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FORAGING BEHAVIOUR OF TROPICAL
FOREST SCARABAEINAE IN PANAMA.

by

BRUCE DOUGLAS GILL, B.Sc.

A thesis submitted to
The Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of
Doctor of Philosophy.

Department of Biology

Carleton University

Ottawa, Canada

March 27, 1986

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FOREST SCARABAEINAE IN PANAMA"

submitted by

BRUCE DOUGLAS GILL, B.Sc.

in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

.....
Chairman, Department of Biology

.....
Thesis Supervisor

.....
External Examiner

Carleton University

April 29, 1986

ABSTRACT

Foraging behaviour of Scarabaeinae was studied in several lowland and montane forests in Panama and adjacent Costa Rica. Ninety-five species were recorded over a two-year period. Data on hourly flight abundance and flying height were collected using flight interception traps. Behavioural data were collected for 35 species that perched on leaves. Food preferences and food relocation techniques were examined by use of baited soil and pitfall traps and by observation of naturally occurring food resources.

Scarabaeine species exhibit distinctive temporal and spatial activity patterns. These patterns appear to have evolved in response to differences in the availability of preferred resources. Canopy based dung of howler monkeys had several specialist dung beetles while ground based rodent pellets were the preferred food of several understory perching species. Other feeding specializations were evident including living in ant refuse piles and bromeliads.

Energetic constraints of foraging mode and predation pressure may have a strong influence on Scarabaeine behaviour. Different foraging strategies may also reduce interspecific competition for food and thereby permit the high diversity exhibited by Neotropical Scarabaeine faunas.

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"It is doubtful whether there is any other large group of beetles which, as a whole, can be pronounced as definitely useful to mankind as the Coprinae."

Gilbert J. Arrow, 1931

ENTOMOLOGICAL
RESEARCH
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You know what I hate about dung beetles?
Their silly little coprophagous grins..

"Multum adhuc restat operis, multumque restabit;
nec ullo nato post mille saecula praecludeture
occasio adhuc adjiciendi"

Seneca, 1st C. A.D.

INTRODUCTION

Detritivores form a vital link in the nutrient cycling and energy flow of ecological systems (Ricklefs 1979; Odum 1983). In the terrestrial environment detritus feeding organisms are of major importance in forest ecosystems (Wiegert and Owen 1971) and are capable of consuming upwards of 90% of the primary production (Woodwell 1970; Ricklefs 1979). In addition to leaf litter and other plant remains, the recycling of animal wastes such as carrion and dung is also dependant upon the activity of detritivores (Putman 1983).

Dung beetles of the subfamily Scarabaeinae are dominant members of the dung and carrion feeding guilds in many grassland and forest ecosystems. Under natural conditions Scarabaeinae are capable of colonizing fresh dung in a matter of minutes and often in very large numbers (Waterhouse 1974; Heinrich and Bartholomew 1979; Beck and Forsyth 1982). Through their activities in burying animal wastes, dung beetles (including some Geotrupinae) aid in the formation of soils (Lindquist 1933; Brussaard and Runia 1984) and increase soil fertility by more efficient recycling of nitrogen and other nutrients (Gillard 1967; Bornemissza and Williams 1970; MacQueen and Beirne 1975; Kabir et al. 1985). The rapid removal of these waste materials is also important.

for the control of potential health hazards, such as parasitic nematodes (Miller 1954; Fincher et al. 1969; Fincher 1975) or pestiferous flies (Bornemissza 1970; Blume et al. 1973; Moon et al. 1980; Ridsdill Smith 1981; Wallace and Tyndale-Biscoe 1983). However, habitat destruction (Howden and Nealis 1975) or the introduction of exotic mammals (Waterhouse 1974) can radically alter the ecological balance and result in the accumulation of fecal material over long periods of time. The introduction of several mammal species to Australia serves to highlight the complex balance between dung beetles and their environment.

Australia has a native Scarabaeine fauna of about 300 species (Matthews, 1972, 1974, 1976; Storey 1977, 1984) that in many cases has evolved to utilize the dung of native marsupials. The small fecal pellets produced by these mammals are easily manipulated by beetles including the primitive ball rolling mentophilines (Matthews 1974). The introduction of rabbits (Oryctolagus cuniculus) and sheep (Ovis aries), two taxonomically distant species, did not upset the ecological balance with the native dung beetles since their fecal pellets were similar in size and consistency to those of the native marsupials. The introduction of cattle (Bos taurus), however, created a problem. The large wet dung pads produced by these grazers were completely unsuitable for most native Scarabaeinae.

One result was that pads persisted in the field for up to a year, with additions at the rate of about 400 million pads per day (Bornemissza 1976). The economic losses associated with this problem led to a major program for the importation of exotic dung beetles adapted to foraging on bovine dung (Waterhouse 1974).

The importance of foraging behaviour to a species' success is well known (Hassell and Southwood 1978). Yet as pointed out by Halffter and Matthews (1966, p.88) "We know little about food-search behaviour in the Scarabaeinae, other than it is carried out on the wing, as a rule." Since that time there has been a wealth of new information on dung beetle communities (Bernon 1981; Breymeyer 1974; Cambefort 1984; Hanski 1983; Hanski and Koskela 1979; Howden and Nealis 1975; Lumaret 1983; Nealis 1977; Olechowicz 1974; Oppenheimer 1977; Peck and Forsyth 1982; Walter 1977 among others) but relatively little work has been directed towards an understanding of the flight activity and foraging behaviour of species, and especially how these relate to community structure. This paucity of information may be due in part to the reliance of most studies upon data collected from baited traps. Pitfall traps, in particular, have a number of limitations (Adis 1979; Bernon 1980) and many dung beetles are known to exhibit strong biases towards different types of food (Halffter and Matthews 1966; Stewart 1967; Gordon and

Cartwright 1979) or quantities of food (Peck and Howden 1984), even though overlap in feeding niches may appear to be high (Halffter and Edmonds 1982). Thus even with a broad range of different types and quantities of bait, trapping studies can never duplicate the spatial and temporal diversity of potential food resources found in nature.

Studies in temperate ecosystems have shown that dung beetles (predominantly Aphodiinae at higher latitudes) exhibit strong temporal patterns in flight activity (Landin 1961, 1968; Fincher et al. 1971; Koskela 1979). Comparable studies in the tropics are scarce, perhaps as a result of the higher diversity and generally poorer state of taxonomic knowledge. Among the few studies available, Cambefort (1984) and Walter (1984) have shown that forest Scarabaeinae in Africa exhibit strong temporal differences in flight activity with some vertical stratification into the upper canopy (Walter 1983). Similar differences have been noted in Neotropical forests (Halffter and Matthews 1966; Howden and Young 1981; Peck and Forsyth 1982) and the observation of beetles perching on leaves (Ohaus 1900; Halffter and Matthews 1966; Howden and Nealis 1978) has been interpreted as a form of foraging behaviour, although different species may perch for a variety of reasons (Young 1982, 1984). The recent review of the Panamanian Scarabaeinae by Howden and Young (1981) now provides the

taxonomic basis for a detailed study of foraging behaviour at the community level. The purpose of this thesis is to examine the foraging behaviour of species in a diverse Neotropical fauna using a variety of baited and unbaited sampling methods.

Scarabaeinae from several forest locations in Panama and neighbouring Costa Rica were sampled with unbaited flight interception traps and a variety of baited pitfall and baited soil traps. Beetles were also collected while perching on leaf surfaces or at natural occurring food resources. The results indicate that species have evolved distinctive temporal and spatial activity patterns that maximize their efficiency in exploiting specific food resources. The habit of perching on leaves is used for a number of different reasons associated with foraging, including the detection of ground based resources (such as rodent pellets among species of the genus Canthidium), or canopy based resources (such as monkey dung among Canthon species). Scarabaeine communities are composed of species with differing food preferences or with complementary foraging behaviours that appear to minimize interspecific competition.

MATERIAL and METHODS

Study Sites

Field studies were conducted for varying periods of time between May 1981 and September 1983 at three major sites in Panama and eastern Costa Rica. Site #1 was on Barro Colorado Island (BCI), located in Gatun Lake, Panama at 9°09'N, 79°51'W. Barro Colorado is a hilltop of approximately 1500 ha that was isolated from the adjoining mainland in 1914 with the damming of the Chagres River during the formation of the Panama Canal. It has been a biological reserve since 1923 and has been administered by the Smithsonian Tropical Research Institute since 1946.

Barro Colorado is situated in the Tropical Moist Forest life zone (Holdridge et al. 1971) with an elevational range from 40 to 170 m above sea level. Located near the midpoint of the Isthmus of Panama, the island has a mean annual rainfall of 260 cm with a distinct dry season starting about late December and lasting until late April (Rand and Rand 1982). At ground level in the forest, seasonal temperature variation is minimal, with daily fluctuations, ranging from a mean minimum of 22°C to a mean maximum of 28°C (Smythe 1974). The forest itself is generally over 100 years of age with half remaining relatively undisturbed for the past 200 to

400 years (Foster and Brokaw 1982). As a result of its isolation and protected status, BCI has maintained a diverse mammal fauna with only the loss of a few species such as white-lipped peccaries and the larger cats during the last 50 years (Glanz 1982). Diversity and biomass estimates of the nonvolant mammals compare favourably with other lowland neotropical areas (Glanz 1982; Eisenberg 1980; Eisenberg and Thorington 1973), and make BCI one of the best studied mammal faunas in the neotropics. Further information on the geology, climate and biology can be found in Leigh et al. (1982).

Site #2 was located at approximately 1500 m elevation on Cerro Pelota, Chiriquí, Panama. Cerro Pelota is about 4 km north of Santa Clara at 8°52'N, 83°46'W in the Lower Montane Rain Forest life zone (Holdridge et al. 1971). This site is composed of relatively undisturbed forest at the upper limit of the coffee growing zone on the Pacific slope of the Chiriquí uplift. The terrain is typically steep with 20-40° slopes and the forest is contiguous with vast expanses extending north into the province of Bocas del Toro. Relatively low hunting and population pressures have resulted in the noticeable disappearance of only a few species such as white-lipped peccaries and Baird's tapir in the last forty years (R. Hartmann personal communication). The mammal fauna of the region was studied at the turn of the century by Bangs (1902). A more recent

summary can be found in the checklist by Handley (1966).

Site #3 was the Las Cruces Tropical Botanical Gardens located 4 km SSE of San Vito, Puntarenas, Costa Rica at 8°47'N, 83°02'W. Las Cruces has a 100 ha tract of remnant Premontane Rain Forest (Holdridge 1967) in the upper Coto Brus valley at 1200 m elevation. Like the previous site, Las Cruces has a slight dry season extending for several months in the early part of the year. With strong population pressure and severe deforestation in much of the surrounding area, many of the larger mammalian species are probably absent or at very low densities (Janzen and Wilson 1983; Wilson 1983).

Additional observations and data were collected from a number of minor study sites. These included the La Fortuna region in Chiriquí, Panama (Site #4); the town of Gamboa in the canal area of Panama (Site #5); the El Llano-Carti Road in eastern Panama Province, Panama (Site #6); and the Perlas Islands in the Gulf of Panama (Site #7). La Fortuna is a remote mountain valley at 800 to 1000 m elevation that is surrounded by a large expanse of Lower Montane Rain Forest. Situated on the continental divide, the region experiences high rainfall and lacks a distinctive dry season (McElravy et al. 1982). The Gamboa and El Llano-Carti Road sites are similar to BCI except that they are located on the mainland of the Isthmus of Panama where hunting pressure is greater, resulting in

mammal populations that are probably reduced, especially near the town of Gamboa. The Perlas Islands include a number of large continental islands that are covered to varying degrees with Tropical Dry Forest. Details of the mammal fauna for these islands can be found in Thayer and Bangs (1905) and Handley (1966). The locations of all study sites are shown in Figure 1.

Sampling Techniques

A variety of baited and unbaited traps, outlined below, were used to sample Scarabaeinae from the various study sites. Behavioural observations of beetles in the field were recorded on a portable cassette recorder. Placing the recorder in a self-sealing plastic bag permitted data collection during heavy rainfall. Where possible observations were recorded on slide film using a 35mm SLR camera. Close-up work was facilitated by the use of a 90mm 1:1 Macro lens and a ring strobe. The strobe permitted slides to be taken of beetles engaged in a variety of activities either at night or under the typical low light conditions of the forest during the day. Nocturnal observations were made with a red filter placed over the lens of a small 6-Volt headlamp.

Perching data were collected from beetles located on foliage up to a maximum height of 2.5 m above the ground surface. Estimates of relative density were conducted by walking through a sample quadrat of known area and removing all perching individuals. Walking counts were also conducted along transects through the forest or in quadrats artificially baited with dung. Heights were measured to the nearest cm above either ground level or surface litter using a pocket tape measure. Walking counts were timed using the countdown alarm function of a digital

wristwatch. Wind direction was checked by use of tobacco smoke drift.

Flight interception traps (FIT's) were used extensively in this study (Fig. 2). Modelled after the simplified version of Peck and Davies (1980), traps consisted of a standardized length and height of green mosquito netting (1.5 by 1.05 m) stretched between two poles and secured with string to neighbouring trees. A series of shallow aluminum pans or a sheet of 6 mil plastic was dug into the ground underneath the screen to form a collecting trough approximately 30 cm wide. The upper surface was positioned to match the surrounding ground level. The trough was then $3/4$ filled with water and an odourless detergent (Extran 300 (R)) was added to break the surface tension. In areas where traps could not be checked on an hourly or daily basis, a solution of propylene glycol was used as a collecting fluid to prevent decomposition of specimens. A large rain roof of clear plastic was also suspended several feet above the top of the screen to prevent flooding of the trough by rain water.

Placement of the traps was essentially at random on flat ground or parallel to the contour line on hillsides. Traps were always placed inside the forest and away from potential funnelling areas such as the margin of clearings or trails. Traps consisting of a collecting trough and

rain roof but lacking the center screen were used as controls.

To test for differences in flying heights, a series of four or five traps of standardized length but differing heights were run concurrently within a study site (Fig. 3). Water in the collecting troughs was changed every few days and had a small amount of sodium benzoate added to prevent any decomposition odours that might have otherwise influenced the flight behaviour of the beetles and hence the trap catch. Traps were serviced at various intervals by removing all specimens and debris with a 10 cm diameter fine mesh kitchen strainer. Contents were placed into whirlpak bags, preserved with 70% ethanol, labelled and subsequently sorted under a dissecting microscope.

