RESOURCE PARTITIONING IN A NEOTROPICAL

NECROPHAGOUS SCARAB GUILD

by

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Cap. 1

APPROVAL SHEET

Title of Thesis: Resource Partitioning in a Neotropical
                   Necrophagous Scarab Guild

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ABSTRACT

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Orrey P. Young, Doctor of Philosophy, 1978

Dissertation directed by: Douglass H. Morse
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Data collected from naturally occurring and artificially

placed vertebrate carcasses were examined for the purpose of revealing

mechanisms permitting the coexistence of carrion feeders in tropical

forests.   Studies concentrated on the necrophagous scarab guild and

were conducted at three sites in the Panama Canal Zone during the

periods January-June 1974, January-May 1975, and September-December

1975.

Only mammalian carcasses were discovered at the principal

study site, Barro Colorado Island (BCI).   The seven species repre-

sented were among the 15 largest mammalian species known to occur on

the island.   Naturally occurring carcasses were most abundant late in

the wet season, but the rate of utilization of carcasses was greatest

in the dry season.   Vertebrate scavengers appeared to be the most

important consumers of carrion on BCI, and were the primary cause of

high carcass utilization rates in the dry season.   Invertebrate

carrion consumers were rare in the dry season, but in the wet season

probably consumed as much as 50% of the available vertebrate carrion.

Field experiments demonstrated that mammalian carcasses were consumed

by arthropods faster than bird carcasses, and that lizard carcasses

were consumed very slowly, if at all. Consumption time by arthropods was directly proportional to carcass size, and fresh carcasses attracted many more species of arthropods than did older carcasses.

Larval dipterans dominated carrion during the wet season. They could render a typical large (2 kg) vertebrate carcass unsuitable for other consumers in three days and consume 80% of the carcass in nine days. Larval dipterans also provided the food of a large group of predators. Potential competitors of larval dipterans (vertebrates, scarab beetles) were only successful if they arrived at the carcass quickly and removed portions of the carcass before larval dipteran populations rendered the food unsuitable.

The necrophagous scarab guild on BCI contained 25 species and partitioned food along several dimensions. Differences in the techniques of removing food from a carcass for subsequent consumption or egg-laying appeared to be the most important in achieving species separation within this guild. Along temporal dimensions, both wet vs. dry season and day vs. night were important in species separation. Also of importance was the ability of species to consume a variety of foods, both carrion and other resources. Body size and trophic apparati were also of some importance.

A linear dominance hierarchy, based on fighting ability, exists in the necrophagous scarab guild and is directly correlated with the type of food removal. Species biomass was also directly correlated with the dominance hierarchy. Ball-rolling species, for example, were always capable of taking food away from other species and represented the largest portion of the guild biomass.

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INTRODUCTION

One of the major pathways for movement of nutrients in tropical forest ecosystems is the detritus food chain (Wiegert and Owen, 1971). Sources of detritus in tropical forests include annual leaf fall, dead plants, fallen seeds and fruits, feces, and dead animals (Richards, 1952). Animal inhabitants of tropical forests exhibit three principal feeding habits: carnivory, the consumption of live animals; phytophagy, the consumption of live plants; and saprophagy, the utilization of dead or dying organic material (Raw, 1967). Two types of saprophages involved in detritus consumption are the coprophages, consumers of fecal material, and the necrophages, consumers of animal carcasses (Wallwork, 1970).

Necrophages may be either vertebrate or invertebrate, as may their food. Vertebrate carcasses may be consumed by vertebrate and/or invertebrate necrophages. With the exception of the largest invertebrate carcasses, the principal consumers of dead invertebrates are invertebrate necrophages and/or microorganisms (Schaller, 1968). In some areas, such as the African savanna, vertebrate necrophages may be the principal consumers of vertebrate carcasses (Kruuk, 1967; 1972). In other areas, such as the sheep-raising districts of Great Britain, invertebrates may be the principal carrion consumers (Cragg, 1955). Most areas, however, such as the southeastern United States (Payne and Crossley, 1966), appear to possess an impressive variety and density of both vertebrate and invertebrate necrophages.

I have investigated the species assemblage associated with vertebrate carcasses and feces in a neotropical forest. This is a

natural grouping of species, as many consumers view these two food types to be similar and unlike other types of detritus (e.g. Halffter and Matthews, 1966). I will consider the necrophages primarily, referring to coprophages where appropriate. Most of my effort was directed toward the invertebrate necrophages, and within this group the Coleoptera received particular attention due to the prominent role they may play in the decomposition of carrion (Raw, 1967). Within the Coleoptera, the necrophagous scarab guild proved to be of special interest and was chosen for detailed analysis. Following Root (1967), I define a guild as "a group of species that exploits the same resource in a similar way". Root was clearly referring to food resources (Root, 1967; 1973), as was Balogh when he proposed a similar term, syntrophia, in 1946. In current usage, a guild is usually composed of species that are similar taxonomically (e.g. Schoener, 1974).

Vertebrate carcasses are usually of large size, morphologically similar, and usually occur on the forest floor. The soil fauna, however, plays a minor role in the decomposition of vertebrate carcasses (Bornemissza, 1957). Invertebrate carcasses are particularly difficult to study because of their small size, diverse morphological characteristics, and three-dimensional distribution in the tropical forest (Wallwork, 1976). Consumption of invertebrate carcasses is performed primarily by members of the soil community (sensu strictu), with minimal attraction of other organisms (Raw, 1967).

Detailed studies of the animal species associated with vertebrate carcasses have usually concentrated on the arthropod fauna.

This attention may result from the proportionately larger number of arthropod species associated with vertebrate carcasses. The most detailed study reported to date indicated that 97% of the 522 animal species associated with pig carrion were arthropods (Payne and Crossley, 1966) (Appendix A). The most important temperate arthropod taxa are the Diptera and Coleoptera, both in number of species and in consumption of carcass material (Fuller, 1934; Walker, 1957; Reed, 1958; Payne, 1965). Several studies have examined the niche relationships of the Diptera and have found the larval forms to be most important in the consumption of carrion (Kamal, 1958; Denno and Cothram, 1975; 1976). In the Coleoptera, adult forms predominate on carrion, and very little is known about the larval feeding habits of most beetles associated with carrion.

Several ecological investigations have focused on the Coleoptera associated with carrion (Howden, 1950; Payne and King, 1969; Shubeck, 1969; Ratcliffe, 1972; Brewer and Bacon, 1975). Behavioral studies on carrion beetles include those concerned with orientation to odor (Shubeck, 1968), beetle-mite interactions (Springett, 1968), diel activity patterns (Shubeck, 1971), and social behavior (Milne and Milne, 1944; 1976). There is an absence, however, of research on the niche relationships and intraguild interactions of any group of coleopteran carrion consumers.

Neotropical investigations of carrion-associated arthropods have been infrequent and limited in scope. Few data exist on tropical species of the principal carrion-feeding dipteran family, Calliphoridae (Norris, 1965), and similarly little information exists for the

principal tropical coleopteran subfamily associated with carrion,

the Scarabaeinae (Halffter and Matthews, 1966). Other arthropod

groups associated with carrion in the neotropics are even less well

known. In the neotropics, the most important taxa involved in carrion

consumption include dipterous larvae (Calliphoridae and Sarcophagidae),

adult Formicidae (Hymenoptera), and Scarabaeidae (Coleoptera) (Cornaby,

1974). Although information on neotropical necrophagous scarabs is

limited, it suggests a large and diverse assemblage (Luederwaldt, 1911;

Pessoa and Lane, 1941; Martinez, 1959; Halffter and Matthews, 1966).

Several recent studies (Cornaby, 1974; Howden and Nealis, 1975) have

provided species lists of scarabs attracted to carrion in Costa Rica

and Colombia, respectively.

It is the objective of this report to consider the question,

"What are the niche dimensions and species characteristics that allow

coexistence of a large species assemblage on the same food resource?"

I will present and discuss data from a neotropical lowland forest

pertaining to the following topics:

1. Seasonal patterns in the occurrence of vertebrate carrion

2. The relative importance of vertebrate and invertebrate
   carrion consumers

3. The rate of carrion removal

4. The influence of carrion size, age, and type on utilization
   patterns

5. Interactions between the dipteran and coleopteran carrion-
   feeding guilds

6. Niche relationships, population characteristics, and intra-
   guild interactions of a group of coleopteran carrion consumers.

SITE DESCRIPTION

Barro Colorado Island

Location and History -- Barro Colorado Island (BCI), Canal Zone,
is a biological preserve and research station operated by the Smith-
sonian Tropical Research Institute. BCI is a hilltop that was
separated from adjoining forests by the damming of the Chagres River
in 1910-1914 to form Gatun Lake, the central part of the Panama Canal.
No agricultural or logging activity has occurred since the island
was made a biological preserve in 1923, but intermittent poaching of
the larger animals has occurred up to the present time. Barro
Colorado (9°10'N, 79°51'W) is about 1,616 ha. in size (Knight, 1975)
with a maximum elevation of 163 m above sea level. Gatun Lake is
about 26 m above sea level.

Forest Characteristics -- The vegetation on BCI has been
classified as semi-evergreen seasonal (deciduous) forest (Beard, 1944)
and as tropical moist forest (Holdridge, 1967). The northeastern half
of BCI contains forest 50-65 years old, averaging 20 m in height,
and has a relatively dense understory. The other half of the island
contains older forest (>130 years), averaging 30 m in height, and
has a relatively open understory (Foster, 1973; Knight, 1975).
Maximum litterfall occurs in December-April (Smythe, 1975), with litter
accumulating to depths of 6 cm or more by the end of the dry season
(personal observation). The rate of litter decomposition increases
dramatically at the start of the wet season (May), such that by August
little or no litter remains, exposing the hard red laterite clay
(Knight, 1975).

Climate -- The average annual rainfall (1926-1973) for BCI is
278 cm, with a mid-December to early May dry season. March has the
lowest average rainfall (3 cm) and November the highest average
rainfall (46 cm) (Croat, 1975). Average hourly windrun values (the
amount of wind (km) passing a fixed point) in a forest clearing
reach a daily maximum (1973) at about 1200 hrs. Monthly windrun
maximums are attained during the dry season (highest in February),
monthly minimums during mid-wet season (August-October). Average
daily temperature maximums (1973) on the forest floor are highest
during April (30.8°C), and lowest during December (26.1°C). Average
daily temperature minimums are highest during March (23.2°C) and
lowest during July (20.9°C). The extremes of temperature observed
on the forest floor during one year (1973) are 16.5°C and 32.5°C.
Average daily relative humidity values at 1200 hrs (1973) are highest
during November (94.2%) and lowest during April (76.4%). Appendix B
contains data derived from Smythe (1975) that illustrate the BCI
climatological data.

Limbo

The Limbo study area is located 8 km NW of Gamboa, Canal Zone
(9°10'N, 79°44'W) within 10 km of BCI, and is under the control of the
Limbo Hunt Club. Much of the forest in the immediate area is undis-
turbed and probably greater than 130 years old. The site is part of
a large forested area (>50 km²) within the Chagres River drainage
system and prior to 1910 was probably contiguous with the forest on
BCI. The forest is tropical moist forest (Holdridge, 1967), approxi-
mately 30 m high, and because of Hunt Club protection contains many

of the larger animals not found in adjacent areas. The climate is essentially the same as BCI, although annual rainfall appears to be somewhat lower (yearly mean of 204 cm for 1959-1968) (Chaniotis et al, 1971).

Buena Vista

Buena Vista is a peninsula extending into Gatun Lake, the tip of which lies within 450 m of the northwest edge of BCI and is the closest mainland to the island. This peninsula is approximately 3 km long and contains mostly secondary forest less than 20 m high. No humans live on the peninsula, but the area has suffered heavy hunting pressure in the recent past, eliminating virtually all of the resident non-volant mammals.

MATERIALS

Several types of traps were used to capture necrophagous arthropods (Fig. 1,2,3,4). All attempted to exclude vertebrates by the use of coarse-mesh wire screening (2.5 cm x 5.0 cm mesh), either staked flush with the top of the trap (Type B, C, D) or in the form of a five-sided cage staked over the carcass (Type A).

Pitfall traps were placed in the ground with the upper lip 2 cm above the soil surface and loose soil packed and sloped up to the trap edge. This prevented ground runoff water from flowing into the traps. To prevent rainwater from filling the pitfall traps, a circular, flat-bottomed plastic bucket with most of the sides removed, leaving only four "legs", was inverted over the trap (Type B, D). A three-pole "tepee" arrangement with plastic sheeting wrapped around the upper portion (within 25 cm of the soil surface) achieved the same result for trap Type C.

Sand or soil was placed beneath the carcass in all traps, functioning to absorb water, to provide material for burrowing arthropods, and to provide space for arthropod prey to escape predators. The fine-mesh screen funnel in each pitfall trap served to restrict the exit of attracted arthropods, although the funnel was not very efficient in retaining adult dipterans.

METHODS

General

Field investigations were conducted at three sites in the Panama

Canal Zone during the periods January-June 1974, January-May 1975,

and September-December 1975, a total of 15 months. All Scarabaeidae

(Coleoptera) obtained were identified to species and are now a part

of the U.S. National Museum collection. Some individuals of each

species were also weighed and measured. Unless otherwise noted, the

animal carcasses utilized in experiments and trapping regimens were

obtained on BCI. The Roof Rats (Rattus rattus) were live-trapped

in the BCI animal house and stored at -20°C. Other animals were

obtained from the Smithsonian Environmental Sciences trapping program

as trap casualties and were also frozen until needed. My usual

procedure was to remove a carcass from cold storage and thaw it at

ambient temperature (±30 C) for 48 hours in a screened, insect-proof

container. The carcass, not yet bloated, was then placed in the field,

releasing odors detectable by humans. This procedure will be referred

to as the "ripening" process. Roof rats were chosen as the principal

carcasses utilized in experiments and trapping because of their

relative ease of procurement and their similarity to the most abundant

rodent in the BCI forest, the Spiny Rat (Proechimys semispinosus)

(Eisenberg and Thorington, 1973).

An extensive network of trails (32 km) is maintained on Barro

Colorado Island, allowing easy access to nearly all parts of the

island (Fig. 5). One section of the island, Lutz Watershed, has been

intensively studied by the Environmental Sciences Program of STRI;

most of the carrion trapping and experiments were conducted here (Fig. 6). Trapping on the island was also conducted on Armour, Zetek, Barbour-Lathrop, Fairchild, Barbour, Wheeler, and Snyder-Molino Trails. Wherever possible, traps were set and/or experiments were performed on ridgetops to maximize the area of odor dissemination.

At the Limbo site, trapping was conducted on 23-24 October 1975 and 29-30 November 1975. At the Buena Vista site, trapping was conducted on 24-25 September 1975 and 2-3 November 1975. At each site a total of five carrion traps (Type B) baited with ripened Roof Rats were placed on slopes or ridgetops, separated by at least 100 meters.

Resource Characteristics

Occurrence -- Almost 2000 hrs were spent in the field on BCI during the 15 months of this study. All island trails (Fig. 5) were traversed at least once during this period, searching for naturally occurring carcasses. Trails within and immediately adjacent to the Lutz Watershed (Fig. 6) were traversed at least once every two weeks. Thus carcass occurrence is expressed as a function of field effort, not of distance travelled. In the field, odors of carcasses, flushed vultures, and other "sign" were investigated for the presence of dead animals. Once a carcass was found, the condition, type, state of decay, and occurrence of arthropods was recorded. Voucher material was retained, both for identification of the carcass and its arthropod consumers.

Availability -- A field experiment was conducted in March 1975, and repeated in November 1975, to determine the relative availability of carrion to the various consumer groups. A series of ten large Roof

Rat carcasses plus controls, averaging 195 g (170 g to 240 g), were placed on the soil surface atop ridges at intervals of 100 m (Fig. 6). Each carcass was examined three times daily for four days or until removed by carrion consumers. Controls included two carcasses, one tied by wire to a stake and the other enclosed in a five-sided, coarse-mesh wire cage anchored to the ground.

To determine the relative importance of the major arthropod groups in the consumption of an animal carcass during November, 1975, a series of nine Roof Rats plus "controls" were placed atop ridges at intervals of 100 m (Fig. 6). Each carcass was placed in a pit-fall trap that excluded vertebrates (Type B), and the traps were located in places different from those of the previously described experiment. At each location, the weights of the carcass, can, and sand were separately recorded immediately before placement, and all traps and their contents were placed in the field on the same morning. On each of the nine days of the experiment, one trap was removed from the field and the total weight of the can, sand, carcass, and attracted arthropods was recorded. The carcass plus arthropod weight was then computed by subtracting the original can plus sand weight from the total post-exposure weight. Arthropods were removed from the carcass by hand-sorting (and then washed), by immersing the trap contents in water and skimming the water surface for specimens, and by sieving the remaining material through fine-mesh screening. Arthropods were then allowed to dry at ambient temperature for at least one hour on absorbent paper before weighing. Specimens were all treated similarly, under similar temperature and humidity conditions, during

the experimental period to minimize the admitted inaccuracies of this procedure. Total arthropod weight was subtracted from the combined carcass plus arthropod weight to determine the remaining carcass weight. Arthropods were subdivided into dipterous larvae, scarabs, and other arthropods; and weights were recorded. The impracticality of obtaining the dry weight of dipterous larvae required the use of wet weight values for all groups. Several Roof Rat carcasses were placed in the field at the same time as the nine experimental carcasses and served as controls for the following conditions;

#1 -- Both vertebrates and invertebrates excluded; monitored for 15 days.

#2 -- Neither vertebrates nor invertebrates excluded.

#3 -- Vertebrates excluded, all dipterous larvae larger than 10 mm removed daily; monitored for 15 days.

#4 -- Vertebrates excluded, all scarabs removed daily.

#5 -- Vertebrates excluded, all Staphylinidae removed daily.

Carcass Type -- Several experiments were conducted, in both the dry and wet seasons, to determine the effect of the type of a carcass on its utilization by carrion consumers. Three carcass types were used: mammal, Roof Rat; bird, Gray-chested Dove (Leptotila cassinii); and lizard, Iguana (I. iguana).

In one experiment, two carcasses of each type were simultaneously placed on the soil surface on ridgetops in Lutz Watershed, separated by at least 100 m. Carcasses were monitored daily for at least five days. This experiment was performed once in the dry season (February 1975) and twice in the wet season (October and December 1975). At var-

ious times in the dry season, 13 Roof Rat and two Iguana carcasses were similarly exposed. At various times in the wet season, 11 Roof Rat, two Gray-chested Dove, and two Iguana carcasses were similarly exposed.

In another experiment, two carcasses of each type were placed on ridgetops in the Lutz Watershed, separated by at least 100 m, using traps (Type A) that excluded vertebrate scavengers. Carcasses were examined daily for 30 days, recording arthropod activity and the state of decay. This experiment was performed once in the dry season (Mar-Apr 1975) and once in the wet season (Oct-Nov 1975). During the wet season experiment, a duplicate experiment was conducted using pitfall traps (Type C).

The average weight of the 36 Roof Rats used in these experiments was 190 g, the average weight of the 12 Gray-chested Doves was 75 g, and the average weight of the 14 Iguanas (head and tail removed) was 550 g.

Carcass Size -- An experiment was conducted in the dry season (April 1975) to determine the influence of carcass size on the rate of utilization by vertebrate scavengers. Eight carcasses of three mammalian species were used: American Oppossum (Didelphis marsupialia) ($\bar{x}$ = 3900 g), Common Agouti (Dasyprocta punctata) ($\bar{x}$ = 1900 g), Roof Rat adult ($\bar{x}$ = 220 g), and Roof Rat juvenile ($\bar{x}$ = 65 g). Carcasses were placed on the soil surface which allowed unrestricted access by scavengers. They were located on ridgetops in the Lutz Watershed, and separated by at least 100 m. Carcasses were monitored daily at 1200 hrs. and 2200 hrs. for presence of scavengers and condition of the carcass.

Another experiment, conducted in the wet season (Nov. 1975) examined the effects of carcass size on the rate of consumption by arthropods. One individual each of the Lesser Anteater (Tamandua tetradactyla) (4300 g), Agouti (1600 g), adult Roof Rat (220 g), and juvenile Roof Rat (95 g) was placed on a ridgetop near the Lutz Watershed, separated by at least 50 m, with vertebrate scavengers excluded (Trap Type A). Carcasses were monitored at 1000 hrs. daily, the condition of the carcass noted, and voucher specimens of arthropods collected. Difficulty in acquiring fresh and intact mammal carcasses larger than the Roof Rat made replication of this and other experiments unfeasible.

Intra-guild Interactions

Scarab specimens and data on intra-guild interactions were acquired both from the field experiments previously described and from a trapping program. Traps (Types B, C, D), baited with "ripened" Roof Rats, were placed at monthly intervals in the Lutz Watershed and irregularly at other locations on BCI. These baited traps were collected 12 to 48 hours after placement and the contents hand-sorted for arthropods. Voucher specimens were retained and the remaining arthropods released within 24 hours near the point of capture. A total of 62 naturally occurring and artificially placed vertebrate carcasses provided data and specimens (Table 1).

Preliminary experiments comparing freshly killed vertebrates with carcasses that were frozen, thawed, and "ripened", demonstrated no significant differences in the rate of utilization by necrophages or in the species and number of individuals attracted to the two types

of carcasses.

Interspecific Competition

A series of pair-encounter experiments with scarabs was conducted in the laboratory on BCI during the period September-December, 1975. Individuals were obtained from pit-fall traps baited with roof rat carcasses or from carcasses exposed on the forest floor. The beetles were brought into the laboratory and retained in holding containers for 24-36 hours, without food but with ample moisture. These containers were of the plastic refrigerator type (15 x 10 x 8 cm), and the bottom of each was covered with 2 cm of soil.

For the experiments, a test chamber was built with a wooden bottom, glass sides, and a removable glass top (30 x 30 x 30 cm). The bottom was covered with 7 cm of packed soil. After each group of species-pairs were exposed, the test chamber was dismantled, cleaned with detergent and alcohol, and fresh soil added. This procedure minimized the influence of residual pheromones on the test results.

A piece of "ripe" muscle tissue from a roof rat was used in these experiments. The piece of carrion was approximately equal in size and shape to the largest species in each species pair competing for it. After each pair was exposed to it, the carrion was replaced with a new piece.

The test procedure was to place the carrion in the center of the chamber on the soil surface and then cover the chamber with the lid. Five minutes later, one individual of each of two species was placed on the soil surface in opposite corners of the chamber. If both individuals had not made contact with the carrion in ten minutes,

the test was terminated. When both individuals made contact with the carrion, ten minutes were allowed for the determination of a winner, after which the test was terminated. This procedure was repeated 10 times for each species-pair combination. A winner was considered to be the individual that had clear possession of the piece of carrion. This always occured within the ten minute period.

Whenever possible, the largest individuals of a species were chosen for testing. Equal proportions of each sex were also employed whenever possible. Diurnal species were tested at 1100-1300 hrs and nocturnal species were tested at 2000-2200 hrs. The nocturnal encounters were observed under dim red light supplied by a 25 watt red light bulb no closer than 60 cm to the beetles.

Analyses of Data

Four statistical tests were employed in the analysis of data. The Student's t-test was used to compare the distribution of sample data with a normal distribution. The Spearman Rank Correlation test was utilized to compare the relative positions in a ranked sequence of values obtained by different techniques. The Chi-square test was employed to compare the distribution of a data set with an even distribution (or some other predicted distribution). In situations where the conditions for a X^2 test appeared to be violated by small cell size, Fisher's Exact test was used. Results always were similar to those obtained by the X^2 test, so the X^2 test was routinely used. In no instance were percentages or proportions used in the computation of the various test statistics; the original data were always utilized (Sokol and Rohlf, 1969).

Resource Characteristics

Many factors may influence the necrophagous scarab guild on BCI.
In this section I will present data and analyses concerning those
factors that define the niche space of the guild. Climatic data are
summarized in Appendix B.

Occurrence of Carcasses

During the fifteen months of the study period, thirteen natural-
ly occurring carcasses were found (Table 2). Although this is a small
sample, the number of hours spent in the field obtaining these and
other data (1944 hrs.) suggests a low natural frequency. The follow-
ing mammalian carcasses were discovered, representing seven species:
Nine-banded Armadillo (Dasypus novemcinctus), Howler Monkey (Alouatta
palliata), Coatimundi (Nasua nasua), Three-toed Sloth (Bradypus infus-
catus), Two-toed Sloth (Choloepus hoffmanni), Collared Peccary (Tayassu
tajacu), and American Opossum (Table 2).

At least 42 species of non-volant mammals occur on BCI, plus
approximately 34 species of bats (Eisenberg and Thorington, 1973). Of
the mammals known to occur regularly on BCI, only fifteen species have
mean individual weights of 2 kg or greater (Table 3). The seven
species observed as carcasses are included in this group, suggesting
a direct relationship between carcass size and likelihood of detection
(at least by humans). Observations on BCI indicate that the various
vertebrate scavengers utilizing carcasses (Table 4) are not capable

of removing an entire carcass larger than approximately 2 kg, thus assuring that some portion of the larger carcasses will remain for subsequent human detection.

Eight of the fifteen species with average individual weights ≥ 2 kg were not observed as carcasses (Table 3). Four of those species, Brocket (Mazama americana), Spider Monkey (Ateles geoffroyi), White-tailed Deer (Odocoileus virginianus), and Tapir (Tapirus bairdii), are present on BCI in small numbers, less than 21 individuals per species (Eisenberg and Thorington, 1973), and in a 1500 hectare area have a high likelihood of escaping human detection as carcasses. One common species, the Agouti, is subjected to relatively heavy predation pressure, particularly by coatis (Smythe, 1970b). The old, sick, and starving individuals of this species are likely to be obtained by predators and not occur as carcasses, as are probably individuals of many other small species. The Paca (Agouti paca) spends much of its time in burrows along stream beds, thus non-predator deaths are likely to occur underground and escape human detection. Both the White-faced Monkey (Cebus capucinus) and the Lesser Anteater are at least semi-arboreal and thus relatively free of predators on BCI, but were not observed as carcasses. They are, however, both relatively small in individual weight and in number of individuals, probably placing them at the threshold of human detectability as carcasses.

The frequency of occurrence of detected mammal carcasses varied through the months of the year (Fig. 7). Comparison of the late wet season period of October through January with the remainder of the year, based on the number of carcasses observed per number of obser-

vation hours, demonstrates a significant deviation from an even distribution (x^2 test, P<0.005). Although the dry season may begin in late December, available food for vertebrates such as insects and fallen fruit may not significantly increase until late January. Thus the mortality that occurs in January I consider to be related primarily to the conditions present in the late wet season. Significantly more carcasses were detected in the late rainy season than at other times of the year. Although only certain mammalian species were detected as carcasses, there is no reason to believe that seasonal patterns of occurrence displayed by these seven species are unrepresentative of the mammal population as a whole. Foster (1973) reported a similar peak of carcass occurrence on BCI during the latter part of the wet season.

Availability of Carcasses

Several field experiments were conducted to determine the relative availability of carrion to the various consumer groups. One series of experiments (Table 5), conducted in both the dry season (March) and the wet season (November), demonstrates definite seasonal differences in carrion utilization. During the dry season, all Roof Rat carcasses were removed by vertebrate scavengers within 24 hours of carcass placement, leaving little if any material for invertebrate consumers. Both species of vultures (Turkey Vulture (Cathartes aura) and Black Vulture (Coragyps atratus)) and solitary male coatis were observed removing carcasses during the day in this and other experiments, and opossums were observed removing carcasses at night. Not all carcasses that disappeared were observed being removed, but

subsequent examination of the carcass site indicated removal by a
vertebrate scavenger (footprints, scat, drag marks, etc.). At least
eleven vertebrate species that are present on the island probably
consume carrion and may account for carcass removal (Table 4).

In the wet season, vertebrate scavengers did not obtain all of
the carcasses available in this experiment (Table 5). Three carcasses
were removed by vertebrate scavengers in the first two nights, two
carcasses were consumed during the first three days by vultures, and
the remaining five carcasses were consumed in four days by inverte-
brates. The results of these experiments suggest, at least for the
size and type of carcass used, that invertebrate consumers of carrion
have little opportunity of obtaining carrion in the dry season on
BCI and that only in the wet season is carrion likely to be available
to invertebrates.

The wet season experimental results presented in Table 4 also
suggest that invertebrate consumers may alter carcass condition to the
extent that at some point in the sequence the carcass is no longer
"suitable" for the vertebrate consumer. The results of feeding
experiments with two captive Coati are consistent with this suggestion
(Table 6). When a single adult Roof Rat was released into a cage
(4m x 4m x 2m) with one adult male Coati, the rat was consistently
killed and eaten within ten minutes (N = 10; repeated 5 times with
each Coati). If the rat was placed freshly killed into the cage, it
was immediately "rekilled" by the Coati but sometimes was not eaten
for up to 24 hours (N = 10; rat always eaten). Rats killed, "ripened",
and then offered to the captive Coati were only consumed if the Coati

was starved from 3 to 7 days (N = 10; rat always eaten). At the end
of a 21 day starvation period, neither Coati would consume a rat car-
cass heavily infested with dipterous larvae (N = 2), even though the
coatis appeared active and healthy.

I conducted a series of experiments in November 1975 to deter-
mine the relative importance of the various invertebrate carrion con-
sumer groups and their patterns of consumption in the wet season
(Table 7). When vertebrate scavengers were denied access to a carcass
in a pit-fall trap, arthropods consumed 80% (wet weight) of the carcass
within nine days, leaving only hair, skin, bone, and cartilage (Fig. 8).
The rate of removal of carcass material reached a maximum on day five
(Fig. 9). If the wet weight of arthropods present each day (Table 7,
column 8) is expressed as a percentage of the carcass material calcu-
lated to have been removed that day (Table 7, column 3), a non-linear
relationship is demonstrated (Fig. 10).

The basis for this relationship can be demonstrated by separating
the data represented in Fig. 10 into dipterous larvae and "other
arthropod" components (Fig. 11). The "other arthropod" component
accounted for most of the missing carcass material in the first two
days, as did the dipterous larvae component from day four to the end
of the experiment. The "other arthropod" component was composed
almost entirely of adult Coleoptera, Scarabaeidae in the first 2-3
days and Staphylinidae during the remainder of the period. Adult
Staphylinidae are predators on dipterous larvae and are not known
to consume carrion. The scarabs of BCI found on carcasses, however,
are known carrion consumers and are probably the principal arthropod

competitors of dipterous larvae for carrion. Although scarabs are most important in the first several days of carcass utilization, relatively little carcass material is removed in that time (Compare Fig. 9 with Fig. 11), suggesting that dipterous larvae are the primary arthropod consumers of carrion on BCI.

Various "controls" were associated with these experiments (Table 8). When all dipterous larvae larger than 10 mm were removed daily from a Roof Rat carcass, only 50% of the carcass was removed by day 15, when the experiment was terminated. This rate of removal is substantially lower than the normal pattern of 80% carcass reduction in nine days when large dipterous larvae were present. When the principal predators on dipterous larvae, Staphylinidae, were removed daily, 80% carcass reduction occurred in seven days. When adult scarabs were removed daily, 80% carcass reduction occurs in nine days. These data suggest that scarab activity did not appreciably affect the duration of the carcass reduction period when dipterous larvae were also present, that staphylinid predators may influence larval dipteran populations, and that in the absence of dipterous larvae a carcass will be partially reduced by adult scarabs.

Type of Carcass

Because of the gross external morphological differences between reptiles, birds, and mammals, it has been suggested (Fuller, 1934; Cornaby, 1974) that the taxonomic class of an animal carcass may influence its utilization by consumers of carrion. This hypothesis was tested on BCI by simultaneously placing in the field carcasses

of mammals (Roof Rat), birds (Gray-chested Dove), and lizards (Iguana).

In one set of experiments (Table 9), no significant differences occurred between the carcass types in the proportion of removal by vertebrate scavengers, in either the dry or the wet season (x^2, $P > 0.5$). When the three types are combined, however, there was a significant between-season difference in removal by scavengers (x^2, $P < 0.005$). Carcasses of all types were removed faster by vertebrate scavengers in the dry season than in the wet season.

