## RESOURCE PARTITIONING IN A COMMUNITY OF
## PHILIPPINE SKINKS (SAURIA: SCINCIDAE)

Walter and Troy Auffenberg

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# RESOURCE PARTITIONING

# IN A COMMUNITY OF PHILIPPINE SKINKS

# (SAURIA : SCINCIDAE)

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## ABSTRACT

   Eleven species of variously sympatric species of skinks were studied in southern Luzon, Philippines. In snout-vent length these species varied from 27 to 117 mm. Species diversity was found to be positively correlated with vegetation density.

   The food analyses were based on a total of 2481 adult specimens collected in monthly samples of about 30 individuals of each species for a period of one year. Excised stomachs contained 10,739 food items. Food size, volume, and seasonal representation were stressed in the analyses of each species. Additionally, seasonal insect abundance data were obtained for all of the major microhabitats of the lizard species. Annual abdominal fat accumulation and degradation cycles were investigated in all species.

   We found almost no evidence of food niche partitioning in most species investigated; exceptions were species that lived in unusual environments (arboreal, semiaquatic, marine littoral) inhabited by single species. However, food selection may be playing a role in the distribution of some terrestrial species living in close contact on the floor of local moist evergreen forests. There is no clear basis for suggesting that prey were selected on the basis of nutritional value. Nor was there a significant correlation between predator and prey size or volume—partly because several species frequently fed on inordinately large prey.

   Seasonal switching of prey types was common among almost all the species. The only exceptions were those that lived in very stable environments, such as the marine littoral. In all instances, such switching could be shown to be directly related to local insect abundances.

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Only about half of the local skinks possess abdominal fat at any time of the year. Of those that do, the annual accumulation and degradation cycle is similar in both males and females. In every species examined the cycle can be shown to be linked to seasonal insect abundance.

The Caramoan Peninsula of southern Luzon contains a number of habitats, and no species of skink ranges through all of them. The local forest is richest in number of species, and this is believed due to its greater structural complexity. Among species inhabiting similar habitats there is significant ecological replacement, both horizontally as well as vertically.


# RESUMEN


Se han estudiado once especies de esquincos (Scincidae) en el sur de Luzón, Filipinas. Estas especies se encuentran simpátricas en varias combinaciones y varían desde 27 a 117 mm de largo (hocico-ano). La diversidad de especies muestra una correlación positiva con la densidad de vegetación.

Análisis de alimento se basan en un total de 2481 ejemplares adultos recolectados en muestras mensuales de aprox. 30 indivíduos de cada especie for un año. Los estómagos analisados cotenían 10,739 unidades de alimento. Se han notado especialmente tamaño de presa, volumen de alimento y representación estacional en el análisis de cada especie. A la vez se han recolectado datos sobre abundancia estacional de insectos en todos los microambientes principales de las especies de lagartija. Se estudiaron los ciclos anuales de acumulación y degradación de sebo abdominal en todas las especies.

Casi no se encontró ninguna evidencia de separación por nicho alimenticio en las especies estudiadas, salvo en algunas especies de ambientes exceptionales (arbóreo, semiacuático, litoral marino) habitadas por especies únicas. Sinembargo, la selección de alimento puede jugar un papel en la distribución de algunas especies terrestres que viven contiguamente en el suelo de las selvas húmedas siempreverdes. No hay base clara para sugerir que escogen sus presas a base de valor nutricional. Tampoco hay una correlación significante entre predador y tamaño o volumen de presa--en parte porque varias especies capturan presas extraordinariamente grandes.

Cambios estacionales en el tipo de presa son frecuentes entre casi todas las especies. Las únicas excepciones son las especies que habitan ambientes muy estables, como el litoral marino. En todos los casos, estos cambios se relacionan directamente a la abundancia de insectos en el ambiente.

Aproximadamente la mitad de los esquincos locales poseen sebo abdominal en alguna época del año. En los que sí lo muestran, el ciclo de acumulación y degradación es semejante en machos y hembras. En cada especie estudiada el ciclo esta ligado a la abundancia estacional de insectos.

La Península de Caramoan del sur de Luzón incluye varios ambientes, y ninguna especie de esquinco se encuentra en todos ellos. La selva es el ambiente más rico en numero de especies, y creemos que esto se debe a su mayor complejidad estructural. Entre las

especies que habitan ambientes parecidos hay reemplazo ecológico, tanto horizontalmente como verticalmente.

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## INTRODUCTION

A major goal of our work was to obtain empirical quantitative data that would help make the relatively specialized, yet morphologically homogeneous scincids more useful in developing theories regarding lizard ecological and reproductive niches and of lizard community structure in general. Whether this group of generally cryptic and difficult-to-study lizards can be used to accomplish this end remains to be seen. For many workers, iguanids have proven to be attractive as research organisms. We hope to show that scincids, representing a different set of niches, may also contribute substantially to a rapidly growing body of herpeto-ecological knowledge at the community level--a point repeatedly stressed in more recent papers, such as those of Barbault (1974a, b). The present study is the first of a two-part series on a skink community in tropical evergreen forests of the Philippines and stresses food niches.

Lizard Niches.-- During the past two decades a number of studies provided herpetologists with many important data on the ecological niches of lizards. Most of these have concerned members of the families Teiidae, Agamidae, Lacertidae, and Iguanidae. The family Scincidae has received less

attention--particularly the tropical species. Most studies published on scincids are of single species; only a few compare sympatric forms or analyze niche dimensions and resource partitioning; none has explored broader patterns governing the structure of scincid assemblages in areas where they dominate the local lizard fauna. With the exception of those by Alcala (1966), no studies have been published on Philippine scincid ecology or reproductive biology. Though a few recent publications have concerned lizard trophic relations (several of which have explored both food and place niches), none has dealt with Asian species.

In the current study, the authors examine aspects of the feeding biology of 11 geographically sympatric species in southern Luzon, Philippines, that bear on the following questions: (1) What dimensions of the ecological niche appear to be crucial and how strongly are resources (food and place) partitioned? (2) Do quantitative measures of overlap among paired species imply possible interspecific competition? and (3) In what ways do these skinks vary in responses to annually changing environmental conditions, even though the changes may be slight in this tropical area?

**Food Habits.--** Because of their high visibility, abundance, and extensive ecological radiation, iguanid lizards have also attracted the most attention of ecologists interested in lizard foraging strategies, and most generalities are based on those studies. However, it is questionable how widely these generalities apply outside of the very specific conditions in which they were conceived. No studies addressing these questions have yet been conducted on scincids, and a primary goal of the present study was to test some of the hypotheses regarding prey utilization patterns in non-iguanid insectivorous lizards.

Most of the documentation of food niche partitioning in reptiles has come from the studies of anoles on relatively small Lesser Antilles islands (see Floyd and Jensen 1983 for review). These islands are characterized by high density, simple lizard communities (1-2 species) and depauperate faunas of potential competitors and predators. On such islands the competition experienced by these lizards is perceived as intense and largely intrageneric, the lizards being considered food-limited. In contrast, studies of lizard food habits in Central and South American mainland sites have not found evidence of food-niche partitioning (see Duellman 1978 for review), implying that food competition is relatively unimportant in these ecologically more complex communities. A strong ecological dichotomy is thus suggested between less diverse island and more diverse mainland lizard communities. Unfortunately, this is based on relatively few studies, and these within restricted and distinctly divergent faunas.

In the Indo-Australian Archipelago the Family Scincidae is a very diverse group, including many potential intrafamilial competitors of diverse habits and residing in many different habitats, varying from some that parallel

those of small island communities to others that parallel those of diverse, rich mainland forest habitats. The data we collected provides the opportunity to (1) determine the pattern of food niche partitioning among scincids in southern Luzon, (2) examine measured variables for possible food limitations, and (3) look at the effect of seasonality upon the diet of a community of scincids.

