

**Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera; Scarabaeidae)**

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Received December 4, 1981

PECK, S. B., and A. FORSYTH. 1982. Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera; Scarabaeidae). *Can. J. Zool.* **60**: 1624-1634.

A guild of neotropical rain forest dung scarabs, collected by baited pit traps, was composed of 11 genera and 31 species of Scarabaeinae. Relative abundances were highly equitable. Population densities were high and stable through the transition from wet to dry season. Competition for dung was intense and removal and burial rates were rapid. Resource use differed between genera and species in diel flight activity, foraging and dung removal methods, and behavior. Interspecific aggression and dung stealing behaviors were well developed. Reproductive activity was inversely correlated with aggression and parental investment.

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Un peuplement de scarabées bousiers de la forêt tropicale pluvieuse, récoltée au moyen de pièges à fosses munis d'appâts, a été étudié; il compte 11 genres et 31 espèces de Scarabaeinae. Il y a une forte régularité dans les abondances relatives. Les densités de population sont élevées et stables durant toute la période de transition entre la saison humide et la saison sèche. La compétition pour le fumier est intense et les taux de prélèvement et d'enfouissement sont rapides. L'utilisation des ressources varie d'un genre à l'autre et d'une espèce à l'autre: le vol ne se fait pas à la même heure chez tous, les méthodes de recherche et de prélèvement du fumier de même que le comportement diffèrent. L'agressivité interspécifique et les comportements de vol de fumier sont bien établis. L'activité reproductrice est en relation inverse avec l'agressivité et le soin apporté aux petits.

[Traduit par le journal]

### Introduction

Dung scarabs are known to be ecologically important in terrestrial habitats which support populations of large vertebrates. By burying and eating dung, scarab beetles increase the rate of soil nutrient recycling, decrease helminth and pest Diptera populations, and act as vectors for vertebrate parasites and disease (Lindquist 1933; Miller 1954; Bormemissa 1960; Halffter and Matthews 1966; Gillard 1967; Fincher et al. 1969; Klemperer and Boulton 1976; Nealis 1977). Most of these studies deal with only a few species inhabiting grassland or open areas in temperate regions. Virtually no quantitative data exist on the role of dung scarabs in tropical rain forest communities. Howden and Nealis (1975) demonstrated that a single locality in the Amazonian rain forest of Columbia supported an abundant and diverse dung scarab fauna of 60 species, and that clearing of the forest reduced the diversity and abundance of this fauna by a factor of 10. Because of the rate of habitat destruction through human population pressures, if quantitative studies of rain forest dung scarab ecology are to be made, they are required now while primary Neotropical rain forest yet remains.

There are theoretical as well as pragmatic reasons for

studying a guild of rain forest dung scarabs. The subfamily Scarabaeinae constitutes a well-defined taxocene (Hurlbert 1971) and in any one area its members constitute a guild (Root 1968). Their high sympatric diversity and abundance and mutual dependence on a clearly defined resource (dung) makes them ideal subjects for the study of competitive interactions.

Most Scarabaeinae exhibit only slight dung preferences (Halffter and Matthews 1966), yet a large number of species coexist on this resource. Thousands of individuals and many species may be attracted to a single deposit of dung within 2 h (Mohr 1943; Woodruff 1972). It is known that species exhibit some differences in flight activity and dung removal behavior (Halffter and Matthews 1966; Fincher et al. 1971). Nealis (1977) found that dung scarabs form communities of species according to soil types and vegetative cover at one site in Texas. We here present general observations and data on a guild of sympatric species and genera of Ecuadorian rain forest dung scarabs.

### Methods and materials

The study was conducted during May 1975, February 1976, and July 1976 at the field station of the Centro Científico de Rio Palenque, 47 km south of Santo Domingo, Pinchincha

0008-4301/82/071624-11\$01.00/0

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Province, Ecuador. The study site consists of 80 ha of primary rain forest surrounded by areas of variously disturbed habitat. The terrain is hilly, dissected by several small streams, and lies at the base of the western slope of the Andes, at an elevation of 200–250 m. The wet season begins in January and rainfall begins to decline in April and May. The dry season is not severe, for rains do occur and forested areas are constantly humid. About 3000 mm of rain falls annually (see Peck and Kukulova-Peck 1980).

Beetles were collected in baited pitfall traps similar to those described by Howden and Nealis (1975) and Newton and Peck (1975). Homogenized human dung collected from several people was wrapped in a double layer of cheese-cloth and used as 200-mL volume baits. Traps used to determine species seasonal abundances and composition were set at the same locations in each study period, along a 700-m transect through apparently homogeneous forest, 35 m from and parallel to Rio Palenque.

Species diversity was calculated from the largest (May) sampling using an information measure  $\hat{H} = -\sum p_i \log p_i$ , where  $p_i$  is the estimated importance value of species  $i$  (Pielou 1969). Importance values were calculated giving equal weight to the number of individuals per species and the number of biomass units per species, to compensate for the wide size range of different species.

Flight activities were measured by collecting all beetles every 4 h at freshly baited traps, beginning at 0100 for a 24-h cycle.

