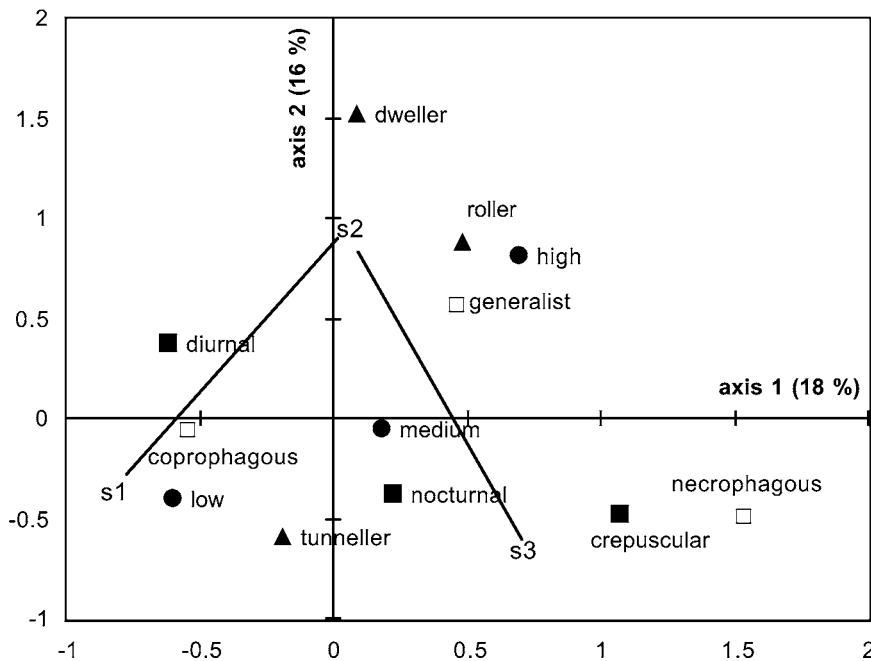
Figure 2. Multiple correspondence analysis. Projection of five niche variables and their modalities (in parentheses) of 57 dung beetle species, activity rhythm (■) (crepuscular, diurnal, nocturnal), food selection (□) (coprophagous, necrophagous, generalist), body size (s1: 3.4–7.9 mm; s2: 8–13.9 mm; s3: 14–45 mm), functional group (▲) (roller, tunneller, dweller) and relative abundance (●) (low: 0.01–0.19%; medium: 0.2–1.9%; high: 2–15% of total) in the plane of the first two factorial axes. Successive sizes are linked by lines.

the plane of the first two factorial axes (Figure 2). The farther a variable was projected from the origin of the axes along a factorial axis, the more it contributed to this axis. The projections of the characteristics of the species in the plane formed by the first two axes revealed three groups with associated modalities. Axis 1 separated small diurnal coprophagous species (32.8% contribution) from large crepuscular necrophagous species (47.5%). Axis 2 separated these two groups from middle-sized dweller and roller species (46.8%). The same axis separated the projections of functional groups, opposing dwellers and rollers to tunnellers. The total contribution of functional groups on this axis is high (40.6%) but non-negligible contributions were revealed on axes 3 and 4 (Table 2). Other variables or modalities also showed high contribution on axes other than 1 and 2. The variable food selection (diet) showed high contribution on axes 1 and 3. The variable rhythm showed a high contribution on the same axes but also on axis 4. The projection of nocturnal species was opposed to the one of species with other activity rhythm in the plane formed by axes 3 and 4.

In the simplest log-linear model that fitted the data, all two-factor effects were absent (loglikelihood-ratio $\chi^2 = 49.1$, df $= 72$, P $= 0.98$). All the four variables were completely independent of one another. Among the cases with the highest Freeman–Tukey deviates, only large necrophagous crepuscular tunnellers showed a

significant deviation (loglikelihood-ratio $\chi^2 = 4.80$, P $<$ 0.05) with a larger number of species than expected.

Body sizes varied significantly according to activity rhythm (Kruskal–Wallis statistic $= 6.84$, df $= 2$, P $= 0.033$). Diurnal species had smaller size (mean $\pm$ SE, 9.6 ± 1.1 mm) than crepuscular species (16.2 ± 2.7 mm, Mann–Whitney U $= 335$, P $= 0.016$). The species of different diet categories showed significant differences in body size (Kruskal–Wallis statistic $= 7.19$, df $= 2$, P $= 0.028$). Coprophagous species had smaller size (10.5 ± 1.2 mm) than necrophagous species (17.2 ± 3.4 mm, Mann–Whitney U $= 89.0$, P $= 0.13$). No significant variation in size was detected among functional groups.

Table 2. Percentage of variance extracted by axes of the multiple correspondence analysis of the species assemblage with the percentages of the contributions of the variables.