Baited pitfall traps (Newton and Peck 1975) were used to sample scarabaeines from the various study sites. Traps were of two sizes; large 2 liter plastic buckets, and small 200 ml plastic cups (Peck and Howden 1984). Traps were placed into the soil with their tops flush with the surrounding ground, and then half-filled with water to which a few drops of detergent were added to break the surface tension. Large traps were baited with either 200 cc of rotting carrion or fresh human dung wrapped in two layers of cheesecloth and suspended from a stick 10 cm above the trap. Small traps were baited with either 2 cc or 0.2 cc of fresh human dung placed on a small stick

wedged across the mouth of the trap. In addition to human dung, small traps were also baited with other types of mammal dung when available. These included fresh agouti (Dasyprocta punctata), paca (Agouti paca) and coati (Nasua narica) dung. Traps were placed at five meter intervals along winding transects in the forest. A small palm leaf or other piece of vegetation was placed in the ground beside the trap to act as a partial rain roof. Care was taken so as not to obscure the opening of the trap. The time of placement of baits was carefully noted and the collection of specimens was accomplished by pouring the trap contents through a fine mesh kitchen strainer. Contents were preserved in 70% ethanol, labelled and subsequently sorted under a dissecting microscope.

Additional data on vertical stratification was obtained using an aerial pitfall trap. This consisted of a one-meter square piece of plywood that had a large circular hole removed from the center. A 2 liter plastic bucket was wedged into the hole with the upper rim level with the surrounding wood. Four pieces of rope connected the corners of the trap and were knotted together in the middle from which a 200 cc bait of human dung was suspended above the opening of the collecting bucket. A sturdy rope placed over a high tree branch was tied to the central knot and used to hoist the trap into the air after the bucket was half-filled with a collecting solution of

water and detergent. The trap was left in place for two days at each height then lowered to remove the beetles. Fresh dung was used at the beginning of each two-day sampling period.

Baited soil traps were used on occasion to examine the behaviour of beetles attracted to dung. Traps consisted of sinking pitfall containers flush with the ground surface, and filling them to within 1 cm of the top with firmly packed soil. A small amount of leaf litter was sprinkled over the surface then fresh dung was placed on the litter in the middle of the trap. After a one to two day period the containers were removed and the contents excavated with a table knife and forceps. The location and depth of all beetles were recorded along with observations on the presence or absence of feeding and nesting burrows.

In areas with a large number of ball rolling species (of the genus Canthon), soil traps with 200 cc of dung were modified as follows. A long strip of 4 cm wide plastic (1 to 2 mm thick) was pressed half-way into the ground to form a fence surrounding the trap at a distance of 50 cm. Soil was added to the outside of the fence to facilitate beetle entry. Two unbaited pitfall traps, similar to the design of Bernon (1980), were placed flush with the ground level along the inside edge of the fence. Fresh dung was then added to the center of the trap.

Taxonomy

The taxonomic scope of this study was limited to the subfamily Scarabaeinae (sensu Halffter and Matthews 1966). While not restricting this study to just the carrion or dung feeding guilds, previous studies of these groups in the Neotropics (Cornaby 1974; Howden and Nealis 1975; Young 1978; Peck and Forsyth 1982; Moron and Terron 1984), have shown that contributions by other groups such as Aphodiinae and Hybosorinae are minimal. Results collected in this study are in agreement with this view and for this reason data on these groups are not included.

The taxonomy and nomenclature of species follows Howden and Young (1981), Arnaud (1982, 1984) and Jessop (1985). Complete species citations are given in the Appendix. Identification of smaller species was verified in the field with either a 20x Coddington hand lens or a 30x stereo microscope. Voucher specimens are deposited in the collections of H.F. Howden and B.D. Gill.

Statistical Analysis

Chi-square and Log-linear analyses were performed using SPSS-X (Release 1.0 A) computer programs. All other statistical work was conducted using BMDP-83 programs. Programs were run on a Honeywell CP-6 operating system.

RESULTS

FLIGHT BEHAVIOUR

Temporal Activity

The diel flight period of species collected from hourly baited pitfall and flight interception traps is summarized in Tables 1, 2 and 3 for BCI, Cerro Pelota and Las Cruces respectively. Diurnal species were proportionately more abundant at the lowland site (Table 1, 27 of 35 species) than at either of the two montane sites (Table 2, 11 of 21 species; Table 3, 11 of 25 species). The flight of diurnal species was normally restricted to the daylight hours with only a few species extending their activity into the first hour after dusk (Canthidium ardens, Table 1; Canthidium leucopterum and Canthidium pallidolatum, Table 2; and Onthophagus praecellens, Table 3). With the exception of O. praecellens, these species were represented by only a few individuals taken after dusk. Nocturnal species generally commenced flight either shortly after dusk (eg. Canthon aequinoctialis, Table 1) or within the first hour of darkness (eg. Ateuchus candezei, Table 1). A few nocturnal species also extended their activity into the morning hours (Uroxys micros, Table 1) or began their flight

activity before dusk (Coprophanaeus chiriquensis, Table 3). In both of these cases the numbers of individuals taken in the day was very low, and appeared to be related to unusual climatic conditions (a rapid drop in light intensity due to thunderclouds in the case of C. chiriquensis), or feeding on fresh howler monkey dung in the case of U. micros (Fig. 12).

In contrast to the diverse diurnal and nocturnal groups, crepuscular species were few in number at all three study sites. Eurysternus caribaeus appeared to be the only crepuscular species on BCI (Table 1) and exhibited both dawn and dusk flight activity. Three species from Cerro Pelota, Deltochilum parile, Onthophagus mirabilis and Onthophagus belorhinus were crepuscular with flight activity only at dusk (Table 2). The same held true for individuals of O. mirabilis from Las Cruces as well as Onthophagus acuminatus and Eurysternus foedus (Table 3). Most species that were found at two or more sites showed very similar flight periods.

A total of three species, two diurnal (Canthidium ardens and Onthocharis panamensis) and one nocturnal (Dichotomius satanas) were common to all three sites and had roughly equivalent flight periods. The two montane sites (Tables 2 and 3) shared 10 species in common: 1 crepuscular (Onthophagus mirabilis), 3 diurnal (Canthidium variolatum, Onthophagus sp.1 and Sulcophanaeus velutinus)

and 6 nocturnal (Canthidium tuberifrons, Coprophanaeus chiriquensis, Coprophanaeus pecki, Ontherus didymus, Uroxys bidentis and Uroxys depressifrons. With the exception of Sulcophanaeus velutinus, all of these species had similar periods of flight activity at the two sites. Sulcophanaeus velutinus was relatively rare at Las Cruces yet its flight period there coincided with the period of peak activity exhibited at Cerro Pelota (Fig. 9). Three other species, Phanaeus pyrois, Onthophagus praecellens and Onthophagus acuminatus were common to BCI and Las Cruces. While P. pyrois had similar flight periods at the two sites, both species of Onthophagus had flight periods extending into the dark at Las Cruces.

Table 1 shows that the flight activity of many diurnal species extends almost continuously from dawn to dusk. The pattern of hourly flight abundance however differs greatly among species. The hourly totals for abundant (more than 15 individuals) diurnal species from BCI (Table 1) are presented in Figures 6, 7 and 8. Similar data are presented for abundant (more than 10 individuals) diurnal and crepuscular species from Cerro Pelota (Table 2) in Figure 9, and for abundant (more than 20 individuals) diurnal species from Las Cruces (Table 3) in Figure 10. The results show a number of activity patterns that can be described as unimodal, bimodal or platykurtic.

Several types of unimodal patterns are apparent

depending upon the degree of skewness and kurtosis (flatness). Distributions with little skewness are characteristic of midday active species such as Canthon lamprimus (Fig. 6), Eurysternus plebejus (Fig. 7) and Onthophagus lebasii (Fig. 8) and of midafternoon species such as Canthidium leucopterum (Fig. 9). These species all show a strong peak of activity about midway through their diel flight period. Crepuscular species such as Onthophagus mirabilis and Onthophagus beloninus (Fig. 9) also have a strong peak of activity, except that their total flight period was greatly compressed, giving a more peaked distribution. These crepuscular species had a very abrupt onset of activity in the field, followed shortly thereafter by a rapid decline. The total flight period of O. mirabilis lasted for only about 40 minutes, with most individuals collected in the first 15 minutes. The midday active species generally had a more gradual onset and cessation of diel flight activity.

Strongly skewed distributions are exhibited by two species of Canthidium. On BCI (Fig. 6) C. ardens began flight shortly after dawn but exhibited only a low level of activity through noon. It was not until midafternoon that activity began to increase, reaching a peak about an hour before dusk. A similar late afternoon peak occurred at Las Cruces (Fig. 10) where C. ardens showed a bimodal activity pattern. Canthidium perceptibile on the otherhand

has a distribution strongly skewed towards the morning (Fig. 10). This species had a burst of activity a few minutes after dawn which lasted for about one hour then diminished very rapidly to background levels for the rest of the day. On BCI (Table 1) C. perceptibile was rare and was only captured during the early morning.

Bimodal activity patterns are characteristic of species that have either a reduction or a total cessation of flight activity during the middle of the day. Species such as Canthidium aurifex, Canthidium haroldi (Fig. 6) and Onthophagus acuminatus (Fig. 8) had a burst of activity shortly after dawn which lasted for several hours then decreased to a relatively constant rate through midday. A second peak of activity equal to the first (C. aurifex), or less pronounced (C. haroldi and O. acuminatus) occurred about an hour before dusk. Canthidium pallidoalatum (Fig. 9), Phanaeus pyrois and Onthophagus nyctopus (Fig. 10) also had a burst of activity just after dawn but experienced a complete cessation of activity by late morning before resuming flight later in the afternoon. A similar pattern seems to hold for Sulcophanaeus velutinus (Fig. 9). Canthon moniliatus (Fig. 7) and Onthophagus stockwelli (Fig. 8) also exhibited bimodal activity but lacked a discrete period of peak activity.

In contrast to the above examples, a number of

species exhibited relatively even flight activity throughout the day. Canthon cyanellus sallei (Fig. 6) and Canthon sp.1 (Fig. 7) were active from an hour after dawn to the hour before dusk with only minor fluctuations in abundance. Onthophagus sharpi and Onthophagus crinitus panamensis on BCI (Fig. 8) and Onthophagus sp.1 at Cerro Pelota (Fig. 9) all commenced flight a little later in the morning but maintained generally even activity levels until dusk. Ateuchus aeneomicans and Canthon septemmaculatus (Fig. 7) had shorter flight periods of about 8 hours centered around midday. At Las Cruces, Onthocharis panamensis (Fig. 10) had a flight period of about 10 hours. It had a similar pattern on BCI except for a small peak of activity at the beginning of its flight period (Fig. 7). Phanaeus pyrois exhibited variation among sites with nearly continuous diurnal activity on BCI (Fig. 8) compared to bimodal activity at Las Cruces (Fig. 10).

Complete hourly flight activity of nocturnal species are not presented since data collection in the sampling regime was suspended for about 8 hours each night. However hourly data from the early evening and cumulative data from the first predawn sample in the morning indicate a number of features. The most noticeable trend is an overall reduction in flight activity in the middle of the night for all species. For example, on BCI a total of 34

Canthon aequinoctialis were taken from flight interception traps in the first hour of darkness over a five-day period. This compares with a total of 17 individuals taken during the second hour and 3 individuals taken during the third hour over the same five-day period. Additional specimens were collected in flight near baited traps during the last hour of darkness before dawn. Five other species from BCI (Table 1), Ateuchus candezei, Canthidium centrale, Dichotomius satañas, Uroxys micros and Uroxys platypyga show similar patterns of evening flight with at least some predawn activity. This pattern is likewise observed in a number of the nocturnal species from Cerro Pelota and Las Cruces (Tables 2 and 3). Whether there is continued or sporadic activity throughout the night or a total cessation of flight followed by a brief resumption of activity before dawn is unclear for most of these species. However a few species did exhibit bimodal activity.

At Las Cruces (Table 3) Coprophanaeus pecki was active for about one hour after dusk and one hour before dawn. Over a five-day period a total of 29 individuals was collected by flight interception or carrion traps. Of this total, 23 were caught in the first half-hour following dusk, 3 in the subsequent half-hour period and 3 in the hour before dawn. At Cerro Pelota C. pecki was less abundant and only a single specimen was collected in the

hour after dusk. Coprophanaeus chiriquensis may also have a bimodal activity pattern (Table 2) since it exhibits crepuscular activity at Las Cruces (Table 3).

A nocturnal species that exhibited both unimodal and bimodal activity patterns was Canthidium tuberifrons. At Cerro Pelota (Table 2) this species was active for about two hours after dusk. Over a five-day period, 19 specimens were collected from flight interception traps in the first half-hour after dusk. A further 7 specimens were collected in the second and third half-hour periods and a final specimen taken in the fourth and fifth half-hour periods after dusk. At Las Cruces (Table 3) the corresponding values were 14, 5 and 2 with an additional 3 specimens collected in the hour after dawn. Early evening activity was also typical of a number of species that were represented by only a few individuals such as Dichotomius femoratus (Table 1), and Deltochilum pseudoparile, Pedaridium pilosum and Scatimus quadridentatus (Table 3). Cumulative data from the first predawn samples indicate that there were no species at any of the three study sites that exhibited peak activity levels between 2200 hours and 0500 hours.

Vertical Stratification

On BCI a total of 2061 beetles comprising 32 species were collected in a ten-day period from five flight interception traps that ranged in net height from 15 to 120 cm (Table 4). Species diversity increased with trap size but not in a direct linear proportion to surface area. A doubling of the height (and surface area) from 15 to 30 cm showed the greatest increase in both number of individuals collected and species diversity. Subsequent doubling of heights to 60 and 120 cm showed less dramatic increases. This is reflected in the estimates of relative density. The 30 cm trap collected an average of 98.2 beetles per square meter per day, a value over twice as high as that of the 15, 60 or 105 cm traps. At Cerro Pelota four traps of 15 to 105 cm in height collected 561 beetles of 16 species in a twelve-day period (Table 5) while a similar series of traps at Las Cruces collected 413 beetles of 15 species over a five-day period (Table 6). At both of these sites, productivity was also highest in the lower traps although the larger traps collected nearly twice as many species. These contrasting results indicate differences in the flying height of the individual species. For species represented by more than 30 individuals at a single site, goodness-of-fit

statistics (Daniel 1978; Fienberg 1977) were used to test a series of models based on the data in Tables 4, 5 and 6.

The first model assumed a uniform distribution of individuals flying over the range of heights sampled. For this test the null hypothesis predicted a set of expected frequency counts based on the total surface area of the trap. Using a Chi-square analysis, only Canthon lamprimus (Table 4; $\chi^2=8.70$, $df=4$, $p=.069$), Onthophagus c. panamensis (Table 4; $\chi^2=7.85$, $df=4$, $p=.097$) and Uroxys bidentis (Table 5; $\chi^2=4.08$, $df=3$, $p=.253$) had observed values close enough to the expected to not reject the null hypothesis. Among these species trap catch appears to be related to overall surface area with no evidence of selectivity in flying heights.