An estimate of population density and dispersal was made by a mark-recapture study after the seasonal species composition study ended. Beetles were trapped alive at dung baits, marked with enamel paint spots on pronotum and elytra, and immediately released at five color-coded stations along trails through the entire forest. The distance between stations varied between 50 and 600 m. Beetles were allowed 24 h to redistribute themselves after all traps had been removed from the area. Traps were then reinstalled.

To measure habitat heterogeneity effects, another five traps were placed at five visibly different sites in the forest. Trap contents were collected at 6-h intervals over 24 h.

Observations were made on preferences for different types of food placed in the forest. These were dung of horses and humans, rotting fruit (bananas), and carrion (chicken).

Behavioral descriptions are based on a total of 35 h of observation of 200-mL dung pads placed in the center of a 1-m diameter area from which surface debris had been removed. Observers sat quietly at the edge of this area and did not use insect repellents (which appear to affect beetle olfaction).

Taxonomic determinations were checked (by S. B. Peck) against collections in the British Museum (Natural History) and by H. F. Howden, Carleton University. Name usage corresponds to that in Howden and Young (1981). Since the determination of many species of neotropical rain forest dung scarabs is difficult (see Howden and Nealis 1975), we have occasionally utilized a generic name with only a species number. A complete species set with numbers is deposited in the H. F. Howden collection. Most of the data analysis is restricted to the subfamily Scarabaeinae and excludes the endocoprid Aphodiinae and other scarab subfamilies.

## Results

### Species diversity and relative abundances

On the 700-m transect, trap samples contained 10 911 beetles in May 1975, 2920 beetles in February 1976, and 2889 beetles in July 1976. These were composed of a total of 11 genera and 31 species of Scarabaeinae. Seven other genera and 12 species of scavenging scarabs were taken at Rio Palenque by other methods but are not incorporated into these numbers. Details of relative abundance of species in the guild are given in Appendix 1. Some species may be "accidentals" since they were represented by less than three individuals each out of a total sample of 16 720 beetles. Two of these, *Canthidium* sp. 6 and sp. 7 were commonly observed perching on low leaves in the forest (see Howden and Nealis 1978). Therefore, they were not rare but were just not attracted to the baits.

The mean dry weight biomass for individual beetles ranged from 0.001 g for *Aphodius* sp. 1 to 0.391 g for *Oxysternon conspicillatus*. The total dry weight biomass of the May collection was 188 g. In addition, the most numerically abundant species tend to be small or medium in size, averaging about 10 mm or less in body length. Table 1 demonstrates the difference in rank order that occurs if biomass is considered. Incorporation of biomass into importance value determinations gives a biologically more realistic measure of relative species abundances.

$\hat{H}$  (species diversity) was 3.257. Basharin (1959) demonstrated the expectation of  $\hat{H} = H - (S - 1/2N)$  where  $S$  is the total number of species,  $H$  is the actual species diversity, and  $N$  is number of individuals. It is reasonable that  $S$  is close to 31 since the last sample yielded no new species.  $\hat{H}$  is expected to differ from  $H$  by only 0.001.

Using the estimated value of  $H$ , the MacArthur-Terborgh species equitability index  $E$  (a measure of evenness of distribution of species abundances) was calculated following May's (1974) formulation:  $E = e^{H/S}$ , where  $e$  is the base of natural logarithms. A completely uniform distribution would give  $E = 1.0$ . Our data indicate  $E = 0.838$ , a more even distribution than a lognormal or even a broken stick model, which would predict  $E$  to be less than 0.65.

### Seasonality

There was no observed seasonality in the relative abundance patterns. The rank order of the dominant species remained identical in the three samples which span the wet-dry season transition. The relative abundance of some of the rare species changed only slightly and may reflect sampling error. Quantitative comparison of absolute abundances were not made because seasonal differences in rainfall cause differences in

TABLE 1. Comparison of rank according to number and biomass for 10 dominant species of Scarabaeidae collected in May 1975

Species	Number	Total biomass (g dry weight)	Rank by numbers	Rank by weight
<i>Onthophagus</i> sp. 1	4018	44.198	1	1
<i>Onthophagus acuminatus</i>	2909	14.545	2	5
<i>Canthon angustatus</i>	2460	29.520	3	4
<i>Onthophagus</i> sp. 3	303	6.363	4	7
<i>Ateuchus</i> sp. 1	243	3.402	5	8
<i>Eurysternus plebejus</i>	217	3.038	6	9
<i>Onthophagus</i> nr. <i>rhinolophus</i>	203	1.218	7	10
<i>Dichotomius batesi</i>	145	6.960	8	6
<i>Dichotomius satanas</i>	129	37.668	9	2
<i>Oxysternon conspicillatus</i>	76	29.716	10	3

TABLE 2. Differences in the total catches of dominant species at five traps at different locations in the forest, showing nonuniform distribution of dung beetles in the rain forest, July 1976

	Trap No.				
	1	2	3	4	5
Site characteristics					
Elevation	Depression	Upland	Upland	Upland	Upland
Understory vegetation	Sparse	Sparse	Sparse	Dense	Dense
Canopy	Dense	Dense	Dense	Dense	Thin
<i>Onthophagus</i> spp.	442	680	577	433	372
<i>Canthon angustatus</i>	27	105	140	36	3
<i>Dichotomius</i> spp.	49	35	47	53	36
<i>Ateuchus</i> sp.	26	56	21	8	14
<i>Oxysternon conspicillatus</i>	0	1	5	12	8
Totals	544	877	790	542	433

available flight time, and thus the efficiencies of traps are lower in the wet season. Our qualitative observations are that abundances are relatively constant through the wet and dry seasons in marked contrast to other groups we have observed such as nocturnal Lepidoptera.