## ACKNOWLEDGEMENTS

## METHODS

Of the 11 skink species studied, 9 are the better represented: *Emoia atrocostata, Lamprolepis smaragdina, Brachymeles boulengeri, Mabuya multifasciata, M. multicarinata, Sphenomorphus jagori, Lipinia pulchella, Otosaurus cumingii,* and *Tropidophorus grayi.* For these species, 30 large individuals were collected each month for a period of one year (July 1962-August 1983) in the environments close to the field camp at the village of Terogo, Caramoan Peninsula, Camarines Sur, southern Luzon, Philippines (123°51'E, 13°55'N). Fewer individuals were obtained of *Dasia grisia* and *Brachymeles samarensis.* Most individuals were collected by hand or sling shot, though *T. grayi* and *O. cumingii* were often caught by "angling" for them with a baited hook lowered into their burrows.

The study area (ca 15 km$^2$) is largely covered with limestone karst mountains, with elevations ranging from sea level to 350 m. Most of the area is clothed with mixed dipterocarp evergreen forest (Whitmore 1975), though secondary forest is extensive, particularly near sea level. Agricultural lands include abaca and coconut plantations, as well as terraced rice lands. Mangrove forest, nipa palm swamp, rocky beaches, and headlands occur along the coast. Details regarding the local vegetation, topography, and climate are available in Auffenberg (in press).

Density estimates for those ecologically sympatric species in which they are discussed were obtained along the marked transect of a small mountain near the base camp at Terogo. The transect was covered in the same fashion on a regular schedule every day (equal daily and hourly representation) over a 5-day period once each month during the entire study period. Climatic and other data were collected during each traverse at eight stations selected to reflect habitat variation in the local forest through which the transect ran. At each station air temperatures were obtained at 10 cm above the surface and at the surface. When lizards were seen, the following data were collected: activity type when sighted (foraging, intraspecific interactions, or basking), angle of sighting in respect to transect path, perpendicular distance between lizard and transect path, elevational position of lizard (in meters above the surface), general lizard size, date, and time of sighting. Technique and analysis of density estimates follow those outlined by Burnham et al. (1980).

Individuals were also collected away from the transect area on a monthly basis. These were immediately preserved and later measured (hereafter, snout-vent length = SVL, total length = TL) to the closest mm. An adequate series of each was weighed immediately after death (but before preservation) to the closest 0.1 g (= Wt hereafter).

The total number of individuals of each species examined for stomach contents are: *E. atrocostata* 318, *L. smaragdina* 358, *B. samarensis* 43, *B. boulengeri* 350, *M. multifasciata* 378, *M. multicarinata* 353, *D. grisia* 61, *S. jagori* 363, *O. cumingii* 305, *T. grayi* 368, and *L. pulchella* 355. Selected individuals were used for other analyses and these totals are indicated in the appropriate places.

Stomach contents were examined by excision and dissection. Data obtained on insect prey found in the stomachs were category type (taxonomic determination to family level) and individual prey length (to closest mm). We recognized 40 prey categories based on both entire and partly digested items. However, the latter were omitted from prey size and volume analyses unless original sizes and volumes could be estimated.

Seasonal diurnal insect abundance was established by placing, once each week for the entire year, four 10 x 15 cm sheets of a good quality flypaper at each of seven stations near the base camp. These were left for an entire day and collected in the late afternoon. The trapped insects then were categorized by family and individuals in each category counted. Locations of the seven stations overlapped part of the transect used for studying lizard densities and activity patterns. All the microhabitats represented along the transect were included in the seven stations used to determine insect abundance and diversity.

In the following section terms used are defined, and where appropriate, analytical techniques are outlined.

**Coefficient of Community.** This is a mathematical measure of the relative similarity of samples from two communities (Whitaker 1970):

$$CC = S_{ab}/(S_a + S_b - S_{ab}),$$

where $S_{ab}$ is the number of species shared by samples a and b, $S_a$ is the total number of species present in sample a, and $S_b$ is the total number of species in sample b.

**Ecological Allopatry.** Two or more species living in the same habitat, but separated by differences in microhabitat and/or diel activity period.

**Ecological Sympatry.** Two or more species living in the same microhabitat and overlapping in their diel activity period.

**Microhabitat.** In the Caramoan primary forest the following lizard microhabitats are recognized: fossorial, leaf litter, ground surface, shrub layer, low tree trunk, high tree trunk (and major branches), and canopy. In agricultural lands the microhabitats recognized are fossorial, surface, and coconut tree trunks.

**Niche.** Our usage follows that of Hutchinson (1957), being an abstract concept of a multidimensional factor. The dimensions are physical factors and biotic relationships necessary for the survival of the species.

**Niche Breadth.** Describes the spectrum of any given dimension of the niche volume (see Pianka 1972),

$$B_i = 1/\text{Sum } p_{ij}^2,$$

where $p_{ij}^2$ is the proportion of individuals of species associated with resource j. Standardized niche breadth values ($B_{st}$) are obtained by dividing the niche breadth value ($B_i$) by the number of resource states.

**Niche Overlap.** This is a measurement of the association of two or more species with respect to some dimension of the niche hypervolume (see Colwell and Futuyma 1971),

$$C_{ih} = 1 \ 1/2 \ S_j \ p_{ij} - p_{hj},$$

where C is the amount of shared resource states between species i and h, $p_{ij}$ is the proportion of individuals of species i associated with resource j, and h is the second species of the matrix. In this measure, C has a value of 0 when species i and h share no resource states, and a maximum value of 1 when the proportional values from two or more independent analyses of different resources provides an overall niche overlap value. The overall values are obtained by multiplying for each pair of species the total of the individual niche overlap values, times 100 (= product alpha of Cody 1975).

**Resource Partitioning.**    The differential utilization of the physical and/or biotic environment by different species.

**Shannon-Wiener Diversity Index (D).**  For the present application, this index describes the average degree of uncertainty of predicting the number of prey categories in a given lizard species.  Two components of diversity are combined in the index:   (1) number of species, and   (2) equitability, or evenness of allotment of individuals among the prey species. A greater number of prey categories increases species diversity, and a more equitable distribution among prey categories will also increase diversity as measured by this function.  The formulas used are,

$$D = - \text{Sum } (p_i \log p_i),$$

where $p_i$ is the decimal fraction of the total individuals belonging to the ith species, $D$ is the information content of sample, i. e. index of diversity, and S is the number of species (prey categories), and,

$$Dmax = - S \ (1/S \log_2 1/S),$$

where Dmax is the species diversity under conditions of maximal equitability and S is the number of species in the community (prey categories in the stomachs), and,

$$E = D/Dmax,$$

where E is equitability (range 0-1), D is the observed species diversity, and Dmax is the maximum species diversity (= $\log_2 S$).

In some instances Simpson's Index (B) is substituted if it is the preferred statistic, where,

$$B = 1/\text{Sum } p_i^2,$$

where B is the diversity index ranging in value from 0 (low diversity) to a maximum of 1-1/S.

Throughout the text, figures and tables, standard symbols are used for the mean ($\overline{X}$), sample size (N), standard error of the mean (SE), standard deviation (SD), correlation coefficient (r) and Spearman rank correlation coefficient ($r_S$).

## RESULTS

### Species Characteristics

Unless otherwise stated, the latest review of the taxonomy and distribution of the skinks examined occurs in Brown and Alcala (1980).

*Emoia atrocostata* (Lesson).    This is a moderate-sized species of the genus, with no Luzon conspecifics.  In the Caramoan area females are larger than males ($p$ = 0.05, $\overline{X}$ SVL females 88.2 ± 2.1 mm, $\overline{X}$ Wt 12.6 = 1.1 g, N=19; males 84.2 ± 3.3 mm, $\overline{X}$ Wt 10.9 g, N=60).    Though widespread in the Philippines, *E. atrocostata* has a completely coastal distribution and is found on rocky beaches, fish pond dikes, and rocky outcrops in mangrove swamps. Alcala and Brown (1967) studied a population of this species on Negros Island, Philippines.