When vertebrate scavengers were excluded (Trap Type A) from these three types of carrion, differences appeared in their rates of consumption by arthropods (Table 10). During the dry season, mammal carcasses under these experimental conditions were consumed (approximately 80% of initial biomass removed) in 12 days and bird carcasses in 16 days. Lizard carcasses were not consumed in 30 days. The difference in decay rate between lizard and either bird or mammal carcasses was statistically significant (x^2, $P < .01$), but the difference between bird and mammal rates was not statistically significant (x^2, $0.5 > P > 0.1$). During the wet season, mammal carcasses were consumed in 6 days, birds in 10 days, and lizards in 20 days. The differences in decay rate between lizard and either bird or mammal carcasses were again statistically significant (x^2, $P < .025$), while the difference between bird and mammal rates was not statistically significant (x^2, $0.5 > P > 0.1$). The rate of consumption of each type differed between the dry and wet seasons, although only at the borderline of statistical significance (x^2: mammal, $0.1 > P > 0.05$; bird, $P \approx 0.1$; lizard, $0.1 > P > 0.05$). The rate of consumption of each type of carcass by arthropods was much faster in the wet season than in the

dry season, the opposite of the pattern produced by vertebrate scavengers. When carcasses in the wet season were exposed in pitfall traps protected from the rain, rather than on the soil surface, consumption took somewhat longer (Table 10), although the difference was not significant (x^2, $P > 0.1$).

Several patterns of utilization of different carcass types can be demonstrated within the necrophagous scarab guild. In the dry season, only six necrophagous scarab species were obtained on BCI (Table 11). Three species occurred on mammal, bird, and lizard carcasses, and three species occurred only on mammal carcasses. In the wet season, 24 necrophagous scarab species were obtained on BCI (Table 12). Four species (_Ateuchus candezei_, _Phanaeus pyrois_, _Onthophagus praecellens_, and _Anaides longeciliata_) occurred on all three types of carrion. The remaining 20 species occurred only on mammal carcasses. Thus no species was found exclusively on lizard and/or bird carrion in either season. Substantially fewer species (x^2, $0.1 > P > 0.05$) in the wet season were distributed on all three carcass types (4/24 = 17%) than in the dry season (3/6 = 50%).

Size of Carcass

The size of a carcass has been shown to influence the species composition of some necrophagous arthropod groups (Kamal, 1958; Denno and Cothran, 1975). A series of experiments was conducted on BCI to investigate the effects of carcass size on the various consumer groups.

During a period of high vertebrate scavenger activity (dry season), an experiment was conducted utilizing eight carcasses of four

different sizes (Table 13). They were Opossum ($\bar{x}$ = 3900 g), Agouti ($\bar{x}$ = 1900 g), adult Roof Rat ($\bar{x}$ = 220 g) and juvenile Roof Rat ($\bar{x}$ = 65 g). (Specimens of a single species in these four sizes would have been prefered, but unfortunately were not available.) Both sizes of rat were removed by vertebrate scavengers on the first night, and the remaining larger carcasses were occupied the first day by vultures. After the vultures had consumed substantial portions of the carcasses on the first day, three of the four carcasses were removed by vertebrate scavengers during the second night. Consumption of the remaining large carcass was completed by a vulture on the second day. These data indicate a pattern of small carcasses disappearing rapidly and larger carcasses requiring up to 48 hours for complete consumption by vertebrates in the dry season. Although I did not perform similar experiments during the wet season, on the basis of this and previously described experiments I would expect the wet season pattern of consumption to be similar, although not as rapid or complete.

Another experiment, conducted in a period of high carrion-consuming arthropod activity (wet season), attempted to demonstrate the effects of carcass size on rate of consumption by arthropods. One individual each of Lesser Anteater (4300 g), Agouti (1600 g), adult Roof Rat (220 g), and juvenile Roof Rat (95 g) was placed in the field with vertebrate scavengers excluded (Table 14). Eighty percent of the juvenile rat was consumed in four days, with each progressively larger carcass requiring more time to reach that stage. Without replication, these results can only suggest that the duration of the

carcass consumption period by arthropods is directly proportional
to carcass size.

Although I did not attempt to quantify the phenomenon, dipterous
larvae appeared to become increasingly important consumers as carcass
size increased. The smallest carcass, juvenile Roof Rat, had no more
than ten dipterous larvae on it at any one time. The largest carcass,
Lesser Anteater, at one time had approximately five liters of dipter-
ous larvae. These observations suggest a possible geometric (rather
than arithmetic) relationship between carcass size and number (or bio-
mass) of dipterous larvae.

Predators on dipterous larvae also appear to increase in number
of species and individuals as carcass size increases. The largest
carcass attracted a minimum of 15 morphospecies of Staphylinidae and
five morphospecies of Histeridae. The smallest carcass attracted
only five morphospecies of staphylinids and no histerids. The number
of individuals was also proportional to the number of morphospecies
on each carcass. The magnitude of this increase suggests an arithmetic
rather than geometric increase. Coleopteran predators on dipterous
larvae thus do not increase in numbers with increasing carcass size
to the same extent that dipterous larvae increase. This suggests
that the effectiveness of staphylinid and histerid predators in
controlling dipterous larvae populations decreases as carcass size
increases. Ants (Formicidae), potential predators on dipterous larvae
(e.g., Lindquist, 1942), were only present on the largest carcass
in these experiments when it had a high density of dipterous larvae.

Members of the necrophagous scarab guild also appear to be

affected by differences in carcass size. In the experiments previously described on carcass size (Table 14), sixteen scarab species were attracted to at least one of the carcasses (Table 15). The largest carcass (4300 g) attracted 7 species, the 1600 g carcass 9 species, the 220 g carcass 12 species, and the 95 g carcass attracted 9 species. That the largest carcass attracted the lowest number of species correlates well with high dipterous larval density and the observed avoidance of masses of dipterous larvae by these scarab species. The smallest carcass, perhaps due to the short availability period (Table 14) and to size constraints, had fewer species present than would be predicted from the number of species found on the larger carcasses. Only four of the sixteen species were found on all carcass sizes; Eurysternus claudicans, Deltochilum parile, Phanaeus pyrois, and Onthophagus praecellens. These were also the four most abundant species in this experiment. Five species were represented by one or two individuals each and were found on only one carcass. The remaining seven species were found on two or three carcasses.

Age of Carcass

The state of decay of a carcass may influence its use by consumers, and there is a high correlation between the age of a carcass and its degree of decay (Payne, 1965). During the dry season on BCI, carcass age may not in effect be important to carrion consumers, however, since carcasses do not "age" appreciably before removal by vertebrate scavengers (Tables 9, 13). In the wet season, mammal carcasses may remain for seven days or more before consumption by

9-day period (Fig. 15). When considered as a component of the total arthropod biomass, however, scarabs represent 64% of the biomass on day 2 and decline to 6% of the biomass by day 8 (Fig. 16).

The sequence of appearance of species within a necrophagous guild has been demonstrated to be of importance in resource partitioning (Fuller, 1934; Denno and Cothram, 1975). In the carcass exposure experiments just described, (Table 7) 14 scarab species were observed (Table 16). Two of those species first appeared on day one, five on day two, four on day three, one on day four, and two on day five, with no new species appearing in the last four days of the observation period. The number of species on a single carcass reached a maximum of ten by day four with a plateau at eight species for the remaining five days (Table 16). The individuals of only one species, Deltochilum parile, arrived at a carcass on each of the nine days of observation. Individuals of most of the other species arrived predominantly within the first five days. Two species, however, Eurysternus claudicans and Canthon septemmaculatum, were found on each of the last five days of the study period, but not on the first four days (Table 16). These are the only two species that may be temporally separated from the remainder of the guild in this way. The two most abundant species found in this experiment, D. parile and Onthophagus praecellens, both appeared to arrive early and frequently, and probably were not partitioning the resource between themselves on a temporal basis.

In the same experiment, the number of scarab individuals reached a peak by day seven (Table 17, column 3), with the maximum rate of

increase in the number of individuals occurring on day two, a five-fold increase in numbers from day one (Table 17, col. 4). Since the values for each day are cumulative (e.g., day seven values produced by one carcass collected after seven days exposure), the number of individuals of a species found on a particular carcass can be divided by the number of days since the first appearance of that species on any carcass to give an estimate of the average daily number of individuals arriving (Table 16; Table 17, col. 2). This estimate produces values that peak at day three, followed by a consistent decline to the end of the observation period. Using average individual biomass estimates for each species (Table 18), and multiplying by the estimated average number of individuals each day for each species (Table 16), a series of values is generated that indicates peak biomass for the guild occurring on day two (Table 17, col. 5). Actual biomass values for each trap (Table 17, col. 6) show a maximum per day increase in biomass occurring on day two (Table 17, col. 7).

Thus, all measures and estimates of number of species, number of individuals, and biomass of the necrophagous scarab guild reveal maximum values on day two, three, or four (Fig. 17).

Intra-guild Interactions

Twenty-five species of scarabs were observed and captured on carrion during the study period on BCI and are considered to constitute the necrophagous scarab guild. A total of 62 naturally occurring and artificially placed vertebrate carcasses provide the data for a consideration of the population characteristics and niche dimensions of the

guild (Table 1).

Population Characteristics

Abundance of Species -- Data will be presented concerning two components of species abundance, the mean number of individuals of each species found on a carcass, and the relative number of carcasses on which a species occurs. The mean number of individuals range from one to seven per species, with only ten species having a mean of two or more individuals per carcass (Table 19, col. 1). Coefficient of Variation values range from zero to 1.30 (Table 19, col. 2). Of the ten species with zero Coefficient of Variation, two species, Canthon lamprimus and Phanaeus corythus, occurred on more than 10% of the carcasses (Table 19, col. 4). These two species thus appear to show a real pattern of occurrence as single individuals. A comparison of the Coefficient of Variation values with frequency of occurrence values for the fifteen species that occur on more than 10% of the carcasses indicates a high positive correlation (Fig. 18) (R_s =+0.759, $P < 0.01$, Spearman Rank Correlation test). This suggests that the more often a species occurs, the more likely it will be variable in numbers on carcasses. Increasing the reliability of the Mean Value, by increasing sample size, does not apparently reduce the variation contained within the Mean Value.

One species, Onthophagus praecellens, is found on over 70% of the carcasses, and three other species are found on over 50% of the carcasses (Table 19, col. 4). A comparison of frequency of occurrence values with the mean number of individuals per carcass for each species

(Fig. 19) indicates a high positive correlation (R_s + +0.648, P< 0.01), suggesting that those species which occur most frequently through time and space also occur in the highest numbers on a carcass. Eight species, however, show a substantially different relationship (greater than four position differences in rank). Four of these species have a low frequency of occurrence but a high mean number per carcass (Fig. 19), with Canthon septemmaculatum strongly characteristic of this pattern. The other four species, Ateuchus candezei, Canthon sallei, C. lamprimus, and Phanaeus corythus, all occur on more than 10% of the carcasses and thus appear to have a pattern of few individuals on many carcasses.

An abundance value for each species was obtained by multiplying the mean number of individuals per carcass by the frequency of occurrence on carcasses (Table 19, col. 6). To determine which variable was more important in determining species abundance ranking, two comparisons were made. A rank correlation between species abundance and mean number per carcass was not significant (R_s= +0.430, P> 0.05), but a rank correlation between species abundance and frequency of occurrence was significant (R_s=+0.535, 0.05> P> 0.01). A graphic presentation of abundance values for each species (Fig. 20) indicates a distribution of species that appears to fit a logarithmic series curve of expected values. This species abundance curve is similar to that found in many other communities (e.g. Williams, 1964). The numerically dominant species, Onthophagus praecellens, is 139 times more abundant than the rarest species.

Size of Species -- Mean individual wet weights were measured for each species (Table 18, col. 1), indicating a size range of 0.009 to 1.37 grams for the 25 species. The frequency distribution of the various sizes (Fig. 21, 22) indicates the presence of many small species and a few large species (e.g. Williams, 1964). A rank correlation between species abundance and size (Fig. 23) indicates a weak positive correlation (R_s= +0.305, 0.10 > P > 0.05). The principal reason that increasing body size is not more strongly correlated with increasing abundance is the presence of four large but rare species; Phanaeus cupricollis, P. corythus, Canthidium n. sp., and Eurysternus caribaeus.

Biomass Estimates of Species -- Estimates of the biomass of the population segment of each species utilizing carrion, and thus an estimate of the relative importance of each species in carrion consumption, were obtained by multiplying the mean individual wet weight (Table 18, col. 1) by the species abundance value (Table 19, col. 6). The resultant values (Table 18, col. 4) fit a logarithmic series curve of expected values, with many minor species and few dominant species (Fig. 24). A ranking of the biomass values (Table 18, col. 5) indicates that Phanaeus pyrois possesses the highest biomass of any species in the guild, over 1800 times larger than the species with the lowest biomass, Uroxys sulcicollis. To determine which parameter was most important in determining the species biomass rank, two relationships were examined. A rank correlation between species biomass and abundance was significant (R_s=+0.785, P < 0.01, as was a rank correlation between species biomass and size (R_s=+0.797, P < 0.01). Since the difference between these correlation values was not significant, both parameters

appear to contribute equally to the biomass ranking.

Species abundance and species biomass values have both been utilized in various arthropod community studies (Price, 1975). To examine further the relationship between these values in a necrophagous scarab guild, both values were converted to "relative dominance" values, which allows a more direct comparison (Table 19, col. 8 and Table 18, col. 6). This method of analysis involves expressing each value as a proportion of the total abundance or biomass of the guild (Norton and Dindal, 1976). A graphic presentation of relative dominance values (Fig. 25) suggests a positive correlation between species abundance and species biomass, although there are several notable deviations. The most abundant species, Onthophagus praecellens, is exceeded in relative biomass by five other species. The species with the largest biomass, Phanaeus pyrois, is exceeded in relative abundance by two other species. The largest-sized species, Phanaeus corythus, is considerably more dominant in biomass than would be expected from its relative dominance in abundance.

It has been suggested by many authors (e.g. Wigglesworth, 1972) that in insects there is a negative correlation between body size and basal metabolic rate (BMR), and that the best estimates of relative biomass take into consideration BMR differences. This relationship may be particularly obvious within individuals of the same species or within congenerics, and is best approximated by the 2/3 power. When this power function is applied to biomass values for the necrophagous scarab guild, a new series of values can be obtained and ranked (Table 18, col. 7 and 8). A rank correlation between biomass

and biomass-BMR values indicates a highly significant relationship (R_s=+0.980). Only two species, Onthophagus praecellens and O. acuminatus, appreciably changed their rank position in the biomass-BMR series. Because there are notable exceptions to the size-BMR relationship (Wigglesworth, 1972), and since there are no specific data concerning this relation in necrophagous scarabs, biomass-BMR values will not be used in subsequent analyses.

Niche Dimensions

The species of the necrophagous scarab guild can be characterized by their response to three niche dimensions: season, diel, and food type. These dimensions were chosen for systematic collection of data and analysis after preliminary observations and a survey of the literature.

Seasonal Activity -- Species occurring on carcasses from 10 January to 10 May, 1974 and 1975, were considered to be present during the dry season and those on carcasses during the period 1 September to 15 December 1975 were considered to be present during the wet season. Six species were present during the dry season and five of those species plus 19 others were present during the wet season (Tables 20 and 21).

The five species that occurred in both seasons did so in different frequencies (Table 22), thus producing potentially different abundance and biomass values for each season. The two Canthon species, however, maintained the same biomass values on carrion in both seasons, while each of the other three species approximately doubled its biomass

in the wet season.

Total biomass values for the six dry season species are 0.225 g and 1.943 g for the 24 wet season species, representing a wet season increase of 8.6-fold. The number of species in the wet season is only an increase of 4.2-fold over the dry season. These differences between seasons are statistically significant (x^2, $P < 0.05$).

Diel Activity -- All species could be classified as primarily diurnal or nocturnal, although there was considerable overlap in activity during crepuscular periods. Thus no species had a twenty-four hour activity pattern (as did some necrophagous ant species) or could be considered primarily crepuscular. Ten species were present on carcasses during the night (1900 hrs to 0500 hrs) and 15 species were present during the day (0700 hrs to 1700 hrs) (Table 21). The distribution of species in the day and night categories is not significantly different from chance (x^2, $.5 > P > .3$), but the distribution of biomass appears not to be due to chance (x^2, $P < 0.05$) (Table 21). Both measures, however, indicate a larger proportion of the guild being active during the day.

Types of Food Consumed -- Contemporaneous studies on dung and fungi scarabs (Young, ms) allow the placing of scarabs found on carrion in one of four feeding categories; (1) carrion, with few or no occurrences on other foods, (2) carrion and dung, with similar frequencies on both, (3) carrion, dung, and fungi, with more than rare occurrence on each type (rare = $< 10\%$ of observations), and (4) dung, with rare occurrence on carrion. Apparently no carrion-fungus, or primarily

fungus-consuming scarabs occur on BCI. Five members of the necro-
phagous scarab guild feed primarily on carrion, nine species feed both
on carrion and dung, five species feed on carrion, dung, and fungi,
and 6 species are primarily dung feeders (Tables 20, 21). The distri-
bution of species in these categories does not differ significantly
from an equal distribution ($x^2 = 1.72$, $.7 > P > .5$), but the distribution
of biomass is significantly different from chance (x^2, $P < 0.005$).
Fifty-six percent of the guild biomass is represented by species that
feed on both carrion and dung and only 30% of the guild biomass is
represented by carrion specialists.

Species Dimensions

Two species characteristics were determined, by preliminary obser-
vations and a search of the literature, to be potentially important
in species separation within the guild: techniques of food removal
and size of beetle.

Food Removal Techniques -- The 25 necrophagous species can be
separated into 2 major categories for food removal, overland and non-
overland transportation. Of the 12 species that remove food from the
site by an overland route, six species roll balls of cut and packed
carrion, and six species "butt" chunks of cut carrion. Thirteen
species do not remove food by an overland technique. One species
buries the entire carcass before consumption, and three species bury
portions of the carcass to the side of the main site. Seven species
dig tunnels below (4 spp.) or to the side (3 spp.) of the carcass and
then pack the ends of the tunnels with carrion for subsequent

consumption. Two species do not remove food from the carcass for consumption elsewhere but consume it in situ (Tables 20 and 21).

The distribution of species in the five principal categories is not significantly different from an equal distribution (x^2, $P > 0.05$). Sixty-six percent of the guild biomass removes food from a site by overland transport, with the rolling technique representing the highest biomass (35%) of any technique employed. Although nine species either consume food in situ or consume after burrowing (36%), only 11% of the guild biomass is represented by these techniques (Table 21).

Size -- The largest and the smallest species in the necrophagoous scarab guild on BCI in effect define the minimal "space" within which subdivision, on the basis of size, can occur. (Possible vacant niche space at either end of this size spectrum will not be considered.) If species size is the only dimension that expresses species separation, then the size of each species should be unique and, according to Hutchinson (1959), separated from its nearest-sized competitor by at least a mass factor of two. The number of subdivisions possible in this guild "space", separated by a mass factor of two, is only eight. The number of species in the present "space" is 25, strongly suggesting that species size is not the only dimension important in species separation.

Mean individual wet weights for each species of the guild show a size range of 0.009 to 1.37 grams (Table 18). When this size range is subdivided into 28 size classes, differing by increments of 0.05 g, a log-normal distribution is demonstrated (Fig. 21). Seventeen of the 25 species in the guild (68%) occur in the two smallest size classes

(Table 23), suggesting that on this account small size may be more successful for guild members. When the relative biomass in each of the 28 size classes is determined, however, only 18% of the biomass of the guild is represented in the two smallest size classes (Fig. 26, Table 23). In addition, the single size class (0.45 g) containing the largest proportion of the guild biomass (28.5%) is approximately ten fold larger in size than the smallest size class (0.05 g) (Fig. 26). Thus if relative biomass, rather than number of species, is used as a measure of "success", small species are the least successful members of the guild.

Multi-Dimensional Considerations

If the five niche and species dimensions examined in this study are the most important dimensions in terms of achieving and/or maintaining species separation within the guild, then most if not all of the possible species-pair combinations should be separated by these dimensions. The four dimensions of season, diel, food type, and food removal technique separate all but two of the 300 possible unique species-pair combinations (Table 24). The remaining two species-pair combinations are separated on the basis of size. I will present first an analysis of the relation between size and each of the other dimensions, and then a consideration of the interrelations between season, diel, food type, and food removal dimensions.

Size Relationships -- Although size alone may not explain the presence of a certain number of species in the necrophagous scarab

guild on BCI, it may explain the distribution of species within the various categories of the niche and species dimensions. The entire guild can be divided into two size classes, with eight species within a weight factor of 10 of the largest species, _Phanaeus corythus_, and 17 species within a factor of 10 of the smallest species, _Uroxys sulcicollis_. There is no overlap between groups and all species are included (Table 23, Fig. 21). I will examine two aspects of this size distribution in each dimension: the number of species and the biomass occurring in each size class (Table 25).

During the dry season one of the six species present is large, and during the wet season eight of the 24 species present are large (Table 25). A Student's t-test on the distribution of species within each season based on size is not significant (t = 0.762, $0.30 > P > 0.20$). A trend exists, however, for large species to occur in the wet season. The eight species in the large size class represent 81.8% of the biomass of the guild (Table 21). Using species abundance values that are corrected for frequency of occurrence in each season (Table 22), during the dry season only 42.7% of the biomass is represented by the large size class (Table 25). Only the dry season distribution is significantly different from the whole-year values (x^2, $P < 0.005$). This result suggests that small-sized species are more important in the dry season than in the wet season.

Three of the 15 diurnal species are large and five of the ten nocturnal species are large (Table 25). This frequency distribution apparently is not due to chance ($x^2 = 3.604$, $P < 0.05$), suggesting some advantage for a species to be large if active nocturnally and small if

active during the day. Diurnally active species in the large size

class represent 71.2% of the biomass of the diurnal portion of the

guild and nocturnally active large species represent 94.7% of the

nocturnal guild (Table 25). This biomass distribution is significantly

different from the combined day-night values (t = 4.27, 0.02>P> 0.01),

which also suggests that there has been a selective advantage in large

size at night and small size during the day.

Two of the five carrion specialists are large, as are three of

the six dung specialists (Table 25). Of the five species that consume

carrion, dung, and fungi, none are large. Nine species consume

carrion and dung only, and three of these are large. The distribution

of species in these eight categories does not differ significantly

from that expected by chance, when considered together (x^2= 3.40,

P = 0.30). If each feeding category is considered separately, however,

a different situation occurs. The distribution of the sizes within

the group of species that consume carrion, dung, and fungi (generalist)

is probably not due to chance (x^2= 2.94; 0.10 > P > 0.05). The group

of species that primarily consume dung may be distributed between the

size classes due to chance (x^2= 1.18, 0.30 > P > 0.20). The frequency

distribution of sizes within the other two feeding classes also have

a likelihood of being due to chance (x^2, P's > 0.30). The data thus

suggest that specialization on carrion or dung by a species is associ-

ated with large size and that increased diversity in food types used

is associated with smaller size.

The distributions of biomass in each of the food utilization

categories were all significantly different from an equal distribution

Page 42 was omitted in

numbering.

(x^2, $P < 0.005$ in each case). The two specialist categories contained biomass values for the large size class higher than the 81.8% value for the entire guild, and the two generalist classes contained lower values for the large size class, suggesting again a relationship between large size and food specialization (Table 25).

The 25 species of the guild can be segregated by size and food removal techniques (Table 25). The frequency distribution of species in these ten subdivisions of the guild does not appear to be due to chance ($x^2 = 8.538$, $0.10 > P > 0.05$), suggesting that the size of a species may affect its ability to obtain food. Examination of each food removal technique may indicate which size is most advantageous.

Roll -- Three of the 6 "rollers" are large. Compared to the size ratio for the guild as a whole (8/25 = large), this distribution is not significantly different from a chance occurrence ($x^2 = 1.18$, $0.5 > P > 0.3$), although the trend is toward more large species than would be expected.

Butt -- Two of the 6 "butters" are large. There is a strong likelihood that this distribution is due to chance, compared to size distributions for the entire guild ($x^2 = 0.01$, $P = 0.9$).

Bury -- Three of the 4 "buriers" are large. This distribution within the size classes apparently is not due to chance ($x^2 = 4.05$, $0.05 > P > 0.02$), suggesting that large size is related to the successful use of this food removal technique.

Burrow -- None of the 7 "burrowers" are large. This distribution is apparently not due to chance ($x^2 = 4.57$, $0.05 > P > 0.02$). Digging tunnels through compacted soil may thus be associated with small size in this guild.

In situ -- Neither of the 2 species that consume food on site
are large. This distribution may be due to chance ($x^2 = 1.03$,
$P = 0.3$).

The distributions of biomass within size classes of each
food removal category are all significantly different from the distri-
bution for the entire guild (x^2, P's all < 0.05). Thus the techniques
of rolling, butting, and burying are each represented in the large
size classes by at least 86% of the biomass performing that particular
technique (Table 25), whereas no large scarabs burrow or consume
carrion in situ. Both species and biomass distributions within the
size classes thus suggest that large size is advantageous in performing
the food removal techniques of rolling, butting, and burying, and
that small size is advantageous in performing burrowing or in situ
techniques.

Other Relationships -- I will consider the relationships among
four niche and species dimensions: season, diel, food type, and food
removal technique. Of particular importance is a determination of
the degree of dependence of each dimension; that is, the degree to
which the possession of a particular characteristic affects the likeli-
hood that a species will possess a particular characteristic of
another dimension. One way to approach this question is to subdivide
each of the four dimensions into two components and determine the
number of species in each component (Table 26). Thus, the guild is
divided into $2^4 = 16$ unique categories. The probability of a species
being in one of these categories is obtained by multiplying together
the observed frequency values for each of the four dimensions

(Table 27, col. 5). The number of species expected in each one of
the 16 categories can then be computed from the probability values
(Table 27, col. 8). Therefore, if the observed frequency of the 16
combinations differs significantly from that predicted by multiplying
the probabilities of each event within each combination, the events
are probably not independent. The standard error of estimate for
this data analysis is 0.90, indicating that all observed values
should be within 1.76 units of the predicted values to be significant
at the 0.05 level. Figure 27 demonstrates that all observed values
are within 1.76 units of the expected values, suggesting that pre-
dicted values are a good indicator of observed values, and that the
events are independent. Thus, for example, the fact that a species
is diurnal probably does not affect the likelihood that it is an
overland transporter of food.

It is significant to note at this point that three of the 16
possible combinations (19%) of the niche and species dimensions
account for 68% of the species in the guild. These three combina-
tions are:

1. wet season: diurnal; non-overland transport: food generalist
2. wet season: diurnal: overland transport: food generalist
3. wet season: nocturnal: non-overland transport: food
   generalist

Another method of analysis is to determine the number of species
and biomass in each of the 80 unique combinations of dimension character-
istics (2/season x 2/diel x 4/food types x 5/food removal). Since
only six species occur in the dry season, and since there are 40

categories possible in that season, only a listing of the character-
istics of those species will be presented, with a detailed presenta-
tion reserved for the wet season species.

None of the six species of scarabs found on carrion during the
dry season are common during this season, either in terms of the
number of carcasses occupied, the number of individuals per carcass,
or in relation to wet season densities. Because of the resultant
low biomass values for the various species (Table 28), it is appro-
priate only to draw attention to certain obvious trends. Two of the
six species are nocturnal and represent 44% of the guild biomass.
Three of the six species feed on carrion, dung, and fungi, but repre-
sent only 15% of the biomass. Three of the six species do not remove
food by an overland route and represent 86% of the guild biomass.
No in situ carrion-consumers are found in the dry season (Table 28).

The wet season distribution of species and biomass in the 40
unique combinations of dimension characteristics is indicated in
Table 29. Considering wet season food removal techniques, rollers
have a higher biomass at night (59%) than in the day (x^2, P < 0.005)
(Table 30), and are primarily specialists on either carrion (58%) or
dung (27%) (x^2, P < 0.005) (Table 31). Butters are almost entirely
diurnal (99%) (x^2, P < 0.005) and feed both on carrion and dung (94%)
(x^2, P < 0.005). Most buriers are nocturnal (95%) (x^2, P < 0.005),
with a majority of the biomass in the carrion and dung category (54%)
(x^2, P < 0.005). Burrowers are primarily diurnal (83%) (x^2, P < 0.005),
and feed on both carrion and dung (94%) (x^2, P < 0.005). In situ
feeders are evenly distributed in biomass day and night (x^2, P > .1)
and are not found as carrion or dung specialists (Tables 30, 31).

Considering wet season feeding niche dimensions, the portion of the guild biomass represented by carrion specialists is primarily nocturnal (88%) (x^2, P < 0.005) (Table 32) and removes food by rolling (67%) (x^2, P < 0.005) (Table 31). The dung specialist portion is primarily diurnal (94%) (x^2, P < 0.005) and rolls carrion (77%) (x^2, P < 0.005). The biomass of those that feed on carrion, dung, and fungi is also mostly diurnal (83%) (x^2, P < 0.005) and rolls carrion (64%) (x^2, P < 0.005). The biomass of those that feed equally on carrion and dung is primarily diurnal (69%) (x^2, P < 0.005) and distributed among butters (51%), buriers (22%), and burrowers (19%) (x^2, P < 0.005) (Tables 31, 32).

When all three dimensions are considered together, the one category that contributes the greatest proportion (28%) of the wet season biomass is characterized by diurnal activity, a butting food-removal technique, and a carrion and dung feeding niche. This category contains one species, _Phanaeus pyrois_.

Interspecific Competition

Preliminary observations in the field suggested a high incidence of combat between species of scarabs when jointly occurring on food (carrion or dung). During the late wet season of 1975, the 16 most abundant necrophagous scarab species were brought into the laboratory and tested for their relative ability to obtain and retain food. A total of 1140 species-pair encounters were performed, involving one individual of each species (Tables 33, 34). Among the nine diurnal species tested, a linear dominance hierarchy exists, with _Canthon_

septemmaculatum capable of taking food away from the other species
and retaining it (Table 33). Among the nocturnal species, a linear
dominance hierarchy also exists, with Deltochilum parile the usual
victor in contests with other species involving food (Table 34).

When both diurnal and nocturnal species are grouped according
to food removal techniques and then arranged by competitive position,
a linear dominance hierarchy can be demonstrated (Table 35). A
species that uses the roller technique of removing food is always
the victor in an encounter with an individual using one of the other
food removal techniques. Individuals using the butter technique will
consistently lose in encounters with rollers but will win contests
with individuals using other techniques. The same general pattern
prevails for individuals using the bury, burrow, and in situ tech-
niques (Table 35).

A correlation also exists between the proportion of the guild
biomass represented by a food removal technique and the rank of a
food removal technique in a dominance hierarchy (Table 35). Rollers
represent the largest proportion of the guild biomass and are the
highest group in the dominance hierarchy. In situ feeders represent
the smallest proportion of the guild biomass and are the lowest group
in the dominance hierarchy.

Species that are burrowers or in situ feeders thus appear to be
competitively inferior to the other scarab species (Table 35).
However, they possess a unique behavior, kleptoparasitism, that may
allow successful competition with rollers, butters, and buriers.
Burrowers and in situ feeders on BCI are all small species, and they

are rather easily buried inside a ball during its formation. Burrowers
will actively tunnel into a moving ball, or into a piece of food that
is being butted. In situ feeders will also attempt to ride on a
moving ball or chunk. Burrowers and in situ feeders will allow
themselves to be buried with a carcass. When individuals using any
of these techniques are discovered, a fight ensues and the roller,
butter, or burier ejects the robber from the food. If the robber is
not detected, it will consume food during the transport period, and
during and after burial. If an egg is laid in the carrion by the
host, the robber will eat the egg or young larva as well as the car-
rion. I have recorded on several occasions an incidence of klepto-
parasitism exceeding 50% in balls and chunks being removed from car-
rion and dung. This behavior, then, may both decrease the success
of rollers and butters and increase the success of burrowers and
in situ feeders.

Predation

When a concentrated food source attracts numerous consumers,
it is likely that predators on those consumers will also be attracted
(Price, 1975). Animal carcasses probably concentrate more arthropods
in one small area at one time than any other food source on BCI.
Evidence of predation on the arthropods associated with carrion (or
the presence of potential predators) was recorded throughout the study
period. Because of the similarity of dung to carrion and the use of
both food types by the same species of arthropods (e.g. Halffter and
Matthews, 1966), the occurrence of predation on dung-associated

arthropods is also presented. Although the analysis of data relating to dung has not been completed, I estimate that dung observations exceed carrion observations by at least a factor of 50.