A second model assumed a uniform distribution of individuals flying only in the zero to 15 cm height interval above the ground. Testing the null hypothesis of equal frequencies among all trap sizes, only Canthidium leucopterum (Table 5; $\chi^2=5.68$, $df=3$, $p=.128$), Canthon c. sallei (Table 4; $\chi^2=4.99$, $df=4$, $p=.288$) and Onthocharis panamensis (Table 6; $\chi^2=6.15$, $df=3$, $p=.104$) failed to reject the null hypothesis. For these three species an increase in trap area above 15 cm did not result in significant increases in the number of individuals collected. The remaining species however exhibited significant departures from this model to reject the null

hypothesis, in many cases at the .001 level. Log-linear analysis was used to discern differences in flying heights among this group of species.

In Log-linear analysis the relationship between frequency count and trap height was modelled through a series of Helmert contrasts utilizing maximum likelihood estimates (Fienberg 1977). With five trap categories for example, the first contrast compares the observed frequency in the lowest trap (Parameter 1) against the observed and expected counts of a model of the four larger traps assuming equal frequencies. The analysis provides both a Pearson Chi-square statistic as a measure of the goodness-of-fit for the model of the four larger traps and also a Z-score to assess the difference between the model and the first parameter. If there is a poor fit between the model and the observed counts in the four traps then a second contrast can be computed. In this case the observed frequencies of the first two traps (Parameter 2) are compared with a model of the observed and expected counts of the last three traps combined. Thus a total of $n-2$ models can be sequentially tested, where "n" equals the number of trap categories.

The results of Log-linear analysis are presented in Table 7. For the first four species in the table, the observed counts in the four larger traps (30, 60, 105 and 120 cm) had a good fit to the model as evidenced by

chi-square values below the critical value of 7.82 at the .05 level with 3 degrees of freedom. Parameter 1, the observed count in the 15 cm trap, was also significantly different from the model with Z-scores more extreme than -1.96. For these species only a few individuals were collected in the 15 cm trap while a relatively uniform number were collected in the 30 cm and larger traps. The model gives no indication of significant increases in numbers collected from traps over 30 cm in height. The same can be said for Onthophagus mirabilis which had a relatively uniform distribution in the 30, 60 and 105 cm traps. The remaining 8 species all exhibited significant departures from this model.

When the 15 and 30 cm counts were tested against a model of the 60 and 105 cm traps, Canthidium pallidoalatum, C. ardens (Las Cruces) and C. perceptibile all showed good agreement to the model (chi-squares less than the critical value of 3.84 at .05 with 1 df) and a significant increase over the two lower traps (Z-scores more extreme than -1.96). For O. acuminatus a good fit was obtained between the observed counts and the model for the 105 and 120 cm traps, and this was significantly different from the counts for the 60 and 30 cm traps (the 15 cm trap collected no individuals and was therefore excluded). With C. haroldi, the 105 and 120 cm traps also gave a good fit to the model and were significantly different from the

third parameter which included the 15, 30 and 60 cm traps. Finally the data for three species, Canthon aequinoctialis, Canthidium ardens (BCI) and Canthon sp. 1 did not show statistically significant patterns.

(Differences in vertical stratification among species were also evident from the dung-baited aerial pitfall trap (Table 8). Species diversity and total number of individuals were greatly reduced above ground level. However there was also a distinct faunal separation between the ground level and above ground level groups. Five of the six species collected at 1 and 8 meters were not present in the trap catch at ground level.

The decrease in species diversity and relative abundance is also seen in long-term blacklight trap data. Two modified Pennsylvania style blacklight traps (Smythe 1982) run for three years at 3 and 27 meters above ground level on BCI (Wolda, 1982) demonstrate reduced diversity and abundance at the higher level (Table 9). Uroxys gorgon was the dominant species and constituted nearly 85% of the individuals at both trap heights. Four of the six species taken at the higher height were also recorded from the two-day dung trap at 8 meters (Table 8). Similar blacklight traps run for 9 months at canopy level and two years at 3 meters height at La Fortuna (Table 10), also exhibited reduced Scarabaeine diversity and abundance at canopy level.

PERCHING BEHAVIOUR

Posture and Orientation

Beetles exhibit a number of characteristic postures associated with their perching activities. The most common is an active searching stance in which beetles sit facing into the wind with their heads elevated above the leaf surface (Figures 4, 5 and 15). This is accomplished by bringing the fore legs together under the prothorax while the mid and hind legs are positioned at varying angles alongside the body. The head is deflected upwards and the antennae are fully extended anterolaterally at a 45 degree angle with the lamellae widely separated. In this posture beetles orient with their heads positioned directly into the wind while gently oscillating their antennal lamellae. Slight changes in the direction of air movement are counterbalanced by shifts of the antennae or head. Larger changes in the direction of wind movement (greater than 10 or 20 degrees) require the beetles to shift their position by turning on the spot or by stepping forward while turning. As many as 15 beetles have been observed to shift 30 degrees nearly in unison while perched at different heights on a single plant. Under the usual conditions of very low wind speed near the ground level (generally less than 0.1 km/hr) beetles maintain this headwind orientation

and respond to changes in wind direction almost instantaneously. During periods of greater wind speed such as those which precede rain storms, beetles appear less capable of maintaining a headwind orientation.

A second posture often exhibited by beetles is apparently a resting stance. Typically a beetle will sit with its body flat and its head deflected downwards onto the leaf surface (Fig. 11). The fore legs are concealed beneath the pronotum and the mid and hind legs are drawn alongside the body. The antennae are often extended so that the widely separated lamellae project outwards from beneath the clypeogenal margin. Although the antennae oscillate gently, beetles rarely change their spatial orientation to correct for shifts in wind direction.

A third posture exhibited by only two species in this study appears to be a defensive display stance. As in the resting stance, beetles sit with their heads deflected downwards onto the leaf surface and their fore legs concealed beneath the pronotum. However the mid and hind legs are extended outwards from the body and the rear of the abdomen is slightly elevated (Fig. 16). The antennae are usually hidden under the head and the beetle does not assume any specific orientation with respect to the wind direction.

Response To Disturbance

When beetles perching in an active searching stance are disturbed by the close approach of a larger animal such as a human observer, one of several different responses is elicited. The simplest response is to quickly take flight and leave the immediate area. This behaviour is exhibited by nearly all of the diurnal perching species studied and can usually be induced by approaching the beetle slowly from an upwind direction. In contrast, nocturnal species rarely take flight even when approached in this manner.

A second response to disturbance among actively searching beetles is to quickly withdraw the legs and antennae under the body and crouch down against the leaf surface. This response is typical of nocturnal perchers and is seen in many diurnal species when approached rapidly or from a downwind position. Most of these species have a strongly concave proepisternum often with a complete and well developed proepimeral carina. When the antennae are withdrawn under the head, the fore femora are retracted into the excavated proepisternum and the head is lowered causing the contracted fore legs to lock between the proepimeral carina and the anterior ventral margin of the clypeus. The antennae and mouthparts are thus effectively sealed off on the ventral side. Beetles will

remain in this posture, similar to the resting posture outlined above (Fig. 11); for a short period of time (usually less than 1 or 2 minutes) before extending their antennae from underneath the clypeogenal margin. If no further disturbance occurs, the beetle will usually resume an active searching stance.

A third type of response is exhibited by two diurnal species of Canthon. Actively searching C. angustatus and C. subhyalinus quickly assume the defensive display posture (Fig. 16) when disturbed. Individuals of C. angustatus often maintain this posture for several minutes before extending their antennae and resuming an active searching stance. Canthon subhyalinus however maintains this posture for a much shorter period of time (up to 10 or 20 seconds) before extending the antennae or jumping up and flying away. This latter activity was not observed in C. angustatus.

In contrast to actively searching individuals, beetles in a resting stance respond to disturbance by withdrawing their antennae (if extended) and adopting the sealed up crouch as outlined above. Individuals of C. angustatus in the defensive display stance respond to disturbance by accentuating their posture. The pygidium is raised higher and the mid and hind legs are extended as far as possible. Individuals of C. subhyalinus will either accentuate their postures or quickly take flight.

Spatial and Temporal Distribution

The distribution of perching beetles varied greatly with respect to the height above ground level and to the presence of mammalian dung. On BCI a total of 22 species were recorded from leaf surfaces (Table 11). The mean perching heights ranged from a minimum of 11.5 cm for Canthidium hespenheidei to a maximum of 86.6 cm for Canthon angustatus. This latter species was also observed to perch above the 2.5 m maximum height sampled. In the absence of howler monkey dung only 14 species were recorded on foliage (Table 12). These individuals were all perching well below the 2.5 m upper limit of sampling. The conspicuous absence of C. angustatus from Table 12 is typical of a number of species that were found to perch only in the vicinity of howler monkey dung. The height distribution of this species (Fig. 19) contrasts sharply with those of two other abundant species Canthidium aurifex (Fig. 20a) and C. haroldi (Fig. 21a). In the absence of howler dung, the perching height distribution of these latter species showed very little change (Figures 20b and 21b). Of the 7 remaining species that perched only in the vicinity of howler monkey dung, Canthon subhyalinus had a perching height distribution similar to that of C. angustatus. The perching height distribution of Uroxys micros in which over 90% of the individuals were

associated with howler monkey dung also resembled the pattern for C. angustatus. Sample sizes of the 6 other species associated only with howler dung were too low to make valid comparisons.

At Cerro Belota a total of 6 species were recorded perching on foliage (Table 13). All of these individuals were found on leaves below 1 m in height. The perching height distributions of the two most abundant species are shown in Figures 22 and 23. There was no apparent mammal dung associated with any of the 278 individuals sampled.

A total of 9 species were recorded from Las Cruces (Table 14). The four most abundant species had similar mean perching heights with all individuals found between 4 and 55 cm above the ground surface. With the exception of the single Onthocharis panamensis, the remaining species at Las Cruces were generally found above this height range. Perching heights for species collected at Gamboa and the Perlas Islands are listed in Tables 15 and 16 respectively.

The diel perching activity of species broken down into nocturnal or diurnal periods (Tables 11-14) show complete congruence with diel flight periods generated from baited pitfall and flight interception traps (Tables 1-3). No individuals were observed perching outside of their respective flight periods nor were there any species that exhibited crepuscular perching activity. The temporal

• distribution of perching species at Gamboa and the Perlas Islands (Tables 15 and 16) also agreed with temporal flight data collected at these same sites. The duration of perch occupancy however differed among species.

Nocturnal species occupied single perches for longer periods of time than did diurnal species. Censusing transects repeatedly showed that many nocturnal species occupied perches for 20 or 30 minutes with occasional individuals remaining on a single leaf for an hour or more. Diurnal species in an active searching stance were more active and were rarely observed on the same perch after a ten minute period. To estimate movement times, two five meter square study plots on BCI had all perching beetles removed. After a five minute relaxation period each plot was repeatedly sampled for a five minute period leaving five minutes of relaxation time between samples.

The results (Table 17) indicate that beetles were capable of recolonizing the study plot within a 5 to 10 minute interval. To determine the effects of mammal dung on the relative movement and abundance of perchers, study plot 2 had five 200 cc pitfall containers placed equidistant from each other in the central two-thirds of the plot. Five minute perching samples separated by ten minute relaxation periods were collected with the five pitfall traps in plot 2 being baited with 2 cc of fresh human dung after sample 1. The results (Table 18) show a substantial increase in

the number of C. aurifex perching in the study plot containing the baited pitfall traps although only a single individual of this species was collected in the traps (Table 19). Similar results were obtained at Las Cruces (Table 20) where Canthidium ardens and to a lesser degree Canthidium perceptibile and Canthidium vespertinum, perched at higher densities in a study plot containing baited pitfall traps although these same species were not readily collected in the traps. Other examples of very localized high perching densities were also observed during foliage censuses.

On four separate occasions 15 to 20 individuals of C. haroldi and C. ardens or C. aurifex (species not determined) were located perching on the leaves of a single tree seedling or shrub. In all cases the majority of individuals dispersed within a five minute period of initial observation. Inspection of the surrounding area (within a radius of approximately 3 m) always failed to reveal any dung or other potential source of attraction. On another occasion a single agouti was observed walking through relatively open understory vegetation at 1030 hrs. After several minutes it sat down and remained in one spot. At the end of 30 minutes, the agouti departed when approached for a closer inspection. A total of 18 C. haroldi and 9 C. ardens or C. aurifex (species not determined) were perching in the sparse vegetation

immediately downwind from the resting site of the agouti. Fourteen of the C. haroldi and several of the smaller Canthidium flew away within two minutes of the departure of the agouti. After a further two minutes all the C. haroldi had departed and only 5 of the smaller Canthidium remained perching. A four-meter square area surrounding the site was carefully searched. However, no beetles nor any trace of dung could be located in the leaf litter or soil beneath.

Other Activities

In addition to the searching and resting behaviours outlined above, a variety of other activities were exhibited by beetles, perching on leaves. These included grooming, brushing, feeding and sunning behaviours.

Grooming of the head and its appendages was observed in a number of diurnal and nocturnal species. This was typically accomplished by rubbing the fore leg against the corresponding part of the head, probably in an attempt to remove small foreign particles. A similar behaviour was often observed in nocturnal perchers when the fore legs were used to remove droplets of water that had landed on the eyes or antennae. A second and very different form of grooming was seen in three species of Canthon.

Individuals of C. angustatus (Fig. 17), C.

subhyalinus and C. septemmaculatus (Fig. 13) were observed to brush the sides of the abdomen and pygidium with the mid and hind legs of one side of the body. To accomplish this, beetles stood on four legs and, while holding the two elevated legs together, rubbed the tarsi back and forth over the abdominal sternites and pygidium several times with a slow brushing action. This behaviour usually lasted for 10 or 20 seconds at the conclusion of which beetles resumed a normal searching stance. A similar behaviour was also seen in Onthophagus coscineus. In this species however only a single leg at a time was used to rub the side of the abdomen and the duration of rubbing was much shorter than in the three species of Canthon.

Several species including U. micros (Fig. 12) and C. subhyalinus were observed to feed upon dung located on leaves. In all cases the dung was from howler monkeys that had recently defecated in the canopy overhead. A number of species also attempted to relocate this dung. Individuals of C. aurifex and C. haroldi could be seen pushing small pieces of howler dung to the edge of a leaf at which point the dung fell to the ground and the beetle lost contact with it. In C. angustatus and C. subhyalinus however beetles removed howler dung by either rolling pieces of it off leaves or by forming it into balls and then rolling these balls off the leaves. Beetles maintained a firm grip on the dung as it left the leaf surface and thereby

maintained contact with it as it crashed to the ground. These two species appeared to ~~collect~~ howler dung from great heights in the canopy and often crashed onto lower story leaves (Fig. 18) in their descent to the ground. Several thousand individuals of C. angustatus were thus observed raining down from the canopy in this fashion.