*Dasia grisia* (Gray).   A large member of the genus, with only one species on Luzon.  In the Caramoan area the sexes are not significantly different in either length or weight (adult $\overline{X}$ SVL 105.0 ± 1.5 mm, $\overline{X}$ Wt 24.3 ± 4.1 g, N=23).  It is widespread in the Philippines and previously has been reported from Luzon, though considered uncommon.   Brown and Alcala (1980) reported finding specimens on rotting tree stumps and under loose bark in forests from 100 to 200 m.   Our specimens were collected from widely scattered localities in the study area from as low as sea level to 250 m, but always in relatively undisturbed forest.

*Lamprolepis smaragdina philippinica* (Mertens).  This is a relatively large species of the genus, with no conspecifics on Luzon.  In the Caramoan area the sexes are not significantly different.  Brown and Alcala (1980) stated that it is almost completely arboreal, being found in gardens, coconut and abaca plantations, and dipterocarp and mangrove forests.   Near Caramoan we found it in all generally open situations, particularly in secondary growth and coconut plantations, from sea level to 350 m (higher elsewhere, Brown and Alcala 1980).  It is one of the most common of the Caramoan lizards.  Alcala (1966) and Reyes (1957) studied a population on Negros Island, Philippines.

*Lipinia pulchella pulchella* Gray.   This is a species of intermediate size within the genus.  Though one other species is said to occur on Luzon, we found only this one at the study area.  Here the sexes were not significantly different in either length or weight (adult $\overline{X}$ SVL 38.1 ± 0.8 mm, $\overline{X}$ Wt 0.6 g, N=106).  It has been reported from most northern Philippine Islands south to Leyte, including the Caramoan area.  We found it common near the ground on the exposed trunks of trees and on large boulders--particularly in primary forest.  Brown and Alcala (1980) found it from 300 to 1000 m; we extend this to sea level in the Caramoan area.

*Mabuya multifasciata multifasciata* (Kuhl). This is a large species of the genus, with no significant sexual difference in either length or weight. In the Caramoan area this species is somewhat smaller than reported elsewhere in the Philippine Islands (adult $\overline{X}$ SVL in study area 90.5 ± 2.0 mm, $\overline{X}$ Wt 22.6 ± 2.2 g, N=135; 109 mm $\overline{X}$ SVL on Negros Island, according to Alcala 1966). The species is widespread over much of Southeast Asia and has previously been reported from Luzon. Wherever it occurs, it is usually very common, being found on the ground in open sunny places, especially field and forest borders, and in secondary forests and abaca and coconut plantations. It hides in heaps of vegetation and under logs, but also in tree holes close to the ground and under loose bark. It has been reported from sea level to over 1200 m. Alcala (1966) and Reyes (1960) studied a population on Negros Island, Philippines. Two other species of the genus occur on Luzon.

*Mabuya multicarinata borealis* Brown and Alcala. This is a medium-sized species of the genus, with no significant sexual differences in either length or weight in the Caramoan area (adult $\overline{X}$ SVL 71.0 ± 2.5 mm, $\overline{X}$ Wt 11.5 ± 0.8 g, N=160). It is widely distributed in the central and northern parts of the archipelago from sea level to 1200 m. At Caramoan it is common in primary forest, but mainly in sunlit openings and along trails, occasionally in secondary forest. In both habitats it is found under leaves, rocks, rotting logs, or climbing about on stumps, tree trunks close to the ground, or on large boulders. There are two congenerics on Luzon, but only one other species locally.

*Brachymeles samarensis* Brown. A small species of the genus, with adults in the Caramoan area having a mean SVL of 60.7 ± 2.3 mm, and a $\overline{X}$ Wt of 1.9 ± 0.6 g, N=43. Locally this species is found from sea level to 100 m, under leaves, vegetation mats on logs and rocks, in rotten logs, in both primary and secondary forests. It previously has been reported from southeastern Luzon. Two other species are known from the same island, but only one other congener occurs in the study area.

*Brachymeles boulengeri boulengeri* Taylor. A moderately large species of the genus, with adult females significantly longer than males ($p < 0.05$, female $\overline{X}$ SVL 86.3 ± 3.0 mm, $\overline{X}$ Wt 13.9 ± 0.8 g, N=97; male $\overline{X}$ SVL 77.0 ± 3.0 mm, $\overline{X}$ Wt 11.0 ± 1.0 g, N=90). It previously has been reported from Luzon. Locally it is usually found under rotting logs, piles of vegetation (particularly leaves and humus) in open situations (pastures, overgrown fields, secondary forests and plantations of abaca and coconut). Brown and Alcala (1980) reported it from 300 to 800 m, but we found it to nearly sea level (18 m). Two conspecifics occur on Luzon, but only one other locally.

*Sphenomorphus jagori jagori* (Peters). A large member of the genus, with a significant difference ($p < 0.05$) in length of adult males and females; overall $\overline{X}$ SVL 76.0 ± 6.1 mm, N=62; adult females $\overline{X}$ SVL 75.0 ± 5.1 mm, $\overline{X}$ Wt 13.9 ± 0.9 g, N=41; males $\overline{X}$ SVL 81.1 ± 4.1 mm, $\overline{X}$ Wt 15.8 ± 0.8 g,

N=121). The species is widely distributed in the archipelago and previously has been reported from Luzon. Locally it is found in areas of primary forest with a rocky substrate; rarely in secondary growth. It may be found under leaves or logs, but is also seen actively clambering over boulders. Brown and Alcala (1980) reported it as occurring from sea level to 1000 m.

*Tropidophorus grayi* Guenther. A relatively large member of the genus. Local males and females are not significantly different in either SVL or Wt; adult $\overline{X}$ SVL 94.1 ± 8.1 mm, $\overline{X}$ Wt 18.9 ± 4.8 g, N=121. It is widely distributed in the Philippines and previously has been reported from Luzon. Locally it is mainly found in holes in banks along small streams (from where we "fished" them with baited hooks). Taylor (1922) and Brown and Alcala (1980) reported finding them under logs and rocks, where we also took them, though less frequently. In the Caramoan area they occur from 80 to 350 m. No congeners are found on Luzon.

*Otosaurus cumingii* Gray. This is the largest species of skink in the Philippine Islands. There is no significant difference in length or weight of males and females from the Caramoan study area, in spite of the fact that the mean SVL for females (121.1 ± 15.9 mm) is greater than that for males (113.9 ± 8.9 mm). Average Wt of adults is 41.1 g (N=63). Widely distributed in the Philippines, this species previously has been reported from Luzon. Locally it is found in rocks at the base of large boulders and cliffs, sometimes along the steep banks of larger streams. Altitudinally it occurs from near sea level to 100 m locally, but probably extends higher into the hills in appropriate habitats. No other species of the genus is known from Luzon.

Besides those species listed above, only one other scincid occurs in the Caramoan District--*Sphenomorphus steerei*. It was captured too infrequently during our study to include in the analysis. *S. steerei* is a very small species ($\overline{X}$ SVL 27 mm, N=4), seen from sea level to 150 m in secondary forest, usually in leaf litter, but once high in the petiole axil of a coconut tree. Table 1 summarizes the meristic data for the Caramoan scincid species studied (see p. 198).

## Body Size Gradation Ratios

Schoener (1968, 1970a, 1970b) showed that the head and jaw sizes of *Anolis* species are positively correlated with body size; Caldwell (1973) reported similar results in hylid frogs and concluded that body size ratios between different species can be used to determine if a regular size progression exists within the reptiles and amphibians of a single community. Both authors ascribed these patterns to prey size and availability. Using SVL ratios of differences between species (mean SVL of each species of

community/mean SVL of smallest species in community), Duellman (1978) found no size groupings, either taxonomic or ecologic in frog and lizard communities of his Ecuadorian study site. Rather, there was a steady increase in SVL from the smallest to the largest *Anolis* species in the environment studied.