No vertebrate was observed feeding specifically on the invertebrates associated with carrion or dung, although some invertebrates probably were inadvertently consumed while vertebrates ate carrion.

No scarab was observed preying on arthropods associated with carrion or dung.

Three observations were made of the presence of Chilopoda at carrion and dung, but prey capture was not seen.

On two occasions, a large lycosid spider was observed capturing small scarabs at dung. The same species of spider was seen at carrion but was not seen capturing prey.

No Reduviidae were observed on either dung or carrion.

Adult Asilidae on two occasions were seen capturing small scarabs and adult Diptera at dung. At carrion, four different individual asilids were observed capturing adult Diptera, but capture of scarabs was not witnessed.

On three occasions, groups of Formicidae were seen capturing small scarabs at dung. At carrion, ten observations were recorded of single ants carrying away adult and larval Diptera. Scarab capture by ants at carrion was not observed.

On numerous occasions (> 50), adult Staphylinidae were seen capturing adult and larval Diptera at dung and carrion. Twice staphylinids were seen capturing adult scarabs at dung, but this was not seen at carrion.

Based on observations at 62 carcasses it appeared that staphylinids were the only predators occurring frequently enough to have any effect on arthropod carrion-consumer populations. This suggestion is supported by the results of the staphylinid removal experiment previously presented (Table 8). Dipterous larvae also appeared to be the only group of organisms suffering appreciable predation.

Comparison with Non-island Sites

Barro Colorado is an island of rather small size, whose flora and fauna have been protected for more than 50 years. Although these factors may be counteracting each other, they suggest that the BCI necrophagous scarab guild may not be typical compared to guilds on adjacent mainland areas. To examine this question dung- and carrion-consuming scarabs were collected at two mainland sites adjacent to BCI.

The closest land, Buena Vista, lies within 450 m of BCI. This 3 km long peninsula presently has no human residents but shows evidence of strong human alteration, including a scrubby, second-growth forest and the absence of monkeys, tapirs, coatis, armadillos, squirrels, and most other mammals. I obtained only four necrophagous scarab species at Buena Vista during the 1975 wet season (two 24 hr trapping periods with a total of five carcasses) (Table 36). Of these species, only Phanaeus corythus was not also captured at dung. Seven additional species, found at carrion on BCI, were trapped at dung but not at carrion on Buena Vista. Thus, with minimal trapping effort, a total of eleven species was trapped on Buena Vista that on BCI are members of the necrophagous scarab guild.

Most of the forested areas in the Panama Canal Zone have suffered from hunting pressure for many years. One of the first mammals to be eliminated from an area is the highly vocal and visible Howler Monkey (Alouatta palliata). The presence of this species may thus indicate relatively undisturbed populations of other mammals. Areas where this monkey is still found in the Canal Zone include BCI and a site 5 km northwest of Gamboa on the Pipeline Road (within 10 km of BCI). This area, Limbo, has a forest very similar to portions of BCI, is at the same elevation, and is part of the same river drainage system. Collecting of scarabs at Limbo during the 1975 wet season (two 24 hour trapping periods with a total of five carcasses) suggests that this area supports a necrophagous scarab guild more similar to BCI than the Buena Vista guild (Table 36). Fourteen species were captured on carrion, two of which are not found on BCI. One of these non-BCI species, Deltochilum gibbosum, is a veritable giant of 28 mm (n = 3) and is larger than any dung or carrion beetle found on BCI. An additional eleven species were found on dung that on BCI occur on both dung and carrion. Thus, with minimal trapping effort, 23 of the 25 BCI necrophagous scarab species were also found at Limbo in addition to two species not found on BCI.

DISCUSSION

The Occurrence of Vertebrate Carcasses

The only direct evidence estimating the abundance of vertebrate carcasses on BCI is a walking strip census (Table 2). It is highly probable that this census detected only a small proportion of the total number of carcasses produced during the observation period. The design of the census also does not allow estimates of the number of carcasses per area or per unit time. What is significant about the census of carcasses, however, is the relative seasonal abundance of carcasses and the species that occur as carcasses.

The data presented are consistent with the hypothesis that carcass abundance is substantially greater in the late wet season than at any other time of the year (Fig. 7). Indirect evidence also suggests that this is the period of the year when vertebrate mortality, and hence the occurrence of carcasses, should be greatest. Several investigators have commented on the hunger stress of a variety of mammals during the late wet season on BCI: agouti (Smythe, 1970a), coati (Kaufmann, 1962), Howler monkey (Hladik and Hladik, 1969), and the white-faced monkey (Oppenheimer, 1968). Wide-spread mammal deaths and the appearance of emaciated individuals during the late wet season have also been reported (Foster, 1973).

Several factors may contribute to this apparent peak in vertebrate mortality in the late wet season. One of the principal food types utilized by many vertebrates on BCI is seeds and fruits (Eisenberg and Thorington, 1973). The general decrease in availability

of this food during the late wet season on BCI has been documented
by Croat (1969, 1975), Smythe (1970b), and Foster (1973). Many
vertebrates on BCI also eat insects (Eisenberg and Thorington, 1973).
Insect light trap collections on BCI (Smythe, 1975) indicate that the
total number and biomass of nocturnal insects is lowest in the months
of September through November (based on three years of weekly collec-
tions). Certain insects associated with fallen fruits and seeds are
also in low density at this time (Pipkin, 1965). Leaf litter inverte-
brates are at peak density in June on BCI and are at relatively low
densities by the late wet season (Willis, 1974). Diurnal sweep
samples from a Costa Rican site similar to BCI indicate that the lowest
arthropod abundances occur in the late rainy season (Buskirk and Bus-
kirk, 1976). A correlation thus exists between the late wet season
peak of mammal carcasses and the relative shortage of insects, fruits
and seeds available to mammals at that time.

All carcasses detected on BCI during the census period were of
species whose average individual weight is $\geq$ 2.0 kg (Table 3). This
predominance of large carcasses suggests that small vertebrate
carcasses may be rapidly consumed, difficult to detect by humans, and/
or may be produced in relatively low numbers. There are a priori
reasons to believe that all three mechanisms are operating in this
situation. Various experiments conducted on BCI (Tables 13, 14)
demonstrated that small mammalian carcasses are consumed more rapidly
than large carcasses. Odors from large carcasses in these experiments
can be detected, at least by humans, at a much greater distance than
the odors of small carcasses (pers. obser.). It is also likely that

small carcasses are produced in smaller quantities on BCI than large
carcasses. Large carnivores, such as the ocelot (Felis pardalis) and
jaguar (Felis onca), are absent or in very low density on BCI (Eisen-
berg and Thorington, 1973). Their potential prey, such as monkeys,
opossums, coatis, and similar-sized vertebrates, thus may exist at
higher than normal densities on BCI and be particularly sensitive to
fluctuations in food abundance and competitive pressure. The old,
sick, and/or starving individuals of these species not being captured
by large carnivores have a high likelihood of appearing as carcasses.
Many of these same species may prey on vertebrates of a smaller size,
such as agoutis, spiny rats, squirrels, and others. The old, sick,
and/or starving individuals in this smaller size class thus have a
high likelihood of being captured by predators and not appearing as
carcasses.

Differences in predation pressures for the various size classes
of vertebrates on BCI may also be the cause of the absence of detect-
able bird, snake, lizard, and frog carcasses. Predators on birds,
reptiles, and amphibians, as well as the smaller mammals, are rela-
tively abundant (Myers and Rand, 1969; Eisenberg and Thorington, 1973;
Willis, ms). Thus the old, sick, and/or starving individuals of
these groups also have a high likelihood of being consumed by predators
and not appearing as carcasses.

Another factor that may influence the occurrence of vertebrate
carcasses on BCI is the portion of the habitat that a particular
species occupies. Arboreal species, such as sloths and monkeys, are
more likely to be found as carcasses than fossorial species such as

the armadillo, paca, and spiny rat. Fossorial individuals, when
dying of starvation, injury, etc., are likely to do so underground,
thus reducing their subsequent exposure to above-ground carrion
consumers, particularly vultures. Vertebrate species that remain
close to water such as the tapir and several iguanids, would also
be unlikely to be detected on a terrestrial carcass census.

Availability of Carcasses to Scarabs

When a vertebrate dies and its carcass is lying on the forest
floor, several potential necrophages are present to initiate con-
sumption. Vertebrate scavengers are the principal carrion consumers
on BCI and may include as many as eleven species (Table 4). The only
carrion "specialists" in this group are the two species of vultures.
Considering vertebrates on a world-wide basis, only large, diurnal,
vulture-like birds have specialized on carrion (Morse, 1975), with
some of the mammals most closely associated with carrion, such as the
hyenas, now known to be quite successful hunters of live prey as
well (Lawick and Lawick-Goodall, 1970; Kruuk, 1972). This phenomenon
suggests that specializing on a food resource, such as carrion, that
is unpredictable in time and space requires large feeding home ranges,
which soaring vultures can accomplish easily. Some vultures find car-
rion by odor (Stager, 1964) and others find it by sight or by following
other vultures (Pennycuick, 1973). In a forested area, all these
techniques require navigating between obstacles such as trees on the
descent to the carcass. This behavior, which probably is possible
only in daylight, coupled with the absence of night-time thermals,

is probably sufficient to explain why all forest vultures are diurnal. If a large home range is thus unattainable for nocturnal vertebrates, then nocturnal species that consume carrion should be omnivores with smaller home ranges, which is indeed the situation on BCI.

Several experiments demonstrate that vertebrate scavengers obtain a larger proportion of the vertebrate carcasses produced in the dry season than in the wet season (Tables 5, 9). This success during the dry season conceivably may only be a function of greater interaction between vertebrate scavengers for a reduced volume of carcasses, relative to the wet season. There is reason to believe, however, that at least the vultures may be more "efficient" scavengers in the dry season than in the wet season. Average hourly windruns in February to April are twice the values for September to November (Appendix B). Wind-borne odors from carrion in the dry season are thus probably detected over a wider area and sooner than in the wet season, even though there may be more carcasses producing odors in the wet season. The rains and calm weather of the wet season may also make soaring by vultures difficult and reduce their hunting time. These factors have been correlated with the nesting period during the dry season of vultures in Panama (McHargue, 1977).

The net effect of the greater relative success of vertebrate scavengers in the dry season, compared to the wet season, is the subsequent low food abundance in the dry season for other necrophages. Potential invertebrate carrion-consumers, such as ants (Formicidae), flies (Sarcophagidae and Calliphoridae), cockroaches (Blattidae), beetles (Scarabaeidae), and bees (Trigona sp.) (Cornaby, 1974), are

all in relatively low densities in the dry season on BCI (Willis, 1974; Smythe, 1975; Young, ms.). This depression of the density of arthropod competitors may either result from the superior food-gathering ability of vertebrate scavengers, or be merely a reflection of the greater sensitivity of arthropods to climatic conditions in the dry season.

The principal invertebrate necrophages on BCI are larval dipterans (Sarcophagidae and Calliphoridae) (Table 7). This group exerts a strong influence on other necrophages, including vertebrate scavengers. Adult flies usually are the first organisms to arrive at a vertebrate carcass and deposit their eggs or larvae immediately. Within three to four days a 200 g carcass in the wet season will be heavily populated with dipterous larvae. At this point a vertebrate scavenger will probably not touch the carcass, as indicated by the experiment with captive coatis (Table 6). In the wet season all carcasses of this study, both naturally occurring and artificially placed, were occupied by dipterous larvae, suggesting that they have the potential to consume all the carcasses on BCI. If all car-casses are occupied by dipterans, and if within four days they can render a carcass unsuitable for other consumers, then the only success-ful feeding technique that a competitor can employ, other than con-suming the larvae, is to arrive at a carcass in the first three or four days and consume or remove the carcass immediately.

Two groups of necrophages employ this strategy of early arrival and removal of carrion, vertebrate scavengers and the Scarabaeidae. Of the two, the vertebrate scavenger group has a far greater effect

on the other necrophages, primarily because one individual can consume
an entire carcass in a relatively short period of time. Scarabaeidae
apparently have no effective strategy of out-competing vertebrate
scavengers although they may to a limited extent share a carcass with
vultures. All other carrion-consumers, beside the three major
groups already mentioned, are found in low densities on carcasses,
do not arrive early, and are not "specialists" on carrion.

Spatial and Temporal Patterns of Carcass Utilization by Scarabs

The fundamental feeding niches (Hutchinson, 1957) of necrophagous
scarabs on BCI include all dead vertebrates. The realized feeding
niche of this group, however, is that portion of the total carcass
material not utilized by more successful competitors. These compe-
titors, interacting with patterns of carcass production, have produced
a spatial and temporal pattern of carcass availability to which the
scarabs must respond.

Spatial patterns -- Published information on the specific loca-
tion of a vertebrate's death is generally lacking (but see Pennycuick,
1975). On BCI observations suggest that the initial location of
dead animals is not correlated with tree density, terrain, or other
habitat features. Carcasses may frequently be moved. Coatis may
drag an entire carcass to a site where it can be consumed in relative
safety, such as between the buttresses of a large tree. Vultures, in
the process of feeding, may dismember and drag the pieces downslope,
occasionally to a streambed. Heavy rains infrequently move all or

part of a carcass downslope. Nocturnal vertebrate scavengers may move all or part of a carcass, eventually feeding in a protected area that may be above, on, or below ground. Scarabs were found on all naturally occurring carcasses, suggesting that they were at least as good as humans in finding carcasses in various situations. Artificially placed carcasses were located in many different areas of the BCI forest, yet scarabs were attracted to all of these carcasses, with no gross differences in species diversity or biomass between the various sites. Thus it appears that the spatial distribution of carcasses on BCI did not noticeably affect their discovery by scarabs.

Although some carcasses probably occur below the soil surface, this location may not significantly affect the scarab guild. A study in Poland by Nabaglo (1973) has demonstrated that in the summer, carcasses of bank voles (approx. 25 g) below ground surface, but connected to the surface by a tunnel, are consumed by invertebrates in 24 days, and similar carcasses on the soil surface are consumed by invertebrates in 10 days. There is a similar number of necrophagous invertebrate species and individuals above and below ground, however, the difference in consumption rates being due to temperature differences. In a study in which piglet carcasses were completely buried (Payne, King, and Beinhart, 1968), decomposition was substantially prolonged and necrophagous Coleoptera reduced in number of species and individuals, as compared with above-ground carcasses.

Temporal patterns -- Necrophagous scarabs are much more abundant, in number of individuals, number of species, and in biomass, in the wet season than in the dry season (Tables 21, 25). This correlates

well with greater carcass abundance and availability during the wet season, suggesting that the guild is food limited. Low population density in the dry season probably is not due to climatic constraints acting directly upon the beetles. Closely related scarab species that feed on dung are more abundant in the dry season than in the wet season (Appendix D). Dung is more available to scarabs in the dry season than in the wet season and correlates well with high species numbers and biomass of scarabs in the dry season (Young, ms.).

There are few data bearing upon the production and availability of vertebrate carcasses during a 24 hr cycle. One investigation in the Serengeti indicated that dawn was the time of maximum carrion availability (Houston, 1974). In a tropical forest, carrion may be generated from predator kills and from animals dying of malnutrition and/or disease. It is likely that carrion is produced both day and night, as the activity of vertebrate scavengers throughout the 24 hr cycle suggests. Although more scarab species are diurnal there is no significant difference between the number of species active in the day or at night. However, the biomass of the diurnal population is significantly larger than the nocturnal population (Table 21). If there is a direct correlation between availability of food and the biomass of a consumer population, then it seems that more carrion is available to scarabs during the day than at night.

The Response of Scarabs to the Size, Type, and State of Decay of Carcasses

Several experiments indicate that necrophagous scarabs do not "prefer" a particular size of carcass but occur on a range of carcass

sizes in proportion to their abundance. In one experiment using four
carcasses ranging in size from 95 g to 4300 g, four species were found
on all four carcasses, but were also the four most abundant species
(Table 15). Five species were found on only one carcass and they
were among the rarest species during the wet season.

Because avian and reptile carcasses appear to be quite rare
on BCI (Table 2), necrophagous scarabs may have little opportunity
to feed on these two carcass types in the dry season. Of the six
scarab species occurring on carrion in the dry season, three species
were found on all three carrion types, with the remaining species
occurring only on mammalian carrion (Table 11). The three species
occurring on all three carrion types were also the most abundant spe-
cies in the dry season (Table 22), suggesting that species occurrence
on different carcass types is a function of scarab species abundance
and not due to a "preference" for a particular carcass type. In the
wet season, vertebrate scavengers may utilize a lower proportion of
the available vertebrate carcasses of any type (Table 9). This
potentially greater supply of avian and reptile carcasses is not
correlated with a greater proportion of wet season scarab species
feeding on these two carcass types (Table 12). Three of the four
species that occur on all three types are among the most frequently
occurring species (Table 19). The fourth species, Anaides longe-
ciliata, is not abundant, and may indeed seek out avian and reptile
carcasses though not ignoring mammalian carrion. A significantly
greater proportion of species in the dry season occur on all three
carrion types than in the wet season. If carrion is actually scarcer

for scarabs in the dry season, one might expect proportionately more species consuming all types of carrion in the dry season than in the wet season, which is indeed what the data indicate (Tables 11, 12). No scarab "specialists" occur on avian or reptile carrion in either season.

State of decay is an important food characteristic for necrophagous scarabs. In the dry season, carrion does not usually "age" appreciably, because of the rapid utilization of carcasses by vertebrate scavengers. Thus only "young" carcasses are available to scarabs, and this factor may contribute to the low rates of utilization of carcasses by scarabs in the dry season. Data from the wet season, however, indicate that "young" carcasses are actually the preferred age, because of the change in carcass condition with increasing age brought about by the action of dipterous larvae. The number of species, the number of individuals, and the biomass of the scarab guild all reach maximum values on the second, third, or fourth day of carcass decay (Fig. 17). Within the guild, however, a differential response to this age pattern occurs. In one experiment (Table 16) new arrivals of five species occurred on each of eight or nine days of the nine day observation period. These five species were also the five most frequently occurring species in the wet season (Table 19). Conversely, those six species with a restricted occurrence on a range of differently-aged carcasses (only occurring on one or two days) were the rarest species in the experiment. This relationship suggests that a species' use of differently aged carcasses is a function of species abundance, and not necessarily related to preference for a particular age range.

Two species (Eurysternus claudicans and Canthon septemmaculatum)

are late arrivers on carcasses (day 5, Table 16) and are not in the
"most abundant" or "most rare" categories. Their arrival time is
substantially different from the two species (<u>Deltochilum</u> <u>parile</u> and
<u>Ateuchus</u> <u>candezei</u>) that arrive on the first day (Table 16). Without
further experimentation, the data can only suggest that one species
pair has a technique of late arrival at a carcass, although low abundance
levels may account for most of that delay.

Consideration of the food resource characteristics of type, size,
and state of decay, indicate that all three characteristics affect the
scarab assemblage as a whole but that they do not play significant roles
in resource partitioning.

<u>Relationship</u> <u>Between</u> <u>Scarabs</u> <u>&</u> <u>Their</u> <u>Potential</u> <u>Competitors</u> <u>&</u> <u>Predators</u>

A variety of arthropods other than scarabs and dipterous larvae
occur on vertebrate carcasses in the neotropics (e.g. Cornaby, 1974).
Some may be competitors or predators of scarabs and may consequently
affect the success of the scarab assemblage.

Potential competitors on carrion include members of the Blatti-
dae (Orthoptera), Diplopoda, Apidae (Hymenoptera), and Diptera. The first
two groups on BCI are rare at carcasses. <u>Trigona</u> sp. (Apidae) occa-
sionally visit carcasses during the dry season, sometimes numbering
50 individuals per carcass. During the wet season, however, they are
rare on carcasses. At least 16 dipteran families occur on carrion in
the tropics (Cornaby, 1974). Their food can be characterized as
either fluid, dry carcasses and/or fungi, or decaying solid organic
matter. Only dipterans consuming decaying solid organic material
would be potential competitors for scarabs, and on BCI larvae of the

Calliphoridae and Sarcophagidae are the principal representatives of this group.

Representatives of several coleopteran families on BCI that are coinhabitants of carcasses are not competitors of scarabs, at least in part because of differences in mouthpart morphology (Arnett, 1968). The presence of one such group on carcasses, however, is in large part due to the activity of dipterous larvae. Larval dipterans produce substances that are able to liquify vertebrate muscle and other tissue (Wigglesworth, 1972). This nutrient "soup" is attractive to various arthropod groups that can suck or "lap" fluids, which scarabs cannot do. In the experiments on carcass size, coleopteran fluid-feeders (Catopidae, Histeridae, Hydrophilidae, and Nitidulidae) were found only on the largest carcasses, when these carcasses had a high density of dipterous larvae. Thus, although one coleopteran group, Scarabaeidae, may be adversely affected in the presence of dipterous larvae, other coleopteran groups may benefit from them.

In the later stages of carcass decay, representatives of several other coleopteran families occur. Some species in the Dermestidae and Cucujidae feed on dried skin, hair, bone, and tissue scraps. Other species in the Cryptophagidae and Tenebrionidae probably feed on the fungi that appear in the later stages of decay.

Observed predation on adult scarabs at carrion, or even at dung, was very rare, suggesting that predation on adults may not be a significant factor. Predation or parasitism on the eggs, larvae, and/or pupae of necrophagous scarabs on BCI may be a significant factor, but no data have been collected on the topic. The literature suggests

that members of the Scarabaeinae (Appendix C), due to nidification

characteristics, are the least affected by predators and parasites

of any of the Scarabaeidae (Balduf, 1935; Clausen, 1940; Ritcher,

1958: Askew, 1971). In fact, the extreme reduction in fecundity

shown by Scarabaeinae (Robertson, 1961) suggests that there is a high

probability that an egg, once produced, will develop into a reproductive

adult. Thus predation on Scarabaeinae may not be a significant

factor in the biology of the group.

Species Abundance

I have characterized each species within the necrophagous scarab

guild by estimates of abundance and of biomass (Tables 18, 19).

Although a strong correlation exists between the two sets of values,

the values are not of equal importance in describing the success of

each species and its relative importance within the guild.

The "success" of a species may be defined in terms of the

ability of individuals to pass genetic material to a subsequent

generation. The toleration of perturbations in the environment is

usually associated with this ability. Since large population size

may minimize the effects of perturbations on a species, population

density alone may be used as a relative measure of "success" for a

species. Onthophagus praecellens may thus be considered the most

successful member of the necrophagous scarab guild on BCI.

O. praecellens is more than twice as abundant on carrion as

Deltochilum parile, the second-ranked species in abundance. Several

characteristics contribute to the success of O. praecellens. It is

one of the few species (5/25) that occur in both the dry and wet seasons, which implies a high level of adaptability to varying climatic conditions. It also feeds equally on carrion and dung, which suggests both a morphology and physiology of a generalist nature, and a certain degree of protection from the fluctuations in availability of any one food type. More species within the guild are generalist feeders (14) than specialists (11), although the difference is not statistically significant. The number of individuals that are generalist feeders, however, represents 70% of the total population of the guild on carrion (Table 37). If the distribution of feeding types in the guild is 14 generalist species and 11 specialists, and feeding type is the principal determinant of the abundance of a species, then the 14 most abundant species should all be generalist feeders. Only 10 of the 14 most abundant species are generalists, however, and this distribution is not significantly different ($x^2 = 1.40$) from what would be expected if the ratio of 14 generalists: 11 specialists applied to all subsets of the 25 species guild. Thus there is not a strong positive correlation between high species abundance and a broad feeding niche.

It is possible that possession of other characteristics may be necessary for a species to have a high population density. Certainly being active in the wet season is important for the "success" of individuals of a species, as 24 of the 25 guild members have this pattern of seasonal activity. It is less obvious how the diel activity pattern of a species is related to population density, as 15 species are diurnally active and 10 species nocturnal (not significantly different from an even distribution). If diel activity was the principal

determinant of species success, then the 15 diurnal species should be either the 15 most abundant species or the 15 least abundant. Nine of the 15 most abundant species are diurnal, exactly the number expected if any subset of 25 had the same ratio of 15 diurnal: 10 nocturnal. Thus diel activity is not the principal species attribute contributing to high population density.

A species characteristic that could be the principal contributor to the relative success of a species is the technique used for removal of food. Twelve species in the guild remove carrion by overland techniques and 13 species by non-overland techniques. Of the twelve most abundant species, six use the overland technique. This is the proportion expected based on the proportion for the entire guild, indicating the absence of a correlation between high population density and the use of a particular food removal technique.

The size of a species could be the principal factor influencing population densities, but increasing body size is only weakly correlated with increasing abundance for the 25 species (R_s = + 0.305; 0.10 > P > 0.05). The presence of four large but rare species account for the lack of a strong correlation (Fig. 23). It does appear, however, that the size of a species has some effect on the population density of that species.

This analysis has demonstrated that the observed patterns of species abundance can not be attributed to the influence of any single niche or species characteristic, although a species must occur in the wet season and probably be of large size to have high population densities.

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Species Biomass

Although the relative "success" of the individuals of a species
may be best estimated by population density, the number of individuals
of a species may be of minimal value when assessing either the rela-
tive importance of a species in a guild or a species' impact upon the
food supply, predators, or competitors. One quantitative measure that
may be adequate for these purposes is the estimation of species biomass.
The numerous statistical tests performed in this study upon the distri-
bution of species and of biomass in various categories demonstrate
that no clear correlation exists between species number and biomass
within subdivisions of the guild.

If the assumption is made that feeding rates, assimilation effic-
iencies, and metabolic rates are similar for all species of the necro-
phagous scarab guild, then estimates of relative biomass should indi-
cate the relative volume of food consumed. This relationship in
effect is a measure of the relative impact of each species upon the
food supply and upon other species within the guild, assuming each
species to be food-limited. Five species constitute 75% of the guild
biomass, and together should have a strong effect upon other members
of the guild. Phanaeus pyrois represents the largest proportion of
the guild biomass, 28.5% (Table 18). In comparison with other guilds,
a value of 0.285 for the relative dominance of the most dominant
species is rather low (e.g. Root, 1973; Norton and Dindal, 1976),
suggesting that Phanaeus pyrois may not have a particularly great
impact on the food supply and on other species.

An examination of the niche and species dimensions of the five

species representing 75% of the guild biomass demonstrates a lack of overlap between species (Table 38). All five species are, however, large and occur in the wet season. Both characteristics have been shown to be strongly correlated with high biomass values within the entire guild (Tables 33, 34). It is tempting to suggest that the possession of these two characteristics is necessary for a species to attain a high biomass.

There is also a strong correlation between high biomass and the possession of the overland transport technique of food removal. The two species with the highest relative dominance in biomass are overland transporters of food, and together constitute 45% of the guild biomass (Table 38), whereas the 13 species in the guild that use the non-overland technique only constitute 34% of the guild biomass (Table 21). Species that utilize the overland technique probably are more efficient in obtaining food and are more aggressive than species using the non-overland technique (p. 72). It is thus possible that in periods of low food availability, species using the non-overland technique of food removal may have difficulty in obtaining carrion.

The correlation between the possession of a particular characteristic and high biomass is not as strong within the diel activity dimension. Exactly one-half of the biomass of these five species occurs diurnally (Table 38), as does 55% of the guild biomass (Table 21). Apparently the possession of either a diurnal or a nocturnal activity pattern is not a requirement for attainment of high species biomass.

The species dominant in biomass consumes both carrion and dung (Table 38), as does the species with the highest population density

(Tables 19, 20). Seventy percent of the guild biomass is also represented by species that are not exclusively carrion consumers. These relationships may only suggest that there is not enough carrion available to support exclusively a large scarab guild.

Feeding Niche Width Within the Scarab Guild

Within the necrophagous scarab guild on BCI, not all of the species are equally dependent on carrion as a food source. Five of the 25 necrophagous scarab species can be considered carrion "specialists", and they comprise only 30% of the guild biomass. This relationship suggests that there may be serious constraints upon the amount of food specialization found within the guild. All five specialist species occur in the wet season, during the period of maximum carrion availability. Two species occur during the day, one being abundant and the other rare. Three species occur at night, one abundant and two rare. This relationship suggests that only one "successful" (= high abundance) specialist species can occur in each half of the 24 hr cycle, which may be due to competitive interactions between species. The two most abundant specialist species are both highly aggressive in obtaining a portion of carrion and actively protective while transporting it to a safe consumption site, characteristics that are correlated with their high competitive position within the guild (Tables 33, 34).

The data also suggest that the number of species and the biomass in the necrophagous scarab guild is in large part due to the availability of non-carrion food. Twenty of the 25 member species also

consume dung or dung and fungi. In fact, 40% of the guild biomass is represented by just 2 species that feed on both carrion and dung (Table 38). Carrion, dung, and fungi appear to represent the principal components of a food type, at least as viewed by the scarabs on BCI. Forty-three scarab species on BCI have been observed feeding on carrion, dung, or fungi, but not on other material (see Appendix D). Most of these species will feed on all three food types (Young, ms). Since most of the necrophagous species can, in effect, shift to alternate food sources when necessary, the guild and its member species should be well insulated from the short-term, unpredictable fluctuations in the food supply.

Food Removal Techniques

Twenty-three species in the necrophagous scarab guild on BCI do not usually consume carrion, or lay eggs on carrion, at the site where it is initially discovered. Carrion is transported in some manner to another site that is usually below the soil surface for subsequent consumption or nidification. This immediate removal of food and individuals from the initial food site may in effect reduce interference at the food source. In fact, it has been demonstrated that adult ball-rollers will consume food in situ and will make and roll balls only when potential scarab competitors become abundant on the food (Young, 1976).

Carrion is removed from the initial site by several methods, but species using the technique of ball-rolling appear to be competitively superior. The pair-encounter experiments demonstrated that ball-rolling

species were superior in combat with species using other food removal techniques. This superiority is related to the degree of contact with the contested food. Once a ball-roller arrives on carrion, it is always in contact with the food, having at least two legs on the carrion at all times until the food ball is finally buried. This contact makes it difficult for another beetle to take the ball away. A butter, however, has legs on the food only when cutting it off from the main food source. The pushing of the food chunk along the ground is accomplished in a head-down position with no legs touching the food. This lack of leg contact allows other individuals rather easily to take the food item away, which ball-rollers do very easily (Tables 33,34).

The ball-rolling technique is probably more efficient energetically than the other food removal techniques. The cutting, shaping, and packing of a ball is likely to require relatively more energy than the mere breaking off or cutting of a section of food as performed by butters. However, once the unit of food is removed from the source, rolling a ball of food is probably energetically less costly than pushing an irregularly shaped piece of food. Since the period of transport is substantially longer than the period of preparation, total energy expenditure for ball-rollers is probably much lower than for butters. Buriers and burrowers probably expend much more energy digging than do the rollers and butters when walking. The relationship between the probable energetic costs of each food removal technique is positively correlated with both the competitive position and the proportion of the guild biomass represented by each technique.

Thus it appears that both competitive ability and energetic

efficiency contribute substantially to the success of species within the necrophagous scarab guild using a particular food removal technique.

Feeding Strategies

The feeding strategy of a species may be divided into four components; search, pursuit, handling, and eating (Schoener, 1971). Within the necrophagous community on BCI, species in different taxonomic groups have maximized efficiency in one or more of these components of their feeding strategy, at the possible expense of other components (Table 39). Vultures are highly efficient "searchers" for carrion, utilizing very little energy during soaring but covering a large area and for a long period of time (Pennycuick, 1973). Compared to other necrophages, their pursuit time is relatively long, due to the long distance that may exist between the detection point and the source of odors. Since consumption may begin immediately upon arrival, handling time is close to zero. The length of consumption time required for satiation in vultures is relatively short, occasionally less than one hour (Houston, 1974).

Adult flies are always the first arrivals at a carcass, suggesting that they either are randomly distributed in the environment or have very good search and pursuit techniques. Blowflies have been demonstrated to have a patchy distribution within a habitat (Macleod and Donnelly, 1957), as well as performing much "random" flight (= search?) (Macleod and Donnelly, 1960). Because dipterans move their wings up and down to fly and do not soar (Chapman, 1969),

it is probable that the relative energetic cost of flying is higher in dipterans than in vultures. Blowflies spend some search time using a sit-and-wait technique, however, thus minimizing energetic costs. On balance, then, blowfly relative search costs may be similar to a vulture's. Both vultures and blowflies may possess superior olfactory detection capabilities (Stager, 1964; Dethier, 1976). Although pursuit time after detection is much shorter in blowflies, the relative energetic costs of pursuit in blowflies and vultures is probably quite similar. Handling time for dipterans is relatively long, since eggs must first hatch after deposition on a carcass before consumption can occur. Some species of Sarcophagidae, however, have reduced handling time to zero by depositing larvae on a carcass. Consumption time may be relatively long for some dipterous larvae, requiring at least five days before departure from the carcass and subsequent pupation (Oldroyd, 1964).