#### Population density and dispersal

A total of 2178 beetles were captured, marked, and released over a 3-day period. The recapture sample of 3184 beetles contained only 41 that were marked.

With a simple Lincoln index (Southwood 1966) the size of the population was estimated at 169 217 individuals in the total area of 80 ha (over 2000 dung beetles/ha). More sophisticated measures were not feasible because of lack of data on mortality rates and other important population parameters. The small proportion of recaptures prevented any estimation of mean dispersal distances or rates, but some data were recovered. Two *Onthophagus* individuals were recaptured 80 and 100 m from their point of marking 1 day after

release. Two other *Onthophagus* were captured 180 and 700 m away 2 days after release. Three *Canthon angustatus* were captured 80, 100, and 300 m away 1 day after release. An *Oxysternon conspicillatus* was recaptured 50 m away less than 2 min after release and another was captured 1 km away 2 days after release.

#### Habitat heterogeneity

There were distinct differences in the proportions and abundances of the species of beetles caught at visibly different localities within the forest, 1 km away from the 700 m transect. Table 2 summarizes the total catch of the dominant genera for each of the traps. An analysis of variance for significant between-trap differences was performed on the capture data for *Canthon angustatus* and *Onthophagus* (mostly sp. 1 and *acuminatus*), the two most abundant genera (see Table 3). The between-trap differences were highly significant with  $p < 0.001$ . The trap localities differed primarily in elevation and in the amount of understory vegetation. Traps 1, 4, and 5,

TABLE 3. Between-trap differences in abundances, significant with  $p < 0.001$ , of *Canthon* and *Onthophagus*. The first value given in each column is for *Canthon*

Sample No.	Trap No.				
	1	2	3	4	5
1	7 99	63 103	59 178	19 77	1 34
2	5 76	26 78	39 77	10 61	0 47
3	11 68	10 118	21 87	4 83	2 118
4	4 199	6 381	21 235	3 212	0 173
Totals	27 442	105 680	140 577	36 433	3 372

TABLE 4. Relative food preferences in five common dung scarab species. Ranking scheme: 0, absent; 1, rare; 2, common; 3, abundant; 4, superabundant

Species	Food type			
	Dung			
	Human	Horse	Carrion	Fruit
<i>Ateuchus</i> sp. 1	3	4	0	0
<i>Canthon angustatus</i>	4	1	2	1
<i>Dichotomius satanas</i>	4	1	3	0
<i>Onthophagus</i> sp. 1	4	2	3	3
<i>Oxysternon conspicillatus</i>	4	1	1	0

which caught the least, were located in a depression and in thick understory vegetation. Traps 2 and 3, which caught the greatest numbers, were both in elevated areas with relatively sparse understory vegetation and a heavy canopy. The soils were the same clays at all sites.

#### Dung preferences

Table 4 ranks the abundances of five common Rio Palenque species at four classes of food. Fresh human dung was generally the most attractive. However, some species were more attracted to older dung. Figure 1 illustrates the general decline in attractiveness of human dung from traps in May 1975. The time of peak abundance varies between species. *Dichotomius satanas* and *Oxysternon conspicillatus*, the two largest species, rapidly decline in abundance, whereas *Canthon angustatus* and *Onthophagus* spp. seemed relatively insensitive to dung age until day 5 when fly larvae finally destroy the dung mass. The interspecific differences in this response may be related to food preference, odor perception, and foraging strategy. The decline is not a "trapping out" phenomenon (Howden and Nealis 1975) because a catch similar to that of day 1 was gained on day 6 when old baits were replaced by fresh baits (data not given). The same generalizations on preferences or "microserre" succession apply to trap results of February and July 1976.

The species succession pattern in Fig. 1 is interesting but probably artificial because the beetles were prevented from actually utilizing the dung. In nature we think the dung would be quickly disposed of, and would not be "available" for 5 days.

#### Diel flight activity

The activity curves and sample sizes for five genera are given in Fig. 2. Nocturnal activity was characteristic of *Ateuchus*, *Dichotomius*, and *Eurysternus* (not shown). Diurnally active genera were *Canthon* and *Oxysternon*. *Canthidium* (not shown) and *Onthophagus* contained nocturnal and diurnal species. *Onthophagus* flew in greatest numbers in early evening. No quantitative data were taken on the remaining genera but all appeared to be primarily nocturnal.