Table 2 shows that among the skinks of the Caramoan area, the ratios of differences in SVL's of skinks arranged in a size series is also an even progression, with the ratios ranging from 1.41 to 4.33. This is a significantly greater order of magnitude than demonstrated in Duellman's analysis of *Anolis* body size in South American forests (1.01-1.46). Thus on the basis of range in body size of the constituent species, the Caramoan skink community is presumably predating a significantly greater range in prey size.
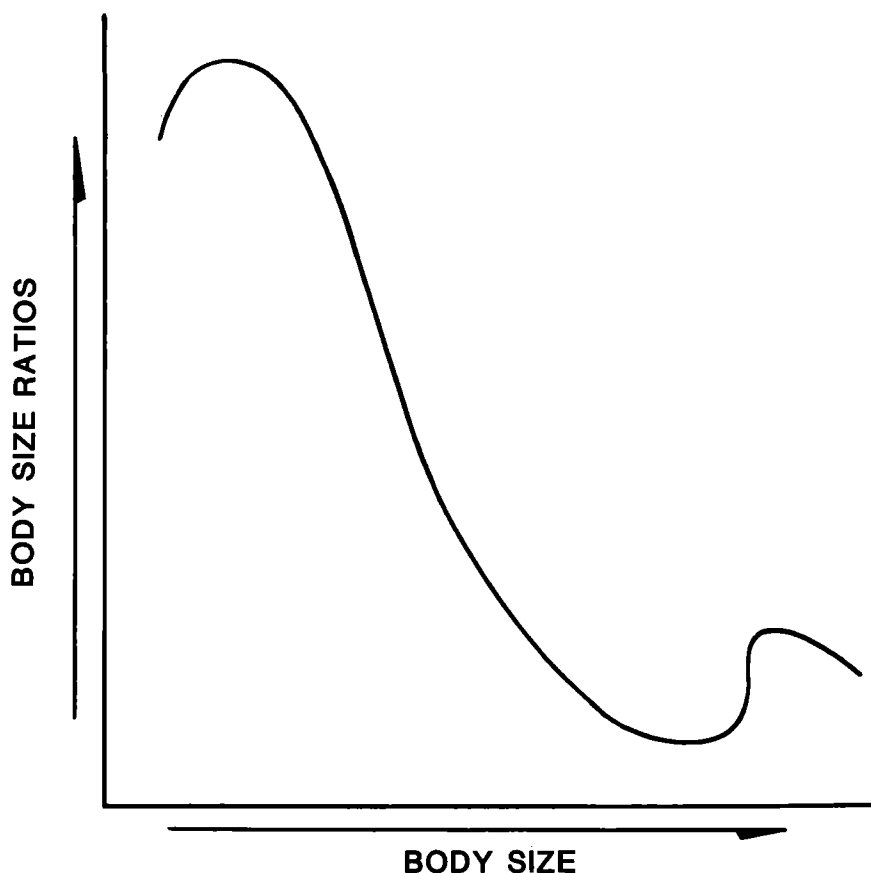


**Figure 1.** General relationship of scincid body size to body size ratio (Otosaurus cumingii used as standard against which all others compared) in Caramoan skink species.

The incremental increase in body size from smaller to larger in any pair of species in Table 2 varies from 1 to 36 percent. The greatest size differences occur among the smallest local species. Interestingly, there are no local agamids that are size equivalents of the smallest local skinks (Fig. 1). However, several local agamids and both varanids are significantly larger than the largest skinks. Half of the local skinks are only from 1 to 5 percent larger than the closest-sized skink species (71 to 94 mm SVL; *S. jagori, B. boulengeri, E. atrocostata, M. multifasciata. L. smaragdina and T. grayi*). The species pair closest to sharing the same microhabitat (*M. multicarinata* and *S. jagori*) are however rather close in mean SVL (ca 4% difference). While the overall pattern is not that predicted by the work of either Schoener or Caldwell, the pattern is clearly not fortuitous.

When the data on Caramoan skink sizes are compared as ratios of SVL's between adjacent species, these ratios vary from 1.0 to 1.6, with a mean of 1.2, SD 0.2. The low value for the latter suggests the presence of a regular, incremental increase within the entire size series from each smaller species to each larger one. Such sequential ratios within closely related organisms in local communities have been described previously. Hutchinson (1959) showed that in sequences of presumably competing organisms, average individuals in successive species have weight ratios about 2, or ratios of 1.3 between typical linear dimensions of successive species. This is nearly identical to the mean value obtained for the Caramoan series. Later studies on different vertebrate and invertebrate organisms have shown that differences of 1.3 in a sequential series is a common ratio among similar animals living in the same habitat (Uetz 1977, and others). Food sizes of such organims also have been shown to differ by the same sequential factor (Horn and May 1977). All these data suggest that this empirical relationship is of some fundamental biological importance, though admitted to be poorly understood.

However, that this ratio may have little or no biological importance in regard to possible competition between community members is suggested by the observations of Horn and May (1977). They show that the same ratio occurs in ensembles of musical instruments that are often played together, whereas instruments traditionally used in solos lack this incremental progression. They also demonstrate that the same ratio applies to the sizes of iron skillets and tricycle wheels. They conclude that the 1.3 rule may derive from generalities about assembling sets of things rather than from any biological peculiarity. We agree and believe that size distributions in Caramoan skinks is more related to local community structure (including the size and density of available prey, species packing, and the complexity of the local biotic environment) than it is to any presumed competition between them.

## Species Diversity

Within the 11-species scincid lizard biocenose studied, several different levels of species combinations are found. The only single-species skink community is on the marine littoral, especially on beaches. Here only *Emoia atrocostata* occurs. Where the littoral is a mangrove association, especially if rocky, the skink community may be a two-species one, with *A. atrocostata* and *Dasia grisia* occurring together. Two-species skink communities are represented by still other combinations. Thus *Otosaurus cumingii* occurs in ecotonal and open forests with *Mabuya multifasciata* or with (separately) *Mabuya multicarinata*. *Tropidophorus grayi* is rather restricted ecologically when compared to many other local species, but in rocky stream side situations it is sometimes found with *M. multicarinata* and/or *Sphenomorphus jagori*. A three-species scincid community occurs only in secondary forests and plantation-type vegetation (most often coconut). This assemblage is comprised of *M. multifasciata, Lamprolepis smaragdina,* and *Brachymeles boulengeri*. The greatest diversity in skink communities is found in primary forest (locally of mixed lowland dipterocarp type), where the following six-species community occurs: *Brachymeles samarensis, M. multicarinata, S. jagori, S. steerei* (rare), *Dasia grisia,* and *Lipinia pulchella*.

Skink species diversity was computed by means of Shannon's Diversity Index and these results were then plotted against density of trees greater than 10 cm DBH. Skink diversity is positively correlated ($r = 0.81, p < 0.01$) with tree density (= vegetation complexity) in the local forests.