In necrophagous scarabs, most of the searching is of the "sit-and-wait" type, but some active flying does occur while searching, although not as much as by blowflies (Dethier, 1976; Young, ms). It is relatively more costly for a beetle to fly than a dipteran, and beetles are also slower (Wigglesworth, 1972). Thus scarab pursuit time is relatively long, and coupled with poor detection abilities (Shubeck, 1968), they usually arrive on a carcass several hours after dipterans. The handling time for scarabs, however, is particularly short compared to dipterans, with complete removal to a safe site for consumption achieved in less than ten minutes in some instances (Young, ms). Consumption times, for the adult, are rather long, in the range

of 1-5 days, but occurring in the absence of competitors or predators (Halffter and Matthews, 1966).

The various food removal techniques exhibited by members of the necrophagous scarab guild all function in a way that maximizes performance in the handling component of their feeding strategy. This is also the component that is exposed to strong competitive pressure, as demonstrated by the pair-encounter experiments. Competition between scarabs within other components of the feeding strategy has not been observed. Handling time for vultures is also very short, and this again is the component that is exposed to strong competitive pressure (Houston, 1975). Within the necrophagous Diptera, performance within the search and pursuit components appears to have been maximized. Since the handling and consumption time for dipterans is relatively long, success for the group is based on the early arrival at food with a subsequent interference in the consumption by other necrophagous groups.

General Considerations

Recent studies of arthropod guilds have attempted to delineate resource exploitation patterns, demonstrate resource partitioning, and/or define the characteristics of guilds (Fager, 1968; Root, 1973; Shapiro, 1974; Rathcke, 1976; Uetz, 1977). Schoener (1974) has also reviewed 81 resource partitioning studies involving at least three species. Thus there is an increasing body of information relating to the question of how species coexist on the same range of food resources.

A review of the guild literature indicates that a variety of factors can be important in food resource partitioning and can be categorized according to the component of the feeding strategy most affected.

Search

  Sensory equipment

  Locomotory ability

Pursuit

  Territoriality

  Dominance hierarchies

Handling

  External trophic structures

  Fighting ability

Consumption

  Nutrient utilization ability

  Energy storage capability

Factors potentially influencing all components

  Body size

  Social interactions

  Predator avoidance

Examination of over 100 published studies involving resource partitioning suggests that the necrophagous scarab guild on BCI is unusual, particularly in the relative importance of foraging techniques as a parameter separating species. Schoener (1974) demonstrated that not one of the 15 arthropod guilds he examined possessed foraging methods that were important in species separation.

The relatively large number of species in the necrophagous scarab

guild may be a function of the use of foraging methods to achieve species separation. Lack (1971) has suggested that ecological isolation, in birds, is accomplished by one or more of three mechanisms; range separation, habitat separation, and use of different food types. Resource partitioning within guilds containing only a few species appears to occur along one or two dimensions, such as habitat and food type (Schoener, 1974). More than two dimensions are utilized within large guilds to achieve species separation (e.g. Root, 1973). Within the necrophagous scarab guild on BCI, both habitat and food type dimensions are partitioned among the species, but in fact may not be able to accomodate further subdivision. This may be related to the unpredictable nature of carrion occurrence. Of the remaining food resource dimensions that could be subdivided, all seem to be correlated with food removal technique. This is particularly obvious for such factors as body size, nature of the trophic structures, and fighting ability. It is tempting to suggest, then, that recent evolution within the necrophagous scarabs has occurred along the food removal dimension and that further partitioning along this dimension is likely.

APPENDIX A

Animal Species Associated with Vertebrate Carcasses in South
Carolina.   Tabulated from Payne, J. A. and D. A. Crossley (1966).
Period of collection restricted to the summer months of 1962
and 1963.

APPENDIX A

Phylum	Mollusca	7
"	Chordata	7
"	Arthropoda	508
		522 species

Phylum Arthropoda		
Class	Arachnida	55
"	Crustacea	6
"	Chilopoda	7
"	Diplopoda	10
"	Insecta	430
		508 spp.

Class Insecta		
Order	Collembola	1
"	Orthoptera	14
"	Isoptera	2
"	Psocoptera	1
"	Hemiptera	16
"	Neuroptera	3
"	Lepidoptera	16
"	Diptera	102
"	Hymenoptera	54
"	Coleoptera	221
		430 spp.

APPENDIX B

Climatic Factors on BCI. Adapted from Smythe, N. (1975).

1. Average Daily Maximum and Minimum Temperature per Month.
   Data presented are for 1973. Obtained at the forest
   floor.

2. Average Hourly Windruns per Month. Data presented are
   for 1973.

3. Average Daily Relative Humidity per Month. Data presented
   are for 1973. Obtained at the forest floor, at 1200 hrs.

4. Average Rainfall per Month. Data are for a 31-month
   period ending in September 1973.

APPENDIX B

1.

Average Daily Maximum and Minimum Temperature per Month

APPENDIX B

Average Hourly Windruns per Month

Average Daily Relative Humidity per Month
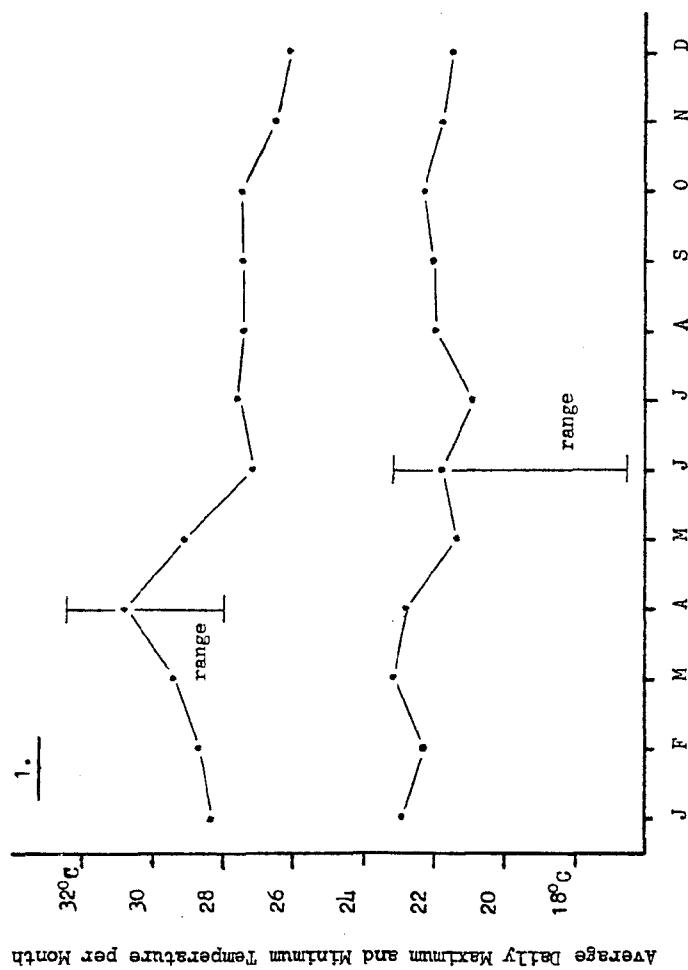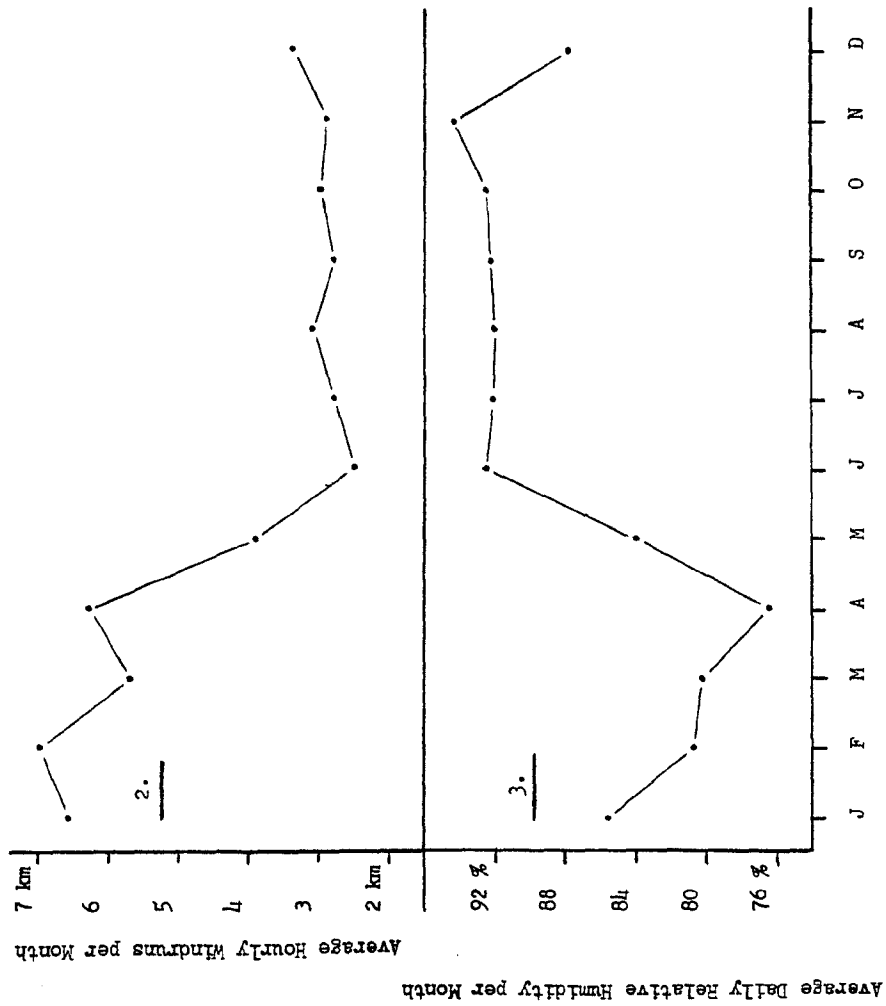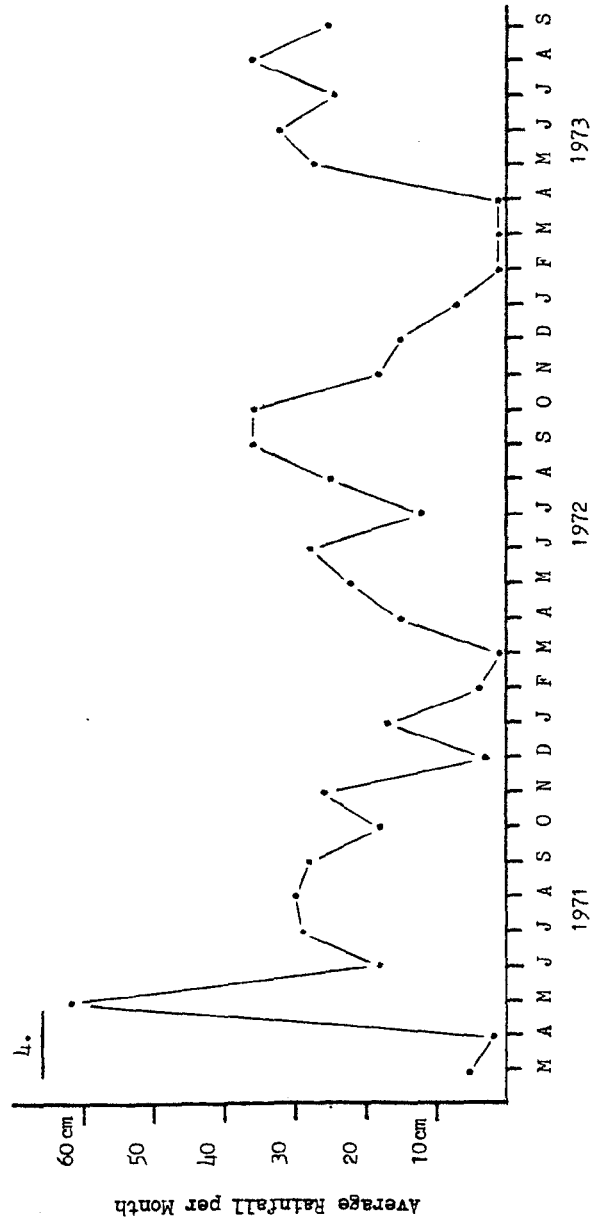
APPENDIX B

APPENDIX C

Phylogenetic Relationships of Genera Represented in the Necrophagous

Scarab Guild on BCI. Classification based on Halffter and

Matthews (1966) and Blackwelder (1944).

APPENDIX C

Family Scarabaeidae

    Subfamily Scarabaeinae (=Coprinae)

        Tribe Onthophagini

            Genus <u>Onthophagus</u>

        Tribe Coprini

            Subtribe Dichotomina (=Pinotina)

                Genus <u>Uroxys</u>

                    "   <u>Ateuchus</u>

                    "   <u>Canthidium</u>

            Subtribe Phanaeina

                Genus <u>Phanaeus</u>

        Tribe Scarabaeini

            Subtribe Eurysternina

                Genus <u>Eurysternus</u>

            Subtribe Canthonina

                Genus <u>Canthon</u>

                    "   <u>Deltochilum</u>

    Subfamily Hybosorinae

                Genus <u>Coilodes</u>

                    "   <u>Anaides</u>

APPENDIX D

Copro-, Necro-, and Mycetophagous Scarabs Collected on BCI in

1974 and 1975. Size values represent mean individual wet

weight.

Symbols:

Seasonal activity. D or d = dry season; W or w = wet season.

A lower case letter indicates a substantially lower

population density for a species, compared to the

other season for that species.

Diel activity. D = diurnal (0700 to 1700 hrs); N = nocturnal

(1900 to 0500 hrs). There were no exclusively crepus-

cular species.

Food Type. C = carrion, D = dung, F = fungi.

Food Removal. O = overland transport, N-O = non-overland

transport.

APPENDIX D

Species	Size (g)	Seasonal Activity	Diel Activity	Food Types Utilized	Food Removal Technique
Eurysternus caribaeus Hbst.	.182	d,W	N	C,D	N-O; Bury
" claudicans Kirsch	.295	d,W	N	C,D	N-O; Bury
" plebejus Har.	.051	D,W	D	C,D	N-O; Bury
Canthon aequinoctiale Har.	.136	D,W	N	C,D	O; Roll
" angustatus Har.	.046	D,W	D	D	O; Roll
" juvencum Har.	.005	D,W	D	D	O; Roll
" lamprimus Bates	.011	D,w	D	C,D	O; Roll
" moniliatus Bates	.034	D,W	D	C,D,F	O; Roll
" sallei Har.	.095	d,W	D	C,D	O; Roll
" septemmaculatum Latr.	.152	d,W	D	C,D	O; Roll
" subhyalinus Har.	.011	D,w	D	D	O; Roll
Deltochilum parile Bates	.205	W	N	C	O; Roll
Pedaridium pilosus Rob.	.004	D	N	D	N-O;
Scatimus ovatus Har.	.029	W	N	D	N-O;
Uroxys gorgon Arrow	.085	W	N	D	N-O;
" micros Bates	.011	D,w	N	D	N-O; Burrow
" sulcicollis Har.	.009	D,W	N	C,D	N-O; Burrow
Ateuchus aeneomicans Har.	.016	D,W	D	C,D	N-O; Burrow
" candezei Har.	.037	D,W	N	C,D	N-O; Burrow
Canthidium ardens Bates	.011	W	D	C	O; Butt
" aurifex Bates	.009	D,W	D	D	O; Butt
" haroldi Preud.	.049	D,W	D	C,D	O; Butt
" laetum Har.	.022	D,W	D	C,D,F	O; Butt
" n. sp.	.085	D,W	N	C,D	O; Butt
" near haroldi	.031	W	D	D	O; Butt
Ontherus n. sp.	.268	W	N	F	N-O;
Dichotomius satanas (Har.)	.762	D,W	N	D	N-O; Burrow
Copris lugubris Boh.	.195	D,W	N	D	N-O; Burrow
Phanaeus corythus (Har.)	1.368	d,W	N	C	N-O; Bury
" cupricollis Nev.	.614	D,W	D	C,D	O; Butt
" pyrois Bates	.405	d,W	D	C,D	O; Butt
" near beltianus Bates	.645	W	D	D	O; Butt
Oxysternon smaragdinum Olsouf.	.329	W	D	D	O; Butt
Onthophagus acuminatus Har.	.024	D,W	D	C,D,F	N-O; Burrow
" coscineus Bates	.009	D,W	D	D	N-O; Burrow
" crinitus Bates	.067	d,W	D	C,D	N-O; Burrow
" lebasi Bouc.	.017	D	D	D	N-O; Burrow
" praecellens Bates	.040	D,W	D	C,D	N-O; Burrow
" sharpi Har.	.030	d,W	N	C,D,F	N-O; Burrow
" n. sp.	.046	D,W	D	D	N-O; Burrow
Coilodes castanea Westw.	.011	W	D	C,D,F	N-O; In situ
Anaides longeciliata Balth.	.030	W	N	C,D	N-O; In situ
Aphodius chapini Hinton	.002	D,w	D	D	N-O;

LITERATURE CITED

Arnett, R.H. 1968. The beetles of the United States. The American
    Entomological Institute, Ann Arbor, Michigan.

Askew, R.R. 1971. Parasitic insects. American Elsevier Publ. Co.,
    New York. 316 pp.

Balduf, W.V. 1935. The bionomics of entomophagous Coleoptera. John
    S. Swift Co., Chicago. 220 pp.

Balogh, J. 1946. The structure of the biocoenoses. Allat. Koslem
    43:1-14.

Beard, J.S. 1944. Climax vegetation in tropical America (2nd ed.).
    Ecology 25:127-158.

Blackwelder, R.E. 1944. Checklist of the coleopterous insects of
    Mexico, Central America, the West Indies, and South America.
    Part 2. Bull. U.S. Nat. Mus. 185:189-341.

Bornemissza, G.F. 1957. An analysis of arthropod succession in carrion
    and the effect of its decomposition on the soil fauna. Aust. J.
    Zool. 5:1-12.

Brewer, J.W., and T.R. Bacon. 1975. Biology of the carrion beetle
    Silpha ramosa Say. Ann. Ent. Soc. Amer. 68:786-790.

Buskirk, R.E., and W.H. Buskirk. 1976. Changes in arthropod abundance
    in a highland Costa Rican forest. Amer. Midl. Nat. 95:288-298.

Chaniotis, B.N., J.M. Neely, M.A. Correa, R.B. Tesh, and K.M. Johnson.
    1971. Natural population dynamics of phlebotomine sandflies in
    Panama. J. Med. Ent. 8:339-352.

Chapman, R.F. 1969. The insects: structure and function. American
    Elsevier Publ. Co., New York.

Clausen, C.P. 1940. Entomophagous insects. McGraw-Hill Book Co.,
    New York. 688 pp.

Cornaby, B.W. 1974. Carrion reduction by animals in contrasting
    tropical habitats. Biotropica 6:51-63.

Cragg, J.B. 1955. The natural history of sheep blowflies in Britain.
    Ann. Appl. Biol. 42:197-207.

Croat, T.B. 1969. Seasonal flowering behavior in central Panama.
    Ann. Missouri Bot. Gard. 56:295-307.

Croat, T.B. 1975. Phenological behavior of habit and habitat classes on Barro Colorado Island (Panama Canal Zone). Biotropica 7:270-277.

Denno, R.F., and W.R. Cothran. 1975. Niche relationships of a guild of necrophagous flies. Ann. Ent. Soc. Amer. 68:741-754.

Denno, R.F., and W.R. Cothran. 1976. Competitive interactions and ecological strategies of sarcophagid and calliphorid flies inhabiting rabbit carrion. Ann. Ent. Soc. Amer. 69:109-113.

Dethier, V.G. 1976. The hungry fly. Harvard Univ. Press.

Eisenberg, J.F., and R.W. Thorington. 1973. A preliminary analysis of a neotropical mammal fauna. Biotropica 5:150-161.

Eisenmann, E. 1952. Annotated list of birds of Barro Colorado Island, Panama Canal Zone. Smiths. Misc. Coll. 117 (5):1-62.

Fager, E.W. 1968. The community of invertebrates in decaying oak wood. J. Anim. Ecol. 37:121-142.

Foster, R.B. 1973. Seasonality of fruit production and seedfall in a tropical forest ecosystem in Panama. Ph.D. Thesis, Duke University, Durham, North Carolina.

Fuller, M.E. 1934. The insect inhabitants of carrion: a study in animal ecology. Aust. Coun. Sci. Ind. Res. Bull. 82:1-62.

Halffter, G., and E.G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entom. Mex. 12-14:1-312.

Hladik, A., and C.M. Hladik. 1969. Rapports trophiques entre vegetation et primates dans la foret de Barro Colorado (Panama). La Terre et la Vie, No. 1-1969:25-117.

Holdridge, L.R. 1967. Life zone ecology (2nd ed.). Tropical Research Center, San Jose, Costa Rica. 206 pp.

Houston, D.C. 1974. The role of griffon vultures as scavengers. J. Zool., Lond. 172:35-46.

Houston, D.C. 1975. Ecological isolation of african scavenging birds. Ardea 63:55-64.

Howden, A.T. 1950. The succession of beetles on carrion. M.S. Thesis, North Carolina State College, Raleigh. 83 pp.

Howden, H.F., and V.G. Nealis. 1975. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). Biotropica 7:77-83.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22:415-427.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals. Amer. Natur. 93:145-159.

Kamal, A.S. 1958. Comparative study of thirteen species of sarco-saprophagous Calliphoridae and Sarcophagidae (Diptera) 1. Bionomics. Ann. Ent. Soc. Amer. 51:261-271.

Kaufman, J. 1962. Ecology and social behavior of the coati, Nasua nasua, on Barro Colorado Island, Panama. Univ. Calif. Publ. Zool. 60:95-222.

Knight, D.H. 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. Ecol. Monogr. 45:259-284.

Kruuk, H. 1967. Competition for food between vultures in East Africa. Ardea 55:171-193.

Kruuk, H. 1972. The spotted hyena. Univ. Chicago Press.

Lack, D. 1971. Ecological isolation in birds. Blackwell Sci. Publ., Oxford. 404 pp.

Lawick, H. van, and J. van Lawick-Goodall. 1970. Innocent killers. Ballantine Books, New York.

Lindquist, A.W. 1942. Ants as predators of Cochliomyia americana C&P. J. Econ. Ent. 35:850-852.

Luederwaldt, H. 1911. Os insectos necrofagos Paulistas. Rev. Mus. Paulista 8:414-433.

Macleod, J., and J. Donnelly. 1957. Some ecological relationships of natural populations of calliphorine blowflies. J. Anim. Ecol. 26:135-170.

Macleod, J., and J. Donnelly. 1960. Natural features and blowfly movement. J. Anim. Ecol. 29:85-93.

Martinez, A. 1959. Catalogo de los Scarabaeidae Argentinos (Coleop.). Rev. Mus. Cien. Nat. Bernardino Rivadavia 5: 126 pp.

Milne, L.J., and M.J. Milne. 1944. Notes on the behavior of burying beetles (Nicrophorus spp.). J. New York Ent. Soc. 52:311-327.

Milne, L.J., and M. Milne. 1976. The social behavior of burying beetles. Sci. Amer. 235:84-89.

Morse, D.H. 1975. Ecological aspects of adaptive radiation in birds. Biol. Rev. 50:167-214.

Myers, C.W., and A.S. Rand. 1969. Checklist of amphibians and reptiles of Barro Colorado Island, Panama, with comments on faunal change and sampling. Smiths. Contrib. Zool., No. 10, 11 pp.

McHargue, L.A. 1977. Nesting of turkey and black vultures in Panama. Wilson Bull. 89:328-329.

Nabaglo, L. 1973. Participation of invertebrates in decomposition of rodent carcasses in forest ecosystems. Ekol. Polska 21:251-269.

Norris, K.R. 1965. The bionomics of blow flies. Ann. Rev. Ent. 10:47-68.

Norton, R.A., and D.L. Dindal. 1976. Structure of the microarthropod community in Lake Ontario beach debris. Envir. Ent. 5:773-779.

Oldroyd, H. 1964. The natural history of flies. Weidenfeld and Nicolson, London.

Oppenheimer, J.R. 1968. Behavior and ecology of the white-faced monkey, Cebus capucinus, on Barro Colorado Island, C.Z. Ph.D. Thesis, Univ. of Illinois.

Payne, J.A. 1965. A summer carrion study of the baby pig Sus scrofa Linnaeus. Ecology 46:592-602.

Payne, J.A., and D.A. Crossley. 1966. Animal species associated with pig carrion. Rad. Ecol. Sec., Oak Ridge Nat. Lab., U.S.A.

Payne, J.A., and E.W. King. 1969. Coleoptera associated with pig carrion. Ent. Mon. Mag. 105:224-232.

Payne, J.A., E.W. King, and G. Beinhart. 1968. Arthropod succession and decomposition of buried pigs. Nature 219:1180-1181.

Pennycuick, C.J. 1973. The soaring flight of vultures. Sci. Amer. 229:102-109.

Pennycuick, L. 1975. Movements of the migratory wildebeest population in the Serengeti area between 1960 and 1973. E. Afr. Wildl. J. 13:65-87.

Pessoa, S.B., and F. Lane. 1941. Coleopteros necrofagos de interesse medico-legal. Rev. Mus. Paulista 25(2):389-504.

Pipkin, S.B. 1965. The influence of adult and larval food habits on population size of neotropical ground-feeding Drosophila. Amer. Midl. Nat. 74:1-27.

Price, P.W. 1975. Insect ecology. John Wiley and Sons, New York.

Ratcliffe, B.C. 1972. The natural history of _Necrodes surinamensis_ (Fabr.) (Coleoptera: Silphidae). Trans. Amer. Ent. Soc. 98:359-410.

Rathcke, B.J. 1976. Competition and coexistence within a guild of herbivorous insects. Ecology 57:76-87.

Raw, F. 1967. Arthropoda (except Acari and Collembola). Pages 323-362 in N. Burges and F. Raw, ed. Soil biology. Academic Press, London.

Reed, H.B. 1958. A study of dog carcass communities in Tennessee, with special reference to the insects. Amer. Midl. Nat. 59:213-245.

Richards, P.W. 1952. The tropical rain forest. Cambridge Univ. Press.

Ritcher, P.O. 1958. Biology of Scarabaeidae. Ann. Rev. Ent. 3:311-334.

Robertson, J.G. 1961. Ovariole numbers in Coleoptera. Can. J. Zool. 39:245-263.

Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monogr. 37:317-350.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (_Brassica oleracea_). Ecol. Monogr. 43:95-124.

Schaller, F. 1968. Soil animals. Univ. Michigan Press, Ann Arbor.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Shapiro, A.M. 1974. Partitioning of resources among lupine-feeding Lepidoptera. Amer. Midl. Nat. 91:243-248.

Shubeck, P.P. 1968. Orientation of carrion beetles to carrion: random or non-random ? J. New York Ent. Soc. 76:253-265.

Shubeck, P.P. 1969. Ecological studies of carrion beetles in Hutcheson Memorial Forest. J. New York Ent. Soc. 77:138-151.

Shubeck, P.P. 1971. Diel periodicities of certain carrion beetles (Coleoptera: Silphidae). Coleop. Bull. 25:41-46.

Smythe, N. 1970a. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Amer. Natur. 104:25-35.

Smythe, N. 1970b. Ecology and behavior of the Agouti (Dasyprocta punctata) and related species on Barro Colorado Island, Panama. Ph.D. Thesis, Univ. of Maryland, College Park.

Smythe, N. 1975. Insect sampling. In: R.W. Rubinoff, ed.,Environmental monitoring and baseline data. Smithsonian Institution Environmental Sciences Program, Tropical Studies.

Sokal, R.R., and F.J. Rohlf. 1969. Biometry. W.H. Freeman and Co., San Francisco.

Springett, B.P. 1968. Aspects of the relationship between burying beetles, Necrophorus spp. and the mite, Poecilochirus necrophori Vitz. J. Anim. Ecol. 37:417-424.

Stager, K.E. 1964. The role of olfaction in food location by the turkey vulture (Cathartes aura). Los Angeles Co. Mus. Contr. Sci., No. 81, 63 pp.

Uetz, G.W. 1977. Coexistence in a guild of wandering spiders. J. Anim. Ecol. 46:531-541.

Walker, E.P. 1975. Mammals of the world (3rd ed.). Johns Hopkins Univ. Press, Baltimore.

Walker, T.J. 1957. Ecological studies of the arthropods associated with certain decaying materials in four habitats. Ecology 38:262-276.

Wallwork, J.A. 1970. The ecology of soil animals. McGraw-Hill, London.

Wallwork, J.A. 1976. The distribution and diversity of soil fauna. Academic Press, London.

Walsh, J., and R. Gannon. 1967. Time is short and the water rises. Thomas Nelson and Sons, Camden, N.J.

Wiegert, R.G., and D.F. Owen. 1971. Trophic structure, available resources, and population density in terrestrial vs. aquatic ecosystems. J. Theor. Biol. 30:69-81.

Wigglesworth, V.B. 1972. The principles of insect physiology (7th ed.). Chapman and Hall, London.

Williams, C.B. 1964. Patterns in the balance of nature. Academic Press, New York.

Willis, E.O. (1972). A revised list of birds of Barro Colorado Island, Panama, Canal Zone. Manuscript.

Willis, E.O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecol. Monogr. 44:153-169.

Young, O.P. 1976. Ball-rolling behavior and competition in a neotropical forest dung beetle. Presented at the XV Inter. Cong. Entom., Washington, D.C.

Young, O.P. (1977). Feeding strategies in a neotropical dung, carrion, and fungi consuming scarab guild. Manuscript.

TABLE I

Naturally Occurring and Artificially Placed Vertebrate Carcasses

on BCI. Each carcass was available to consumers only for the period

indicated.

Table 1

	Day only	Night only	Both Night and Day	Total
Dry Season	6	--	8	14
Wet Season	12	--	36	48
Total	18	--	44	62

TABLE 2

Naturally Occurring Carcasses Observed on BCI During the Period
Jan-Jun 1974, Jan-May 1975, and Sept-Dec 1975.

Table 2

Date of Discovery	Species	Developmental Stage	Estimated Interval Since Death
Jan 15 75	Nine-banded Armadillo (Dasypus novemcinctus)	Adult	3 days
Jan 20 74	Howler Monkey (Alouatta palliata)	Adult	3 days
Feb 12 75	Coatimundi (Nasua nasua)	Old adult	14+ days
May 21 74	Three-toed Sloth (Bradypus infuscatus)	Adult	1 hour
May 23 75	Two-toed Sloth (Choloepus hoffmanni)	Adult	7 days
Oct 11 75	Three-toed Sloth	Adult	5 days
Oct 15 75	Opossum (Didelphis marsupialis)	Juvenile (±6 months)	3 days
Oct 31 75	Opossum	Adult	7 days
Nov 2 75	Howler Monkey	Adult	1 day
Nov 14 75	Howler Monkey	Adult	1 day
Nov 15 75	Howler Monkey	Infant (<2 months)	1 hour
Dec 7 75	Collared Peccary (Tayassu tajacu)	Old adult	14+ days
Dec 8 75	Collared Peccary	Adult	3 days

TABLE 3

Mammals of BCI $\geq$ 2 kg in Average Individual Biomass.

Table 3(a)

Observed as Carcass (b)	Species	Estimated no. of Individuals	Average Individual Weight (kg)	Percent of Nonvolant Mammalian Biomass
X	Bradypus infuscatus	11,400	2.8	48.0
X	Choloepus hoffmanni	2,800	3.5	14.7
X	Dasypus novemcinctus (c)	1,724	4.0	9.4
	Dasyprocta punctata	1,400	2.0	4.2
X	Didelphis marsupialis	1,050	2.0 (d)	1.5
X	Alouatta palliata	1,000	5.5	8.3
X	Nasua nasua	600	3.0	2.7
	Agouti paca	500	8.0	6.0
	Tamandua tetradactyla (c)	374	4.0	2.2
	Cebus capucinus	250	2.6	0.9
X	Tayassu tajacu	100	23.0	3.5
	Mazama americana	20	15.0	0.4
	Ateles geoffroyi	14	5.0	0.1
	Odocoileus virginianus	10	40.0	0.6
	Tapirus bairdii	8	300.0	3.6

(a) Data from Eisenberg and Thorington (1973) unless otherwise noted

(b) Carcass observations by Young

(c) Data extrapolated from Walsh and Gannon (1967)

(d) Data from Walker (1975)

TABLE 4

Probable Vertebrate Consumers of Carrion on BCI.