Each dominant genus exhibited a different activity pattern (Fig. 3). There were always some individuals active throughout the entire 24-h cycle. The biomass curve peaked in the evening primarily as a result of *Dichotomius* and *Onthophagus*. During the day *Oxysternon* activity was responsible for the small activity peak while *Canthon* contributed heavily to over-all diurnal activity.

#### Foraging strategies

Dung scarabs are known to employ two relatively

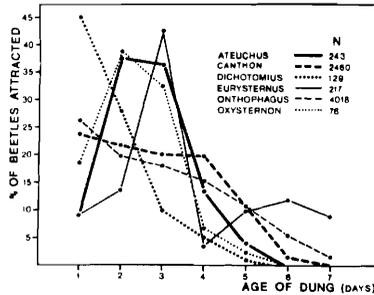


FIG. 1. The response of different genera to dung of different ages; *N* indicates sample size.

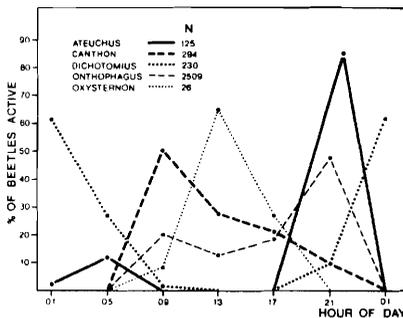


FIG. 2. Flight activities of different genera over 24 h. *N* indicates sample size and each point sums the trap catches of the previous 4 h.

distinct foraging "strategies" (Halfiter and Matthews 1966). One is perching on leaves waiting for an odor current, and the other is to fly or cruise and search for odor trails. Howden and Nealis (1978) have studied dung beetle perching at Rio Palenque. We present observations which corroborate, and in some ways add to, their findings.

*Canthon angustatus*, several *Canthidium* spp., and *Onthophagus accuminatus* were frequently observed sitting immobile on the broad leaves of the understory vegetation, usually at less than 1 m in height. Beetles often sat with the antennae exposed, presumably searching for odor currents since it is the antennal lamellae which are the principal site of long-distance olfactory organs (Warnke 1934). This searching posture was induced in resting beetles by exposing dung nearby. The characteristic response of the beetle was to raise the body, extend the antennae, lift the head, and expand the

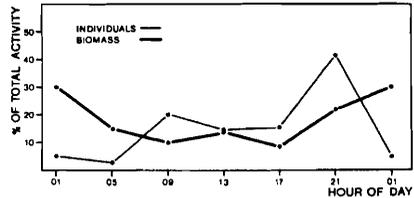


FIG. 3. The pattern of total dung scarab activity over 24 h.

antennal lamellae. The beetle then alternately moved the antennae and often slowly turned the body. At this point the beetle usually began a cruising flight. All cruising behavior observed in perching species took place at heights of less than 1 m.

The larger species such as *Oxysternon* and *Dichotomius* were not observed perching but appeared to spend much time in cruising. Observations and mist net captures of *Oxysternon* indicate a cruising height of 1–2 m, usually just above the understory vegetation. Using a red light at night, we observed *Dichotomius* making similar flights.

#### Discovery times

As Figs. 2 and 3 suggest, the time that elapsed before dung was found depended on the time at which it was made available. Average discovery times were short, with beetles usually arriving within 1 min during the day. The longest recorded discovery time during the day was 5 min at 1740. Late afternoon and predawn had the longest discovery times because of reduced flight activity. Arrival rates during the day were as high as 150 beetles during the 1st h.

Discovery time was approximately proportional to species size and abundance. During the day *Canthon*, *Canthidium* spp., and *Onthophagus* spp. all had first arrival times of less than 1 min in 10 trials while *Oxysternon* never discovered the dung in less than 5 min.

#### Approach behavior

The manner in which different dung scarab genera approached the dung was distinctive. There were also specific differences within the more diverse genera such as *Onthophagus* and *Canthidium*. Differences in approach behavior are probably indicative of differences in cruising behavior, but approach behavior was more readily observed than cruising.

*Onthophagus* flew relatively directly and rapidly toward the dung, making an occasional tight, low circle before plunging down, and often landing heavily. Some landed directly on the dung mass while others landed on the soil within 20 cm of the dung and crawled rapidly towards it. All *Onthophagus* immediately burrowed

TABLE 5. Distribution of different dung acquisition and nidification behaviors in common genera at Rio Palenque (see text for descriptions of these behaviors)

Genus	Ball rolling	Pushing	Direct burial under dung mass	Feeding in dung mass	Stealing	Klepto-parasitism	Male-female cooperation
<i>Aphodius</i>	-	-	-	+	-	+	-
<i>Ateuchus</i>	-	-	+	+	-	-	-
<i>Canthidium</i>	-	+	?	-	+	-	?
<i>Canthon</i>	+	-	-	-	+	-	+
<i>Dichotomius</i>	-	+	+	-	?	-	+
<i>Onthophagus</i>	-	-	+	-	-	+	-
<i>Oxysternon</i>	-	+	+	-	+	-	+

beneath the dung mass, but *O. accuminatus* occasionally perched on leaves near the dung before flying to the dung.