	Axes			
	1	2	3	4
Eigenvalue	0.369	0.325	0.267	0.244
% variance	18.4	16.3	13.4	12.2
Size	20.8	31.2	8.93	1.23
Rhythm	28.0	10.1	24.2	31.0
Diet	34.2	6.76	34.7	1.21
Functional group	4.42	40.6	25.6	27.0
Abundance	12.7	11.3	6.57	39.6

DISCUSSION

Factors such as temperature, humidity and light are known to regulate the flight activity of dung beetles (Landin 1968). In the Panamanian forest, several distinctive patterns were observed among diurnal species that reflect variation in temperature preferences (Gill 1991, Young 1984). Davis (1999) noted that in the Bornean forest species with peak activity during the hottest part of the day are more abundant in riparian forest where microclimatic conditions are brighter and less humid. Similarly, Gill (1991) observed in Panama that such species are commonly found in drier forests. In our study, the presence of species more active towards midday suggests tolerance to warm and dry conditions. Nevertheless it has been observed that most of them avoided forest gaps where extreme conditions prevail (S. Pincebourde *pers. obs.*). The species trapped in open habitats near forest edges are mostly nocturnal (F. Feer *pers. obs*). As in other studies, at Nouragues we observed a greater diversity of diel activity patterns among diurnal than among nocturnal species. This may be related to different physiological adaptations in response to a greater amplitude of microclimatic factors during daytime. Nevertheless, microclimatic fluctuations in the understorey of tropical forests are relatively buffered, which can explain why it is less easy to uncover distinct activity groups in this habitat than in savannas (Krell *et al.* 2003, Walter 1985). In the Nouragues forest, diurnal species tend to be smaller than nocturnal and crepuscular species (Figure 2). This widespread tendency in dung beetles (Cambefort 1991) may partially relate to thermoregulatory constraints during flight and following activity, which decline with increasing body size (Bartholomew & Heinrich 1978). Within the mostly diurnal tribe Canthonini small species are diurnal but large species (i.e. *C. bicolor*, *Deltochilum* spp.) are nocturnal or dawn–dusk active for the extreme sizes. Most species of the Phanaeini are diurnal but the largest species of *Coprophanaeus* are crepuscular (Edmonds 2000). Such a trend does not appear in the tribe Ateuchini because all species are small.

As a rule nocturnal species are black or dark in body colour whereas diurnal species show colour patterns. In French Guiana, nocturnal species differed from mostly coloured diurnal species. Crepuscular species are known for their dark iridescent colours (Edmonds 1972). A study on light environment and body colour of Phanaeini species of French Guiana, using spectrometry, suggested that their colours optimize intraspecific visual communication and/or avoidance of visual predators in the ambient light of their flight activity (Pincebourde 2002), see also (Vulinec 1997).

In this study, diurnal species were more numerous than nocturnal species. This has been found in other neotropical sites (Andresen 2000, Gill 1991), which contradicts the view of Halffter & Matthews (1966). Dominant diurnal species also characterize the tropical forests of Asia (Davis 1999, Hanski 1989) and Zaïre (Walter 1985), but equal or higher numbers of nocturnal species exist in other forests (Cambefort 1984, Escobar & Chacon de Ulloa 2000, Halffter *et al.* 1992, Howden *et al.* 1991, Walter 1985). These differences probably reflect variation in resource supply between different areas. In French Guiana, diurnal non-flying mammal species are less numerous than nocturnal species (Bongers *et al.* 2001) but their proportion among common species with body weight larger than 1 kg is clearly larger than for nocturnal species (67% vs. 30%) (Feer 2000). The dominance of diurnal over nocturnal species among dung beetles seems also to be related to a greater dung production during the day, as in Panama (Gill 1991) and Borneo (Davis 1999), whereas the reverse may be true in the Australian tropics (Howden *et al.* 1991). The defecation of large mammals usually peaks at the beginning and at the end of their activity period. For example the howler monkey, an important provider of dung in neotropical forests, defecates preferentially early in the morning and during the afternoon (Julliot 1997). Dung beetles showing bimodal flying activity (i.e. *G. semiopacus*) or a preference for the first half of the day may have adapted to this pattern of resource production. Such a coincidence was reported for *Canthon* species in Panama by Howden & Young (1981). Possibly because of the relatively small proportion of large nocturnal mammals, nocturnal dung beetles are active early in the night to exploit the remaining late afternoon dung production.

Many species considered as nocturnal in the literature are in fact crepuscular species which remain unnoticed because of inadequate sampling. In this study we differentiated 14 species with a short activity period limited to dawn and dusk, that is more than in any other neotropical forest areas. Most of these species are large carrion specialists (i.e. species of *Deltochilum* and *Coprophanaeus*). Their short, high-speed flight may be a good strategy to locate rare and unpredictable fresh carrion. But the fact that some species with different diets have adopted similar flight patterns suggests that it may be also a response to a temporally lower predation risk at twilight. In particular, large vulnerable ball-rollers such as *Deltochilum icarus* and *D. orbiculare* may escape from predators by restricting their foraging activity to this time.