## Pattern of Habitat Differences

To interpret adequately the scincid fauna of our study area it was necessary to examine the ecological distribution of the species within the area. Figure 2 shows that almost all the species studied are restricted to rather distinct microhabitats, with little overlap between them. *Lamprolepis smaragdina* is characteristically found in open habitats with scattered trees, and within this habitat it is found on tree trunks and shrubs from near the ground surface to 25 m high ($\overline{X}$ 2.7 m). *Dasia grisia* occurs only in densely forested situations, on tree trunks and larger limbs (including mangroves) from 3 to 25 m high ($\overline{X}$ 5.3 m, sample probably biased towards the lower parts of the tree due to collecting methods). *Lipinia pulchella* is found in the same habitat, but is restricted to a lower stratum within the environment, being found on rocky outcrops and tree trunks from near the surface to about 3 m
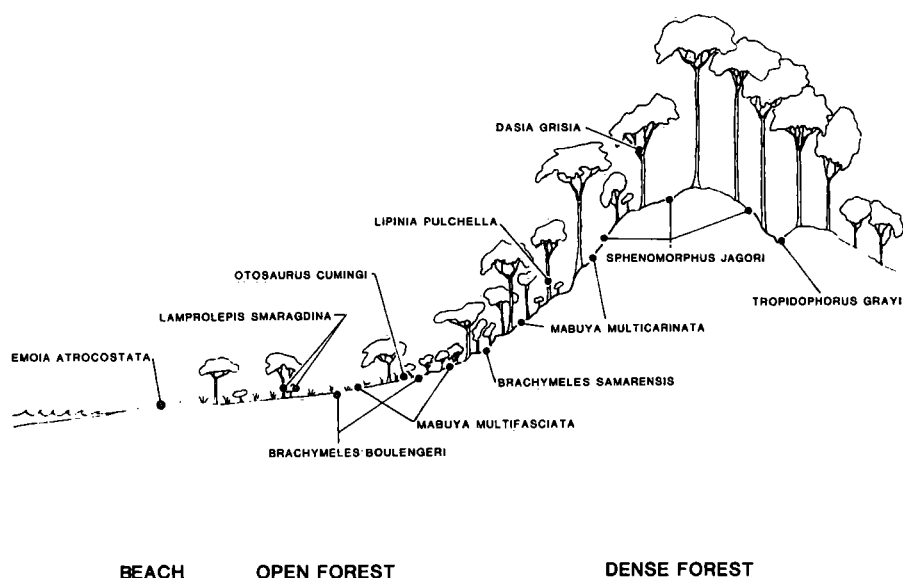
**Figure 2.** General habitats of common skink species in the Caramoan area.

above it ($\overline{X}$ 1.5 m). Thus there are three arboreal skinks in the Caramoan area, and none is ecologically overlapping from the standpoint of microhabitats. Within the same general size class there are three other local arboreal lizards--all agamids. These are *Calotes marmoratus* (shrub species), *Draco volans* (trunk species of more open situations), and *Goniocephalus sophiae* (a tree canopy species of dense forests).

Two local scincids are fossorial, though each is found in slightly different situations. *Brachymeles boulengeri* is most common in open areas, where it burrows under grass tussocks and surface debris (piles of dead vegetation, household trash, and logs). *B. samarensis* is more common in forests and along their edges. Here it burrows under leaf litter and root mats covering logs and rocks. There are no other fossorial lizards in the immediate area, though three different-sized species of typhlopid snakes are locally common.

The most diverse scincid group is that composed of the surface forms. Some of these occur in restricted and special habitats, while others are found throughout a rather broad ecological spectrum. In the Caramoan area, *Emoia atrocostata* is an almost exclusive inhabitant of sandy beaches with rocky outcrops; occasionally it is found on dikes and rocky outcrops in mangrove and nipa swamps. *Tropidophorus grayi* is primarily found in crevices and burrows in clayey or rocky banks and flood plains of small mountain

streams in dipterocarp forests. No other local lizard utilizes this microhabitat as regularly. *Otosaurus cumingii* is found in forest ecotones, on the flood plain of larger streams, and in secondary forests. It is not found in primary forest. In all these situations it is most common in sites with abrupt changes in surface topography, such as near banks and cliffs. Here it spends considerable time in crevices and holes.

Because the remaining three scincid species studied (*Sphenomorphus jagori, Mabuya multifasciata* and *M. multicarinata*) are often found in the same general area and under similar conditions, more detailed study of these species was conducted. This included gathering data on their density, diel activity patterns, and microecological distributions along a 346 m transect established near the base camp (see Methods and Fig. 3).

Table 3 shows the use of different environments by these three similar species. While *M. multifasciata* is the only terrestrial species in open local habitats, it is most common in ecotonal situations. The two remaining species are significantly more abundant in densely forested situations. However, within these lower illumination habitats, *M. multicarinata* occurs in forested situations in which the lowest vegetation stratum is more dense, often with scattered boulders in the Caramoan area. While found in this microhabitat, *S. jagori* is more common in open, rocky situations, including sloping (but usually not vertical) rock faces. *M. multicarinata* and *S. jagori* are separated further by their vertical distribution within the lowest forest stratum. Thus only one of the 34 *S. jagori* found along the transect was above the forest ground surface (at a height of 1 m, on a fallen log resting against a rock face). Though *M. multicarinata* usually forages on the ground, it regularly climbs to at least 4 m above it (surface 58%, to 1 m 21%, 1-2 m 18.4%, and 2-4 m 2.6%).

Table 4 shows the relationship between mature size (SVL) and habitat preference. From it (when *S. steerei* is additionally considered) one concludes that on Luzon tropical forests have the same number of skink species than more open forests. However, the forest species are significantly smaller ($\overline{X}$ 63.2, SD 21.7) than those in more open situations ($\overline{X}$ 93.4, SD 13.8; means significantly different when *S. steerei* included; $p < 0.02$, t = 3.37, df = 9). There is also less size variation among forest skinks than among those living in more open environments.


### Temporal Patterns


All the terrestrial and arboreal skinks of the Caramoan area forage only during daylight hours. There is, however, evidence that, at least in captivity, *Tropidophorus grayi* sometimes feeds during the night. Data on diel activity
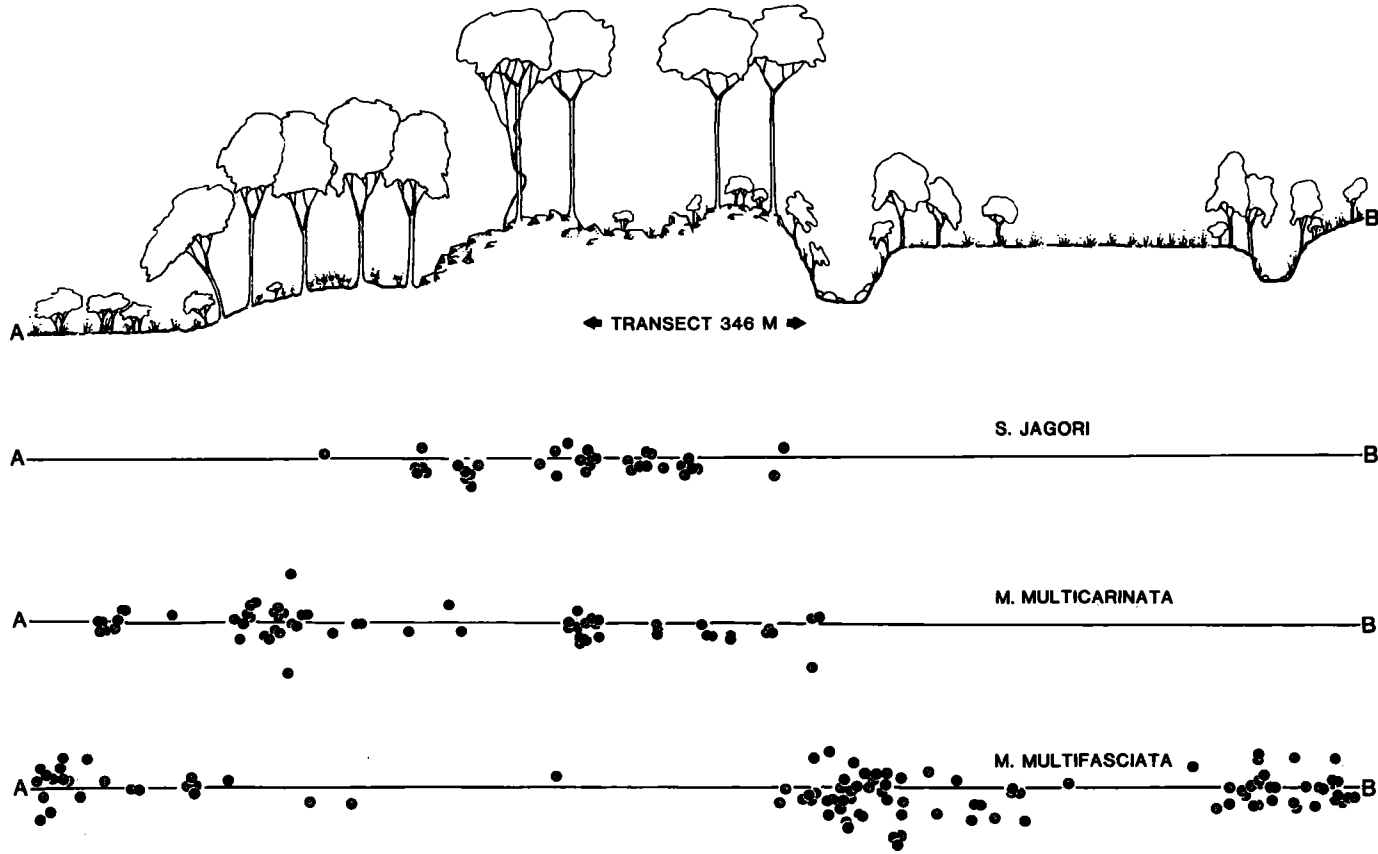
**Figure 3**. Spatial distribution of three ecologically similar skink species along a forest transect (see text).