The diurnal *Canthidium* species exhibited a similar but less direct approach behavior, flying more slowly and making several zig-zag circles. They frequently perched on leaves or landed on the soil or dung. Nocturnal *Canthidium* sp. were not observed approaching the dung.

*Canthon angustatus* flew to the dung using a slow, zig-zagging circling pattern 10–20 cm above the ground. Individuals usually landed directly on the dung mass and began cutting a dung ball. Some landed on or beside dung balls of other *Canthon* and the dung fragments of *Canthidium* individuals up to several meters from the main dung mass.

*Oxysternon* approached the dung in wide zig-zags, often taking many passes to locate the dung. They frequently collided with dense vegetation. Individuals landed clumsily on the ground or dung and immediately burrowed under the dung.

#### Dung removal

Six modes for acquiring and removing dung for feeding and (or) reproduction were observed. Dung was transported by either rolling a formed ball, pushing an unformed piece, or excavating a burrow beneath the dung and pulling dung into the burrow. Other species fed directly in the main dung mass, stole dung from other beetles, or utilized a kleptoparasitic strategy, laying their eggs or feeding in the dung mass of another beetle. Table 5 summarizes the distribution of these behaviors for the common genera of scarabs at Rio Palenque.

*Canthon angustatus*, as the main ball-roller, was the scarab most important in dispersing the dung over a wide area. Balls were rapidly cut within 4–30 min after arrival, depending on the consistency of the dung mass. Up to 30 individuals were found cutting balls at one time on a single piece of dung. Balls were usually 5 mm in

diameter. Balls were rolled 1–6 m away from the dung before burial. The factors affecting the distance rolled were not discerned. Individuals prevented by a barrier from rolling dung more than 15 cm from the main dung mass eventually abandoned the dung. Burial was rarely initiated unless the beetles were concealed under leaf litter or other debris. Balls were buried in shallow vertical burrows several centimetres in depth. Beetles retained contact with the ball while building a burrow.

Diurnal *Canthidium* spp. were the only other beetles which consistently transported dung away from the main dung mass. *Canthidium* cut irregular pieces, using the head while grasping onto the main dung mass or soil. The size of the piece cut varied greatly but usually exceeded the size of the beetle. The dung was pushed by the head for distances usually less than 2 m. Sexual pairs and burrows were never observed.

*Oxysternon conspiciellatus* was the most rapid and vigorous diurnal dung burier. Burrows from 15 to 45 cm in depth were usually constructed directly under the dung mass, and descended at a 30–45° angle from the surface. Excavated soil was pushed up under the dung mass. Feeding burrows were unbranched, usually less than 23 cm in depth and inhabited by a single beetle. Brood burrows resembled those described for *Phanaeus* by Halffter and Matthews (1966). Burrow construction took between 15 and 20 min. If several *Oxysternon* burrows existed under a dung mass, individuals arriving later were often physically repulsed by those already present. Displaced individuals then cut and pushed away a large piece of dung in a manner similar to that of the diurnal *Canthidium*. Other *Oxysternon* individuals often fought for these pieces, which resulted in their being pushed up to 7 m from the main dung mass. Usually they were only moved 1 m away before burial. While the burrow was being constructed, dung remained unattended on the surface unless a pair worked together. Dung was pulled into the burrow entrance using the forelegs and then pushed with the head into a solid wad at the end of the burrow.

*Dichotomius* behavior at night was similar to that of *Oxysternon*. It was the most important nocturnal species in terms of quantity of dung utilized.

*Onthophagus* and *Ateuchus* built shallow vertical burrows directly under the dung, usually less than 15 cm deep for *Onthophagus* and less than 8 cm deep for *Ateuchus*. No overt spacing or aggressive behavior was observed in these genera. Burrows were densely packed with dung and often contained several individuals. Examination of *Onthophagus* burrows revealed all possible sexual combinations and even different species in the same burrow. As many as 314 beetles were recovered from a 0.5-L volume of soil directly under a dung mass. When horse or cow dung was available, *Ateuchus* and *Aphodius* fed directly in the dung and hundreds of individuals were found in single pieces.

Dung burial rates were extremely fast. During the day or evening 200 g of human dung were invariably buried in less than 2 h. Cow or horse dung remained on the forest floor much longer because it attracted mainly *Ateuchus*, *Aphodius*, *Eurysternus*, and *Onthophagus* which fed directly in the dung rather than burying it.

In contrast to the forest observations, 200 g of human dung in cleared areas remained for over a day. *Ateuchus* and *Aphodius* were the only frequent genera at dung in open habitat.