Table 4

Species	Activity Period
Wooly Opossum (Caluromys derbianus)	Nocturnal
Mouse Opossum (Marmosa robinsoni)	"
Gray Four-eyed Opossum (Philander opossum)	"
Brown Four-eyed Opossum (Metachirus nudicaudatus)	"
American Opossum (Didelphis marsupialis)	"
Nine-banded Armadillo (Dasypus novemcinctus)	"
Tayra (Eira barbara)	"
Collared Peccary (Tayassu tajacu)	"
Coatimundi (Nasua nasua)	Nocturnal and Diurnal
Black Vulture (Coragyps atratus)	Diurnal
Turkey Vulture (Cathartes aura)	"

Sources: Eisenberg and Thorington (1973)
          Walker (1975)
          Eisenmann (1952)

TABLE 5

Experimental Determination of Carcass Fate on BCI. Carcasses were
Rattus rattus, average weight 195 g (170-240 g). The value given for
the number of carcasses consumed by arthropods is the number of days
necessary for 80% (wet wt.) of the carcass to be consumed.

Symbols: -- = N/A

      0 = Not Present

     + = Present,   10 Individuals

    ++ = Present, 10-100 Indiv.

   +++ = Present,   100 Indiv.

Table 5

		Carcasses Present	Carcasses Occupied by Vultures	Carcasses Removed by Vertebrates	Adult Diptera Activity	Larval Diptera Activity	Adult Scarab Activity	Carcasses Consumed by Arthropods
March 1975								
(Dry Season)								
		Start						
Day 1	0900	10	--	--	--	--	--	--
	1500	10	2	0	++	0	+	0
	2100	5	0	5	0	0	+	0
Day 2	0900	0	--	5	--	--	--	0
- - - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -
November 1975								
(Wet Season)								
		Start						
Day 1	1800	10	--	--	--	--	--	--
	0600	8	0	2 (noct.)	0	0	++	0
	1200	8	2	0	++	0	+	0
Day 2	1800	7	0	1 (vult.)	0	+	+	0
	0600	6	0	1 (noct.)	0	+	+++	0
	1200	6	1	0	+	++	+	0
Day 3	1800	5	0	1 (vult.)	0	+++	+	0
	0600	5	0	0	0	+++	++	0
	1200	5	0	0	0	+++	+	0
Day 4	1800	5	0	0	0	++	+	0
	0600	0	--	0	--	--	--	5

Table 6

Exposure of Roof Rats to Captive Coatis. Rats placed individually in cage with one coati, with only one rat exposed per coati per day. Coatis not fed for 24 hrs. or more prior to each exposure. Tests performed during Sept-Dec 1975.

Table 6

Rat Condition	Response of Coatis (2)
Alive and active N=10	All killed and eaten within ten minutes.
Freshly killed N=10	All rekilled immediately, then eaten within 24 hrs.
Killed, ripened for 48 hrs. N=10	Not eaten if coati fed in last 48 hrs. All eaten when coati starved 3-7 days.
Killed, ripened, heavily infested with maggots N=2	Not eaten, even after 21 day starvation period.

TABLE 7

Utilization of Rat Carcasses by Arthropods. Nine carcasses were
placed in the field on the same day, with one carcass collected on
each of the nine days.

Table 7

Day	Initial Carcass Weight (g)	Final Carcass Weight (g)	Amount of Carcass Missing (g)	Cumulative % Reduction	Daily % Reduction	Dipterous Larvae (g)	Other Arthropods (g)	Total Arthropods (g)	Dipterous Larvae as % of Missing Carcass	Other Arthropods as % of Missing Carcass	Arthropods as % of Missing Carcass	Dipterous Larvae as % of Total Arthropods	Other Arthropods as % of Total Arthropods	Scarabs as % of Total Arthropods	Scarabs as % of Other Arthropods	Scarabs as % of Missing Carcass
1	168.7	168.0	0.7	<1	--	<0.1	0.5	0.6	<1	71.4	85.7	16.6	83.4	33.3	40.0	28.6
2	243.3	233.6	9.7	4	4	0.6	3.0	3.6	6.2	31.4	37.6	16.6	83.4	63.9	76.6	23.7
3	185.7	163.2	22.5	12	8	1.9	2.6	4.5	8.4	11.6	20.0	42.2	57.8	48.9	84.6	9.8
4	205.6	149.8	55.8	27	15	8.4	4.4	12.8	15.1	7.8	22.9	65.6	34.4	24.2	70.5	5.6
5	160.7	89.1	71.6	44	17	16.9	4.7	21.6	23.6	6.6	30.2	78.2	21.8	17.1	78.7	5.2
6	181.3	76.4	104.9	58	14	37.7	6.2	43.9	35.9	5.9	41.8	85.9	14.1	12.1	85.5	5.1
7	165.0	50.7	114.3	69	11	51.3	9.6	60.9	44.9	8.4	53.3	84.2	15.8	9.5	60.4	5.1
8	194.8	48.9	145.9	75	6	62.2	7.1	69.3	42.6	4.9	47.5	89.8	10.2	5.9	57.7	2.8
9	205.1	40.6	164.5	80	5	54.9	9.9	64.8	33.3	6.1	39.4	84.7	15.3	7.6	49.4	3.0
Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16

TABLE 8

Fate of Roof Rat Carcasses when Various Consumer Groups are Excluded.
One carcass in each availability category was placed in the field during
November, 1975, and observed daily.

Table 8

Carcass Availability to Consumers	Experimental Treatment of Carcass	Length of Observation Period	Fate of Carcass
Both vertebrates and invertebrates excluded	None	15 days	Reached dried state by day 15 with no utilization
Neither vertebrate or invertebrate excluded	None	Until removed	Disappeared second night
Vertebrates excluded	None	Until carcass consumed	80% carcass reduction in nine days
Vertebrates excluded	All dipterous larvae larger than 10 mm removed daily	15 days	50% carcass reduction by day 15
Vertebrates excluded	All scarabs removed daily	Until carcass consumed	80% carcass reduction in 9 days
Vertebrates excluded	All Staphylinidae removed daily	Until carcass consumed	80% carcass reduction in 7 days

TABLE 9

Vertebrate Scavenger Removal of Three Carrion Types. Carcasses placed in field in late afternoon and observed daily.

Table 9

Species and Type	Dry Season		Wet Season		
	No. of Carcasses	No. removed in first 24 hours	No. of carcasses	No. Removed in first 24 hours	No. Removed in Entire 5 Day Period
Mammal 　Rattus rattus	15	15	15	4	9
Bird 　Leptotila cassinii	2	2	4	1	2
Lizard 　Iguana iguana	4	4	4	0	2

TABLE 10

Rate of Consumption of Three Carcass Types. All numerical values indicate the number of days required for the carcasses to attain the indicated condition. The dry season lizard carcasses reached a deflated condition by the 18th day and were mummified by the end of the experiment.

Table 10

Season	Carcass Type (a)	Detect- able Odor	Bloated	Puncture of Skin	Flesh from Head and Anal Areas Removed	Most of Flesh Removed	Only Skin, Bone, Carti- lage Remain
Dry Season[b]	Lizard	3	8	-	-	-	-
"	Bird	2	5	9	11	13	16
"	Mammal	1	3	6	8	10	12
Wet Season[c]	Lizard	2	5	10	13	17	20
"	Bird	2	4	7	8	9	10
"	Mammal	1	2	3	4	5	6
Wet Season[c] (Pitfall traps)	Lizard	3	6	12	15	19	22
"	Bird	2	4	8	10	11	13
"	Mammal	1	3	5	7	8	10

(a) Two carcasses of each type in each situation

(b) No rain in first 17 days of experiment; terminated after 30 days

(c) Rain in every 24 hour period

TABLE 11

Occurrence of Different Species of Scarabs on Three Types of Carrion

in the Dry Season. Naturally occurring and artificially placed

carcasses included.

Table 11

Species	Lizard	Bird	Mammal
<u>Canthon</u> <u>lamprimus</u>	++	++	++
<u>Canthon</u> <u>moniliatus</u>	++	++	++
<u>Canthidium</u> <u>laetum</u>	--	--	++
<u>Phanaeus</u> <u>corythus</u>	--	--	++
<u>Onthophagus</u> <u>praecellens</u>	++	++	++
<u>Onthophagus</u> <u>sharpi</u>	--	--	++

-- = Absent

++ = Present

TABLE 12

Occurrence of Different Species of Scarabs on Three Types of Carrion
in the Wet Season.   Naturally occurring and artificially placed carcasses
included.

Table 12

Species	Lizard	Bird	Mammal
Eurysternus caribaeus	--	--	++
" _claudicans_	--	--	++
" _plebejus_	--	--	++
Canthon aequinoctiale	--	--	++
" " _lamprimus_	--	--	++
" _moniliatus_	--	--	++
" _sallei_	--	--	++
" _septemmaculatum_	--	--	++
Deltochilum parile	--	--	++
Uroxys sulcicollis	--	--	++
Ateuchus aeneomicans	--	--	++
" _candezei_	++	++	++
Canthidium ardens	--	--	++
" _haroldi_	--	--	++
" _n. sp._	--	--	++
Phanaeus corythus	--	--	++
" _cupricollis_	--	--	++
" _pyrois_	++	++	++
Onthophagus acuminatus	--	--	++
" _crinitus_	--	--	++
" _praecellens_	++	++	++
" _sharpi_	--	--	++
Coilodes castanea	--	--	++
Anaides longeciliata	++	++	++

-- = Absent

++ = Present

TABLE 13

Rate of Utilization of Four Carcass Sizes by Vertebrate Scavengers in
the Dry Season. The two D. marsupialis carcasses were fresh, intact,
off-island road kills. The other carcasses were obtained on BCI, frozen,
thawed, and "ripened" before placement. All carcasses placed in field
at approx. 1800 hrs.

Table 13

Species	Approx. Weight (g)	Removed First Night	Vultures on Carcass First Day	Removed Second Night	Vultures on Carcass Second Day
Didelphis marsupialis	4100		X	X	
Didelphis marsupialis	3700		X		X
Dasyprocta punctata	1800		X	X	
Dasyprocta punctata	2000		X	X	
Rattus rattus (Adult)	200	X			
Rattus rattus (Adult)	240	X			
R. rattus (Juvenile)	70	X			
R. rattus (Juvenile)	60	X			

TABLE 14

Rate of Utilization of Four Carcass Sizes by Arthropods in the Wet Season. Numerical values indicate the number of days after carcass placement required to reach a particular stage of decay. Each size category represented by one carcass.

Table 14

Species (approx. weight)	Detectable (by humans) Odor	Bloated	Most of Fur Detached	Large Holes in Skin	Flesh from Head and Anal Areas Removed	Most of Carcass Flesh Removed	Only Skin, Bones, and Cartilage Remaining
Tamandua tetradactyla (4300 g)	2	2	3	4	5	6	7
Dasyprocta punctata (1600 g)	2	2	3	3	4	5	6
Rattus rattus (Adult) (220 g)	1	-	2	2	3	4	5
R. rattus (Juvenile) (95 g)	1	-	2	2	3	3	4

TABLE 15

Occurrence of Scarabs on Four Sizes of Mammal Carcasses in the Wet

Season.   Each size category represented by one carcass.

Table 15

Species	Tamandua tetradactyla (4300 g)	Dasyprocta punctata (1600 g)	Rattus rattus (Adult, 220 g)	R. rattus (Juvenile, 95 g)
Eurysternus caribaeus	X	-	-	-
" claudicans	X	XX	X	X
" plebejus	X	X	X	-
Canthon aequinoctiale	-	X	X	-
" lamprimus	X	-	-	X
" moniliatus	-	X	X	-
" sallei	-	X	X	X
" septemmaculatum	-	-	X	X
Deltochilum parile	X	X	X	X
Ateuchus candezei	-	-	X	X
Phanaeus corythus	-	-	X	-
" cupricollis	-	X	-	-
" pyrois	X	X	XX	X
Onthophagus acuminatus	-	-	-	X
" praecellens	X	X	XX	X
Anaides longeciliata	-	-	X	-
Number of Species	7	9	12	9

- = Absent   X = Present, less than five individuals
XX = Present, five or more individuals

TABLE 16

Succession of Scarabs on Adult Roof Rat Carcasses in the Wet Season.
Nine carcasses were placed in the field on the same day, with one
carcass and its inhabitants collected on each of the nine days. Each
numerator represents the number of individual beetles captured. The
denominators represent the estimated number of individuals arriving
daily, obtained by dividing the numerator by the number of days
since first appearance of species.

TABLE 16

Species	1	2	3	4	5	6	7	8	9	Total No. Individuals
Eurysternus plebejus			1/1.0	1/.50	1/.33	2/.50	3/.60	2/.33	2/.29	12
Eurysternus claudicans					1/1.0	2/1.0	1/.33	1/.25	1/.20	6
Canthon sallei		1/1.0	2/1.0	1/.33	1/.25	1/.20	2/.33	1/.14	1/.12	10
Canthon lamprimus				1/1.0						1
Canthon moniliatus		1/1.0		1/.33						2
Canthon septemmaculatum					2/2.0	1/.50	2/.67	2/.50	4/.80	11
Deltochilum parile	1/1.0	1/.50	2/.67	6/1.50	8/1.60	16/2.67	10/1.43	9/1.12	14/1.55	67
Ateuchus aeneomicans			1/1.0							1
Ateuchus candezei	1/1.0	2/1.0	1/.33	2/.50	1/.20	2/.33	4/.57	2/.25	3/.33	18
Phanaeus corythus		1/1.0								1
Phanaeus pyrois		1/1.0	2/1.0	2/.67	1/.25	1/.20	5/.83	2/.29	1/.12	15
Onthophagus parecellens		3/3.0	15/7.5	18/6.0	22/5.5	16/3.2	18/3.0	14/2.0	11/1.38	119
Onthophagus sharpi			1/1.0	2/1.0						3
Anaides longeciliata			2/2.0	2/1.0						4
Total No. of Species	2	7	9	10	8	8	8	8	8	
Estimated Av. Biomass (g)	0.242	2.161	1.106	0.971	1.396	1.103	1.031	0.662	0.641	

TABLE 17

Analysis of Scarab Succession on Carcasses in the Wet Season. Based on data presented in Table 16.

TABLE 17

Day	No. of Species	Estimated Av. Number of Individual Arrivals/Day	No. of Individuals on Carcass	Proportional Per Day Increase in No. of Individuals	Estimated Average Biomass (g)	Actual Biomass for Each Trap (g)	Increase in Biomass/Day
1	2	2	2	--	0.242	0.242	--
2	7	8.5	10	10/2=5.00X	2.161	2.301	9.51X
3	9	15.5	27	2.70	1.106	2.204	0.96
4	10	12.8	36	1.33	0.971	3.145	1.43
5	8	11.1	37	1.03	1.396	3.707	1.18
6	8	8.6	41	1.11	1.103	5.338	1.44
7	8	7.8	45	1.10	1.031	5.885	1.10
8	8	4.9	33	0.73	0.662	4.085	0.69
9	8	4.8	37	1.12	0.641	4.926	1.21
Column Number	1	2	3	4	5	6	7

TABLE 18

Species Biomass Characteristics for Members of the Necrophagous Scarab Guild. Biomass values were obtained by multiplying abundance values by the mean individual wet weight in grams. Relative dominance values represent the proportion of the total biomass of each species. Biomass Basal Metabolic Rate (BMR) values were obtained by raising body size (weight) values to the 2/3 power and then multiplying by abundance values.

TABLE 18

Species Number	Species	Mean Indiv. Wet Wt. (g)	Rank	Sample Size	Guild Biomass (g)	Rank	Relative Dominance	Biomass-BMR	Rank
1.	Eurysternus caribaeus	.182	6	15	.015	13	.008	.027	13
2.	" claudicans	.295	4	16	.217	3	.113	.325	5
3.	" plebejus	.051	12	96	.024	12	.012	.064	11
4.	Canthon aequinoctiale	.136	8	1128	.082	7	.043	.158	7
5.	" lamprimus	.011	22	15	.001	22	.001	.006	20
6.	" moniliatus	.034	16	15	.025	11	.013	.077	10
7.	" sallei	.095	9	15	.071	8	.037	.156	8
8.	" septemmaculatum	.152	7	20	.178	5	.092	.332	4
9.	Deltochilum parile	.205	5	15	.318	2	.165	.538	2
10.	Uroxys sulcicollis	.009	25	8	.0003	25	.0002	.001	25
11.	Ateuchus aeneomicans	.016	21	21	.0006	24	.0004	.003	24
12.	" candezei	.037	15	19	.031	9	.016	.092	9
13.	Canthidium ardens	.011	22	7	.001	23	.001	.006	21
14.	" haroldi	.049	13	24	.008	14	.004	.022	15
15.	" laetum	.022	20	15	.003	18	.002	.011	18
16.	" n. sp.	.085	10	15	.002	21	.001	.005	22
17.	Phanaeus corythus	1.368	1	15	.190	4	.099	.171	6
18.	" cupricollis	.614	2	18	.026	10	.013	.030	12
19.	" pyrois	.405	3	30	.550	1	.285	.739	1
20.	Onthophagus acuminatus	.024	19	492	.003	19	.002	.005	23
21.	" crinitus	.067	11	46	.003	20	.002	.007	19
22.	" praecellens	.040	14	26	.160	6	.083	.467	3
23.	" sharpi	.030	17	17	.007	15	.004	.023	14
24.	Coilodes castanea	.011	22	11	.005	17	.003	.012	17
25.	Anaides longeciliata	.030	17	11	.006	16	.003	.019	16
	Column Number	1	2	3	4	5	6	7	8

TABLE 19

Species Abundance Characteristics for Members of the Necrophagous

Scarab Guild. Frequency of occurrence values represent the propor-

tion of carcasses upon which a species was found. Abundance values

were obtained by multiplying freq. of occurrence values by the mean

number of individuals per carcass. Relative dominance values repre-

sent the proportion of the total abundance of each species.

TABLE 19

Species Number	Species	Mean No. per Carcass	Coef. of Variation	Rank	Freq. of Occurrence	Rank	Species Abundance	Rank	Relative Dominance
1.	Eurysternus caribaeus	1.0	0	17	.083	16	.083	19	.006
2.	" claudicans	2.4	1.27	7	.306	7	.734	8	.053
3.	" plebejus	1.6	0.52	11	.292	8	.467	10	.034
4.	Canthon aequinoctiale	2.7	0.46	6	.222	9	.599	9	.043
5.	" lamprimus	1.0	0	17	.129	14	.129	17	.009
6.	" moniliatus	2.2	0.58	8	.339	6	.745	7	.054
7.	" sallei	1.5	0.33	13	.500	3	.750	6	.054
8.	" septemmaculatum	7.0	1.18	1	.167	10	1.169	4	.084
9.	Deltochilum parile	3.1	1.28	4	.500	3	1.550	2	.111
10.	Uroxys sulcicollis	1.0	0	17	.028	24	.028	24	.002
11.	Ateuchus aeneomicans	1.0	0	17	.042	21	.042	21	.003
12.	" candezei	1.6	0.88	11	.528	2	.845	5	.061
13.	Canthidium ardens	2.0	0.50	9	.063	18	.126	18	.009
14.	" haroldi	1.3	0.37	15	.125	15	.163	14	.012
15.	" laetum	2.0	0	9	.071	17	.142	15	.010
16.	" n. sp.	1.0	0	17	.028	24	.028	24	.002
17.	Phanaeus corythus	1.0	0	17	.139	13	.139	16	.010
18.	" cupricollis	1.0	0	17	.042	21	.042	21	.003
19.	" pyrois	3.1	1.30	4	.438	5	1.360	3	.098
20.	Onthophagus acuminatus	1.0	0	17	.063	18	.063	20	.005
21.	" crinitus	1.0	0	17	.042	21	.042	21	.003
22.	" praecellens	5.5	1.02	2	.726	1	3.990	1	.287
23.	" sharpi	1.4	0.35	14	.167	10	.234	12	.017
24.	Coilodes castanea	4.0	0.25	3	.063	18	.252	11	.018
25.	Anaides longeciliata	1.2	0.33	16	.167	10	.200	13	.014
	Column Number	1	2	3	4	5	6	7	8

TABLE 20

Characteristics of Members of the Necrophagous Scarab Guild within
Four Niche and Species Dimensions.

TABLE 20

Species	Authority	Seasonal Activity (Wet/Dry)	Diel Activity (Noct./Diurn.)	Food Preference (Dung-Carr.-Fungi)	Food Removal Technique (Overland/ Non-Overland)
Eurysternus caribaeus	Herbst	W	N	D	N-O, Bury-side
" claudicans	Kirsch	W	N	C,D	N-O, Bury-side
" plebejus	Harold	W	D	C,D	N-O, Bury-side
Canthon aequinoctiale	Harold	W	N	C,D	O, Roll
" lamprimus	Bates	D,W	D	D	O, Roll
" moniliatus	Bates	D,W	D	C,D,F	O, Roll
" sallei	Harold	W	D	C	O, Roll
" septemmaculatum	Latreille	W	D	D	O, Roll
Deltochilum parile	Bates	W	N	C	O, Roll
Uroxys sulcicollis	Harold	W	N	C	N-O, Burrow-side
Ateuchus aeneomicans	Harold	W	D	C,D	N-O, Burrow-side
" candezei	Harold	W	N	C,D	N-O, Burrow-side
Canthidium ardens	Bates	W	D	C	O, Butt
" haroldi	Preud.	W	D	D	O, Butt
" laetum	Harold	D	D	C,D,F	O, Butt
" n. sp.		W	N	C,D	O, Butt
Phanaeus corythus	(Harold)	D,W	N	C	N-O, Bury-below
" cupricollis	Nevermann	W	D	D	O, Butt
" pyrois	Bates	W	D	C,D	O, Butt
Onthophagus acuminatus	Harold	W	D	C,D,F	N-O, Burrow-below
" crinitus	Harold	W	D	D	N-O, Burrow-below
" praecellens	Bates	D,W	D	C,D	N-O, Burrow-below
" sharpi	Harold	D,W	N	C,D,F	N-O, Burrow-below
Coilodes castanea	Westwood	W	D	C,D,F	N-O, in situ
Anaides longeciliata	Balthazar	W	N	C,D	N-O, in situ

TABLE 21

Distribution of Species and Biomass among Subdivisions of Niche and

Species Dimensions in a Necrophagous Scarab Guild. All categories

are mutually exclusive except Dry and Wet Season.

Table 21

Dimension		Number of Species	%	Guild Biomass (g)	%
Season	Dry	6[a]	24		
	Wet	24[a]	96		
Diel	Day	15	60	1.059	54.9
	Night	10	40	0.868	45.1
Food Type	Carrion	5	20	0.580	30.1
	C. and Dung	9	36	1.073	55.7
	C., D., and Fungi	5	20	0.043	2.2
	Dung	6	24	0.231	12.0
Food Removal Technique	Roll	6	24	0.675	35.0
	Butt	6	24	0.590	30.6
	Bury	4	16	0.446	23.2
	Burrow	7	28	0.205	10.6
	In situ	2	8	0.011	0.6
Body Size	Large	8	32	1.576	82.0
	Small	17	68	0.351	18.0

(a) 5 species found both dry and wet seasons

TABLE 22

Frequency of Occurrence, Abundance, and Biomass Values for the Five

Necrophagous Scarab Species that Occur in Both Dry and Wet Seasons.

Frequency of occurrence values represent the proportion of carcasses

upon which a species was found. Abundance values were obtained by

multiplying frequency of occurrence values by the mean number of

individuals per carcass. Biomass values were obtained by multiplying

species abundance values by the mean individual wet weight in grams.

Table 22

Species	Dry Season			Wet Season			Composite		
	Freq. of Occurrence	Abundance	Biomass	Freq. of Occurrence	Abundance	Biomass	Freq. of Occurrence	Abundance	Biomass
Canthon moniliatus	.357	.785	.027	.333	.733	.025	.339	.745	.025
Canthon lamprimus	.142	.142	.002	.125	.125	.001	.129	.129	.001
Onthophagus praecellens	.429	2.360	.094	.813	4.471	.179	.726	3.992	.160
Phanaeus corythus	.071	.071	.096	.139	.139	.190	.139	.139	.190
Onthophagus sharpi	.071	.099	.003	.167	.234	.007	.167	.234	.007

TABLE 23

Distribution of Species and Biomass among 28 Size Classes in a
Necrophagous Scarab Guild.

Table 23

Size Class (g)	No. of Species	% of Total No. of Species	Guild Biomass (g)	% of Total Biomass
.05	13	52	.251	13.0
.10	4	16	.100	5.2
.15	1	4	.082	4.3
.20	2	8	.193	10.0
.25	1	4	.318	16.5
.30	1	4	.217	11.3
.35				
.40				
.45	1	4	.550	28.5
.50				
.55				
.60				
.65	1	4	.026	1.3
.70				
1.35				
1.40	1	4	.190	9.9
Totals	25	100	1.927	100

TABLE 24

Separation of Necrophagous Scarabs among Five Dimensions. All cate-
gories are mutually exclusive except those within the seasonal
dimension.

Table 24

Seasonal Activity	Diel Activity	Food Type	Food Removal Technique	Size (g)	Species
Dry Season	Diurnal	Carrion & Dung			Onthophagus praecellens
		C., D., & Fungi	Butt		Canthidium laetum
			Roll		Canthon moniliatus
		Dung			Canthon lamprimus
	Nocturnal	Carrion	Burrow		Onthophagus sharpi
			Bury		Phanaeus corythus
Wet Season	Diurnal	Carrion	Roll		Canthon sallei
			Butt		Canthidium ardens
		Carrion & Dung	Butt		Phanaeus pyrois
			Bury		Eurysternus plebejus
			Burrow-below		Onthophagus praecellens
			Burrow-side		Ateuchus aeneomicans
		C., D., & Fungi	Roll		Canthon moniliatus
			Burrow		Onthophagus acuminatus
			In situ		Coilodes castanea
		Dung	Roll	0.011	Canthon lamprimus
				0.152	Canthon septemmaculatum
			Butt	0.614	Phanaeus cupricollis
				0.049	Canthidium haroldi
			Burrow		Onthophagus crinitus
	Nocturnal	Carrion	Roll		Deltochilum parile
			Bury		Phanaeus corythus
			Burrow		Uroxys sulcicollis
		Carrion & Dung	Roll		Canthon aequinoctiale
			Butt		Canthidium n. sp.
			Bury		Eurysternus claudicans
			Burrow		Ateuchus candezei
			In situ		Anaides longeciliata
		C., D., & Fungi			Onthophagus sharpi
		Dung			Eurysternus caribaeus

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TABLE 25

Distribution of Species and Biomass among Size Categories of Niche and Species Dimensions in a Necrophagous Scarab Guild.

Table 25

Dimension		Large (Size Class)				Small (Size Class)				Total	
		No. of Species	Propor.	Biomass (g)	Propor.	No. of Species	Propor.	Biomass (g)	Propor.	No. of Species	Biomass (g)
Season	Dry	1	.17	0.096	.427	5	.83	0.129	.573	6	0.225
	Wet	8	.33	1.576	.811	16	.67	.367	.189	24	1.943
Diel	Day	3	.20	.754	.712	12	.80	.305	.288	15	1.059
	Night	5	.50	.822	.947	5	.50	.046	.053	10	.868
Food Type	Carrion	2	.40	.508	.876	3	.60	.072	.124	5	.580
	C-Dung	3	.33	.849	.791	6	.67	.224	.209	9	1.073
	C-D-Fungi	0	-	-	-	5	1.0	.043	1.0	5	.043
	Dung	3	.50	.219	.948	3	.50	.012	.052	6	.231
Food Removal Technique	Roll	3	.50	.578	.856	3	.50	.097	.144	6	.675
	Butt	2	.33	.576	.976	4	.67	.014	.024	6	.590
	Bury	3	.75	.422	.946	1	.25	.024	.054	4	.446
	Burrow	0	-	-	-	7	1.0	.205	1.0	7	.205
	In situ	0	-	-	-	2	1.0	.011	1.0	2	.011

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TABLE 26

Frequency of Occurrence of 25 Necrophagous Scarab Species in Sub-
divisions of Four Niche and Species Dimensions.

Table 26

Season	Diel	Food Type	Food Removal Technique
Dry 6/25	Day 15/25	Carrion Only 5/25	Overland 12/25
Wet 24/25	Night 10/25	Carrion Plus 20/25	Non-overl. 13/25

TABLE 27

The Number of the 25 Necrophagous Scarab Species Observed and Predicted
in 16 Niche and Species Dimension Categories. Each of four niche and
species dimensions has been subdivided into two categories (Table 26).
There are thus 16 unique combinations (2^4), and the observed fre-
quencies of these combinations are presented in the first four
columns. The probability of a species occurring in one of these 16
combinations (Column 5) was obtained by multiplying together the
observed frequency values in each of the four dimensions (Column 1
x Col. 2 x Col. 3 x Col. 4). These probability values are ranked
in Column 6 and are used to predict the number of species (out of
25) that should be in each of the 16 combinations (Column 8). The
number of species observed in each combination is presented in
Column 7. Abbreviations used in Column 5 refer to a particular
category in each of the four dimensions and are as follows:

Season

   D = dry

   W = Wet

Diel

   D = day

   N = night

Food removal technique

   O = overland

   N = non-overland

Food type

   S = specialist on carrion

   G = generalist consumer

Table 27

Season	Diel	Food Removal Technique	Food Type	Probabil.		Rank	No. Species Observed in Category	No. Species Predicted in Category
24/25	15/25	13/25	20/25	.240	(WDNG)	1	6	6.0
24/25	15/25	12/25	20/25	.221	(WDOG)	2	6	5.5
24/25	10/25	13/25	20/25	.160	(WNNG)	3	5	4.0
24/25	10/25	12/25	20/25	.148	(WNOG)	4	2	3.7
24/25	15/25	13/25	5/25	.060	(WDNS)	5	-	1.5
6/25	15/25	13/25	20/25	.060	(DDNG)	5	1	1.5
24/25	15/25	12/25	5/25	.055	(WDOS)	7	2	1.37
6/25	15/25	12/25	20/25	.055	(DDOG)	7	3	1.37
24/25	10/25	13/25	5/25	.040	(WNNS)	9	2	1.0
6/25	10/25	13/25	20/25	.040	(DNNG)	9	1	1.0
24/25	10/25	12/25	5/25	.037	(WNOS)	11	1	0.92
6/25	10/25	12/25	20/25	.037	(DNOG)	11	-	0.92
6/25	15/25	13/25	5/25	.015	(DDNS)	13	-	0.37
6/25	15/25	12/25	5/25	.014	(DDOS)	14	-	0.35
6/25	10/25	13/25	5/25	.010	(DNNS)	15	1	0.25
6/25	10/25	12/25	5/25	.009	(DNOS)	16	-	0.22

Column number

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |

TABLE 28

Characteristics of Necrophagous Scarab Species Occurring in the Dry

Season.

Table 28

Species	Diel Activity	Food Type	Food Removal	Biomass
Canthon moniliatus	Day	All	Overland-Roll	0.027
Canthon lamprimus	Day	Dung	Overland-Roll	.002
Onthophagous praecellens	Day	Carrion and Dung	Non-overl.-Burrow-Below	.094
Phanaeus corythus	Night	Carrion	Non-overl.-Bury-Below	.096
Onthophagous sharpi	Night	All	Non-overl.-Burrow-Below	.003
Canthidium laetum	Day	All	Overland-Butt	.003
			Total	0.225

TABLE 29

Distribution of Species and Biomass among Forty Possible Combin-

ations of Niche and Species Dimensions in a Necrophagous Scarab

Guild during the Wet Season.