Graphically, two groups of species based on body size, rhythm and food selection were identified. Small diurnal coprophagous species were opposed to large crepuscular necrophagous species. A third group introduced a difference based on functional groups, opposing tunnellers to other groups. The association between modalities of the

niche variables means that they are present in a relatively large number of species. This suggests that species packing exists in our species assemblage. However one must be careful with such an interpretation because the analysis showed that our associated modalities have projections dispersed on more than two axes. Further analysis showed that the distribution of the species fitted with a log-linear model where all the variables were completely independent of one another. This suggest that species distribution along the selected set of niche variables structures the community in such a way that it supposes a minimum interspecific competition. Only the large necrophagous crepuscular tunneller species, all of them members of the genus *Coprophanaeus*, comprised a larger number of species than expected. These species correspond to one of the groups previously delimited. Note that the diverse group of small coprophagous diurnal species is less taxonomically homogeneous. Our study suggests that activity rhythm may facilitate species coexistence with apparently the same efficiency as body size and food selection. Hanski (1989) gave prominence to a similar structure in the species assemblage of Scarabaeinae of Barro Colorado Island in Panama. Surprisingly, differentiation by functional group seemed comparatively less important. Hanski & Cambefort (1991a) established a competitive hierarchy among tropical dung beetles based on the functional group and size that may facilitate the coexistence of inferior competitors with the top competitors. Further studies are needed to classify our species according to such a hierarchy. Our analysis showed no clear effect of species relative abundance. Abundance differences of the species between guilds may be less important in terms of ecological separation than those between two adjacent species. Indeed, clear differences in abundance were found between species of *Dichotomius* or *Oxysternon* with similar size (Feer 2000). Niche variables other than those we adopted may lead to a finer segregation. Arboreal dung-relocation behaviour among small diurnal species exploiting primate dung has been observed in several tropical forests (Davis *et al.* 1997, Gill 1991, Walter 1984). In French Guiana, two *Glaphyrocanthon* species feed on primate dung caught up to 25 m high on canopy vegetation (Feer 2000), allowing them to reduce competition with other rollers with same food preference and diel activity. This example of small species foraging on small dung patches is not restricted to canopy-foragers. Some other small-dung specialists are known to exhibit species-specific preferences for small dung (Peck & Howden 1984). A preference for dung of howler monkeys characterizes five *Canthidium* and three *Glaphyrocanthon* species. Such a feeding specialization of diurnal species seems to be common in neotropical forests (Estrada *et al.* 1993) but it is documented less in other areas.

Hanski (1989) pointed out that size distribution and species diversity appeared reasonably similar in species assemblages of dung beetles from forests of Sarawak, Liberia and Panama, though there were taxonomic differences among faunas. He called for new and comparable data on dung and carrion beetles suitable for studies on convergence at the community level. Quantitative trapping data are newly available that allow a study of abundance relations in tropical communities. Recent studies generally provided data on species traits like body size, rhythm and diet. However, data on reproductive traits that may intervene in competitive hierarchies are comparatively less documented. Seasonal variation of abundance when present, is an important factor in temporal segregation. Moreover a comparative study should take into account the size of the vertebrates in the region and the consequences on resource volume and renewal (see Cambefort 1984).

Do dung and carrion insects in tropical forests exemplify equilibrium assemblages of species where coevolutionary niche separation through interspecific competition prevails? Comparative studies across a variety of communities must be undertaken in order to interpret the observed degree of species packing in light of species interactions. A critical approach to the selection of niche dimensions as the basis of the construction of models is needed. There is also a need for experimental studies on actual patterns of resource use or on competitive interactions. Comparative study of patterns may be becoming more difficult because many local communities are impoverished by various disturbances to the forest and the vertebrate fauna.

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Appendix 1. List of species with flight activity over a 24-h period [time of collection is Coordinated Universal Time (UTC) + 1], with number of animals taken by pitfall trap (n = 150 trap-days).