#### *Combative and stealing behavior*

Combat was observed to result from attempts at dung stealing. *Canthon* and the diurnal *Canthidium* frequently stole from each other, although intraspecific encounters were more frequent. Female *Canthon* occasionally attempted to displace a female riding on a brood ball rolled by a male. Combat consisted of butting another individual from the dung and then attempting to push or roll the dung. Larger individuals almost invariably displaced smaller ones. For this reason *Oxysternon* was interspecifically unrivaled. *Canthon* could usually defeat species of *Canthidium* because of its larger size and superior ability to move the dung. Both sexes fought for dung, but male-male fighting was more frequently observed. Occasionally, male *Canthon* would repulse females attempting to mount the dung ball, and females frequently resisted attempts by males to take command of the dung ball. *Oxysternon* not only fought over dung pieces by butting and pushing but also attempted to force individuals out of their burrows, which was not observed to be successful. Occasionally, the dung pieces of *Canthon*, *Canthidium*, and *Oxysternon* were divided by the combatants.

Large species such as *Oxysternon* and *Dichotomius satanas* were occasional victims of kleptoparasitism. Brood balls were sometimes found containing *Aphodius* and Diptera larvae. *Onthophagus* adults were found in *Dichotomius* burrows and may act as kleptoparasites

(see Howden (1955), Halffter and Matthews (1966), and Hammond (1976) for reviews of kleptoparasitic habits).

#### *Sexual behavior and physiological state*

Detailed observations on mate acquisition and cooperation in nidification were made on *Canthon* and *Oxysternon*. *Canthon angustatus* male-female pairs were formed when a male constructed a ball and a female mounted the ball. The nuptial ball was usually larger than a food ball and was rolled by the male. Marked females sought males with a brood ball at the edge of the dung mass. On one occasion a female rolling a food ball abandoned it and mounted the nuptial ball of a male who passed nearby. Males often repulsed the initial mounting attempts of other individuals but if they discovered it was a female they then allowed her to mount the ball. If a male was removed from a male-female pair the female often remained immobile on the ball for several minutes and then abandoned the ball and searched for a new male with a ball. On occasion females began to roll the ball alone. When a female was present males buried the ball by burrowing beneath it while the female sat on it.

In *Oxysternon conspiciellatus* pairing occurred when males encountered a female building a burrow. If the male was accepted it began to drag dung from the main mass to the burrow entrance. The female remained in the burrow, excavating and pushing the dung down the burrow. Pairing also took place when a female was pushing a dung piece. A male would land and attempt to maintain contact with the moving dung until the female began to burrow. This male behavior remained the same even when two females were fighting for the dung. Males were not observed fighting for dung. This is remarkably similar to behavior reported for the related genus *Phanaeus* (Halffter and Lopez 1972; Halffter et al. 1974).

Male-female pairs of any species were observed relatively infrequently. Table 6 suggests reasons for this. Only a relatively small percentage of females in each species were reproductive, at least in July 1977. Dissection of preserved specimens revealed most females to have no well-developed eggs present. Reproductive females had a single large egg ranging from 0.5 mm in diameter in *Ateuchus* to 2 mm in diameter in *Dichotomius satanas*. By contrast most males were reproductive since they contained well-developed spermatophores. Mature beetles usually possessed 8-12 spermatophores. Older beetles (age indicated by wear on body parts) had fewer spermatophores. Spermatophores were 2 mm in length in *D. satanas*.

The nonreproductive males were usually newly emerged individuals as indicated by the comparative lack of pigmentation and weak chitinization of abdominal sterna and penis.

TABLE 6. Proportion of reproductive females and males of five species (July 1977 sample) arranged in order of increasing body size and parental investment

Species	Sample size	Male/female ratio	% males reproductive	% females reproductive
<i>Ateuchus</i> sp. 1	100	0.66	92.50	42.86
<i>Canthon</i>	100	1.63	82.25	31.57
<i>Dichotomius batesi</i>	94	1.09	97.96	9.76
<i>Dichotomius satanas</i>	126	1.11	83.58	1.69
<i>Oxysternon conspicillatus</i>	22	3.4	100	0.00

Only 18% of the 442 individuals dissected had discernable intestinal contents. A wide range of variation in individual body size exists within most species, and may be due to differences in the amount of dung supplied for larval consumption.

### Discussion

Competition for dung among the forest Scarabaeinae at Rio Palenque appeared to be intense and was the most obvious ecological factor influencing their behavior. Population density may be determined by dung availability, which we assume to be a limited resource. This is suggested by the small proportion of individuals which contained intestinal contents, the rapid removal or consumption of dung, and the development of aggressive combat and interference behaviors in many genera. "Partitioning" of the limiting resource seems not to have occurred through the development of specific dung preferences. Most species seem to utilize a spectrum of dung types, at least for adult feeding. Rather, it is the existence, as we have found, of different activity periods, foraging behaviors, body sizes, dung removal methods, and feeding behaviors that suggest that relatively specialized resource utilization characteristics exist for Neotropical forest dung beetles.

Most Scarabaeinae utilize mammalian dung (Halffter and Matthews 1966). This should be available throughout the year, and populations should be relatively stable in relation to the life expectancy of the scarabs throughout the year if there is no climatically induced seasonal mortality. This is probably responsible for the observed aseasonality and stability of the species abundance relationships at Rio Palenque. The dependence on a single and continuously available resource appears to produce the high equitability of the relative species abundance as predicted by May (1974, 1975).