Table 29

Diel Activity	Food Type	Food Removal	Biomass	Species
Diurnal	Carrion	Roll	0.071g	Canthon sallei
14 spp	2 spp	Butt	0.001	Canthidium ardens
1.075g	0.072g	Bury		
		Burrow		
		In situ		
	Carrion &	Roll		
	Dung	Butt	0.550	Phanaeus pyrois
	4 spp	Bury	0.024	Eurysternus plebejus
	0.754g	Burrow	0.180	O. praecellens ; A. aeneomicans
		In situ		
	Carrion, Dung,	Roll	0.025	Canthon moniliatus
	& Fungi	Butt		
	3 spp	Bury		
	0.033g	Burrow	0.003	Onthophagus acuminatus
		In situ	0.005	Coilodes castanea
	Dung	Roll	0.179	Canthon lamprimus ; C. 7-maculatum
	5 spp	Butt	0.034	Phanaeus cupricollis ; C. haroldi
	0.216g	Bury		
		Burrow	0.003	Onthophagus crinitus
		In situ		
Nocturnal	Carrion	Roll	0.318g	Deltochilum parile
10 spp	3 spp	Butt		
0.869g	0.509g	Bury	0.190	Phanaeus corythus
		Burrow	0.001	Uroxys sulcicollis
		In situ		
	Carrion &	Roll	0.082	Canthon aequinoctiale
	Dung	Butt	0.002	Canthidium n.sp.
	5 spp	Bury	0.217	Eurysternus claudicans
	0.338g	Burrow	0.031	Ateuchus candezei
		In situ	0.006	Anaides longeciliata
	Carrion, Dung	Roll		
	& Fungi	Butt		
	1 sp	Bury		
	0.007g	Burrow	0.007	Onthophagus sharpi
		In situ		
	Dung	Roll		
	1 sp.	Butt		
	0.015g	Bury	0.015	Eurysternus caribaeus
		Burrow		
		In situ		

TABLE 30

Distribution of Guild Biomass among Categories of the Diel and Food

Removal Dimensions.

Table 30

Food Removal Technique	Day	Night	Totals
Roll	0.275 g (40.7%)	.400 (59.3%)	.675 (100%)
Butt	.585 (99.6%)	.002 (0.4%)	.587
Bury	.024 (5.4%)	.422 (94.6%)	.446
Burrow	.186 (82.6%)	.039 (17.4%)	.225
In situ	.005 (45.4%)	.006 (54.6%)	.011
All techniques	55%	45%	

TABLE 31

Distribution of Guild Biomass among Categories of the Feeding Niche
and Food Removal Dimensions. Each box in the table contains three
values (or none). The number in the upper left is the biomass (g)
of scarabs in a feeding niche using the indicated food removal
technique. The biomass values can be summed vertically or horizon-
tally in the table. The center value in each box represents the
proportion of the total biomass using the food removal technique
that also is in the indicated feeding niche. These values can be
summed horizontally in the table. The lower right number is the
proportion of the total biomass in a feeding niche that also used
the indicated food removal technique. These values can be summed
vertically in the table.

Table 31

	Feeding Niche				
Food Removal Technique	Carrion	Carrion and Dung	Carrion, Dung, and Fungi	Dung	Totals
Roll	0.389g 57.6% 66.9%	0.082g 12.1% 7.5%	0.025g 3.8% 62.5%	0.179g 26.5% 77.4%	0.675g 100%
Butt	0.001g 0.3% 0.2%	0.552 94.0 50.5		0.034 5.7 14.7	0.587g 100%
Bury	0.190g 42.6% 32.7%	0.241 54.0 22.0		0.015 3.4 6.4	0.446g 100%
Burrow	0.001g 0.6% 0.2%	0.211 93.7 19.3	0.010 4.4 25.0	0.003 1.3 1.5	0.225g 100%
In situ		0.006 54.6 0.5	0.005 45.4 12.5		0.011g 100%
Totals	0.581g 100%	1.092g 100%	0.040g 100%	0.231g 100%	1.944g

TABLE 32

Distribution of Guild Biomass among Categories of the Diel and

Feeding Type Dimensions.

Table 32

Food Type	Day	Night	Totals
Carrion	0.072 g (12.4%)	.509 (87.6%)	.581 (100%)
Carrion and Dung	.754 (69%)	.338 (31%)	1.092
Carrion, Dung, and Fungi	.033 (82.5%)	.007 (17.5%)	.040
Dung	.216 (93.5%)	.015 (6.5%)	.231
All types	55%	45%	

TABLE 33

Summary of Results of Pair-encounter Experiments Involving Diurnal

Scarabs. Experiments were conducted in the laboratory on BCI during

the period September-December, 1975.

Table 33

	Diurnal Species	Canthon septemmaculatum	Canthon sallei	Canthon moniliatus	Phanaeus pyrois	Canthidium haroldi	Canthidium laetum	Eurysternus plebejus	Onthophagous praecellens	Coilodes castanea	Wins	Losses
					LOSER							
WINNER	Canthon septemmaculatum	X	9	10	10	10	10	10	10	10	79	1
	Canthon sallei	1	X	10	10	10	10	10	10	10	71	9
	Canthon moniliatus	-	-	X	10	10	10	10	10	10	60	20
	Phanaeus pyrois	-	-	-	X	10	10	10	10	10	50	30
	Canthidium haroldi	-	-	-	-	X	9	10	10	10	39	41
	Canthidium laetum	-	-	-	-	1	X	10	10	10	31	49
	Eurysternus plebejus	-	-	-	-	-	-	X	8	10	18	62
	Onthophagus praecellens	-	-	-	-	-	-	2	X	10	12	68
	Coilodes castanea	-	-	-	-	-	-	-	-	X	0	80

TABLE 34

Summary of Results of Pair-encounter Experiments Involving Nocturnal Scarabs. Experiments were conducted in the laboratory on BCI during the period September-December, 1975.

Table 34

		Nocturnal			LOSER							
	Species	Deltochilum parile	Canthon aequinoctiale	Phanaeus corythus	Eurysternus claudicans	Ateuchus candezei	Onthophagous sharpi	Anaides longeciliata	Wins	Losses
WINNER	Deltochilum parile	X	9	10	10	10	10	10	59	1
	Canthon aequinoctiale	1	X	10	10	10	10	10	51	9
	Phanaeus corythus	–	–	X	9	10	10	10	39	21
	Eurysternus claudicans	–	–	1	X	10	10	10	31	29
	Ateuchus candezei	–	–	–	–	X	7	10	17	43
	Onthophagous sharpi	–	–	–	–	3	X	10	13	47
	Anaides longeciliata	–	–	–	–	–	–	X	0	60

TABLE 35

Comparison of Dominance Hierarchy Rank and Guild Biomass represented
by Five Categories of the Food Removal Dimension. Biomass percentages
refer to the entire guild (Table 21). Hierarchy rank was determined
by pair-encounter experiments involving 16 species (Tables 33, 34).

Table 35

Food Removal Technique	Guild Biomass (%)	Hierarchy Rank	No. Species Tested	N
Roll	35	1	5	360
Butt	31	2	3	240
Bury	23	3	3	200
Burrow	10	4	3	200
In situ	1	5	2	140

TABLE 36

Comparison of Species Composition and Food Type of the Necrophagous
Scarab Guild on BCI with that of Mainland Sites.

Table 36

Species	BCI Food Type	Buena Vista Dung	Buena Vista Carrion	Gamboa Dung	Gamboa Carrion
Eurysternus caribaeus	Dung			X	
" claudicans	Carrion-Dung	X			
" plebejus	C-D			X	
Canthon aequinoctiale	C-D			X	
" lamprimus	D	X		X	
" moniliatus	C-D-Fungi	X	X	X	X
" sallei	C	X	X	X	X
" septemmaculatum	D	X		X	X
Deltochilum parile	C			X	X
Uroxys sulcicollis	C				X
Ateuchus aeneomicans	C-D	X		X	
" candezei	C-D			X	X
Canthidium ardens	C				X
" haroldi	D	X		X	
" laetum	C-D-F	X		X	
" n. sp.	C-D			X	
Phanaeus corythus	C		X	X	X
" cupricollis	D				
" pyrois	C-D			X	X
Onthophagus acuminatus	C-D-F	X	X	X	X
" crinitus	D			X	
" praecellens	C-D			X	X
" sharpi	C-D-F			X	
Coilodes castanea	C-D-F			X	
Anaides longeciliata	C-D	X		X	X
Deltochilum gibbosum				X	X
Chaetodus irregularis					X
Totals	25	10	4	22	14

TABLE 37

Distribution of the Mean Number of Scarabs per Carcass among several

Feeding Categories. Tabulated from Table 18.

Table 37

Feeding Category	$\bar{X}$ no. individuals per carcass	Proportion	
Generalist			
Carrion and Dung (9 spp.)	8.27	.594	
Carr., Dung, and Fungi (5 spp.)	1.44	.103	.697
Total	9.71		
Specialist			
Carrion (5 spp.)	2.59	.186	
Dung (6 spp.)	1.63	.117	.303
Total	4.22		
Total	13.93	1.000	

TABLE 38

Characteristics of the Five Scarab Species Dominant in Biomass.

Table 38

Species	Biomass: Rel. Dominance	Season	Diel	Food Type	Food Removal Technique	Size Rank
Phanaeus pyrois	.285	W	D	C, D	O; Butt	3
Deltochilum parile	.165	W	N	C	O; Roll	5
Eurysternus claudicans	.113	W	N	C, D	N-O; Bury, Side	4
Phanaeus corythus	.099	D, W	N	C	N-O; Bury, Below	1
Canthon septemmaculatum	.092	W	D	D	O; Roll	7
Total	.754					

TABLE 39

Comparison of the Feeding Strategies of Three Groups of Necrophages.

Table 39

Component	Vultures	Adult Flies	Adult Scarabs
Search	Excellent olfactory or visual capabilities Soaring flight technique	Excellent olfactory capabilities Mostly flying, some sit-and-wait	Good olfactory capabilities Mostly sit-and-wait, some flying
Pursuit Time	Long	Very short	Short
Handling Time	Very short (consumption begins immediately upon arrival at carcass)	Long (2-3 days for eggs to hatch)	Short ($\pm$ 10 minutes)
Consumption Time	Short ($\pm$ 2 hours)	Very long (5-10 days for larvae to pupate)	Long (1-5 days for adult)

FIGURE 1

Trap Type A

Coarse-mesh Wire Screen

Soil

Carcass

Iron Rod

Fine-mesh Wire Screen

Soil Surface

FIGURE 2

Trap Type B

Plastic
Bucket-bottom

Coarse-mesh
Wire Screen

Iron Rod

Soil
Surface

Fine-mesh
Wire Screen
Funnel

Metal Can

Sand

Carcass

177

FIGURE 3

Trap Type C

Plastic
Cover Sheet

Coarse-mesh
Wire Screen

Soil
Surface

Wood
Support Pole

Iron
Rod

Plastic
Container

Fine-mesh
Wire Screen
Funnel

Carcass

Sand

FIGURE 4

Trap Type D

Plastic
Bucket-bottom

Coarse-mesh
Wire Screen

Iron Rod

Soil
Surface

Fine-mesh
Wire Screen
Funnel

Plastic
Container

Carcass

Sand

FIGURE 5

Map of Barro Colorado Island, Panama Canal Zone.

BARRO COLORADO ISLAND

Smithsonian Tropical Research Institute
Canal Zone
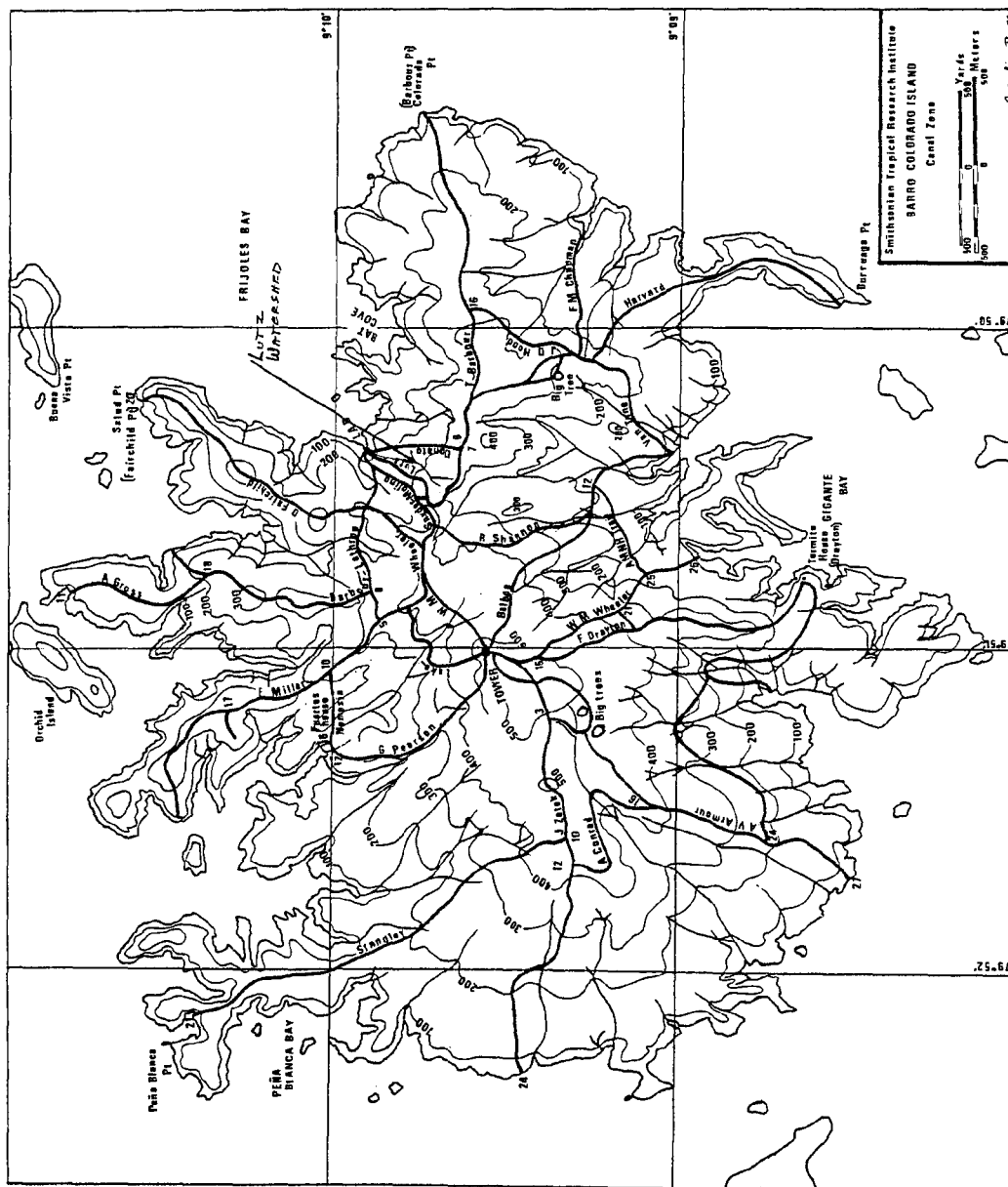
FIGURE 6

Map of Lutz Watershed, BCI.   Trail markers are separated by 100 m.
Location of trapping or experimental sites indicated by X.

N ←

DC5

TB7

DC4

DC2

DC3

TB6

200 m

TB5

100 m

300 m

LUTZ
STREAM

FRL2

100 m

300 m

FRL3

200 m

SM1

SM2

FRL4

TB4

SM3

TB3

TB1

TB2
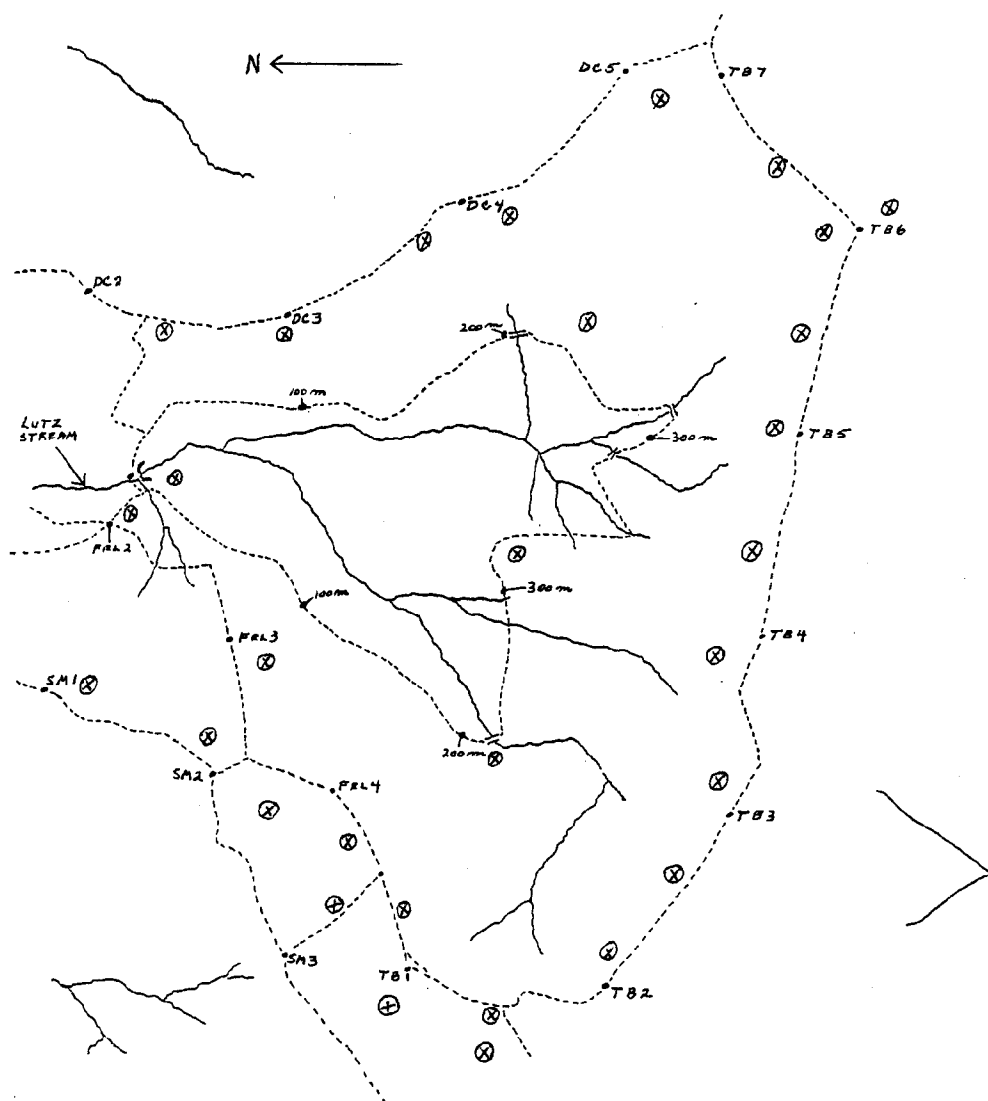
FIGURE 7

Occurrence of vertebrate carcasses on BCI. Data points represent
the estimated date of death for each carcass (Table 2).

	J	F	M	A	M	J	J	A	S	O	N	D
No. of Carcasses	3	0	0	0	2	0	–	–	0	3	3	2
No. of Hours of Observation	180	288	252	216	288	180	–	–	144	144	180	72
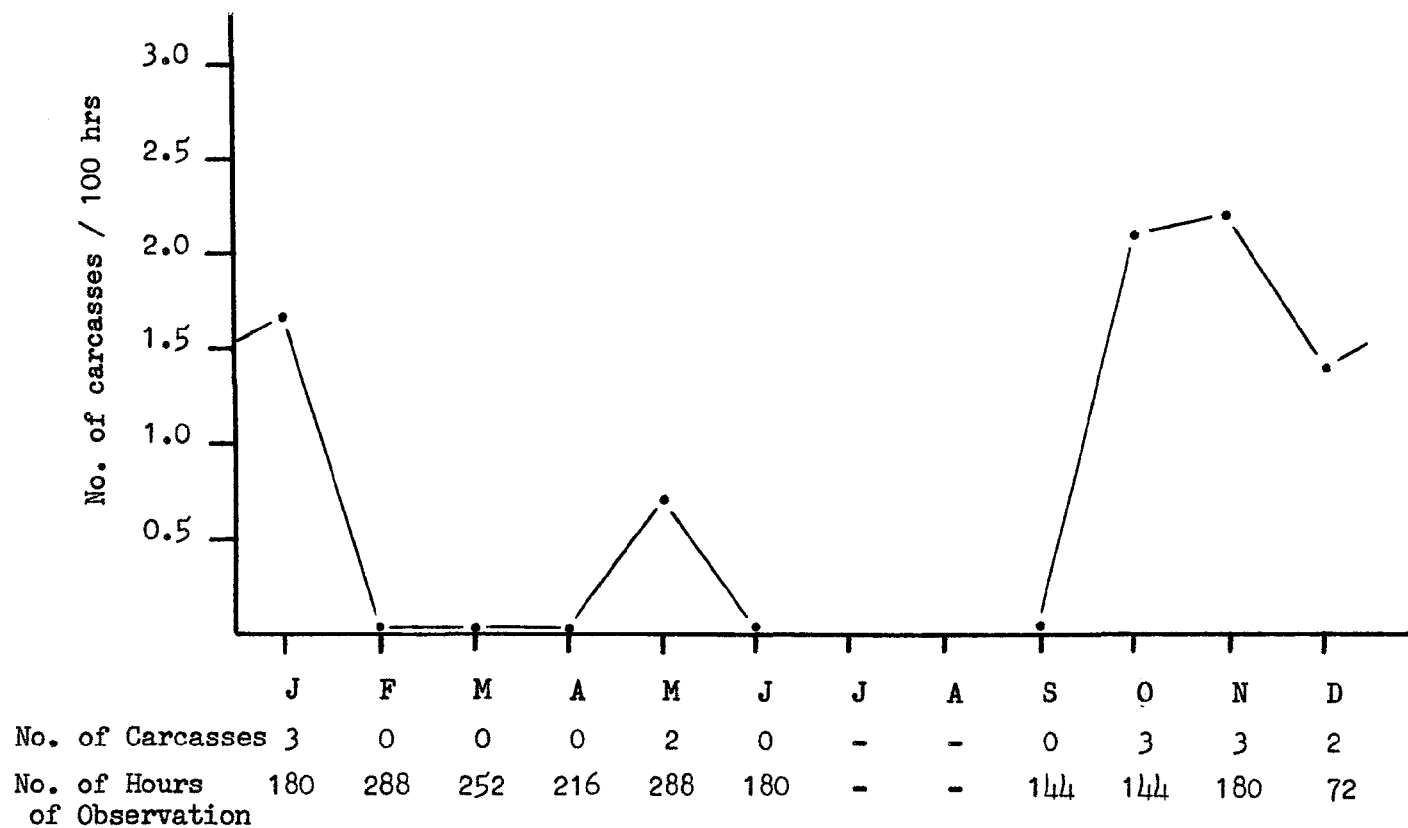
FIGURE 8

Cumulative daily carcass reduction due to arthropod activity.

Experiment performed in the wet season with nine roof rat

(<u>Rattus</u> <u>rattus</u>) carcasses (Table 7, col. 4).

189
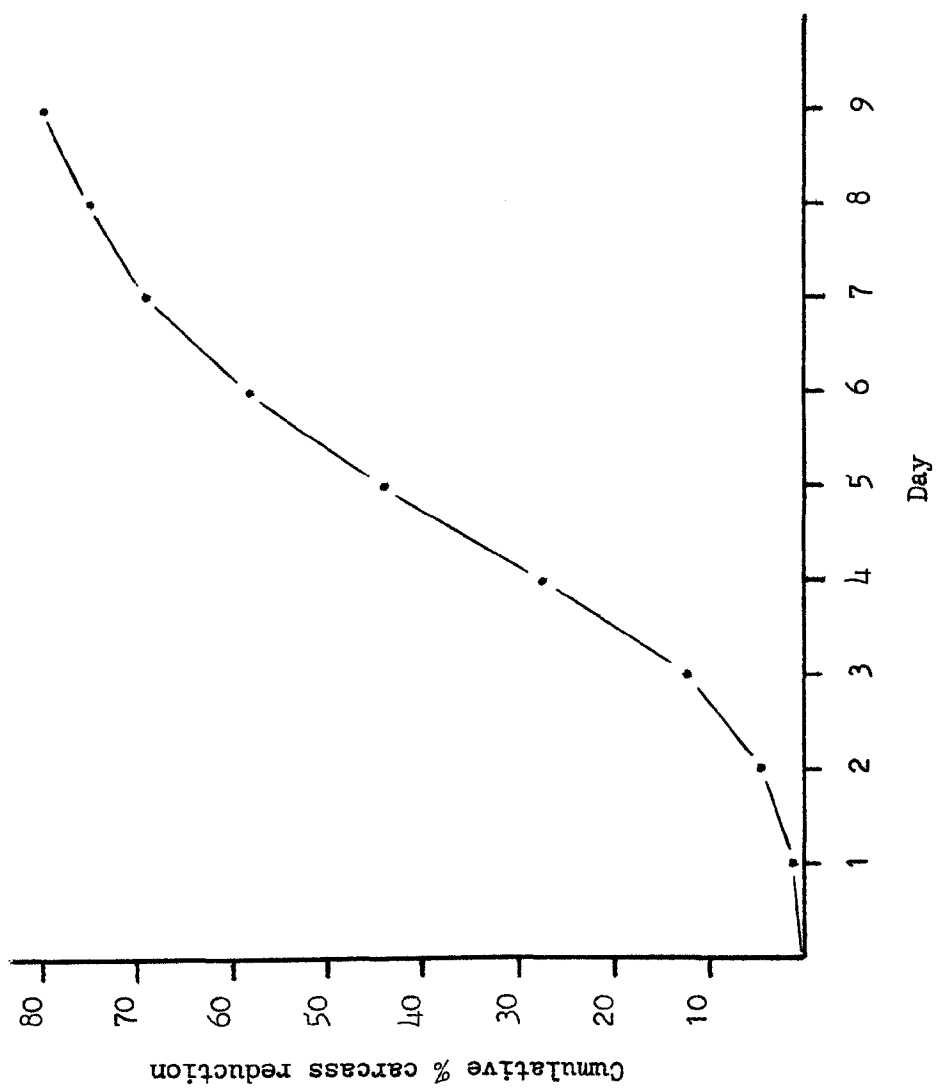
FIGURE 9

Daily carcass reduction due to arthropod activity. Experiment performed in the wet season with nine roof rat carcasses (Table 7, col. 5).
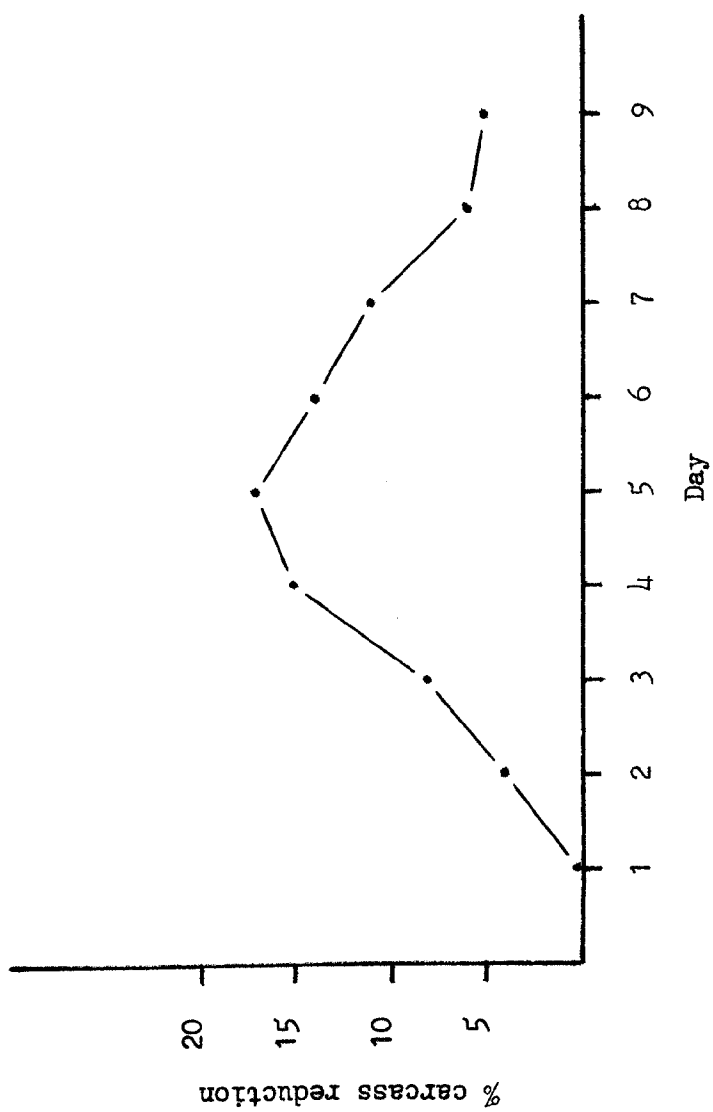
FIGURE 10

Relationship between arthropod biomass and the amount of carcass material removed daily. Experiment performed in the wet season with nine roof rat carcasses (Table 7, col. 11).
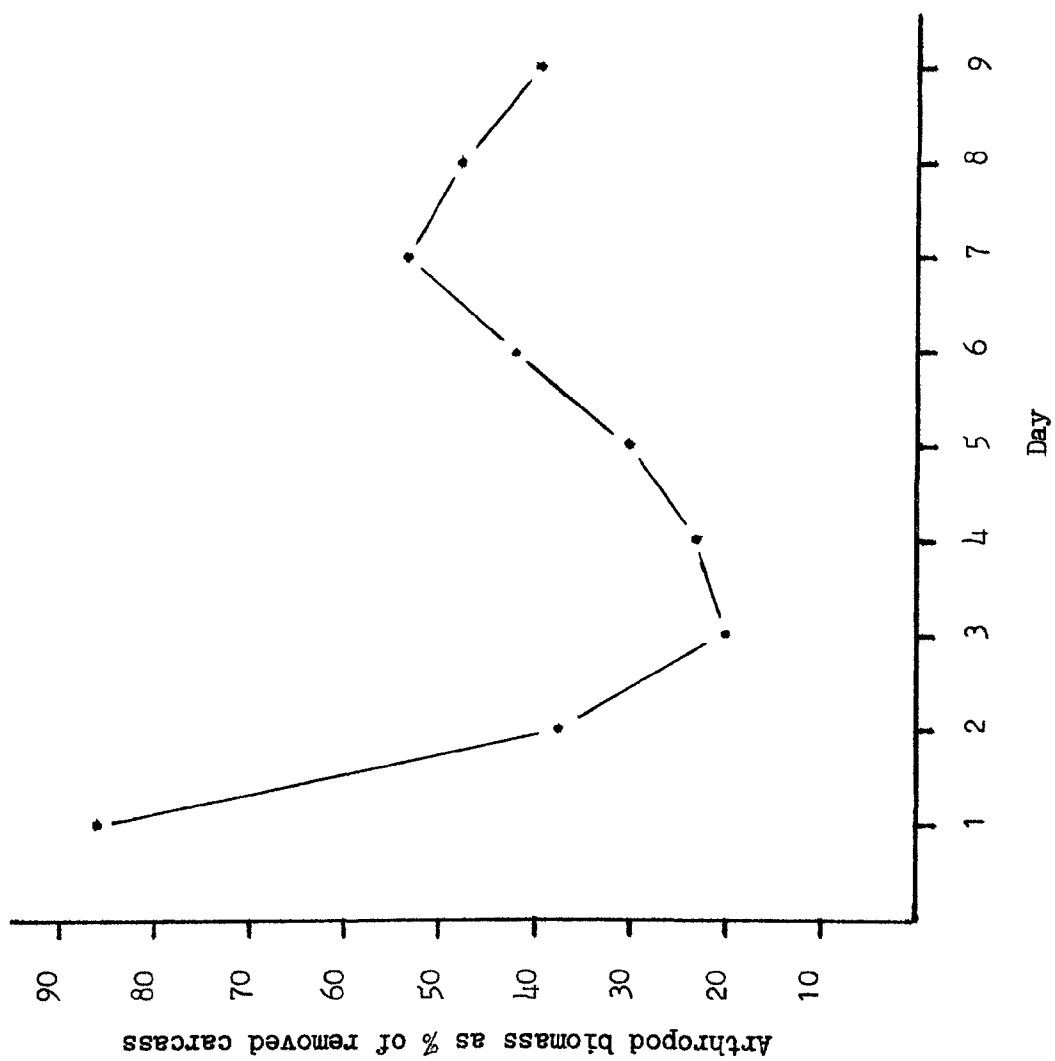
FIGURE 11

Relationship between the biomass of dipterous larvae and other

arthropods and the amount of carcass material removed daily.