Finally, two species of diurnal perchers, Eurysternus plebejus and Canthon septemmaculatus appear to selectively perch on leaves exposed to direct sunlight under certain conditions. Four of the five individuals of E. plebejus found perching were located on leaves in light gaps. The fifth individual was located in the shade but was busy grooming its antennae and mouthparts. All five beetles were perching between 1100 and 1330 hrs on warm sunny days and the four individuals in light gaps were very alert and flew away when approached. On the Perlas Islands (Table 16), C. septemmaculatus perched in light gaps and in shade on sunny days, but also perched on overcast or rainy days. On BCI however, 6 of 10 individuals were located on brightly illuminated leaves (Fig. 14) and these individuals were more alert than beetles sitting in the shade, flying away when approached.

FEEDING BEHAVIOUR

Baited Traps

Beetle species exhibited great differences in the degree of attraction to different types and quantities of baits placed in the field. In May and June 1981 on BCI (Table 21), 38 species were recorded from flight interception traps over a sixteen-day period. Over a similar twenty-day period pitfall traps baited with human dung collected substantially fewer species and of very different proportions than the FIT's.

Canthon aequinoctialis was the dominant species at all dung baited pitfall traps. It accounted for 70 and 74% of the totals collected from the two May samples, and 91% for the June sample (Table 21). In the flight interception traps this species ranked 4.5 and 14th in abundance for the May and June samples, corresponding to only 7.6% and 1.2% of the total individuals collected, respectively. After C. aequinoctialis the 200 cc baited traps were dominated by D. satanas, two species of Onthophagus and U. micros. With the exception of D. satanas, these species were all abundant in the FIT samples of May and June. At the smaller 2 cc baits, these species were surpassed in rank abundance by one of two species of Canthon.

A single pitfall trap baited with 200 cc of carrion

collected several hundred Canthon cyanellus sallei over a three-day period. Only a few individuals of other species such as C. aequinoctialis and Canthon moniliatus were also collected (data not shown).

A number of species were commonly collected in the flight interception traps but were rare or absent in the baited traps (Table 21). The genus Canthidium with seven species constituted 27% and 59% of the FIT totals for May and June respectively, yet were absent from the 200 cc baited traps and only rarely taken in the 2 cc traps. In June of 1983 a similar pattern emerged with large numbers of Canthidium collected in FIT's (Table 4) but only a few taken at 2 cc baited traps (Table 22). Canthon aequinoctialis once again dominated the baited pitfall traps and numerous individuals were observed removing bait from the soil traps. In the case of the 200 cc soil traps, unbaited pitfalls placed along the perimeter wall collected 505 individuals of this species, many with a ball of dung. After a two-day period the soil was excavated and 10 D. satanas were located in dung-filled tunnels at the bottom of the 16 cm deep containers (Table 22). Over three-quarters of the O. acuminatus were found in the bottom half of the traps alongside the burrows of D. satanas, including 12 individuals that were actually located inside the dung masses at the bottom of the containers. Uroxys micros were found down to a depth of 10

cm but were generally much shallower with 70% located in the top 4 cm of soil. Pedaridium pilosum were also found in the top 4 cm of soil. Scatimus ovatus were found at all depths but were most abundant around the 10 cm level.

In the 2 cc soil traps all specimens were located in the top 2 cm of soil except for the single Onthophagus stockwelli found at the bottom of the .9 cm deep container. At the bottom of another trap a Phanaeus pyrois brood cell was found, the beetle(s) having departed.

At Cerro Pelota, 22 species were recorded from baited pitfall and flight interception traps during a five-day period in July 1981 (Table 23). As at the previous site, the relative abundance of species differed greatly among the different trap types. Species such as C. leucopterus, C. pallidoalatum and O. mirabilis were abundant in FIT's but were rare or absent in baited traps. Other species such as C. chiriquensis, D. satanas and O. didymus were rare in FIT's but common in baited traps. Comparing the three series of baited pitfalls, the 200 cc dung traps collected more beetles per day than the 2 cc traps (7 compared with 4.9) although the species diversity was lower in the larger traps (9 compared with 12). The larger baited traps also collected greater numbers of three small species, Onthophagus nyctopus, S. quadridentatus and P. pilosum. The 200 cc carrion trap had the highest productivity of the baited traps (10.1 beetles/day) but

also the lowest diversity with 7 species only 2 of which, C. chiriquiensis and O. didymus were abundant.

Over a three-day period in July 1982, baited pitfall and flight interception traps once again collected 22 species at Cerro Pelota (Table 24). Seventeen species were common to both years and with the exception of O. nyctopus, the species present in only one year were collected in low numbers (usually only a single individual, but up to 5 or 6 in some species). In the flight interception traps C. leucopterum, C. pallidoalatum and O. mirabilis were again the most abundant species while only a single C. pallidoalatum was taken from the baited traps. The carrion trap had very low numbers while the 200 cc dung traps were the most productive (46 beetles/day), collecting large numbers of O. didymus. The 2 cc dung traps collected three times as many individuals as the 0.2 cc traps, although both had equal species diversity. Surprisingly the 0.2 cc traps collected several species that were not present in the larger baited traps. This pattern was repeated in a subsequent three-day period in August (Table 25) when 0.2 and 2 cc human dung traps each collected 9 species.

During August pitfall traps baited with several agouti pellets (0.2 cc) collected large numbers of O. mirabilis (Table 25), although species diversity at these traps was much less than that of similar sized human dung

traps. Onthophagus mirabilis was also collected in abundance at traps baited with several paca pellets (2 cc), a bait that attracted even fewer species than agouti dung. Traps baited with 2 cc of coati dung collected very similar species and numbers to traps baited with 2 cc of human dung. The 2 cc cow dung traps collected numbers intermediate between the rodent and human dung traps. The 200 cc baited traps did not collect a single Canthidium species nor any individuals of O. mirabilis. Traps with 200 cc of human dung were dominated by O. didymus while the soil trap with cow dung collected large numbers of Uroxys depressifrons. Five of the U. depressifrons were located in the dung masses of O. didymus and D. satanas at the bottom of the trap while the remaining 19 specimens were distributed in the top 2 cm of soil.

At Las Cruces, 21 species were recorded from baited traps over a combined ten-day period in February and July 1983 (Table 26). Pitfall traps baited with 2 cc of human dung collected almost twice as many species as traps baited with 0.2 cc although the smaller traps collected slightly more beetles per day (7.7 compared with 5.9). In contrast to the pitfalls, soil traps baited with 0.2 cc of dung collected very few beetles per day. Nearly all of those collected were species of Canthidium while other species such as P. pyrois were observed to land at the traps and consume the bait but leave shortly thereafter.

The 2 cc baited soil traps however were much more productive and collected almost as many beetles per day (5.8) as the 2 cc pitfall traps. Excavated 12 to 24 hours after being placed in the field, all individuals of the larger species (C. chiriquensis, D. satanas, O. didymus, P. pyrois and S. velutinus) were found at the bottom of the 9 cm deep containers, usually with most of the bait. On four occasions though, single beetles were found in the last stages of consuming the bait. Thirty of the forty O. nyctopus collected were found in the dung baits at the bottom of the containers along with the larger species. Seven more beetles were found without any apparent dung at the bottom of traps that did not contain individuals of the larger species. Only three individuals were found in the upper levels of the soil. The single O. acuminatus and one U. depressifrons were also located at the bottom of traps beside the dung masses brought down by larger species. The remaining beetles were generally found within the top 6 cm of soil.

In the 200 cc baited soil traps at Las Cruces, all specimens of C. pecki, D. satanas, O. didymus and Sulcophanaeus noctis were collected at the bottom of the standard 16 cm deep containers. Several D. satanas were also taken from greater depths in a modified trap that extended to 50 cm in depth. In the standard traps over 70% of the O. nyctopus were located at the bottom or around

the large masses of dung that had been carried down by the bigger species. A number of small burrows extending from the surface to the bottom of the traps were presumably made by this species. Five S. quadridentatus and several O. acuminatus and U. depressifrons were also located beside the large dung masses at the bottom of these 16 cm containers. In the modified trap three individuals of D. satanas were found with dung supplies at 20, 36 and 46 cm depths. Several specimens of O. acuminatus and O. nyctopus were also found alongside the dung at each of the three depths. The remaining species and individuals were generally found within the top 6 to 8 cm of soil.

At La Fortuna a single flight interception trap collected 15 species over a six-week period (Table 27). Dilution of the trap preservative with rain water resulted in a strong odour of decomposition. The most abundant species in the trap, Deltochilum mexicanum was also the dominant species at carrion baited pitfall traps. Dung baited pitfall traps at this site were dominated by O. didymus.

Nineteen species were recorded from baited traps at Gamboa (Table 28). At the baited soil traps the two largest species, Coprophanaeus telamon corythus and Phanaeus howdeni were found at the bottom of the containers together with the dung baits. Two-thirds of the O. acuminatus collected at these traps were also found at

the bottom of the containers, with half of them in or beside the dung masses of the 2 larger species. Onthophagus landolti, the most abundant species at the 2 cc pitfall traps, was rare in the soil traps but was readily attracted in large numbers (more than 100 individuals) to 200 cc dung baits placed on the ground (data not shown). Like the previous sites, the flight interception trap collected different species proportions than the baited traps.

Natural Deposits

A number of naturally occurring resources were discovered in the field. On BCI fresh howler monkey (Alouatta palliata) dung was observed on a regular basis during the early morning hours by locating troops of monkeys when they were vocalizing. Canthon angustatus was present at every one of the several dozen occurrences. Upwards of several thousand individuals were censused at single localities where a large troop of monkeys had defecated. Many of these individuals were observed in the act of dropping to the ground with balls of dung that they had collected from leaves and branches in the canopy above (Fig. 18). Canthon subhyalinus was also observed to utilize howler monkey dung in the same fashion. A number of other species were also regularly observed perching on

leaves with fresh howler dung nearby, and also feeding on it (Fig. 12). Dung which reached the ground was often colonized by large species such as Sulcophanaeus cupricollis, P. pyrois and P. howdeni and a variety of smaller Onthophagus species such as O. stockwelli, O. sharpi and O. acuminatus. On another occasion fresh capuchin monkey (Cebus capucinus) dung was discovered on the ground in the mid-afternoon. Twenty-four O. coscineus were removed from within the scattered feces and the soil immediately below, along with one O. c. panamensis and one E. plebejus. Several other O. coscineus were observed perching on leaves in the immediate vicinity of the dung. In the late afternoon a small pile of elongate rodent pellets (probably from an agouti) were discovered on the ground. Six C. haroldi and 8 C. aurifex were rapidly pushing individual pellets away from the central pile. The only other species present was a single U. micros sitting under a pellet. There were no beetles present in the soil beneath the pellets. A pile of white-tailed deer (Odocoileus virginianus) pellets were found beside the base of a large tree at night and contained a total of 12 U. micros and 8 C. aequinoctialis. Several of the C. aequinoctialis had begun burrowing into the soil beneath the dung.

Invertebrate carrion was observed on several occasions on BCI. Crushed land snails of approximately 1

cm length were located on forest trails and were often attended by one or two individuals of C. moniliatus or C. c. sallei. The carcass of a dead Melolonthine scarab (Phyllophaga sp.) was also observed being rolled down a forest trail by a single C. c. sallei.

A number of species were collected from different types of rotting plant material. On BCI twenty Ontheus brevipennis were removed from vertical burrows at a depth of 10 to 20 cm in the refuse pile of a large leaf-cutting ant nest (Atta sp.). The occurrence of several teneral beetles and the immaculate condition of all specimens indicated that they had probably pupated in situ. At Cerro Pelota one C. tuberifrons and five O. belorhinus were collected from three rotting Solanus fruits on the ground. The C. tuberifrons and three of the O. belorhinus were located with pieces of fruit in burrows below the ground surface. Several individuals of O. mirabilis were also collected from burrows beneath fallen avocado fruits (Persea sp.) at Cerro Pelota. At Las Cruces Onthophagus sp.3 and O. praecellens were very abundant under rotting bananas (Musa sp.) and jackfruit (Artocarpus sp.). Both sexes could be found provisioning burrows at depths between 4 and 12 cm. At the El Llano site the occurrence of Bdelyrus seminudus in a flight interception trap (Table 29) led to the discovery of a dozen individuals living in a mass of rotting plant material on the rain roof. Leaves

and flowers which had accumulated in the middle of the plastic sheet, created a depression that had trapped a small pool of water. The beetles were found in the wet debris just above the waterline.

Relocation Techniques

Most species of beetles attracted to dung or carrion baits exhibited some form of relocation behaviour, and removed food from the site where it was first encountered. Notable exceptions were species of Eurysternus, individuals of which were usually found within the dung mass or in the soil interface immediately below. The most common form of relocation behaviour was the paracoprid method of burying the food directly beneath or slightly off to the side of the spot on which it was found. This was seen in many of the dung feeding species as well as in the carrion-frequenting Coprophanaeus which on several occasions buried dead mice within 10 minutes of arrival. Phanaeus and Sulcophanaeus species were typical paracoprids but sometimes started their burrows at a distance of 5 to 20 cm away from the edge of a dung pile. Beetles could then be observed pushing and pulling fragments of dung over the ground surface towards the burrow entrance.

A number of small species including Onthophagus

nyctopus and O. acuminatus exhibited a form of paracoprid behaviour best described as a cleptocoprid strategy. While these species often buried small amounts of dung at 2 cc baits, beetles at the 200 cc baits would burrow deep into the soil and remove dung from the galleries of large paracoprid species such as Dichotomius satanas. Placing a fine-mesh screen over the dung prevented colonization by the larger beetles, however the cleptocoprid species were still found deep in the soil, but without any dung.

The other major form of food relocation was the telocoprid strategy of overland transport. This was typically observed in the ball rolling genera Canthon and Deftochilum. These species generally formed balls of dung within 5 to 10 minutes of arriving at a dung source, then rapidly rolled the balls away in a head-down stance. A few individuals that did not make balls fed underneath the dung. Similar rolling behaviour was observed in Canthon moniliatus and C. c. sallei with small pieces of carrion. A very different form of telocoprid behaviour was seen in perching species of Canthidium.