periods were obtained only for the three terrestrial species inhabiting generally similar microhabitat (i.e. *M. multifasciata, M. multicarinata,* and *S. jagori*). All three are active about 25 percent of the total daylight hours available to them at this latitude (*M. multifasciata* 22%, *M. multicarinata* 21%, and *S. jagori* 27%; values not significantly different than expected). However, the way in which they allocate their time during the day is different. In general, the daily pattern of *S. jagori* is more distinctly bimodal than the other two (Fig. 4), which tend to be active throughout the day. In all three species, basking is the most common behavior early in the day and occurs most between 0800 and 0900 hr. During the following hour there is a peak in social activity. *M. multifasciata* and *S. jagori* intersperse this morning socializing with foraging, while *M. multicarinata* feeds rather regularly throughout the middle of the day; basking is also a common behavior at the same time, but with most of it shifted later in the day. *M. multifasciata* feed primarily in the heat of the day (Fig. 4) from 1300 to 1400 hr. All three species show a decided late afternoon peak in social activity, and this tends to be the last behavior of the day for all three species. It is particularly significant that the behavior of *M. multicarinata* and *S. jagori* are so very different in both basking and foraging, in spite of the fact that they both occur in the same forest type, with similar surface temperatures and humidities (Figs. 5, 6), albeit slightly different surface textures. Whitford (1978) has demonstrated that temporal partitioning in narrowly sympatric species is an important factor in species packing in ant communities. It may also be important among the more narrowly sympatric terrestrial species of the local evergreen tropical forest. However, the degree of asynchrony in temporal partitioning may not be a reliable index of competition via dietary overlap

Though asynchrony in time of activity is often used as an indication of dietary or spatial competition, there is little verified justification for doing so on the basis of studies of lizards in the field. Pianka et al. (1979) suggest that rapidly renewed prey (as apparently occurs in tropical forest termite communities of the leaf litter) could suffice as an alternative explanation for reduced exploitative competition. In spite of the appeal of food competition as a major driving factor in bringing about temporal separation of activity patterns, many data suggest that this is not an important factor. Thus, the diets of closely related nocturnal and diurnal organisms are often surprisingly similar. One of the clearest cases of this is the work of Jasic' et al. (1981), comparing the diets of diurnal and nocturnal vertebrates in Chile. They concluded that temporal asynchrony in hunting does not always result in lowered dietary overlap. Thus the different temporal activity patterns of *Mabuya multicarinata* and *Sphenomorphus jagori* does not necessarily suggest that they are competing for prey.
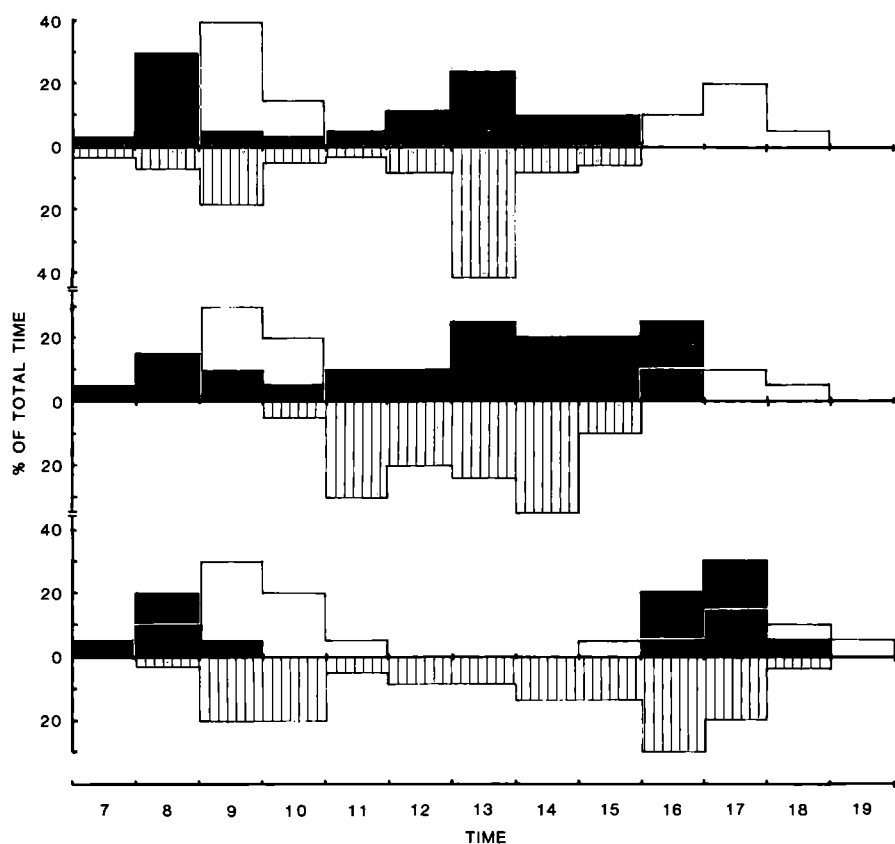
**Figure 4**. Daily allocation of basking (solid), foraging (lined), and social (open) behaviors in three ecologically similar skink species.

## Food

One of the goals of this study is to determine the patterns of food niche partitioning among skinks in a tropical evergreen forest.  To do so we examine each measured variable for possible limitations, and finally ask the question, "What are the effects of seasonality upon the diets of these different scincids?".