Experiment performed in the wet season with nine roof rat carcasses

(Table 7, columns 9, 10).
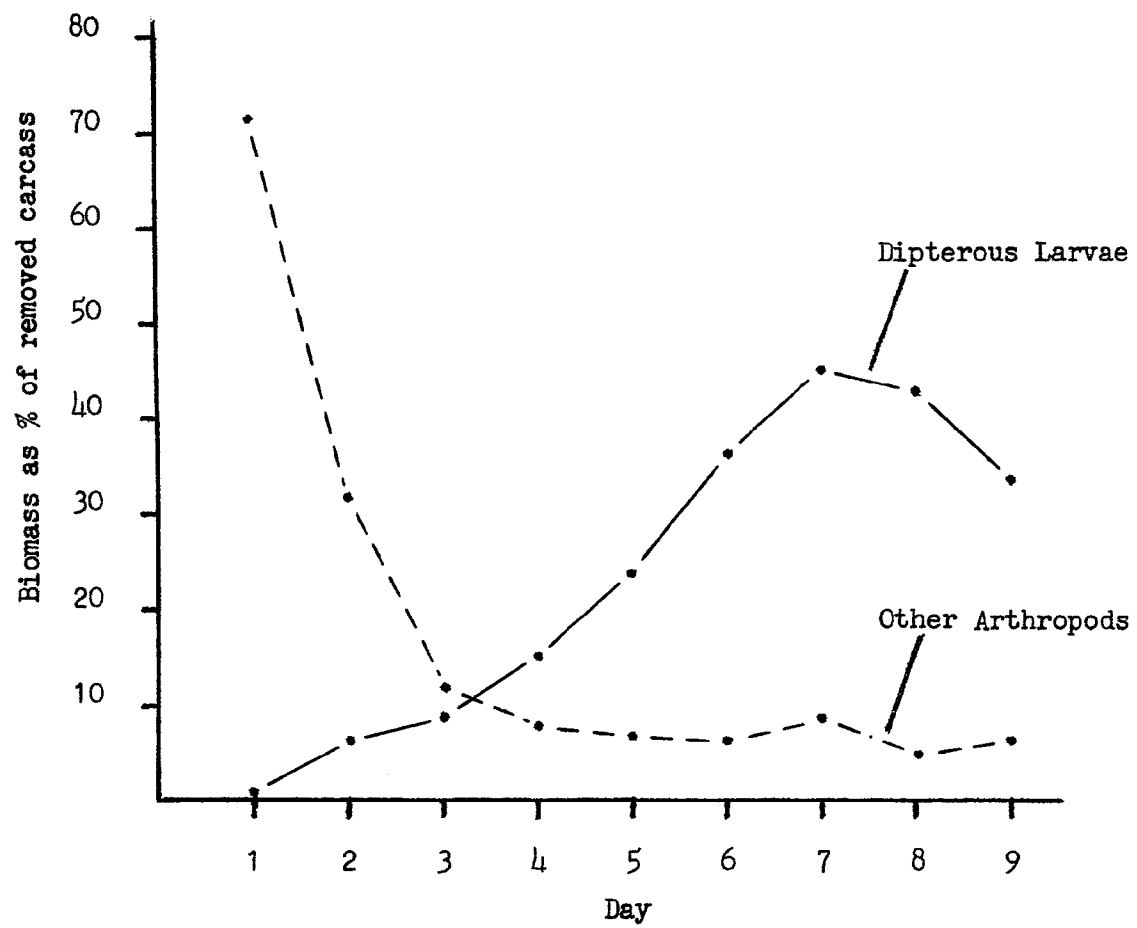
FIGURE 12

Relationship between scarab biomass and the amount of carcass

material removed daily. Experiment performed in the wet season

with nine roof rat carcasses (Table 7, col. 16).
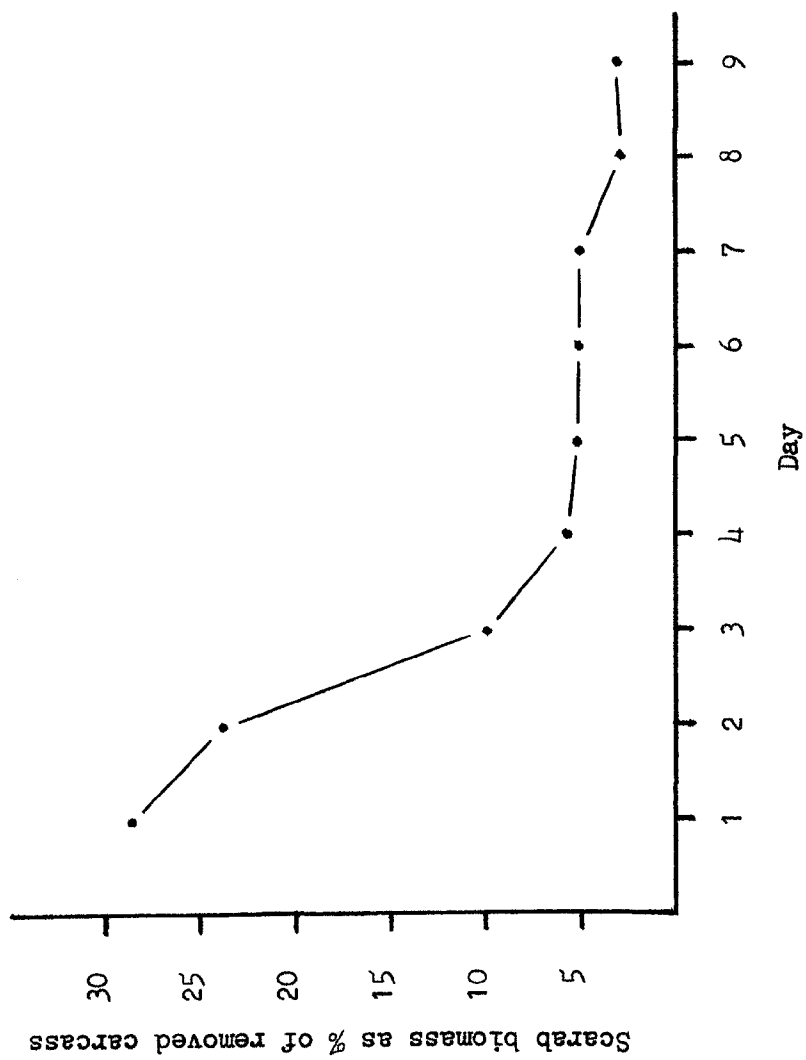
FIGURE 13

Biomass of dipterous larvae and other arthropods on carcasses.
Biomass expressed as a daily percentage of the total arthropod
biomass. Data from an experiment performed in the wet season
with nine roof rat carcasses (Table 7, columns 12, 13).

Day

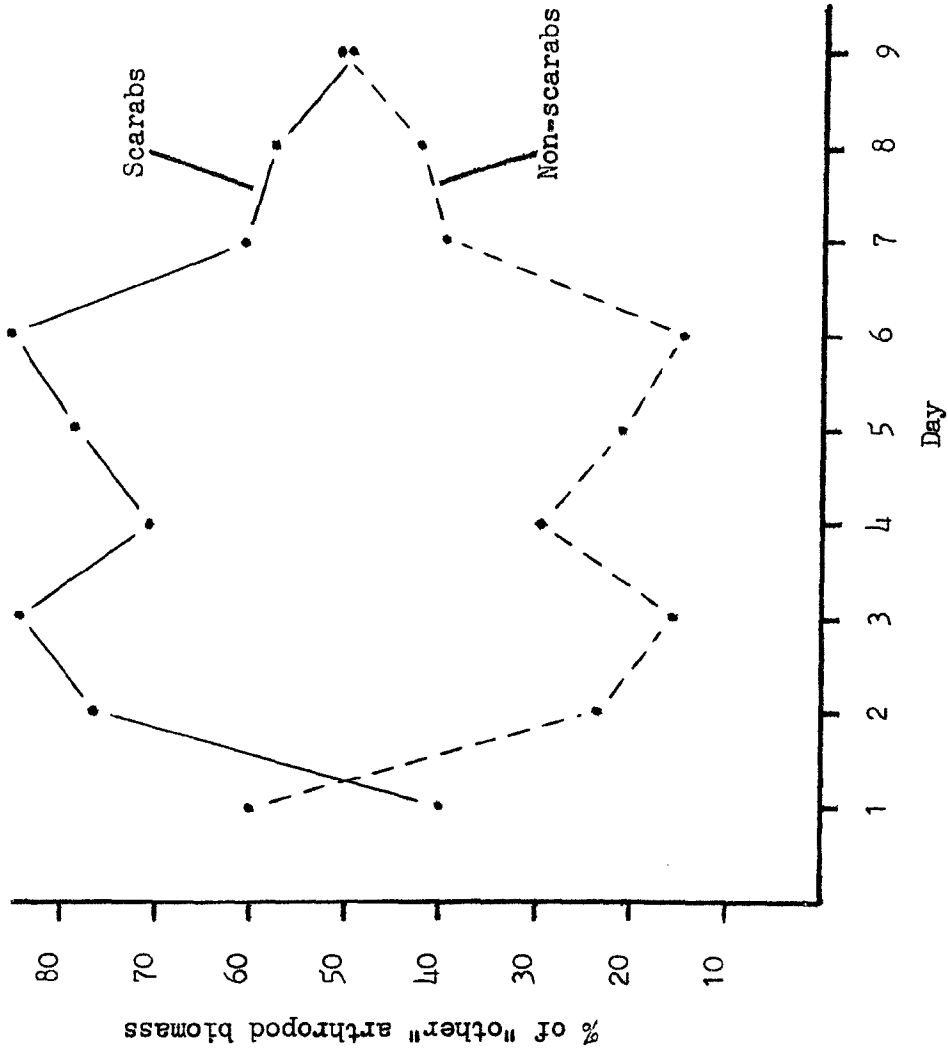% of total arthropod biomass

Dipterous Larvae
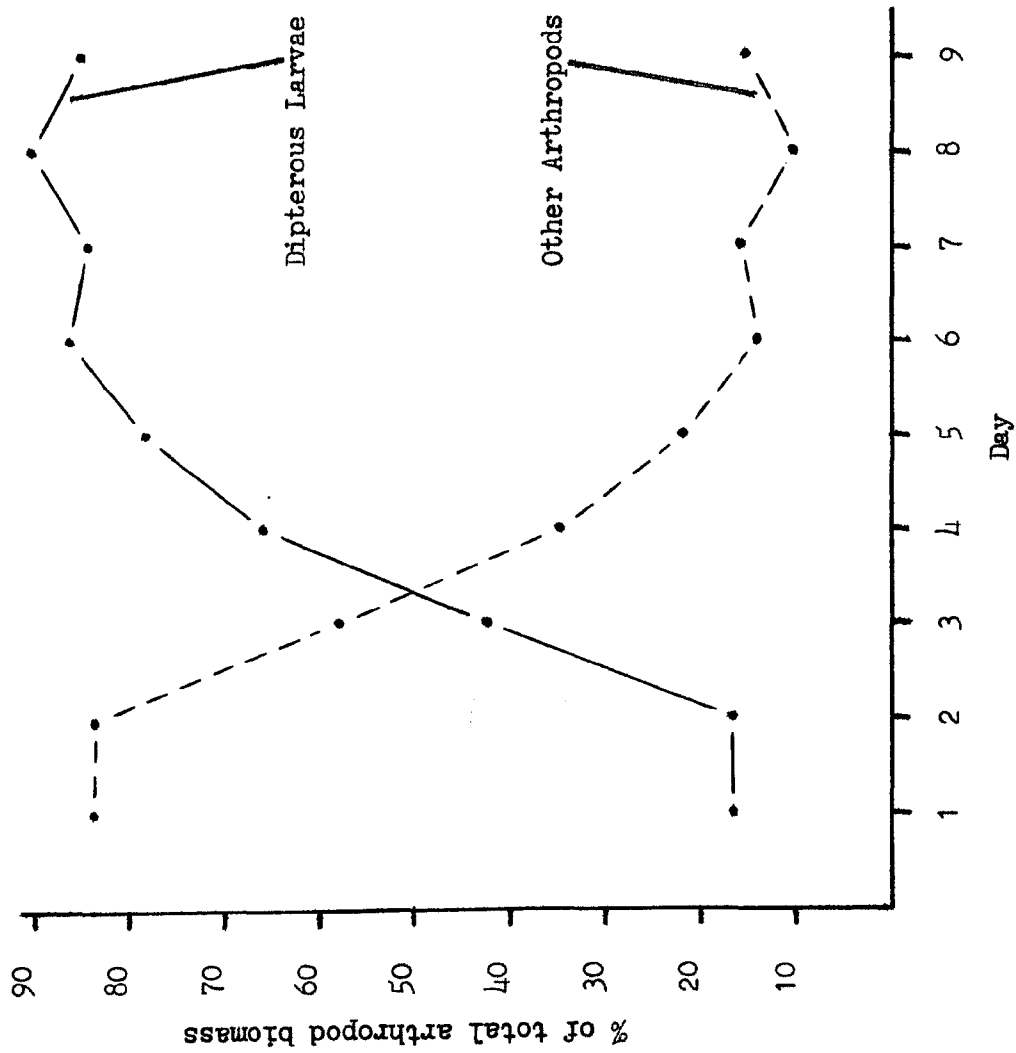
Other Arthropods

FIGURE 14

The relationship between available carcass material and the

biomass of dipterous larvae and other arthropods. Data points

represent the percentage of the total arthropod biomass of

dipterous larvae (. . . . .) and other arthropods (- - - - -),

and the % of the carcass remaining (----------). Data from an

experiment performed in the wet season with nine roof rat

carcasses (Table 7; columns 12, 13, reciprocal of 4).
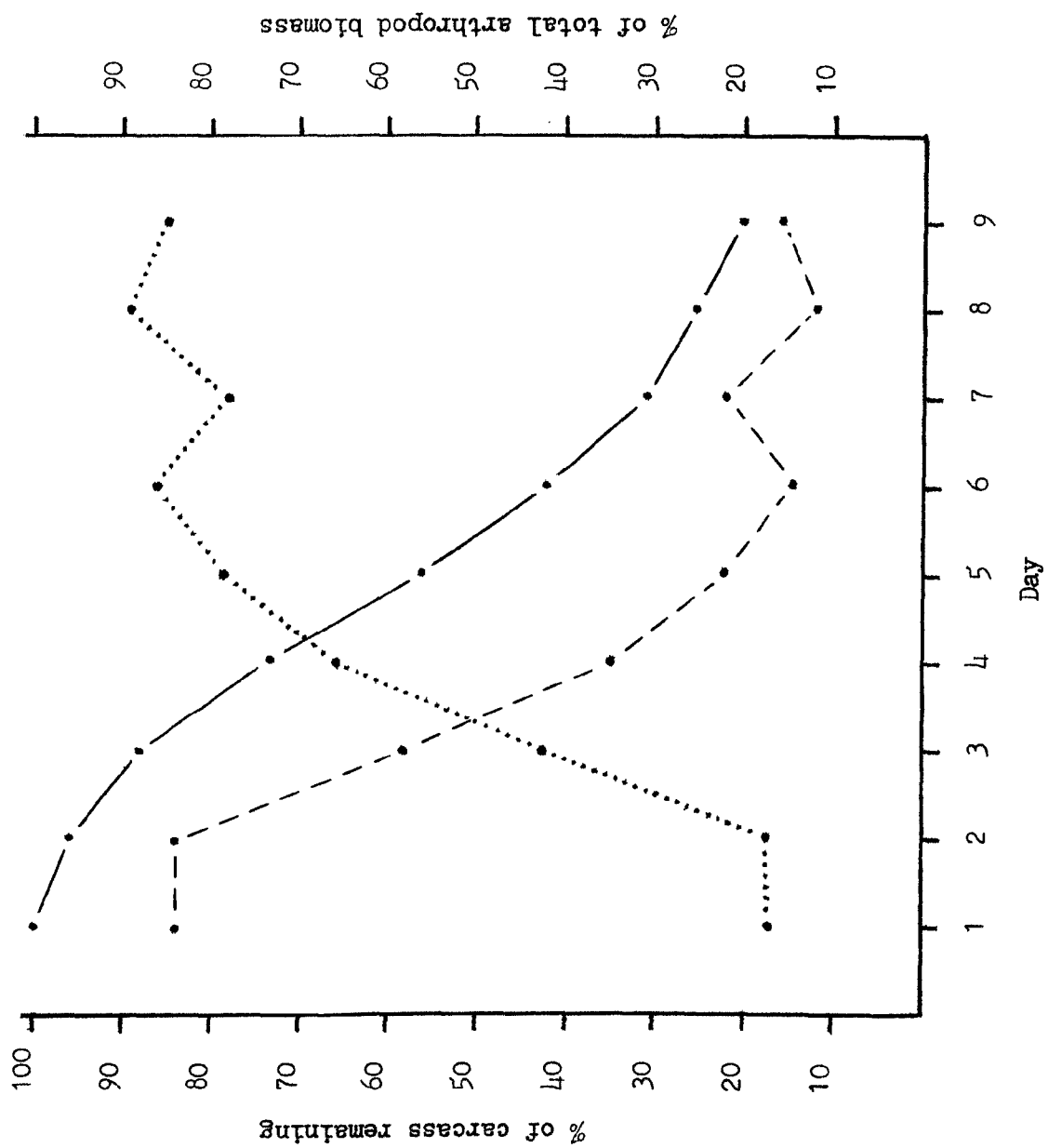
FIGURE 15

Relative biomass of scarabs and other non-dipterous arthropods

on carcasses. Data points represent the respective percentages

of the non-dipterous larva portion of the total arthropod biomass.

Data from an experiment performed in the wet season with nine

roof rat carcasses (Table 7, col. 15).

Scarabs

Non-scarabs

% of "other" arthropod biomass

Day

FIGURE 16

Scarab biomass on carcasses. Data points represent the daily percentage of the total arthropod biomass. Based on an experiment performed in the wet season with nine roof rat carcasses (Table 7, col. 14).
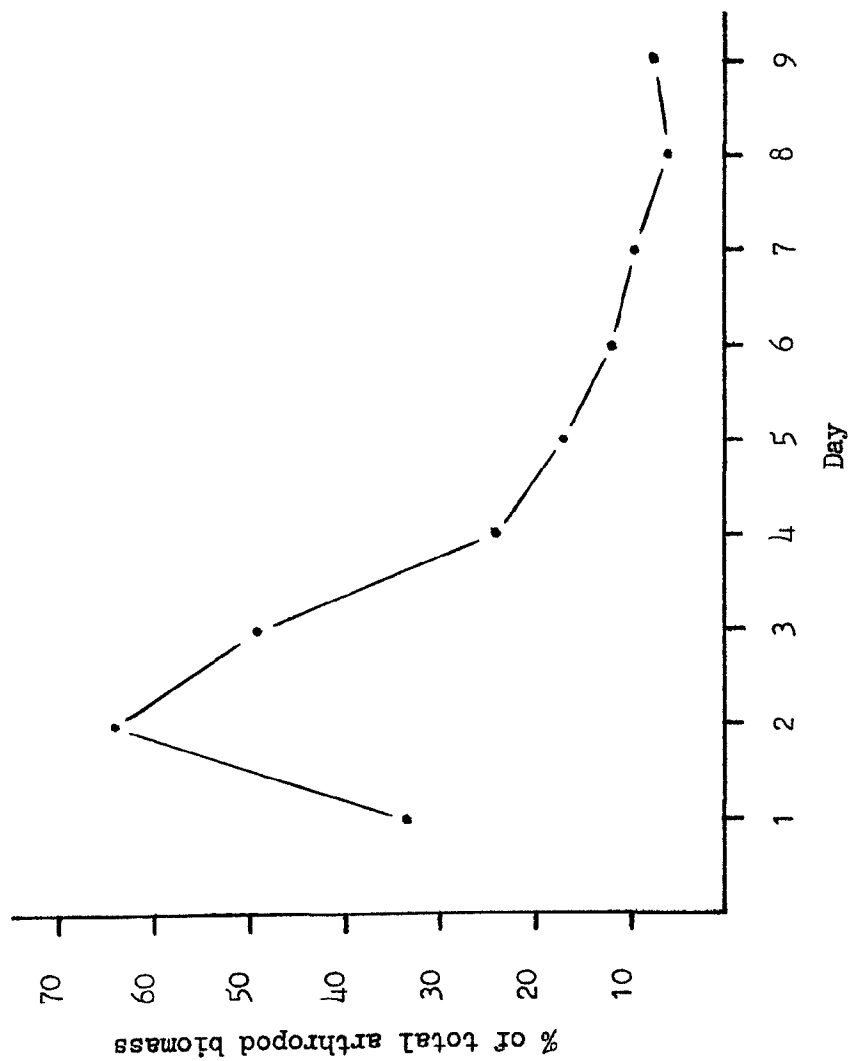
FIGURE 17

Summary of the characteristics of a scarab guild as determined by a nine-day carcass exposure experiment. Conducted during the wet season on BCI, utilizing nine roof rat carcasses. Data from Tables 16 and 17.

A. Number of species occurring each day.

B. Number of species that first occur on each day.

C. Estimated average number of individuals arriving each day.

D. Daily proportional increase in the number of individuals.

E. Estimated average biomass (g) per day.

F. Daily proportional increase in biomass.
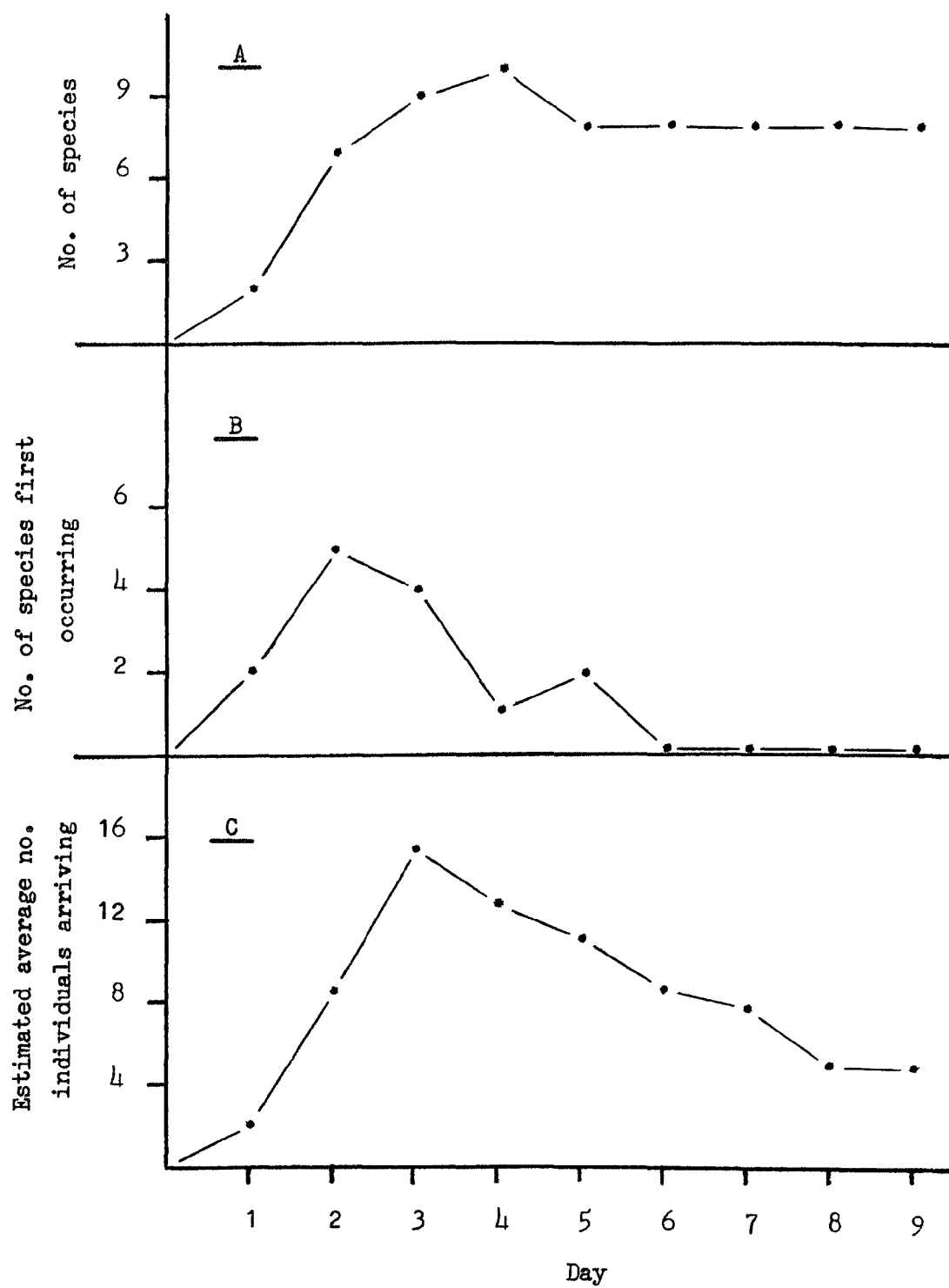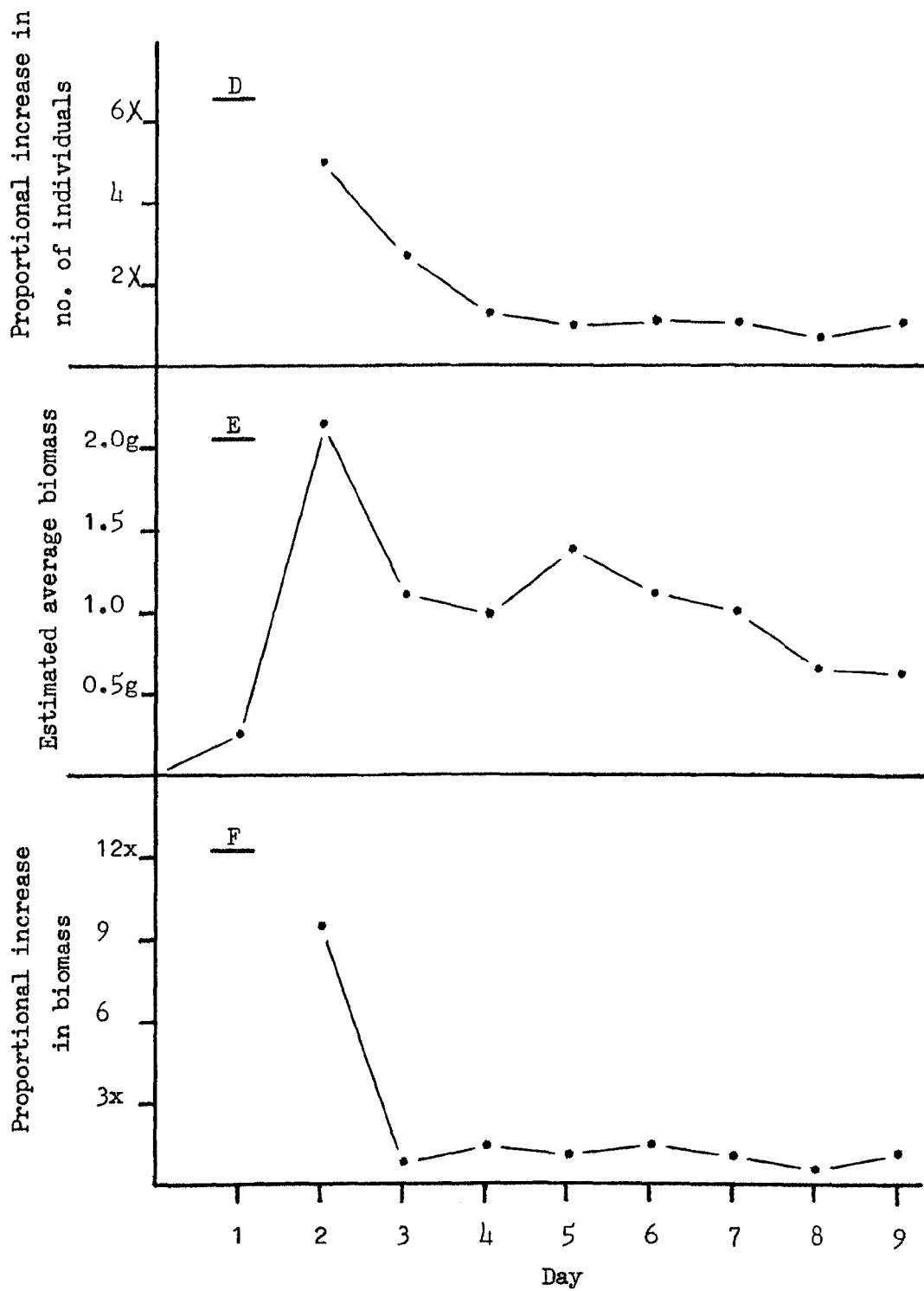
FIGURE 18

Relationship between the Coefficient of variation of the mean

number of individuals per carcass and the frequency of occurrence

for 15 scarab species. The ten species occurring on less than

10% of the carcasses are not considered here. Each species is

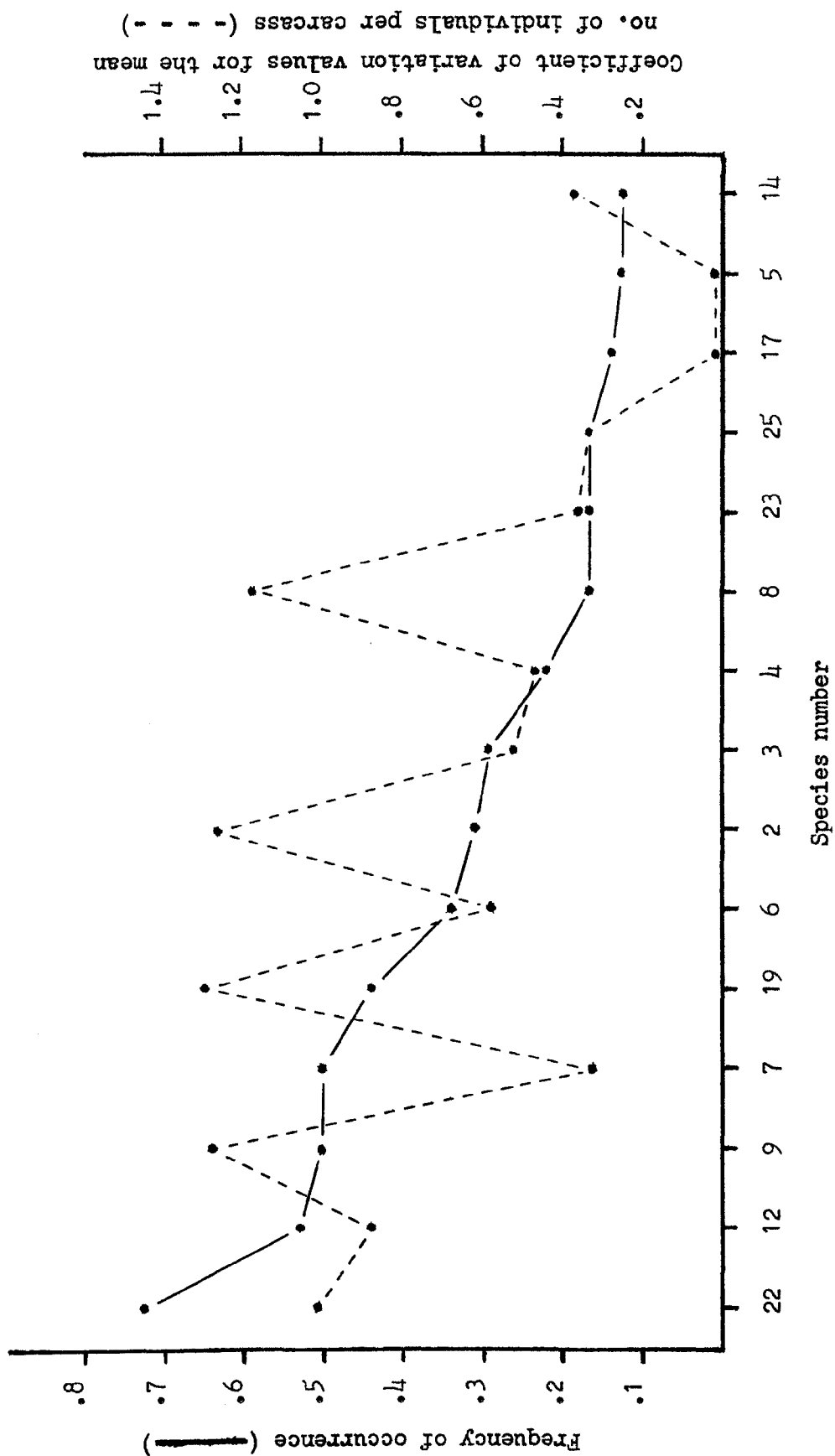identified by a code number (Table 18).