At human dung, individuals of several species of Canthidium were observed to push small fragments of dung across the ground using their heads. The irregular shape of the fragments, combined with the tendency of ground litter to stick to the moist surfaces, resulted in very slow progress by the beetles. However, at agouti and other

rodent droppings, beetles rapidly pushed single pellets away from the site of first encounter. Beetles placed the anterior margin of the clypeus under the middle of the pellet then flexed the head up and down while running forward with the pellet balanced in front of them. This pellet-pushing behaviour was not observed in non-perching species of Canthidium nor in any other genus.

DISCUSSION

Resource Availability

As noted by Peck and Howden (1984) and supported by the present study, naturally occurring fecal deposits are rarely observed in Neotropical rainforests. However, nonvolant mammal faunas are diverse (Fleming 1975; Eisenberg 1980) and often characterized by large biomasses, although individual species may be rarely observed (Terwilliger 1978). The substantial amount of dung produced each day must therefore be rapidly utilized by the local Scarabaeine fauna. On BCI three-toed sloths (Bradypus infuscatus) constitute approximately 48% of the nonvolant terrestrial mammalian biomass (Eisenberg and Thorington 1973). Assuming individual production of 7.9 g dry weight of dung per day (Montgomery and Sunquist 1975), the 8000 sloths on the island (Glanz 1982) should produce 59.2 kg dry weight of dung per day. The less abundant howler monkeys (Alouatta palliata) on BCI consume an average of 1 kg wet weight of food per day of which approximately 60% is voided as feces (Nagy and Milton 1979). With a population size of 1300 individuals (Glanz 1982), 780 kg of fresh dung would be produced by this species every day. Feeding rates and digestive efficiencies of other species are not readily available

but estimates of total dung production for the island could be very high. For example, assuming that all species consumed (on average) 15% of their body weight per day (an overly conservative estimate for many of the smaller mammalian species) and had a 50% digestive efficiency, the 66,465 kg of nonvolant mammalian biomass on BCI (Eisenberg and Thorington 1973) could conceivably produce nearly 5000 kg wet weight of dung per day. The availability of this dung to Scarabaeines though, may differ greatly depending upon the defecation patterns of the different mammals.

Three-toed sloths defecate at weekly intervals by descending to the ground and burying their dung in a shallow depression made by their tail (Montgomery and Sunquist 1978). The paucity of dung beetles attracted to these feces has been noted by Montgomery and Sunquist (1975) and others (Ratcliffe 1980; Young 1981). A number of Scarabaeine species, however, have been recorded from the fur of sloths (Boucomont 1928; Arrow 1933; Ratcliffe 1980) and are believed to be specialist feeders on sloth dung, riding on the animal until it descends to defecate (Young 1981). How the beetles get back to the sloths is an interesting problem (Ratcliffe 1980). The presence of Uroxys gorgon (a known sloth associate) in blacklight traps of the upper canopy (Tables 9 and 10) suggests that beetles search for sloths or move between them when the sloths are in the upper canopy and not on the ground.

In contrast to the unusual behaviour of the sloth, howler monkeys and most other arboreal mammals probably defecate from the canopy at least once a day. Much of this dung lands on lower story leaves and branches where it is utilized on BCI by only a few species including Canthon angustatus and C. subhyalinus. The ball rolling behaviour of these two species permits them to move dung to the ground where it can be buried. Other groups such as Canthidium push the dung off leaves but are unable to hold onto it as it falls to the ground. Dung that does reach the ground is quickly colonized in an apparent scramble competition by a number of taxa including several species of Onthophagus, Phanaeus pyrois, P. howdeni and Sulcophanaeus cupricollis.

The dung of ground-dwelling mammals is likely scattered in a variety of patterns along the ground surface although some species such as tapir prefer to defecate in water (Terwilliger 1978; Janzen 1983a). The dung of larger mammals is probably distantly spaced as a consequence of the greater home range requirement associated with increased body size. In contrast small mammals such as rodents might be expected to produce more even temporal and spatial distributions of dung, because of their higher metabolic rates (Schmidt-Nielsen 1975) and smaller home ranges. The use of dropping boards in a temperate rodent fauna (Emlen et al. 1957) suggests

patterns of widely scattered droppings with continual production during much of a species diel activity period. However, data on defecation rates and patterns for small mammals in the Neotropics are not available.

Foraging Strategies

Scarabaeines exhibit a number of different strategies to successfully utilize the diverse array of available resources. Beetles presumably rely upon olfaction to locate food since they arrive at baits from a downwind position. The initial detection of a food odour, however, appears to be accomplished by two different methods. Most species employ a cruising or searching flight to encounter suitable resources. The distance covered by this method can be quite large as shown by Schoof and Silverly (1954) and MacLeod and Donnelly (1963) for flies that breed in carrion and dung. An alternative foraging mode used by a number of small species appears to be a sit-and-wait tactic (Pianka 1973) of perching on leaves. These disparate foraging modes have a number of ecological consequences for predators (Huey and Pianka 1981) that can also be applied to Scarabaeines.

Flight is an efficient method of locomotion but it is also a very energetically demanding activity (Schmidt-Nielsen 1972). For most flying organisms this

energetic cost (power) does not follow a linear relationship with flight speed (Pennycuik 1972) but rather exhibits a U-shaped curve. One result is that the minimum power requirement for staying aloft occurs at a lower speed than the power requirement for maximum range. Among the Panamanian Scarabaeinae, widely foraging species seem to select one of these two relative flight speeds. Canthon c. sallei has a flight period extending from dawn to dusk and can often be observed in the forest flying about 20 cm above the ground in slow meandering curves. Coprophanaeus pecki like most species in the genus is generally active for only a short period of time after dusk and flies very rapidly about a meter in height above ground level. Both species are carrion specialists although individuals of either can occasionally be taken at dung baits. Coprophanaeus pecki however is much larger than C. c. sallei and presumably is forced to search for larger amounts of food. Assuming that larger carrion resources are more patchy in space and time, then C. pecki appears to minimize its foraging time by flying at a higher speed to cover as much ground as possible. If there are no suitable resources in a given area, then it is probably inefficient to continue flying while waiting for a large resource to become available. In contrast C. c. sallei may attempt to stay aloft as long as possible by flying at the minimum power speed while it waits for small

carriion resourcres to become available. The chemical secretions that the nominate subspecies (Canthon c. cyanellus) uses to protect its food supplies (Belles and Favila 1983), may also confer some protection against potential predators. The bright colour pattern of C. c. sallei may thus serve as an aposematic warning to predators allowing it to forage conspicuously (at a slow speed) for longer periods of time. Slow flying nocturnal species may be easy targets for insectivorous bats so C. pecki may also be attempting to minimize its foraging time (Schoener 1971) to decrease its exposure to predators. The remains of large slow flying nocturnal Scarabaeinae such as Dichotomius in fecal piles at bat roosts (pers. observ.) would tend to support this conclusion.

Search height is an important variable for effective foraging (Anderssen 1981) and so it is not surprising that flying height differed among many species in this study. Howden and Nealis (1978) hypothesized that small fecal deposits should have commensurately smaller "odour cones" than larger deposits. To detect these small resources beetles would have to forage close to the ground. Likewise, for larger species that require bigger resources, it would be more efficient for them to fly at higher levels so that they only pick up odours from suitable resources. The flying heights of the two carrion specialists mentioned above certainly support this.

hypothesis. Among the dung feeding group several small species such as Onthophagus nyctopus, Pedariidum pilosum, Scatimus quadridentatus and Uroxys depressifrons were more abundant at large resources and probably all exhibit some form of cleptocoprid behaviour. While these species were rarely collected in flight interception traps, they were always taken in the taller 60 and 105 cm traps. Individuals of the latter 3 species were also occasionally found on leaves, but at greater heights than the more common perchers such as Canthidium. It thus appears that the flying height of a species is related to the size of the preferred food resource, at least in species that forage for ground based resources. Species that utilize vertically distributed resources such as monkey dung (Canthon angustatus, C. lamprimus, and C. subhyalinus), sloths (Uroxys gorgon) and even bromeliads (Bdelyrus seminudus) should not be expected to show narrow vertical stratification. The random flying height of C. lamprimus (up to 120 cm) and the perching height distributions of the other 2 Canthon species support this.

Thirty-two species in this study were recorded perching on leaves at least once. In this type of diversity, Young (1984) is correct in assuming that there is not a unitary cause for perching among Scarabaeines. In fact, many of the species collected on leaves only once or twice were probably just pausing between cruising flights

and happened to land on a leaf instead of the ground. Other species exhibited a range of behaviours such as feeding on dung-covered leaves or basking in light gaps. While certain African dung beetles are capable of endothermic temperature regulation (Bartholomew and Heinrich 1978; Heinrich and Bartholomew 1979), basking in light patches has thermoregulatory significance for a number of insects (Casey 1981; Shelley 1982). Perching Scarabaeines may also take advantage of sunning, but this behaviour does not seem related to the detection of special food resources. However other species of Scarabaeines that do not bask, utilize perching as a specialized foraging mode for the detection of small scattered resources.

Diurnal species of Canthidium (Fig. 24) and nocturnal species of several genera (Fig. 25) perch close to the ground and exhibit the characteristic stance of monitoring air borne odours. The average perching height for these species is correlated with body size and the observation that sympatric species have either different perching heights or activity periods suggests some form of resource partitioning (Schoener 1974). Canthidium species in particular appear to specialize on rodent pellets and have evolved an efficient method for their relocation. The observation of numerous beetles located downwind of a resting agouti raises the possibility that Scarabaeines

may orient towards the odour of potential dung producing mammals. Many of the Panamanian mammals including agouti, opossum, armadillo and peccaries are known for their strong scents, which are probably used in host detection by a number of blood-feeding groups such as Psychodids (Christensen and Herrer 1980). Dung beetles that use the energetically conservative method of perching as opposed to flying, may locate mammals by their odours and then be able to sit downwind and wait until fresh feces become available.

Perching may also be used by some species to extend their diel foraging period without incurring excessive costs associated with flight. For example, Ontherus didymus is commonly observed flying shortly after dusk and is collected in large numbers at a variety of baits. As the night progresses fewer individuals are observed in flight while many more are seen perching on leaves. If mammal activity (and presumably defecation) is greatest at dusk and dawn, which is true for a number of bat species in Panama (Bonaccorso 1979) then species such as O. didymus may tend to employ cruising flights at the most productive times of the night then shift to a more conservative perching strategy during periods when mammal activity is reduced.

While nocturnal Scarabaeines face a number of predators including hawking and gleaning bats (Bonaccorso

1979), diurnal perchers are very conspicuous on leaves and are probably exposed to a large number of potential predators. The pygidial rubbing exhibited by several Canthon species may be a method of distributing repellent compounds over the body from possible exocrine glands located on the abdominal sternites (Pluot-Sigwalt 1982). The bright colouration of these species coupled with a display stance may be an effective deterrent against some predators. Most diurnal perchers however lack these defenses and assume a tight crouch when disturbed. Aerial foraging predators such as Asilidae are abundant in Panama (Shelley 1984) and often feed on insects only when they are in flight (Lavigne 1964; Fisher 1983). On BCI the asilid Senobasis corsair commonly feeds on small perching Scarabaeines that it captures when the beetles are in flight (T. Shelley, pers. comm.). Other predators such as staphylinids (Janzen 1983b) and cicindelids (Young 1980) feed on dung beetles when they arrive at food resources. Predators may therefore have an effect on dung beetle foraging at several levels. Any type of optimal foraging model that might be applied to Scarabaeinae, would therefore have to include both energetic considerations of foraging mode as well as predation risks to be biologically meaningful.

CONCLUSIONS

Forests in Panama support a large and diverse fauna of Scarabaeinae. Diversity was highest at lowland sites where diurnal species were more abundant. Montane sites had approximately equal numbers of nocturnal and diurnal species and shared only a few species in common with the lowland sites. Species showed distinctive patterns of diel flight activity and exhibited differences in flying height, foraging mode, food relocation technique and food preference. Leaf perching was used by species for resting, basking in light gaps or searching air currents for possible food odours. Several perching species appear to specialize on rodent droppings and have evolved a pushing behaviour to handle the dry elongate pellets. The temporal and spatial heterogeneity of dung and carrion resources in tropical forests together with the abundance of rotting fruit, leaf litter and ant nest refuse appears to have resulted in the evolution of diverse foraging strategies that minimize interspecific competition. Energetic costs of foraging and the risk of predation have probably also had a major impact on foraging strategies. Studies that rely upon baited traps may give a distorted view of community structure and competition because many of the spatial and temporal characteristics that influence Scarabaeine activity are eliminated.

TABLE 2

Diel flight activity of species from Cerro Pelota. Dawn at 0600 hrs; dusk at 1830 hrs. AP = activity period: C = crepuscular, D = diurnal, N = nocturnal.

Time of Day (x100 = Hr.)

Species	AP	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Canthidium ardens	D			XXX		XXX		XXX		XXX								
Canthidium leucopterum	D					XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX
Canthidium pallidoalatum	D					XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX		XXXXXXXXXXXXXXXXXXXX
Canthidium tuberifrons	N																	
Canthidium variolosum	D							XXX		XXX								XXXXXXXXXXXX
Canthon sp. 2	D							XXX		XXX		XXX		XXX				
Coprophanaeus chiriquensis	N																	XXXXXXXXXXXX
Coprophanaeus pecki	N																	XXX
Deltochilum parile	C																	XXX
Dichotomius satanas	N							XXXXXX										XXXXXXXXXXXX
Eurysternus magnus	D							XXXXXXX										
Ontherus didymus	N							XXXXXXXXXXXX										XXXXXXXXXXXX
Onthocharis panamensis	D							XXX		XXXXXX								
Onthophagus belorhinus	C																	XXXXXX
Onthophagus cyanellus	D							XXXXXXXXXXXX										
Onthophagus incensus	D							XXXXXXXXXXXX										
Onthophagus mirabilis	C																	XXXXXX
Onthophagus sp. 1	D																	XXXXXXXXXX
Sulcophanaeus velutinus	D							XXXXXXXXXXXX		XXXXXXXXXXXX		XXXXXXXXXXXX		XXXXXXXXXXXX		XXXXXXXXXXXX		XXXXXXXXXXXX
Uroxys bidentis	N							XXXXXXXXXXXX		XXXXXXXXXXXX		XXXXXX		XXXXXX				XXXXXXXXXX
Uroxys depressifrons	N							XXXXXXXXXXXX										XXXXXXXXXXXX

TABLE 4

Beetles collected from five sizes of flight interception traps on BCI over a ten-day period in June 1983.