Food Type.-- Of the Caramoan skinks examined, 58-81% contained food remains (Table 5).  A total of 10,739 food items was taken from the 2,093
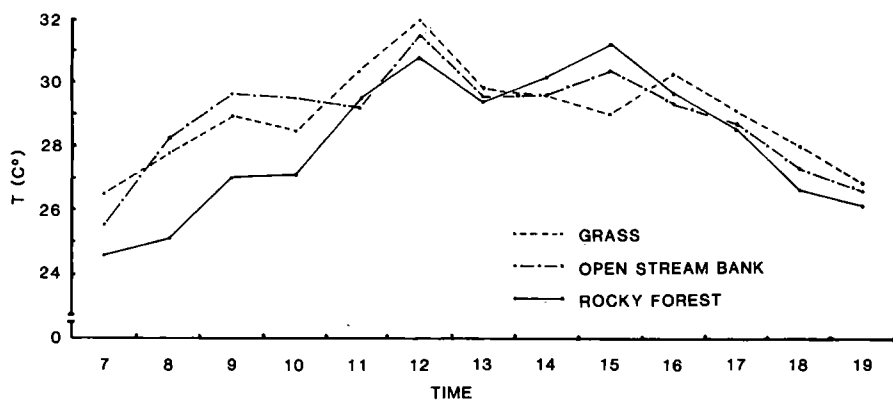
**Figure 5.** Annual mean daily shade temperatures (10 cm above surface) in the major microhabitats of three ecologically similar skink species.
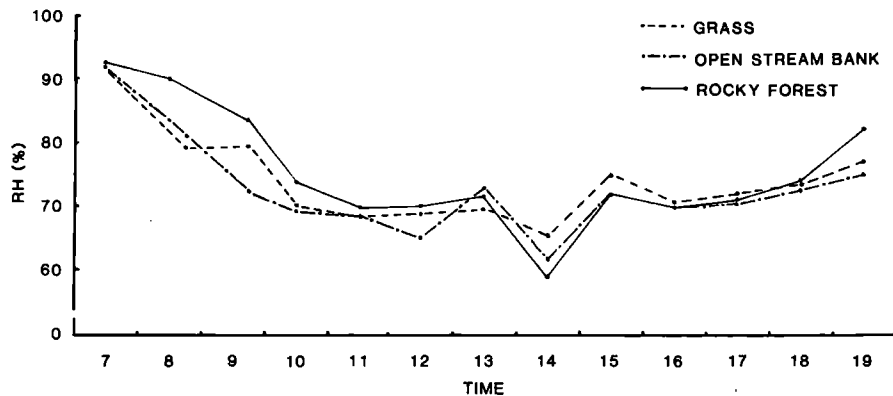


**Figure 6.** Annual mean daily relative humidity in the major microhabitats of three ecologically similar skink species.

specimens with food in their stomachs. The distribution of food categories is shown in Table 6. Ninety percent of all food items found are arthropods. Of the 17 arthropod orders represented, 7 constitute the vast bulk of the prey (Isoptera, Coleoptera, Orthoptera, Lepidoptera, Hymenoptera, Araneida, and Diptera, Table 6). Molluscs (including their eggs) are the next common item (0.7%), followed by fruits (0.4%). Chordates are among the prey types eaten rarely. They are represented primarily by lizards and snakes (0.3 and 0.1% respectively, including the eggs of both). Fishes comprise 0.1 %; frogs and birds occur only once and twice respectively in the entire sample. Annelids are also rare items.

Table 7 shows that termites are the primary to tertiary food category of almost all species of scincids in the Caramoan area. There is no rank order correlation between termite feeding and habitat or lizard body size. The only exceptions are *Otosaurus cumingii* (the largest skink in the area) and *Lamprolepis smaragdina*, which lives in rather open situations on exposed tree trunks, where termites are less common. However, even in the marine littoral zone, *Emoia atrocostata* feeds on many termites. Pianka (1969) found that termites are also the primary food of lizards in desert communities in Australia.

Crustacea are eaten by most of the skinks studied, though almost all are members of the Isopoda, commonly found in leaf litter. In most species, crustacean-feeding is not common. The outstanding exception is the marine littoral *Emoia atrocostata*, which feeds extensively on both isopods and decapods (Alcala and Brown 1967 and this paper). Many of the latter are larval forms and are apparently exhumed from the beach sand. Other skink species living on tropical beaches in other parts of the world are also known to feed extensively on littoral amphipods and decapods (Australia, Cogger et al. 1983; Indonesia, Auffenberg 1980; East Africa, Canaris and Murphy 1965; United States, Mount 1963).

Ants (Formicidae) are frequently the major food of arboreal lizards in the New World tropics (Schoener 1969, Duellman 1978) and constitute the only food of the arboreal agamid *Draco volans* in the Caramoan area (and in study by Alcala 1966 on Negros Island, Philippines). Among the local skinks only the two arboreal species of dense forests, *Lipinia pulchella* and *Dasia grisia*, regularly eat ants. The arboreal species of more open situations, *Lamprolepis smaragdina*, eats relatively few ants. None of the local terrestrial species eat many ants--nor do the fossorial species. There are only a few species of terrestrial frogs locally and no terrestrial agamids in the Caramoan area, and one wonders who then feeds on ants in the Philippine primary forests.

Fishes (unidentified) were found only once in *Emoia atrocostata*, but more commonly in *Tropidophorus grayi*. A terrestrial frog (*Platymantis* sp,

found in the same microhabitat) occurred in the stomach of one *Sphenomorphus jagori*.

Lizard remains were found in the stomachs of 8 of the 11 skink species examined, proving that they are eaten by most of the local scincids. Most lizard prey consisted of entire individuals of several of the local gecko species. Reyes (1957, 1960) has reported that two species of skinks on Negros Island, Philippines also occasionally eat geckos. In the Caramoan area, *Hemidactylus* sp. and *Cyrtodactylus monarchus* were occasionally eaten by *Mabuya multifasciata, Emoia atrocostata, Sphenomorphus jagori*, and *Tropidophorus grayi*. *Hemidactylus* sp. and *Mabuya* sp. were found in a few *Lamprolepis smaragdina*. In this same predator species some tails (only) were found with scalation matching that of *L. smaragdina*, but in every case the tail was too digested to be absolutely certain of the identification. Almost all of the *Brachymeles boulengeri* collected at Caramoan had regenerated tails. Though such loss is often explained as resulting from predation, very little data exists that supports this contention. Some tail loss in lizards may, of course, be due to intraspecific agonistic encounters. Carr (1940) reported that tails of *Leilopisma laterale* found in the stomachs of Florida skinks sometimes match the part missing from the tail of the same individual, suggesting that autophagy is possible. In the Caramoan study, all lizard remains found in the stomachs of *Brachymeles boulengeri* are tails (only) of conspecifics, but clearly not of the same individual, for they all possessed tails. Thus individuals of this species are eating one another's tails. We assume that they snap these off conspecifics as they make contact during movements just below the soil surface and in leaf litter. *B. boulengeri* also eats snakes, but these are also fossorial types (*Ramphorhynchus braminus* and *Typhlops manilae*). Reyes (1960) is of the opinion that *Mabuya multifasciata* may eat conspecific young on Negros Island.