We think it evident that a large and diverse mammal fauna should be important for the support and maintenance of a large and diverse population of forest dung scarabs, but to what extent is not clear. The list (unpublished) of native mammals for the Rio Palenque Station forest contains 26 species, excluding Chiroptera, and includes four marsupials, eight carnivores,

three primates, four rodents, three artiodactyls, and five edentates. Domestic animals only rarely enter the Rio Palenque forest. A significant but variable dung contribution is probably made by human residents of the station. We can only guess at the importance of the dung contribution of each forest mammal species in the support of the dung scarab guild, without doing a careful population census of each. We suppose that monkey dung is important in maintaining the scarab fauna that is attracted to human dung, but the low numbers of the three species at Rio Palenque (the Squirrel and Woolly monkey and a marmoset) suggests that the beetles must also use other dungs or other foods. This is in contrast with the large dung beetle populations found on Barro Colorado Island, Panama and elsewhere (Howden and Young 1981; G. Halffter, personal communication) that seem to be mostly supported by a single vertebrate species, the Howler monkey. Yet, significant dung scarab guilds can exist in the absence of this species, such as at Leticia, Columbia, where Howden and Nealis (1975) found over 50 species in a forest from which Howlers had been hunted-out several years earlier, and where the other mammals had been actively hunted by the local people for at least the previous 10 years.

Mammalian dung may be produced at a relatively constant rate in the rain forest but distributed in an unpredictable manner. Competitive success depends to a large degree on the ability of a beetle to rapidly locate dung. Much of the competition is in the form of a scramble. However, some genera have evolved behaviors that decrease competition; the most obvious being the removal and burial of dung. In the Rio Palenque scarab guild, the degree to which this interference behavior was developed correlates well with many life history traits such as reduced fecundity and increased parental care. It is known that the Scarabaeinae have reduced reproductive capacity relative to other subfamilies of Scarabaeidae (Robertson 1961; Halffter and Matthews 1966; Halffter 1977). They possess a single ovary instead of several, mature a single egg at a time, and require an extended adult feeding period before becoming sexually active. We found that only a small proportion of females at Rio Palenque are sexually

active at one time. The proportion of reproductively active females was clearly and inversely proportional to the amount of parental effort invested in the offspring if we consider burrow construction and provisioning a good qualitative measure of investment. It was the larger genera and species such as *Oxysternon* and *Dichotomius satanas* that were observed to be relatively aggressive, sexually dimorphic, with heavy investment, and the most male-female cooperation in nidification. These had the lowest level of reproductive capacity in anatomical and physiological terms. *Ateuchus* and *Onthophagus*, anatomically the most reproductively competent genera, show almost no aggressive behavior and invest little in nidification.

Reduced female reproduction has several potential effects on social and competitive behavior. In our study the majority of males were sexually active. Strong sexual selection operates on males if a Bateman (1948) effect is present, producing a high variance in male reproductive success relative to females. As Trivers (1972, 1976) has emphasized, as females invest more heavily in their offspring, their mate selection behavior may be expected to evolve towards choosing males which are also making an increased investment. Consideration of Scarabaeinae life histories (Halffter and Matthews 1966; Wilson 1971; and our observations) appear to confirm this expectation. In *Canthon angustatus* the males do the preliminary work on nidification, but the female transforms the ball to a brood ball. In *Oxysternon conspicillatus*, males adopt the above-ground role in cooperative nidification. This presumably exposes them to a greater predation risk than females. Males in the closely related genus *Phanaeus* are known to exhibit a predator avoidance behavior (Halffter et al. 1974) and are known to be eaten by birds (Woodruff 1973).

Aggressive behavior appears to have been underestimated by previous authors. Halffter and Matthews (1966) state "fights are invariably between members of the same species." We routinely saw interspecific combat in *Canthidium* and intraspecific combat in *Oxysternon* and *Canthidium*. Lack of observation of interspecific aggressive behavior probably results from the fact that most scarab ethology has been observed in open and often agriculturally disturbed areas with a low number of species, but large numbers of individuals. The Neotropical rain forest has many species and perhaps a comparatively lower number of individuals of each species, which should lead to greater opportunity for interspecific combat. For example, Rio Palenque forest, with over 40 species of dung scarabs contains a diversity similar to that of the entire state of Florida (Woodruff 1973).

Aggression in large species may be selected for by both intraspecific and interspecific competition. Larger

species take more time for dung discovery and aggressive removal of dung may be compensation for this. Small species can compete with larger species by utilizing smaller pieces of dung, which may be more abundant, and by discovering these more quickly. We suggest that small species may also use a wider variety of dung, including those of invertebrates such as land snails, caterpillars, and millipeds. Amongst the combative species, combat favors larger-sized individuals. This could select for increased body size until opposed by the increased energy expenditure required by foraging for the larger but scarcer dung source. This situation is similar to that reported by Johnson and Hubbell (1974) for meliponine bees.