Species	Trap Height in cm				
	0-15	0-30	0-60	0-105	0-120
<i>Ateuchus aeneomicans</i>	1	4	0	2	4
<i>Ateuchus candezei</i>	0	0	1	1	1
<i>Canthidium angusticeps</i>	0	1	1	0	1
<i>Canthidium ardens</i>	18	57	45	73	48 *
<i>Canthidium aurifex</i>	14	102	81	99	89 *
<i>Canthidium centrale</i>	0	0	0	7	1
<i>Canthidium elegantulum</i>	0	2	1	1	0
<i>Canthidium haroldi</i>	6	103	83	122	116 *
<i>Canthidium perceptibile</i>	2	0	0	0	1
<i>Canthon aequinoctialis</i>	0	13	21	46	25 *
<i>Canthon c. sallai</i>	-25	29	16	23	18 *
<i>Canthon lamprimus</i>	7	28	37	90	74 *
<i>Canthon moniliatus</i>	0	3	0	2	1
<i>Canthon septemmaculatus</i>	0	1	0	1	0
<i>Canthon sp. 1</i>	3	11	4	11	3 *
<i>Dichotomius satanas</i>	0	0	0	0	1
<i>Eurysternus caribaeus</i>	0	0	1	2	1
<i>Eurysternus plebejus</i>	3	5	4	4	8
<i>Onthocharis panamensis</i>	1	7	3	9	4
<i>Onthophagus acuminatus</i>	0	6	4	21	11 *
<i>Onthophagus coscineus</i>	4	20	27	38	31 *
<i>Onthophagus c. panamensis</i>	1	8	4	11	13 *
<i>Onthophagus dicranus</i>	0	2	0	2	5
<i>Onthophagus lebasii</i>	0	1	1	9	6
<i>Onthophagus praecellens</i>	0	3	2	11	5
<i>Onthophagus sharpi</i>	3	16	18	16	15 *
<i>Onthophagus stockwelli</i>	0	4	2	10	3
<i>Phanaeus howdeni</i>	0	0	3	1	3
<i>Phanaeus pyrois</i>	2	14	15	9	6 *
<i>Sulcophanaeus cupricollis</i>	0	2	1	2	2
<i>Uroxys micros</i>	0	0	2	17	5
<i>Uroxys platypyga</i>	0	0	4	5	2
Total	90	442	381	645	503
$\bar{x}/(m^2 day^{-1})$	40.0	98.2	42.3	41.0	27.9
No. Species	14	24	25	29	30

* Species with more than 30 individuals.

TABLE 5

Beetles collected from four sizes of flight interception traps at Cerro Pelota over a twelve-day period in August 1983.

Species	Trap Height in cm			
	0-15	0-30	0-60	0-105
<i>Canthidium ardens</i>	0	0	1	0
<i>Canthidium leucopterum</i>	32	32	38	50 *
<i>Canthidium pallidoalatum</i>	5	48	94	106 *
<i>Canthidium tuberifrons</i>	0	4	2	13
<i>Canthidium variolosum</i>	0	0	1	0
<i>Canthon sp. 2</i>	0	0	2	1
<i>Coprophanaeus chiriquensis</i>	0	0	1	2
<i>Dichotomius satanas</i>	0	0	1	0
<i>Ontherus didymus</i>	0	0	0	2
<i>Onthocharis panamensis</i>	0	0	1	0
<i>Onthophagus belorhinus</i>	0	0	0	1
<i>Onthophagus mirabilis</i>	3	21	19	30 *
<i>Onthophagus sp. 1</i>	0	1	4	6
<i>Sulcophanaeus velutinus</i>	0	3	0	4
<i>Uroxys bidentis</i>	1	5	13	11 *
<i>Uroxys depressifrons</i>	0	0	2	1
Total	41	114	179	227
$\bar{x}/(m^2 day^{-1})$	15.2	21.1	16.6	12.0
No. Species	4	7	13	12

* Species with more than 30 individuals.

TABLE 6

Beetles collected from four sizes of flight interception traps at Las Cruces over a five-day period in July 1983.

Species	Trap Height in cm			
	0-15	0-30	0-60	0-105
<i>Canthidium angusticeps</i>	0	0	1	1
<i>Canthidium ardens</i>	27	23	45	53 *
<i>Canthidium perceptibile</i>	34	31	60	44 *
<i>Canthidium tubrifrons</i>	0	1	4	1
<i>Canthidium vespertinum</i>	1	0	0	1
<i>Coprophanaeus chiriquensis</i>	2	3	1	5
<i>Coprophanaeus pecki</i>	2	0	3	0
<i>Deltochilum pseudoparile</i>	0	0	1	0
<i>Dichotomius satanas</i>	0	0	0	1
<i>Onthocharis panamensis</i>	12	3	7	11 *
<i>Onthophagus mirabilis</i>	0	0	4	6
<i>Onthophagus nyctopus</i>	0	0	4	2
<i>Onthophagus praecellens</i>	0	2	0	2
<i>Onthophagus</i> sp. 1	0	0	5	5
<i>Phanaeus pyrois</i>	2	0	0	3
Total	80	63	135	135
$\bar{x}/(m^2 day^{-1})$	71.2	28.0	30.0	17.2
No. Species	7	6	11	13

* Species with more than 30 individuals.

TABLE 7

Pearson Chi-square goodness-of-fit statistics with degrees of freedom for Log-linear models and corresponding Z-scores for the parameters tested.

Species	Site	Parameter 1			Parameter 2			Parameter 3		
		X ²	df	Z-Score	X ²	df	Z-Score	X ²	df	Z-Score
Canthidium aurifex	1	2.98	3	-6.94**						
Onthophagus coscineus	1	5.86	3	-3.90**						
Onthophagus sharpi	1	0.29	3	-2.86*						
Phanaeus pyrois	1	4.91	3	-2.38*						
Onthophagus mirabilis	2	2.94	2	-3.48**						
Canthon aequinoctialis +	1	11.76	2	-2.90	6.21	1	-2.11			
Onthophagus acuminatus +	1	12.17	2	-1.57	3.12	1	-2.61*			
Canthidium pallidoalatum	2	22.68	2	-6.21	0.72	1	-4.57**			
Canthidium ardens	3	11.97	2	-1.89	0.65	1	-3.26**			
Canthidium perceptibile	3	9.38	2	-1.46	2.46	1	-2.53*			
Canthidium ardens	1	8.52	3	-4.61	8.54	2	0.19	5.17	1	-1.70
Canthidium haroldi	1	8.43	3	-6.98	8.24	2	-0.34	0.15	1	-2.83*
Canthon sp. 1	1	7.83	3	-1.45	6.33	2	1.58	4.57	1	-0.99

* Indicates significant Z-score for parameter at .01(*) or .001(**) level when the corresponding chi-square value of the model does not exceed X² critical at the .05 level with degrees of freedom as indicated.

+ Species in which a zero count in the lowest trap resulted in the first model corresponding to the 30 cm trap height.

TABLE 8

Beetles collected from an aerial dung-baited pitfall trap run for two days each at three heights during May 1981 on BCI.

Species	Trap Height		
	Ground	1 Meter	8 Meters
<i>Ateuchus aeneomicans</i>	2	0	0
<i>Ateuchus candezei</i>	1	0	0
<i>Canthon aequinoctialis</i>	344	5	4
<i>Canthon angustatus</i>	0	0	2
<i>Canthon lamprimus</i>	0	2	0
<i>Canthon septemmaculatus</i>	1	0	0
<i>Canthon subhyalinus</i>	0	1	37
<i>Copris lugubris</i>	1	0	0
<i>Dichotomius satapas</i>	15	0	0
<i>Eurysternus caribaeus</i>	1	0	0
<i>Onthophagus acuminatus</i>	43	0	0
<i>Onthophagus coscineus</i>	2	0	0
<i>Onthophagus praecellens</i>	1	0	0
<i>Onthophagus sharpi</i>	0	1	1
<i>Onthophagus stockwelli</i>	10	0	0
<i>Pedariidium pilosum</i>	4	0	0
<i>Uroxys gorgon</i>	0	0	1
<i>Uroxys microps</i>	15	0	0
<i>Uroxys platypyga</i>	2	0	0
Total	442	9	45

TABLE 9

Scarabaeinae collected from two blacklight traps run at 3 and 27 meters above ground level on BCI for three years. (Data from H. Wolda, STRI, Panama)

Species	Trap Height	
	3 Meters	27 Meters
<i>Ateuchus candezei</i>	6	1
<i>Canthidium elegantulum</i>	9	0
<i>Canthidium haroldi</i>	2	0
<i>Canthon aequinoctialis</i>	11	2
<i>Canthon angustatus</i>	23	3
<i>Canthon subhyalinus</i>	26	0
<i>Dichotomius femoratus</i>	1	0
<i>Eurysternus foedus</i>	2	0
<i>Ontherus brevipennis</i>	1	0
<i>Onthophagus sharpi</i>	72	6
<i>Phanaeus pyrois</i>	1	0
<i>Uroxys gorgon</i>	2207	338
<i>Uroxys macrocularis</i>	2	0
<i>Uroxys micros</i>	183	20
Total	2613	392

TABLE 10

Scarabaeinae collected from two blacklight traps run at 3 meters above ground level (24 months) and at canopy height (9 months) at La Fortuna. (Data from H. Wolda, STRI, Panama)

Species	Trap Height	
	3 Meters	Canopy
<i>Bdelius seminudus</i>	144	17
<i>Canthidium</i> sp. 1	2	0
<i>Copris costaricensis</i>	50	0
<i>Deltotilum mexicanum</i>	5	0
<i>Ontherus didymus</i>	46	0
<i>Onthophagus mirabilis</i>	3	0
<i>Uroxys bidentis</i>	4	0
<i>Uroxys depressifrons</i>	35	0
<i>Uroxys gorgon</i>	27	14
<i>Uroxys metagorgon</i>	9	1
<i>Uroxys</i> sp. 1	4	0
<i>Uroxys</i> sp. 2	2	0
<i>Uroxys</i> sp. 3	1	0
Total	332	32

TABLE 11

Mean perching height and activity period of beetles from BCI. N = sample size; $\bar{x} \pm SE$ = mean $\pm$ standard error in cm; Range = minimum and maximum values; AP = activity period: N = nocturnal, D = diurnal.

Species	N	$\bar{x} \pm SE$	Range	AP
Canthidium aurifex	297	29.9 $\pm$ 0.60	8-81	D
Canthidium haroldi	250	47.7 $\pm$ 0.90	3-94	D
Canthon angustatus	197	86.6 $\pm$ 3.26	15-250+	D
Uroxys platypyga	69	26.1 $\pm$ 1.50	9-69	N
Canthidium ardens	64	15.2 $\pm$ 0.74	5-38	D
Canthon lamprimus	59	37.8 $\pm$ 2.93	11-132	D
Uroxys micros	36	58.8 $\pm$ 5.02	5-120	N
Uroxys macrocularis	24	24.7 $\pm$ 2.31	9-53	N
Canthon septemmaculatus	17	39.2 $\pm$ 3.55	11-66	D
Canthon subhyalinus	14	72.3 $\pm$ 8.91	19-124	D
Onthophagus coscineus	14	25.3 $\pm$ 3.46	11-60	D
Canthidium elegantulum	12	25.3 $\pm$ 3.34	12-52	D
Onthophagus acuminatus	9	79.0 $\pm$ 7.32	45-109	D
Ateuchus aeneomicans	5	49.0 $\pm$ 4.94	31-58	D
Eurysternus plebeus	4	53.2 $\pm$ 9.34	30-75	D
Onthophagus sharpi	3	30.0 $\pm$ 10.4	15-50	D
Onthophagus lebasi	2	55.0 $\pm$ 33.0	22-88	D
Canthidium hespenheidei	2	11.5 $\pm$ 1.50	10-13	D
Canthidium perceptibile	1	23		D
Ateuchus candezei	1	44		N
Onthophagus c. panamensis	1	32		D
Canthon sp. 1	1	16		D

TABLE 12

Mean perching height and activity period of beetles from BCI excluding individuals associated with howler monkey dung. N = sample size; $\bar{x} \pm SE$ = mean + standard error in cm; Range = minimum and maximum values; AP = Activity period: N = nocturnal, D = diurnal.

Species	N	$\bar{x} \pm SE$	Range	AP
Canthidium aurifex	165	31.2 0.77	14-67	D
Canthidium haroldi	161	47.5 1.10	13-94	D
Uroxys platypyga	53	23.1 1.25	9-46	N
Canthidium ardens	26	15.7 1.40	5-38	D
Canthon lamprimus	25	32.9 2.22	14-52	D
Onthophagus coscineus	14	25.3 3.47	11-60	D
Canthon septemmaculatus	11	34.2 4.45	11-58	D
Canthidium elegantulum	6	28.2 2.78	18-36	D
Uroxys macrocularis	5	19.2 3.99	9-32	N
Onthophagus acuminatus	4	68.5 10.2	45-89	D
Eurysternus plebejus	4	53.2 9.34	30-75	D
Uroxys micros	3	54.0 22.9	9-84	N
Canthidium perceptibile	1	23		D
Canthon sp. 1	1	16		D

TABLE 13

Mean perching height and activity period of beetles from Cerro Pelota. N = sample size; $\bar{x} \pm SE$ = mean $\pm$ standard error in cm; Range = minimum and maximum values; AP = activity period: N = nocturnal, D = diurnal.

Species	N	$\bar{x} \pm SE$	Range	AP
<i>Uroxys bidentis</i>	160	16.2 0.56	3-42	N
<i>Canthidium leucopterum</i>	34	14.3 1.00	5-31	D
<i>Canthidium vespertinum</i>	29	17.2 0.83	8-25	N
<i>Canthidium pallidoalatum</i>	27	32.8 2.75	15-70	D
<i>Ontherus didymus</i>	17	41.1 3.60	18-66	N
<i>Uroxys depressifrons</i>	11	61.9 7.08	17-89	N

TABLE 14

Mean perching height and activity period of beetles from Las Cruces. N = sample size; $\bar{x} \pm SE$ = mean $\pm$ standard error in cm; Range = minimum and maximum values; AP = activity period: N = nocturnal, D = diurnal.

Species	N	$\bar{x} \pm SE$	Range	AP
<i>Canthidium vespertinum</i>	148	20.0 0.60	7-43	N
<i>Canthidium ardens</i>	102	24.7 0.89	8-55	D
<i>Canthidium perceptibile</i>	41	24.7 1.61	4-48	D
<i>Uroxys bidentis</i>	26	21.4 1.83	4-42	N
<i>Scatimus quadridentatus</i>	5	71.8 9.33	50-98	N
<i>Uroxys depressifrons</i>	4	74.0 17.2	50-125	N
<i>Onthophagus praecellens</i>	1	56		D
<i>Pedariidum pilosum</i>	1	80		N
<i>Onthocharis panamensis</i>	1	86		D

TABLE 15

Mean perching height and activity period of beetles from Gamboa. N = sample size; $\bar{x} \pm SE$ = mean + standard error in cm; Range = minimum and maximum values; AP = activity period: N = nocturnal, D = diurnal.