Subfamily / Tribe (Functional group) / Species	17	21	1	5	9	13	Rhythm[a]	Diet[b]	Size[c]
Coprinae (Tunnellers)									
Ateuchini									
Ateuchus near *aeneomicans* (Harold)					1	1	D	C	1
A. near *obscurus*					3		D	C	2
A. simplex (Audinet-Serville)		501	31	7	73	13	N D	G	1
Ateuchus murrayi (Harold)	33	99	24	12	25	47	N D	C	1
Ateuchus sp. 1	3				3	15	D	C	1
Ateuchus sp. 2		2	1		2		N	G	1
Canthidium aterrimum Harold		20	1	1	1		C	C	1
C. aurichalceum Preudhomme de Borre	2					8	D	N	2
C. bicolor Boucomont					1	1	D	C	1
C. near *angusticeps* Bates	*					*	D	N	2
C. near *chrysis* Fabricius	1					2	D	N	1
C. near *guyanense* Boucomont		3					C	C	1
C. deyrollei Harold		4			38		C	C	1
C. dohrni Harold	3	2			3	3	D	C	2
C. gerstaeckeri Harold					4	4	D	C	2
C. gracilipes Harold	1					1	D ?	C	2
C. onitoides (Perty)	4				3	4	D	C	1
Canthidium sp. 1	5	4			4	6	D	C	1
Canthidium sp. 2		4	3	2	2		N	C	2
Canthidium sp. 7	*					*	D	C	1
Uroxys sp. 1			14	3	4		N	C	1
Uroxys sp. 2	10	21	15	5	16	2	N D	C	1
Uroxys sp. 3				1			N ?	C	1
Pedaridium sp. 1					1		D ?	C ?	1
Coprini (Tunnellers)									
Dichotomius lucasi (Harold)		96	4	1	7		N	G	2
D. apicalis (Luederwaldt)		2					N	G	3
D. subaeneus (Laporte de Castelnau)		1	8	1	2		N	C	3
Dichotomius sp. 1		3	1				N	G	3
D. near *robustus* (Luederwaldt)			1		4		N	C	3
D. boreus (Olivier)		14	33	12	8		N	C	3
Onthophagini (Tunnellers)									
Onthophagus haematopus Harold		12			9		C	C	1
O. rubrescens Blanchard	28	21	1		28	72	D	C	1
O. xanthomerus Bates	1	3					D ?	G	1

Appendix 1. Continued.

Subfamily Tribe (Functional group) Species	Time of collection (h)						Rhythm[a]	Diet[b]	Size[c]
	17	21	1	5	9	13			
Phanaenini (Tunnellers)									
Coprophanaeus parvulus Olsoufieff		2			3		C	N	3
C. dardanus Mac Leay		2					C	N	3
C. christophorowi Olsoufieff					1		C	N	3
C. jasius (Olivier)		2			1		C	N	3
C. (Megaphanaeus) lancifer (Linné)		4					C	N	3
Oxysternon durantoni Arnaud	19	12			24	32	D	C	3
O. festivum (Linné)	7	1			3	13	D	C	3
Phanaeus cambeforti Arnaud					9	1	D	C	3
P. chalcomelas (Perty)	6				2	8	D	C	3
Sulcophanaeus faunus (Fabricius)					*		D	C	3
Scarabaeinae (Rollers)									
Canthonini									
Agamopus castaneus Balthasar			2	3	2		N	C	1
Canthon bicolor Laporte de Catelnau		17	6	1			N	C	2
C.(Glaphyrocanthon) quadriguttatus (Olivier)						1	D	C	1
C.(G.) femoralis bimaculatus Schmidt	1						D	C	2
C.(G.) semiopacus Harold	14				11	8	D	C	2
Trichocanthon sordidus Harold	51	2			14	201	D	G	2
Hansreia affinis (Fabricius)	7	2			44	13	D	C	2
Scybalocanthon pygidialis (Schmidt)		1			8	8	D	C	2
Sylvicanthon candezei (Harold)		1			1		D	C	2
Canthonella sp. 1					1		C ?	C	1
Deltochilum septemstriatum Paulian		86	3		27	1	C	N	2
D. guyanense Paulian		9			2		C	G	2
D. submetallicum (Laporte de Castelnau)		47	2	2	29	1	C	N	2
D. carinatum (Westwood)		6	9	4	8		N	N	3
D. orbiculare Van Lansberge		*					C	C	3
D. icarus (Olivier)		1					C	G	3
Eurysternini (Dwellers)									
Eurysternus hirtellus Dalman	3						D	C	1
E. confusus Jessop	34	4				44	D	C	2
E. cayennensis Laporte de Castelnau	10	1				24	D	G	2
E. balachowskyi Halffter & Halffter	4					2	D	G	2
E. caribaeus (Herbst)		5			5		D	C	3
E. hamaticollis Balthasar					1		C ?	G	3
E. velutinus Bates					53		C	G	3
Aphodiinae									
Aphodius sp. 1	1	34	18	44	38	3	N	C	1

* Direct observation.
[a] D: diurnal; N: nocturnal; C: crepuscular.
[b] C: coprophagous; N: necrophagous; G: generalist.
[c] 1: 3.4–7.9 mm; 2: 8–13.9 mm; 3: 14–45 mm.