The result of the observed competition, high diversity, and high density of the dung scarabs is the rapid location, burial, and consumption of dung in tropical rain forests. From this study and other field experience, we agree with Howden and Nealis (1975) that the clearing of rain forest effectively eliminates the native forest dung scarabs. With clearing and the introduction of cattle into an area comes the establishment of a different but smaller group of eurytopic species that are associated with human activity. The rapidity of establishment of these species depends on the time the region has been open and in contact with neighboring clearings. These are the species that are already comparatively well known. In contrast, where undisturbed Neotropical rain forest still remains, diverse opportunities still remain for ecological and ethological studies on the poorly known guild of forest dung-feeding scarab beetles.

#### Acknowledgements

Assistance in the field was provided by the 1976 Earthwatch Expedition to Ecuador. We also thank Ken Miyata, Jarmila Peck, and Richard Webster for field help. Henry F. Howden provided unpublished observations and aided in identifying the beetles. E. O. Wilson and Harvard University provided A. Forsyth with facilities and financial support. The Natural Sciences and Engineering Research Council of Canada provided operating grants to S. B. Peck. Turid Hölldobler prepared the figures. Above all, we thank Caloway Dodson (Marie Selby Botanical Gardens), Earl Rich (University of Miami), and the Rio Palenque Corporation who were instrumental in having the land of the Rio Palenque station set aside as a protected biology field station of the University of Miami and the Catholic University of Quito. Gonzalo Halffter and H. F. Howden suggested improvements to the manuscript.

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APPENDIX 1. Summary of collections of rain forest scavenging Scarabaeid beetles of the Rio Palenque Field Station, Ecuador

Dung-baited pit trap catches in the species composite study				
	May 1975 (6 traps, 7 days)	Feb. 1976 (5 traps, 5 days)	July 1976 (5 traps, 3 days)	Other habits and studies
<b>Scarabaeinae</b>				
<b>Scarabaeini</b>				
<i>Eurysternus caribaeus</i> Herbst	21	2	6	Carrion
<i>Eurysternus plebejus</i> Harold	217	79	24	Perching, carrion
<i>Eurysternus claudicans</i> Kirsch	1		2	
3 <i>Canthon angustatus</i> (Harold)	2460	376	394	Perching, carrion
<i>Canthon bimaculatus</i> (Schmidt)			1	
<i>Canthon</i> sp. 13				Perching
<i>Deltochilum parile tolimensis</i> Paul.				Carrion
<i>Deltochilum gibbosum</i> group, sp. 2				Carrion
<b>Coprini</b>				
<i>Ateuchus</i> sp. 1	243	259	194	Fruit
<i>Pedariidum pilosum</i> Robinson	61	3	7	
<i>Scatium</i> , nr. <i>furcatum</i> Balt.	5	33	5	
<i>Uroxys gorgon</i> Arrow	2			
<i>Uroxys</i> sp. 2	1	2		
<i>Canthidium</i> , nr. <i>haroldi</i> P. de Borre	20	7	28	Perching, carrion
<i>Canthidium</i> , nr. <i>tuberifrons</i> Howden & Young	4		1	
<i>Canthidium aurifex</i> Bates	17	7	5	Perching
<i>Canthidium</i> , nr. <i>centrale</i> Boucomont,	10	48	23	Carrion
<i>Canthidium</i> sp. 5				Perching
<i>Canthidium</i> sp. 6		1		Perching
<i>Canthidium</i> sp. 7		2		Perching
<i>Canthidium</i> sp. 8		1		Perching
<i>Dichotomius satanas</i> (Harold)	129	188	252	Carrion
<i>Dichotomius batesi</i> (Harold)	145	293	46	Perching
<i>Copris lugubris</i> Boh.	2	7	2	
<i>Coprophanes ohausi</i> (Felsche)				Carrion
<i>Phanaeus apollinaris</i> Gillet				Fruit
<i>Phanaeus noctis</i> Bates	8	6	1	
2 <i>Onthophagus accuminatus</i> Harold	2909	669	1150	Perching, carrion
4 <i>Onthophagus</i> sp. 3	303	50	16	
<i>Onthophagus batesi</i> Say	13	84	43	
<i>Onthophagus</i> , nr. <i>rhinolophus</i> Harold	203	49	32	Carrion
<i>Onthophagus</i> , nr. <i>bidentatus</i> Drap.	8	15	39	Fruit
<i>Onthophagus conscineus</i> Bates	25	18	10	
<i>Onthophagus criniis panamensis</i> Bates	7			
<i>Onthophagus</i> , nr. <i>canellinus</i> Bates	3	3	18	Fruit, perching, carrion
<i>Onthophagus sharpi</i> Harold				Fruit
Totals	10 911	2920	2889	1,120
Beetles per trap per day	260	117	193	
<b>Aphodiinae</b>				
<i>Aphodius</i> sp. 1	320	805	222	Carrion
<i>Aphodius</i> sp. 2	2	1		
<i>Ataenius</i> sp. 1				Horse dung
<b>Hybosorinae</b>				
<i>Pseudohybosorus</i> sp. 1		2		
<b>Melolonthinae, Macroductylini</b>				
<i>Ceraspis</i> sp. 1		1		Fruit
	5	25	24	23