Species	N	$\bar{x} \pm SE$	Range	AP
<i>Canthidium aurifex</i>	44	28.1 2.91	9-50	D
<i>Uroxys microcularis</i>	29	17.9 1.34	8-38	N
<i>Onthophagus coscineus</i>	3	23.7 6.35	15-36	D
<i>Canthon lamprimus</i>	2	33.0 0.99	32-34	D
<i>Canthidium hespenheidei</i>	1	14		D
<i>Eurysternus plebejus</i>	1	32		D

TABLE 16

Mean perching height and activity period of beetles from the Perlas Islands. N = sample size; $\bar{x} \pm SE$ = mean + standard error in cm; Range = minimum and maximum values; AP = activity period: N = nocturnal, D = diurnal.

Species	N	$\bar{x} \pm SE$	Range	AP
<i>Canthon septemmaculatus</i>	20	23.8 3.31	8-62	D
<i>Canthidium</i> sp. 3	13	21.6 2.02	13-38	D

TABLE 17

Perching beetles removed from two 5-meter square plots on BCI between 1540 and 1640 hrs, September 8, 1983. Samples 1 to 4 refer to consecutive five minute sampling periods separated by five minute relaxation intervals.

Species	Sample	Plot 1				Plot 2			
		1	2	3	4	1	2	3	4
Canthidium ardens		5	4	5	6	6	3	1	4
Canthidium aurifex		5	4	1	3	4	5	1	3
Canthidium haroldi		5	2	1	2	2	4	1	0

TABLE 18

Perching beetles removed from two 5-meter square plots on BCI between 1000 and 1130 hrs, September 9, 1983. Plot 2 with five pitfall traps each baited with 2 cc of dung at the end of sample 1. Samples 1 to 4 refer to consecutive five minute sample periods separated by ten minute relaxation intervals.

Species	Sample	Plot 1				Plot 2			
		1	2	3	4	1	2	3	4
Canthidium ardens		0	0	0	1	2	0	1	2
Canthidium aurifex		1	2	3	3	0	40	13	17
Canthidium haroldi		1	4	0	3	0	4	0	2

TABLE 19

Beetles collected into five baited pitfall traps from perching plot 2 on BCI between 1005 and 1130 hrs, September 9, 1983.

<i>Canthidium aurifex</i>	1
<i>Canthidium haroldi</i>	9
<i>Canthon angustatus</i>	1
<i>Canthon moniliatus</i>	2
<i>Canthon septemmaculatus</i>	1
<i>Onthophagus acuminatus</i>	2
<i>Phanaeus pyrois</i>	9

TABLE 20

Beetles collected during five 10-minute perching samples from each of two 10-meter square study plots and from five baited pitfall traps at Las Cruces. Traps baited with 2 cc of dung and located in study plot 2.

Species	Plot 1	Plot 2	Traps
<i>Canthidium ardens</i>	5	29	2
<i>Canthidium perceptibile</i>	4	9	3
<i>Canthidium vespertinum</i>	9	18	1
<i>Uroxys bidentis</i>	2	3	0
Other	0	0	21

Beetles collected from pitfall traps (PFT) baited with human dung and from a standard size flight interception trap (FIT) during a ten-day period in May (V) and in June (VI) 1981 on BCI. Quantity of bait measured in cc. Effort expressed as number of trap days.

Species	Trap Type:		PFT		FIT	
	Bait:	Effort:	2	200	-	2
Month:	V		VI		VI	
	V		VI		VI	
<i>Ateuchus aeneomicans</i>	0	3	32	0	25	
<i>Ateuchus candezei</i>	1	1	10	3	10	
<i>Ateuchus guatemalensis</i>	0	0	4	1	1	
<i>Canthidium ardens</i>	0	0	22	0	32	
<i>Canthidium aurifex</i>	0	0	97	1	455	
<i>Canthidium centrale</i>	0	0	10	3	9	
<i>Canthidium elegantulum</i>	0	0	5	1	7	
<i>Canthidium haroldi</i>	3	0	61	4	153	
<i>Canthidium hespenheidei</i>	0	0	2	0	1	
<i>Canthidium perceptibile</i>	0	0	11	0	3	
<i>Canthon aequinoctialis</i>	154	577	61	795	14	
<i>Canthon angustatus</i>	0	0	1	1	61	
<i>Canthon c. sallei</i>	8	0	27	4	21	
<i>Canthon lamprimus</i>	26	3	51	2	0	
<i>Canthon moniliatus</i>	0	2	6	2	1	
<i>Canthon septemmaculatus</i>	1	1	6	26	9	
<i>Canthon sp. 1</i>	0	0	1	0	4	
<i>Copris lugubris</i>	0	1	0	0	0	
<i>Deltochilum v. acropyge</i>	0	0	1	0	0	
<i>Dichotomius satanas</i>	0	31	1	5	0	
<i>Eurysternus caribaeus</i>	0	1	0	0	1	
<i>Eurysternus foedus</i>	0	1	0	0	2	
<i>Eurysternus plebejus</i>	0	3	1	0	19	
<i>Onthocharis panamensis</i>	0	0	13	0	5	
<i>Onthophagus acuminatus</i>	9	44	36	2	31	
<i>Onthophagus coscineus</i>	1	56	119	6	78	
<i>Onthophagus c. panamensis</i>	0	0	0	1	2	
<i>Onthophagus dicranus</i>	0	0	28	0	0	
<i>Onthophagus praecellens</i>	1	1	6	7	32	
<i>Onthophagus sharpi</i>	0	0	2	0	11	
<i>Onthophagus stockwelli</i>	8	10	13	0	2	
<i>Pedariidium pilosum</i>	0	10	3	0	0	
<i>Phanaeus howdeni</i>	0	0	0	0	11	
<i>Phanaeus pyrois</i>	1	0	12	5	24	
<i>Scatimus ovatus</i>	0	2	1	1	9	
<i>Uroxys gorgon</i>	0	0	0	0	1	
<i>Uroxys macrocularis</i>	0	0	2	0	0	
<i>Uroxys micros</i>	5	23	100	1	63	
<i>Uroxys platypyga</i>	1	7	58	1	21	
Total	219	777	804	872	1118	

TABLE 22

Beetles collected from pitfall (PFT) and soil traps (SLT) baited with human dung during a five-day period in June 1983 on BCI. Unbaited pitfall traps (UPT) placed along perimeter wall surrounding 200cc baited soil trap. Quantity of bait measured in cc. Effort expressed as number of trap·days.

Species	Trap Type: Bait: Effort:	PFT 2 28	PFT 200 2	SLT 2 8	SLT 200 3	UPT - 3
<i>Ateuchus aeneomicans</i>		2	0	0	1	0
<i>Ateuchus candezei</i>		2	0	0	0	0
<i>Canthidium ardens</i>		3	1	1	0	0
<i>Canthidium aurifex</i>		4	0	2	0	0
<i>Canthidium centrale</i>		4	0	0	0	0
<i>Canthidium haroldi</i>		2	0	0	0	0
<i>Canthon aequinoctialis</i>		184	96	(+)	(+)	505
<i>Canthon angustatus</i>		1	0	0	0	0
<i>Canthon c. sallei</i>		14	0	0	0	0
<i>Canthon lamprimus</i>		27	8	4	1	3
<i>Canthon moniliatus</i>		5	0	0	0	0
<i>Canthon septemmaculatus</i>		8	0	0	0	1
<i>Dichotomius satanas</i>		3	0	0	10	5
<i>Eurysternus caribaeus</i>		0	1	0	0	0
<i>Eurysternus plebejus</i>		12	18	0	0	0
<i>Onthophagus acuminatus</i>		33	19	3	43	1
<i>Onthophagus coscineus</i>		10	2	1	0	0
<i>Onthophagus c. panamensis</i>		5	13	0	7	3
<i>Onthophagus lebasi</i>		4	17	0	0	0
<i>Onthophagus praecellens</i>		0	1	0	0	0
<i>Onthophagus stockwelli</i>		1	0	1	4	1
<i>Pedariidium pilosum</i>		0	0	0	3	0
<i>Phanaeus pyrois</i>		10	0	0	0	0
<i>Scatimus ovatus</i>		1	0	0	48	1
<i>Uroxys micros</i>		44	10	13	58	5
<i>Uroxys platypyga</i>		2	0	0	0	0
Total		381	186	25	175	525

(+) Individuals observed removing bait from traps.

TABLE 23

Beetles collected from pitfall traps (PFT) baited with carrion (C) and human dung (D) and from a standard size flight interception trap (FIT) during a five-day period in July 1981 at Cerro Pelota. Quantity of bait measured in cc. Effort expressed as number of trap days.

Species	Trap Type:	PFT	PFT	PFT	FIT
	Bait Type:	D	D	C	-
	Quantity:	2	200	200	-
	Effort:	40	10	5	5
Canthidium leucopterum		0	0	1	16
Canthidium pallidoalatum		0	0	0	33
Canthidium tuberifrons		2	1	0	5
Canthidium variolosum		0	0	0	2
Coprophanaeus chiriquensis		43	0	23	5
Coprophanaeus pecki		1	0	0	0
Deltochilum mexicanum		0	2	1	0
Deltochilum parile		1	0	3	1
Dichotomius c. colonicus		0	1	0	0
Dichotomius satanas		40	14	2	0
Ontherus didymus		92	10	20	2
Onthocharis panamensis		0	0	0	1
Onthophagus cyanellus		1	0	0	0
Onthophagus mirabilis		1	0	0	33
Onthophagus nyctopus		1	31	0	0
Onthophagus sp. 1		0	0	0	1
Pedariidum pilosum		1	5	0	0
Phanaeus pyrois		0	0	0	1
Scatimus quadridentatus		0	5	0	0
Sulcophanaeus velutinus		7	0	0	0
Uroxys bidentis		0	0	0	1
Uroxys depressifrons		7	9	1	4
Total:		197	78	51	105

TABLE 24

Beetles collected from pitfall traps (PFT) baited with carrion (C) and human dung (D) and from 3 standard size flight interception traps (FIT) during a three-day period in July 1982 at Cerro Pelota. Quantity of bait measured in cc. Effort expressed as number of trap days.

Species	Trap Type:	PFT	PFT	PFT	PFT	FIT
	Bait Type:	D	D	D	C	-
	Quantity:	0.2	2	200	200	-
	Effort:	8	8	1.5	1.5	9
Canthidium ardens		0	0	0	0	1
Canthidium leucopterum		0	0	0	0	42
Canthidium pallidoalatum		1	0	0	0	79
Canthidium tuberifrons		4	4	0	0	15
Canthidium variolosum		1	0	0	0	0
Canthon sp. 2		0	0	0	0	5
Coprophanaeus chiriquensis		6	2	3	2	2
Coprophanaeus pecki		0	0	1	0	0
Deltochilum mexicanum		0	0	0	1	0
Deltochilum parile		0	0	0	1	0
Dichotomius satanas		0	11	0	0	3
Ontherus didymus		12	55	55	2	1
Onthocharis panamensis		0	0	0	0	2
Onthophagus belorhinus		0	0	0	0	2
Onthophagus cyaneellus		0	1	1	0	0
Onthophagus incensus		0	1	0	0	0
Onthophagus mirabilis		0	0	0	0	52
Onthophagus sp. 1		0	0	0	0	3
Onthophagus sp. 2		1	0	0	0	0
Sulcophanaeus velutinus		0	6	0	0	2
Uroxys bidentis		1	0	0	0	16
Uroxys depressifrons		3	6	9	0	9
Total		29	86	69	6	234

2 OF/DE 2

MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

TABLE 26

Beetles collected from pitfall (PFT) and soil traps (SLT) baited with various quantities of human dung over a ten-day period in February and July 1983 at Las Cruces. Quantity of bait measured in cc. Effort expressed as number of trap days.

	Trap Type:	PFT	PFT	SLT	SLT	SLT
	Bait:	0.2	2	0.2	2	200
Species	Effort:	10	30	5	25	7
Canthidium ardens		0	11	0	0	0
Canthidium perceptibile		13	12	1	11	0
Canthidium tuberifrons		14	20	2	9	3
Canthidium vespertinum		12	5	4	16	3
Coprophanaeus chiriquensis		0	7	0	1	0
Coprophanaeus pecki		0	7	0	0	1
Deltochilum pseudoparile		0	0	0	0	(+)
Dichotomius satanas		0	29	0	7	15
Eurysternus foedus		0	0	0	0	1
Ontherus didymus		0	7	1	6	6
Onthophagus acuminatus		0	0	0	1	8
Onthophagus incensus		0	0	0	0	1
Onthophagus nyctopus		1	30	0	40	77
Onthophagus praecellens		1	4	0	7	6
Pedariidum pilosum		3	7	0	6	37
Phanaeus pyrois		14	15	0	12	0
Scatimus quadridentatus		0	8	0	0	11
Sulcophanaeus noctis		0	8	0	0	2
Sulcophanaeus velutinus		0	1	0	2	0
Uroxys bidentis		11	1	0	14	1
Uroxys depressifrons		8	4	0	14	19
Total		77	178	8	146	191

(+) Individuals observed removing bait from trap.

TABLE 27

Beetles collected from pitfall traps (PFT) baited with carrion (C) and human dung (D) during a six-day period in June and from a standard size flight interception trap (FIT) during a six-week period in June and July 1981 at La Fortuna. Quantity of bait measured in cc. Effort expressed as number of trap-days.

Species	Trap Type:	PFT	PFT	FIT
	Bait Type:	D	C	-
	Quantity:	2	200	-
	Effort:	15	3	42
<i>Bdelyrus seminudus</i>		0	0	2
<i>Canthidium ardens</i>		3	0	103
<i>Canthidium vespertinum</i>		0	0	15
<i>Canthidium</i> sp. 1		0	0	1
<i>Canthon</i> sp. 3		0	0	4
<i>Coprophanaeus chiriquensis</i>		1	1	70
<i>Cryptocanthon</i> sp. 1		1	0	0
<i>Deltochilum mexicanum</i>		6	30	200
<i>Deltochilum parile</i>		5	2	6
<i>Eurysternus velutinus</i>		0	0	1
<i>Ontherus didymus</i>		29	7	22
<i>Onthophagus</i> sp. 2		3	0	50
<i>Onthophagus mirabilis</i>		0	0	3
<i>Onthophagus praecellens</i>		0	0	22
<i>Sulcophanaeus velutinus</i>		1	0	0
<i>Uroxys depressifrons</i>		2	2	1
<i>Uroxys</i> sp. 1		0	0	72
<i>Uroxys</i> sp. 2		3	0	0
Total		54	42	572

TABLE 28

Beetles collected from pitfall (PFT) and soil traps (SLT) baited with human dung and from a standard size flight interception trap (FIT) during a two-day period in June 1983 at Gamboa. Quantity of bait measured in cc. Effort expressed as number of trap days.