Coefficient of variation values for the mean no. of individuals per carcass (- - - -)

Species number

Frequency of occurrence (——)

FIGURE 19

Relationship between frequency of occurrence and mean number of

individuals per carcass within the necrophagous scarab guild.

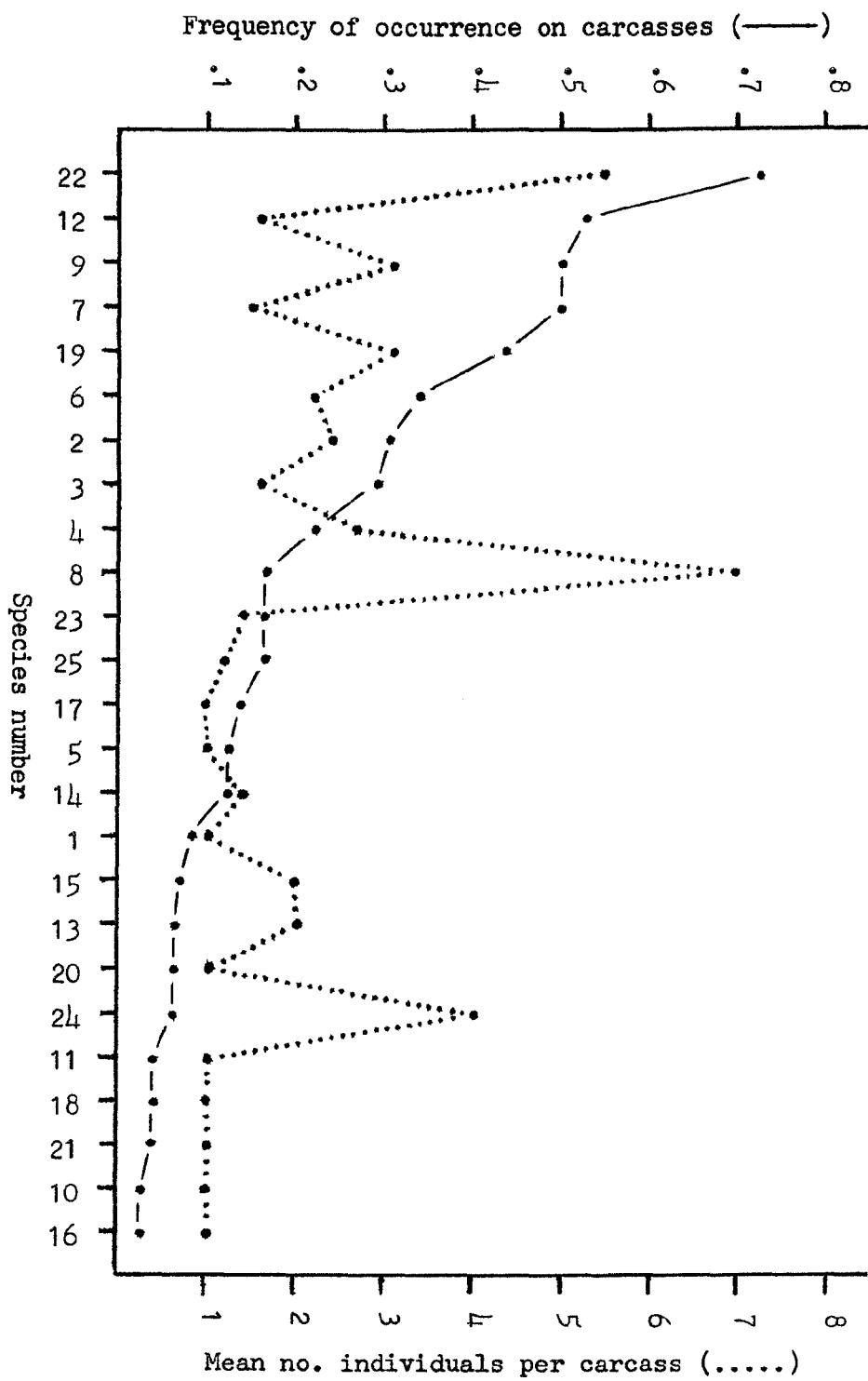Each species is identified by a code number (Table 18).

Frequency of occurrence on carcasses (———)

Species number

Mean no. individuals per carcass (......)

FIGURE 20

Relative abundance of the members of a necrophagous scarab guild.
Abundance values for each species were obtained by multiplying
the mean number of individuals per carcass by the frequency
of occurrence on carcasses (Table 18). Each species is identified
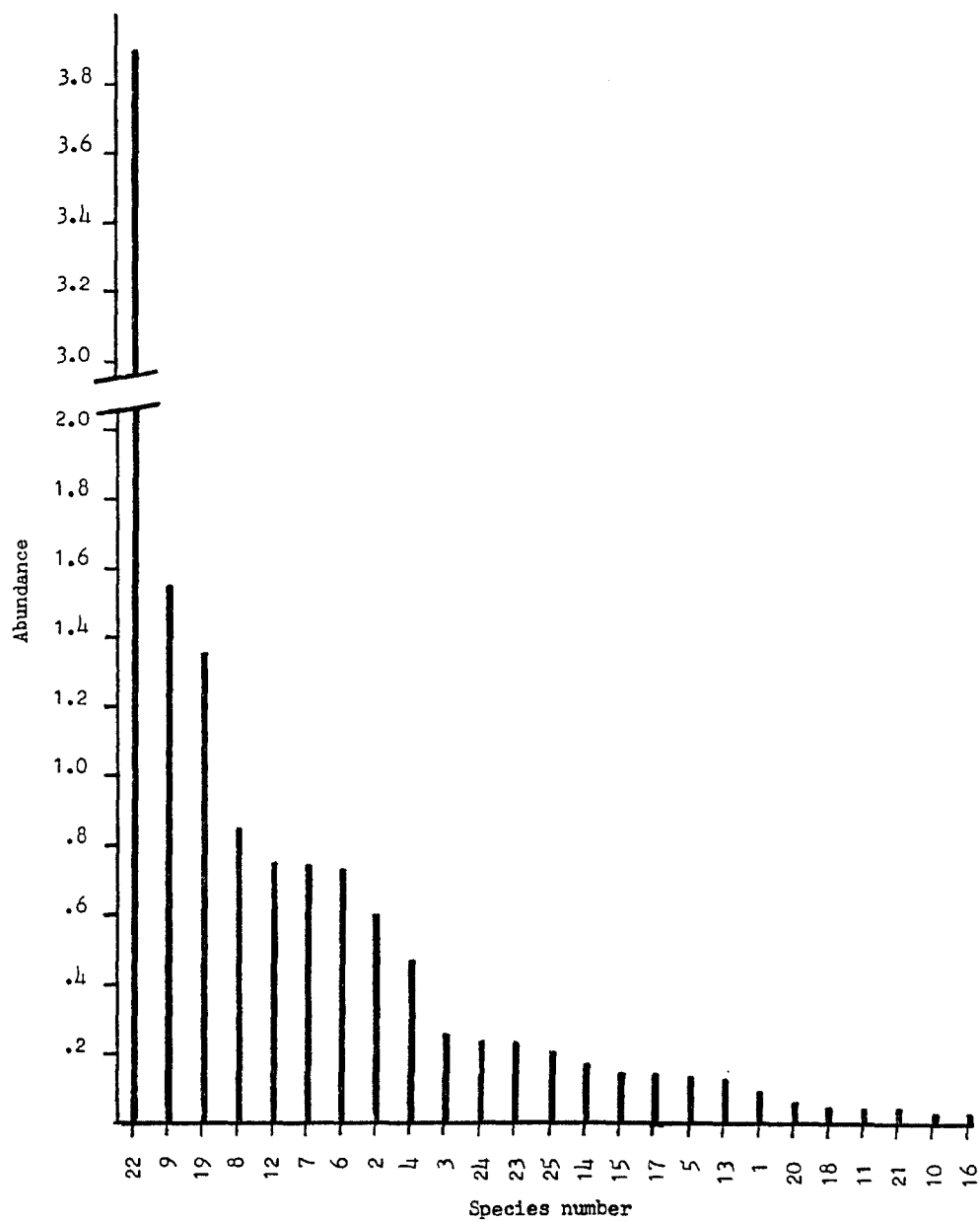by a code number (Table 18).

Abundance (y-axis)

Species number (x-axis): 22, 9, 19, 8, 12, 7, 6, 2, 4, 3, 24, 23, 25, 14, 15, 17, 5, 13, 1, 20, 18, 11, 21, 10, 16

FIGURE 21

Distribution of necrophagous scarabs along a species size

gradient. Size is expressed as the mean individual wet weight (g)
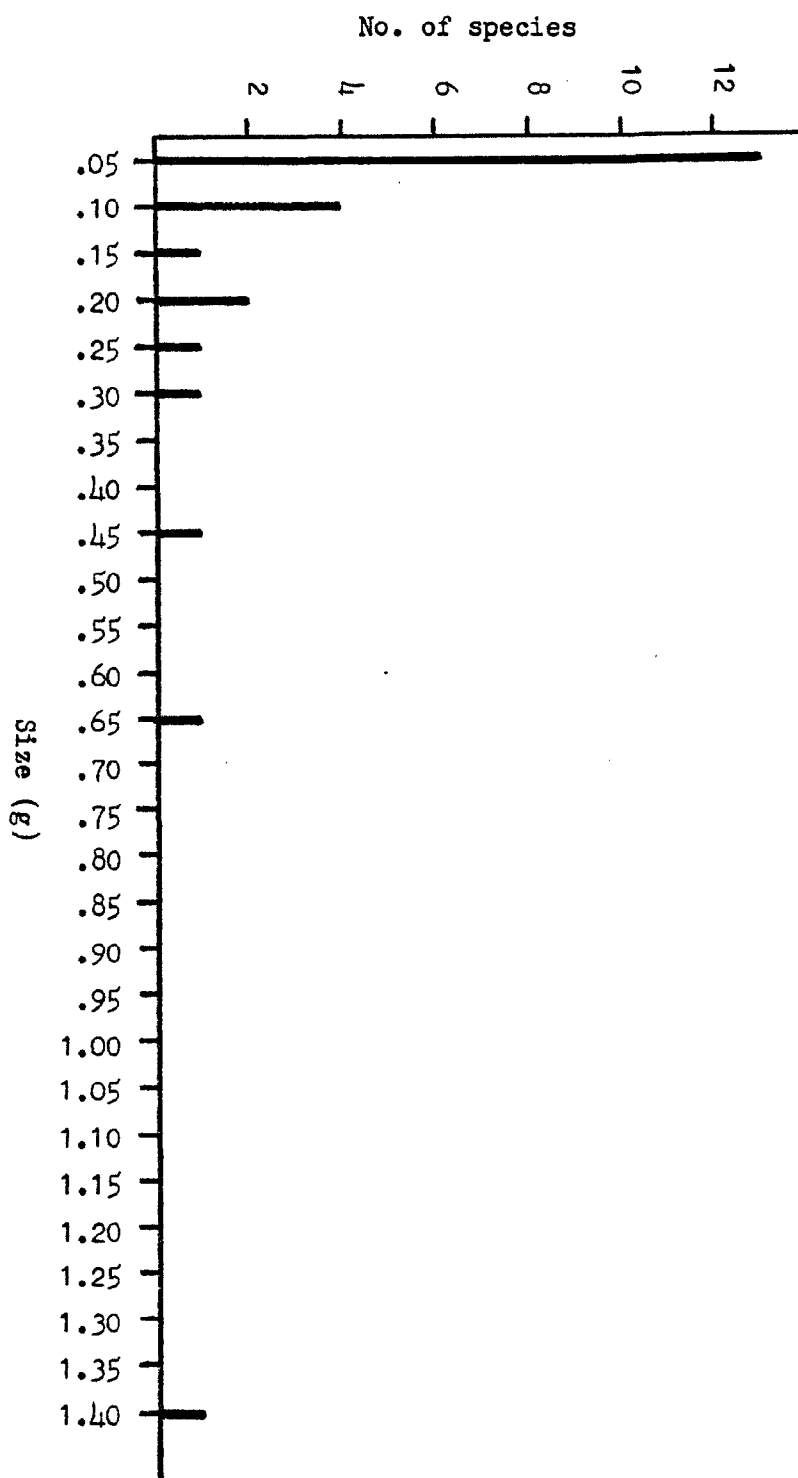
for each of 25 species (Table 19).

No. of species

2   4   6   8   10   12

.05
.10
.15
.20
.25
.30
.35
.40
.45
.50
.55
.60
.65
.70
.75
.80
.85
.90
.95
1.00
1.05
1.10
1.15
1.20
1.25
1.30
1.35
1.40

Size (g)

FIGURE 22

Distribution of 18 scarab species among 15 size classes. These
data represent a subdivision of the first three size classes
(0.05, 0.10, and 0.15 g) of Figure 21.

FIGURE 23

Relationship between abundance and size for 25 necrophagous

scarab species. Each species is identified by a code number

(Table 18). Both sets of values have been converted to loga-

rithms. Those data points connected by a line represent species

abundance values, those not connected represent species size (g)

values (Table 19).

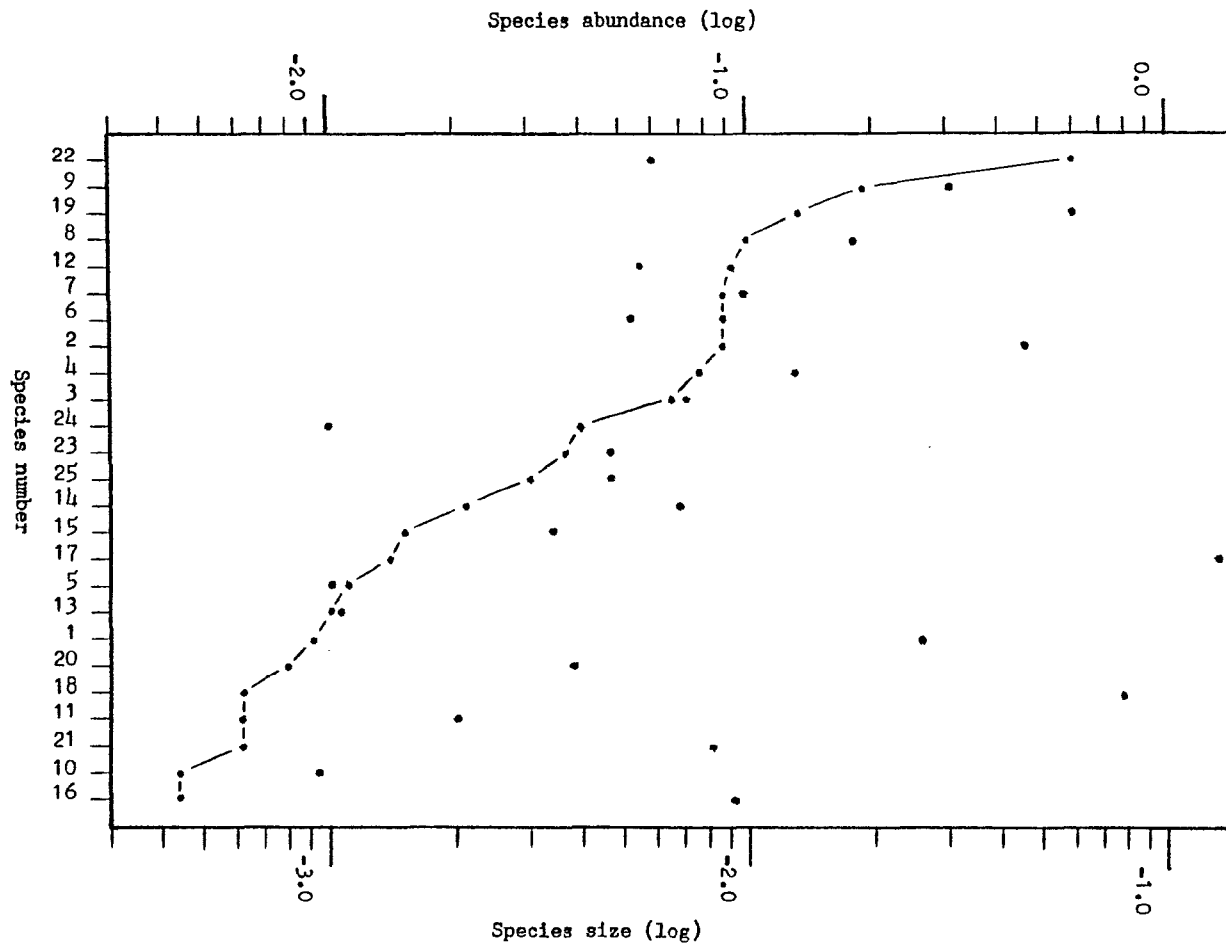Species abundance (log)

Species size (log)

Species number

FIGURE 24

Biomass of 25 necrophagous scarab species. Each species is identified by a code number (Table 18). Biomass values for each species were obtained by multiplying mean individual wet weight (g) values by species abundance values (Tables 18, 19).
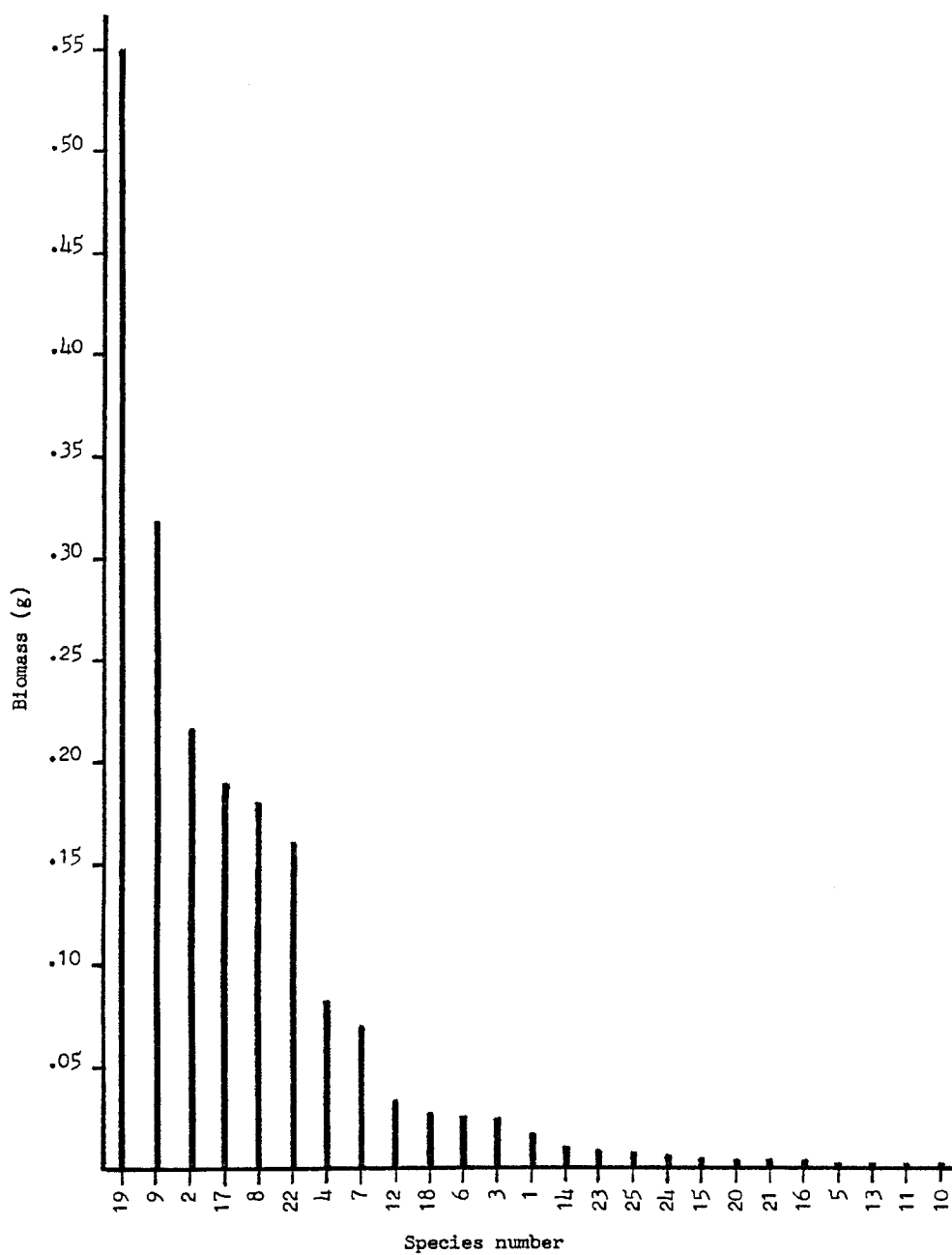
FIGURE 25

Relationship between species abundance and species biomass for members of a necrophagous scarab guild. Each species is identified by a code number (Table 18). Values represent for each species the proportion of the total abundance or biomass of the guild (= relative dominance) (Table 18, col. 8 and Table 19, col.6).
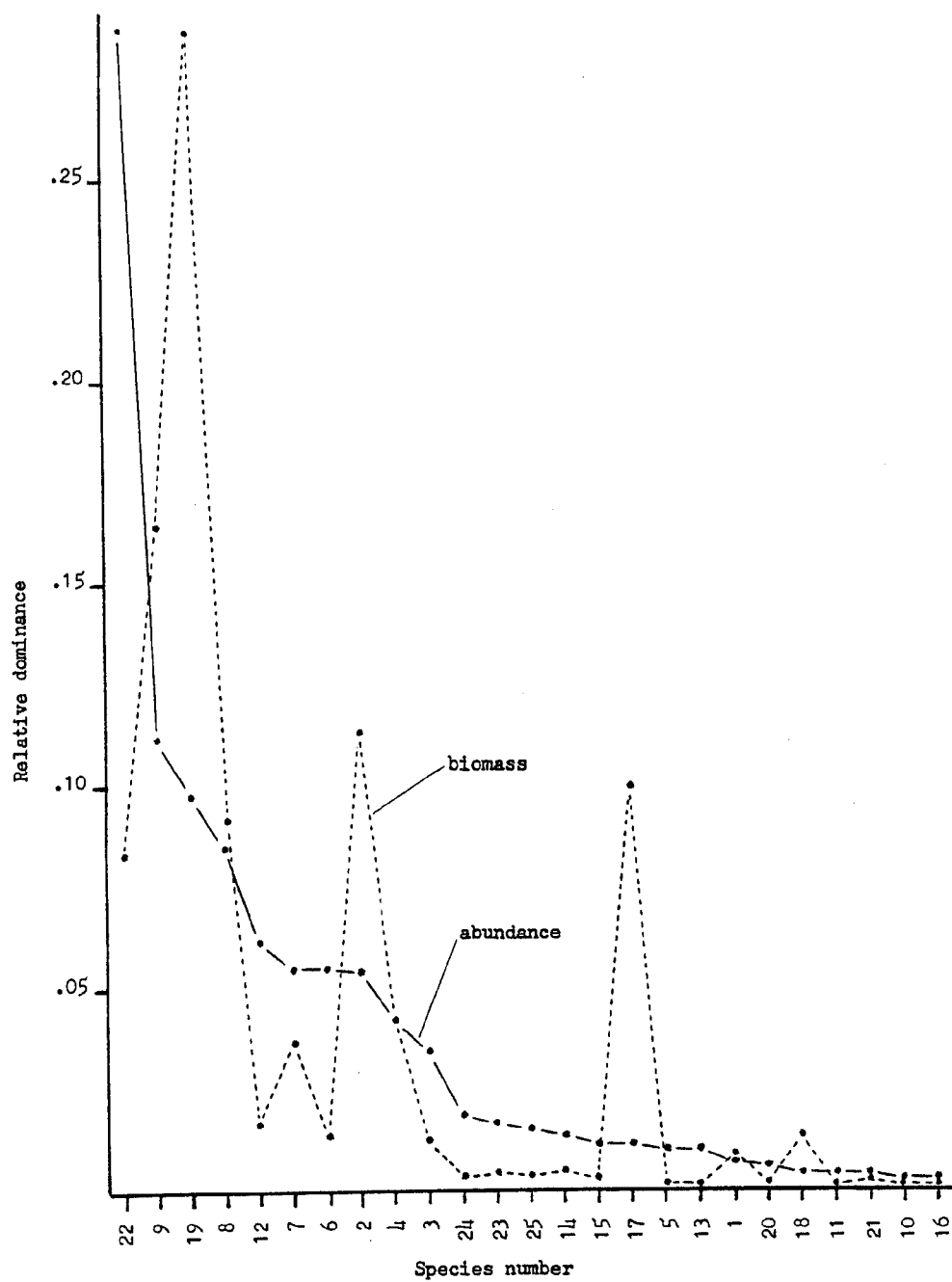
FIGURE 26

Distribution of biomass within a necrophagous scarab guild along

a size gradient. The size of a species is considered to be the

mean individual wet weight (g) (Table 19). The number of species

and biomass in each size category is presented in Table 32.

% of total scarab biomass

10 20 30 40 50

Size (g)

.05
.10
.15
.20
.25
.30
.35
.40
.45
.50
.55
.60
.65
.70
.75
.80
.85
.90
.95
1.00
1.05
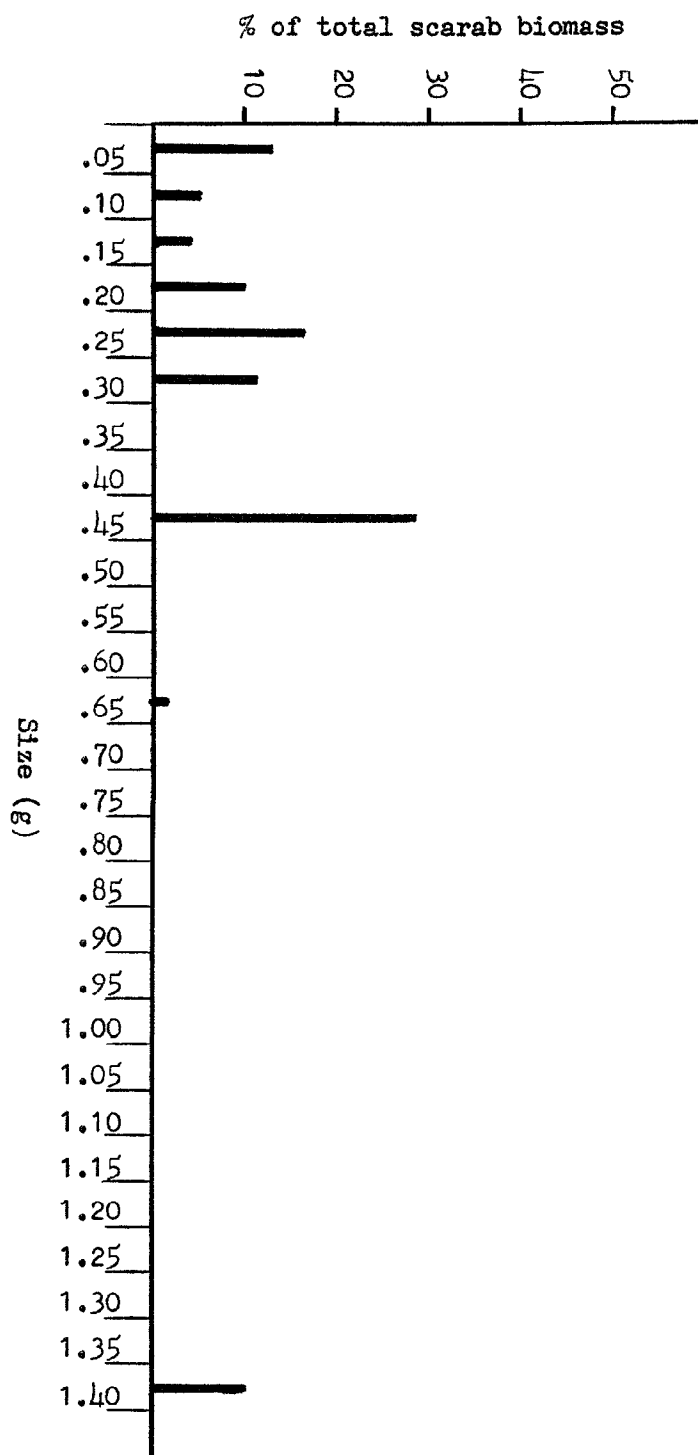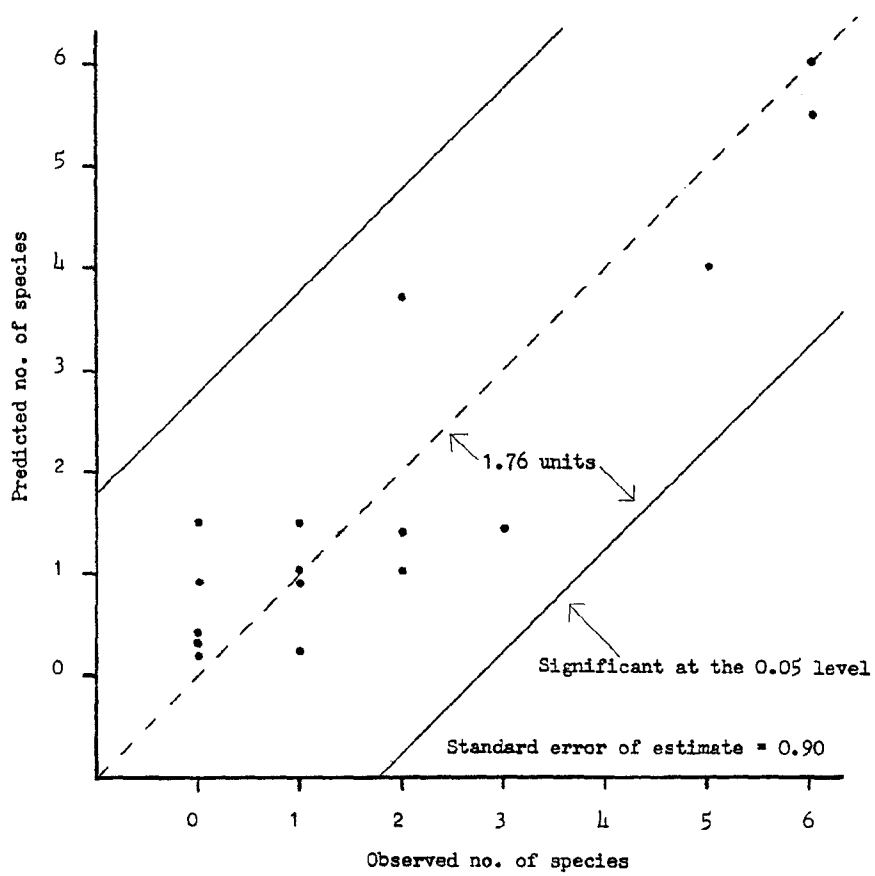1.10
1.15
1.20
1.25
1.30
1.35
1.40

FIGURE 27

Relationship between the number of observed species and the

number of predicted species in each of 16 combinations of niche

and species dimensions. Rationale, protocol, and interpretation

of this figure are presented on page 44. Data from Tables 24 and

25.

Observed no. of species

Predicted no. of species

1.76 units

Significant at the 0.05 level

Standard error of estimate = 0.90

CURRICULUM VITAE

Name: Orrey Pierce Young

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                     Columbia, Maryland 21045

Degree and date: Ph.D., May, 1978

Date of birth: August 23, 1940

Place of birth: Pittsfield, Massachusetts

Secondary education: Pittsfield High School, 1958

Collegiate institutions attended	Dates	Degree	Date of Degree
University of Massachusetts	1958-62		
University of Maryland	1969-72	B.S.	1972
University of Maryland	1972-78	Ph.D.	1978

Major: Zoology

Minor: Behavior and Ecology