Species	Trap Type:		
	Bait:	PFT	SLT
	Effort:	32	14
			FIT
Ateuchus candezei	5	0	2
Canthidium aurifex	14	36	43
Canthidium centrale	2	0	0
Canthon c. sallei	1	1(+)	3
Canthon juvenis	18	2(+)	5
Canthon lamprimus	3	1(+)	9
Canthon moniliatus	5	1(+)	0
Canthon subhyalinus	4	1(+)	0
Coprophanaeus t. corythus	1	4	1
Eurysternus plebejus	1	0	1
Onthophagus acuminatus	53	137	7
Onthophagus coscineus	7	1	6
Onthophagus landolti	82	8	25
Onthophagus praecellens	7	16	10
Pedariidum pilosum	0	1	0
Phanaeus howdeni	18	12	7
Pseudocanthon perplexus	1	0	0
Scatimus ovatus	0	1	0
Uroxys microcularis	7	11	12
Total	229	233	131

(+) Additional beetles observed removing bait from trap.

TABLE 29

Beetles collected in a standard size flight interception trap between June 5 and August 22, 1982 at El Llano.

<i>Ateuchus aeneomicans</i>	3
<i>Ateuchus guatemalensis</i>	1
<i>Bdelyrus seminudus</i>	4
<i>Canthidium angusticeps</i>	6
<i>Canthidium ardens</i>	4
<i>Canthidium aurifex</i>	26
<i>Canthidium centrale</i>	23
<i>Canthidium elegantulum</i>	2
<i>Canthidium haroldi</i>	12
<i>Canthidium hespenheidei</i>	5
<i>Canthidium perceptibile</i>	3
<i>Canthidium</i> sp. 2	5
<i>Canthon aequinoctialis</i>	220
<i>Canthon moniliatus</i>	2
<i>Canthon</i> sp. 1	23
<i>Coprophanaeus morenoi</i>	26
<i>Cryptocanthon humidus</i>	2
<i>Deltochilum g. panamensis</i>	4
<i>Deltochilum pseudoparile</i>	31
<i>Deltochilum v. acropyge</i>	1
<i>Dichotomius gamboaensis</i>	10
<i>Dichotomius satanas</i>	7
<i>Eurysternus caribaeus</i>	5
<i>Eurysternus foedus</i>	4
<i>Eurysternus plebejus</i>	2
<i>Eurysternus velutinus</i>	2
<i>Onthocharis panamensis</i>	1
<i>Onthophagus acuminatus</i>	4
<i>Onthophagus dicranus</i>	12
<i>Onthophagus marginicollis</i>	1
<i>Onthophagus nyctopus</i>	4
<i>Onthophagus praecellens</i>	12
<i>Onthophagus sharpi</i>	3
<i>Onthophagus stockwelli</i>	1
<i>Phanaeus pyrois</i>	78
<i>Scatimus ovatus</i>	1
<i>Sulcophanaeus cupricollis</i>	1
<i>Uroxys gatunensis</i>	20
<i>Uroxys macrocularis</i>	7

Total 575

Figure 1. Locations of study sites in Panama and adjacent Costa Rica. 1 - Barro Colorado Island; 2 - Cerro Pelota; 3 - Las Cruces (Costa Rica); 4 - La Fortuna; 5 - Gamboa; 6 - El Llano-Carti Rd; 7 - Perlas Islands.

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Figures 2 - 5

Figure 2. Standard size flight interception trap with rain roof at Cerro Pelota.

Figure 3. Series of 15, 30 and 60 cm high flight interception traps on BCI.

Figure 4. Canthidium pallidoalatum perching at 0930 hrs, Cerro Pelota. Note the active searching stance with head elevated and antennal lamellae widely separated. Actual beetle length 4.5 mm.

Figure 5. Canthidium vespertinum perching at 2100 hrs, Las Cruces. Searching stance as in Fig. 4. Actual beetle length 5 mm.

Figure 6. Hourly flight abundance of selected species from BCI.
Arrows indicate dawn and dusk.

Figure 7. Hourly flight abundance of selected species from BCI. Arrows indicate dawn and dusk.

Figure 8. Hourly flight abundance of selected species from BCI. Arrows indicate dawn and dusk.

Figure 9. Hourly flight abundance of selected species from Cerro Pelota. Arrows indicate dawn and dusk.

Figure 10. Hourly flight abundance of selected species from Las Cruces. Arrows indicate dawn and dusk.

Figures 11 - 14

Figure 11. Canthidium ardens in defensive crouch at 1000 hrs, Las Cruces. Note the presence of phoretic mite on hind tarsus. Actual beetle length 4.5mm.

Figure 12. Uroxys micros feeding in fresh howler monkey dung on leaf at 0830 hrs, BCI. Actual beetle length 4 mm.

Figure 13. Canthon septemmaculatus brushing pygidium with mid and hind legs at 1530 hrs, BCI. Actual beetle length 13 mm.

Figure 14. C. septemmaculatus sunning on leaf at midday, BCI. Photo taken using ambient light. Actual beetle length 12 mm.

Figures 15 - 18

Figures 15 - 18. Perching behaviours of Canthon
angustatus between 0830 and 0845 hrs, RCI.
Average beetle length 6.5 mm.

Figure 15. Active searching stance of C. angustatus.

Figure 16. Defensive display stance of C. angustatus.

Figure 17. C. angustatus brushing pygidium with mid
and hind legs.

Figure 18. C. angustatus removing howler monkey dung
from upper canopy leaves.

Figure 19. Distribution of *Canthon angustatus* perching heights above ground level from BCI (N=197). Note that all individuals found within 10 meters of fresh howler monkey dung.

Figure 20. Distribution of *Canthidium aurifex* perching heights above ground level on BCI.
 Fig. 20a: All individuals observed (N=297).
 Fig. 20b: Excluding individuals within 100m of less than 1 day old howler monkey dung (N=165).

Figure 21. Distribution of *Canthidium haroldi* perching heights above ground level on BCI.
 Fig. 21a: All individuals observed (N=250).
 Fig. 21b: Excluding individuals within 100m of less than 1 day old howler monkey dung (N=161).

Figure 22. Distribution of *Uroxys bidentis* perching heights above ground level at Cerro Pelota (N=160).

Figure 23. Distribution of *Canthidium leucopterus* perching heights above ground level at Cerro Pelota (N=34).

Figure 24. Linear regression of perching height on body length for eight species of diurnal Canthidium.

Figure 25. Linear regression of perching height on body length for six nocturnal species of Canthidium, Ontherus and Uroxys.

APPENDIX

List of species with their major foraging characteristics. Order of taxa follows that in Howden and Young (1981). Activity Period: C- crepuscular; D- diurnal; N- nocturnal. Foraging Mode: F- cruising flight; F/P- cruising flight with perching; P- perching. Food Relocation: BR- ball roller; CC- cleptocoprid; PC- paracoprid; PP- pellet pusher. A cross (+) indicates presence at food type either as a natural deposit or in a trap. Two crosses (++) indicates a greater abundance at that food type.

Species	Activity Period	Foraging Mode	Food Relocation	Dung	Carion	Fruit	Plant Litter
<u>Eurysternus foedus</u> Guérin-Meneville	C	F	?	+			
<u>Eurysternus plebejus</u> Harold	D	F/P	?	+			
<u>Eurysternus velutinus</u> Bates	?	F	?	+			
<u>Eurysternus caribaeus</u> (Herbst)	C	F	?	+			
<u>Eurysternus magnus</u> Laporte	D	F	?	+			
<u>Canthon moniliatus</u> Bates	D	F	BR	+	+		
<u>Canthon septemmaculatus</u> (Latreille)	D	F/P	BR	++	+		
<u>Canthon cyanellus sallei</u> Harold	D	F	BR	+	++		
<u>Canthon aequinoctialis</u> Harold	N	F	BR	++	+		
<u>Canthon juvenis</u> Harold	D	?	BR	+			
<u>Canthon angustatus</u> Harold	D	F/P	BR	+			
<u>Canthon subhyalinus</u> Harold	D	F/P	BR	+			
<u>Canthon lamprinus</u> Bates	D	F/P	BR	+			
<u>Canthon</u> sp. 1	D	F/P	BR	+			
<u>Canthon</u> sp. 2	D	F	?				
<u>Canthon</u> sp. 3	D	?	?	+			
<u>Pseudocanthon perplexus</u> (LeConte)	D	F	BR	+			
<u>Deltochilum gibbosum panamensis</u> Howden	N	F	BR	+	+		
<u>Deltochilum mexicanum</u> Burmeister	N	F	BR	+	++		
<u>Deltochilum parile</u> Bates	C	F	BR	+	+		
<u>Deltochilum pseudoparile</u> Paulian	N	F	BR	+	+		
<u>Deltochilum valgum acropyge</u> Bates	?	F	?				
<u>Cryptocanthon humidus</u> Howden	?	?	?				
<u>Cryptocanthon</u> sp. 1	?	?	?	+			
<u>Pedaridium pilosum</u> (Robinson)	N	F	CC?	+			
<u>Bdelyrus seminudus</u> (Bates)	?	F	?				+
<u>Onthocharis panamensis</u> Paulian	D	F	?				
<u>Scatimus quadridentatus</u> Balthasar	N	F	CC?	+			
<u>Scatimus ovatus</u> Harold	N	F	CC?	+			

APPENDIX Continued

Species	Activity Period	Foraging Mode	Food Relocation	Dung	Carion	Fruit	Plant Litter
<u>Uroxys gorgon</u> Arrow	N	F	?	+			
<u>Uroxys metagorgon</u> Howden & Young	N	F	?				
<u>Uroxys depressifrons</u> Howden & Young	N	F/P	CC	++	+		
<u>Uroxys micros</u> Bates	N	F/P	PC	+			
<u>Uroxys microcularis</u> Howden & Young	N	P	PC	+			
<u>Uroxys platypyga</u> Howden & Young	N	P	PC	+			
<u>Uroxys macrocularis</u> Howden & Young	N	P	PC	+			
<u>Uroxys bidentis</u> Howden & Young	N	P	PC	+			
<u>Uroxys gatumensis</u> Howden & Young	?	?	?				
<u>Uroxys</u> sp. 1	N	P	?	+			
<u>Uroxys</u> sp. 2	N	P	?	+			
<u>Uroxys</u> sp. 3	N	P	?	+			
<u>Ateuchus candezei</u> (Harold)	N	F	PC	+			
<u>Ateuchus aeneomicans</u> (Harold)	D	F	?	+			
<u>Ateuchus guatemalensis</u> (Bates)	D	F	?	+			
<u>Canthidium centrale</u> Boucomont	N	F	PC	+			
<u>Canthidium tuberifrons</u> Howden & Young	N	F	PC	+			+
<u>Canthidium haroldi</u> Preudhomme	D	P	PP	+			
<u>Canthidium angusticeps</u> Bates	D	F	?				
<u>Canthidium elegantulum</u> Balhasar	D	P	?	+			
<u>Canthidium perceptibile</u> Howden & Young	D	P	PP	+			
<u>Canthidium vespertinum</u> Howden & Young	N	P	PP	+			
<u>Canthidium pallidoalatum</u> Howden & Young	D	P	PP	+			
<u>Canthidium variolosum</u> Howden & Young	D	?	?	+			
<u>Canthidium leucopterum</u> Howden & Young	D	P	PP	+			
<u>Canthidium ardens</u> Bates	D	P	PP	+			
<u>Canthidium aurifex</u> Bates	D	P	PP	+			
<u>Canthidium hespenheidei</u> Howden & Young	D	P	?				
<u>Canthidium</u> sp. 1	N	P	?	+			
<u>Canthidium</u> sp. 2	N	P	?	+			
<u>Canthidium</u> sp. 3	N	P	?				
<u>Onthophagus incensus</u> Say	D	F	PC	✓			
<u>Onthophagus crinitus panamensis</u> Bates	D	F	PC	+			
<u>Onthophagus stockwelli</u> Howden & Young	D	F	PC	+			
<u>Onthophagus nyctopus</u> Bates	N	F	CC	+			
<u>Onthophagus acuminatus</u> Harold	D	F	CC?	+			
<u>Onthophagus marginicollis</u> Harold	D	F	?	+			

APPENDIX Continued

Species	Activity Period	Foraging Mod.	Food Relocation	Dung	Carion	Fruit	Plant Litter
<i>Onthophagus lebasii</i> Boucefont	D	F	?	+			
<i>Onthophagus coscineus</i> Bates	D	F/P	PC	+			
<i>Onthophagus dicranus</i> Bates	D	F	?				
<i>Onthophagus landolti</i> Harold	D	F	PC	+			
<i>Onthophagus atrosericeus</i> Boucefont	?	F	?	+			
<i>Onthophagus cyanellus</i> Bates	D	F	PC	+			
<i>Onthophagus mirabilis</i> Bates	C	F	PC	++		+	
<i>Onthophagus sharpi</i> Harold	D	F	PC	+		++	
<i>Onthophagus praecellens</i> Bates	D	F	PC	+		+	
<i>Onthophagus belorhinus</i> Bates	C	F	PC	+		++	
<i>Onthophagus</i> sp. 1	D	F	?	+			
<i>Onthophagus</i> sp. 2	?	F	?	+			
<i>Onthophagus</i> sp. 3	?	F	PC			+	
<i>Ontherus brevipennis</i> Harold	N	F	PC				+
<i>Ontherus didymus</i> Erichson	N	F/P	PC	++	+		
<i>Dichotomius satanas</i> (Harold)	N	F	PC	++	+		
<i>Dichotomius lemoratus</i> Howden & Young	N	F	?				
<i>Dichotomius gamboaensis</i> Howden & Young	N	F	?	+			
<i>Copris lugubris</i> Boheman	N	F	PC	+			
<i>Copris costaricensis</i> Gahan	?	F	?	+			
<i>Phanaeus howdeni</i> Arnaud	D	F	PC	+			
<i>Phanaeus pyrois</i> Bates	D	F	PC	++	+		
<i>Sulcophanaeus velutinus</i> (Murray)	D	F	PC	+			
<i>Sulcophanaeus cupricollis</i> (Nevinson)	D	F	PC	+			
<i>Sulcophanaeus noctis</i> (Bates)	D	F	PC	+			
<i>Coprophanaeus telamon corythus</i> (Harold)	N	F	PC	+	++		
<i>Coprophanaeus chiriquensis</i> Olsoufieff	N	F	PC	+	++		
<i>Coprophanaeus morenoi</i> Arnaud	N	F	PC	+	++		
<i>Coprophanaeus pecki</i> Howden & Young	N	F	PC	+	++		

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