Leaves and other plant debris were sometimes found in the gut, but in all cases these seem accidentally ingested. However, fruits, often complete, were found in 7 of the 11 skink species examined, showing that they represent part of the food spectrum of most local scincids. This proportion is high when compared with the food of skinks in other parts of the world, suggesting that frugivory is probably more common among Asian forest-dwelling skinks than in skinks from other areas (Greene 1982 has already suggested that herbivory is probably more common among small lizards than presently assumed). Fruits are most commonly found in the larger arboreal species *Dasia grisia* and *Lamprolepis smaragdina*, where they represent 6.5 and 11.6% of the total diet respectively. That diets may be remarkably different for some species in different habitats is suggested by the food data of *L. smaragdina* on Negros, where no fruits are taken (Reyes 1957). In the Caramoan area, *Sphenomorphus jagori* also regularly eat fruits (1%), which are apparently found on the ground. The only local skink species in which fruits are never
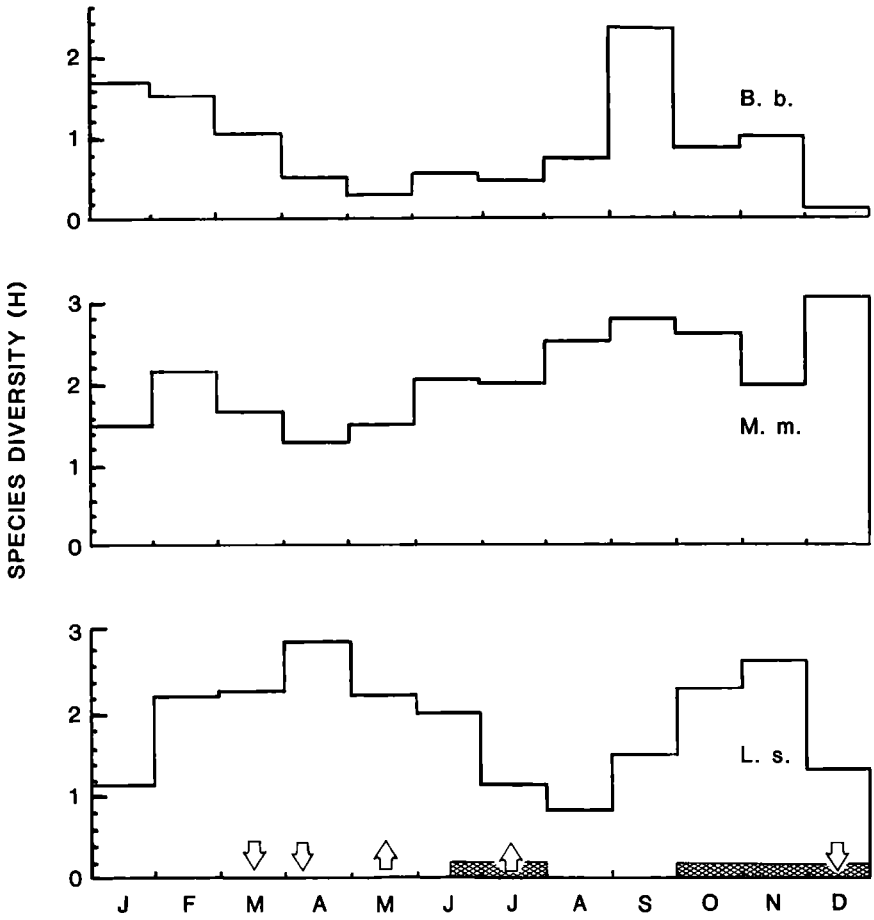
**Figure 7.** Distribution of monthly Shannon-Wiener Diversity Indices for prey categories taken by three skinks of open forest and inhabiting different microhabitats.    B. b., Brachymeles boulengeri; M. m., Mabuya multifasciata; L. s., Lamprolepis smaragdina. Arrows show months of high (arrow up) and low (arrow down) insect abundance in same area. Cross-hatched sections represent periods of high rainfall.
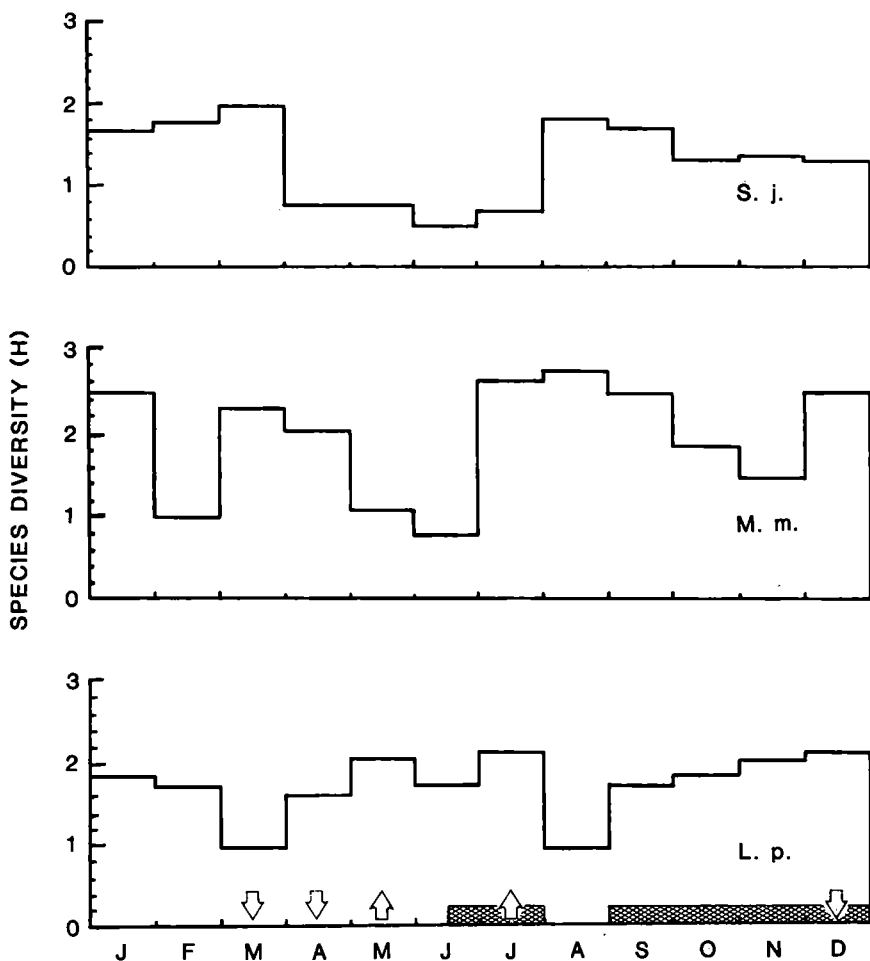
**Figure 8**. Distribution of monthly Shannon-Wiener Diversity Indices for prey categories taken by three skinks of dense forest and inhabiting different microhabitats. S. j., Sphenomorphus jagori; M. m., Mabuya multicarinata; and L. p., Lipinia pulchella. Arrows and cross hatching as in Figure 7.

found are *Emoia atrocostata* (marine littoral), *Brachymeles boulengeri* and *B. samarensis* (both fossorial), and *Mabuya multicarinata* (terrestrial forest species).  The absence of fruits in the latter is surprising, because all other local terrestrial skinks eat them and because this species often climbs in low shrubs.

At least six different fruit species are eaten by the Caramoan skink community.  However, because of the difficulty of identifying poorly known small tropical forest fruits, none can be precisely determined.

**Food Diversity Indices.**-- The prey category diversity indices for the local skinks represent two basic patterns.  The more common one is seasonally variable, with distinct high and low peaks (Figs. 7, 8).  The second pattern, found in only *Emoia atrocostata* and *Lipinia pulchella*, shows little seasonal variation in prey diversity.  The pattern of the former is, however, different from that of the latter in representing a consistently lower prey diversity throughout the year.  Both habitats (terrestrial marine littoral and arboreal dense forests) are probably relatively stable when compared to the ones used by the other skink species in the area.  The differences in the two species patterns are illustrated by the differences in the mean monthly prey diversity values (mean monthly diversity indices for *E. atrocostata* 1.03 and for *L. pulchella* 1.76).

Shannon-Wiener Diversity Indices for species representing the more common annual pattern with notable high and low peaks show different patterns among syntopic skink species.  Figure 7 shows that within the local open forests *Brachymeles boulengeri* not only has a generally low prey diversity index through the year, but that the monthly diversity index for prey categories presents a very different pattern from particularly the arboreal *Lamprolepis smaragdina*.  Figure 8 shows the prey diversities of skinks living in densely forested areas. *Sphenomorphus jagori* and *Mabuya multifasciata* (both terrestrial) have very similar patterns, whereas the arboreal *Lipinia pulchella* is different in respect to the monthly distribution of high and low peaks.

In general, many of these patterns show a depression in diversity values during the dry season and through part or all of the first monsoon.  This is not correlated with monthly overall insect abundances, for the premonsoon period is characterized by having high insect numbers (see Figs. 7, 8, and 10).  Thus in general, the diets of these skinks are narrower when food supplies are abundant, and broaden when food supplies are more limited.  This is also indicated by the data in Table 8.  However, the diversity of insects available is not always related to total overall insect abundance.  In fact, though insects are locally abundant preceding the first monsoon, they are not represented by many orders--only a few making up the bulk of the masses of insects moving at this time of year.  Thus the low diversity of insects in nature during the premonsoon season is reflected in the low diversity of prey in the stomachs.
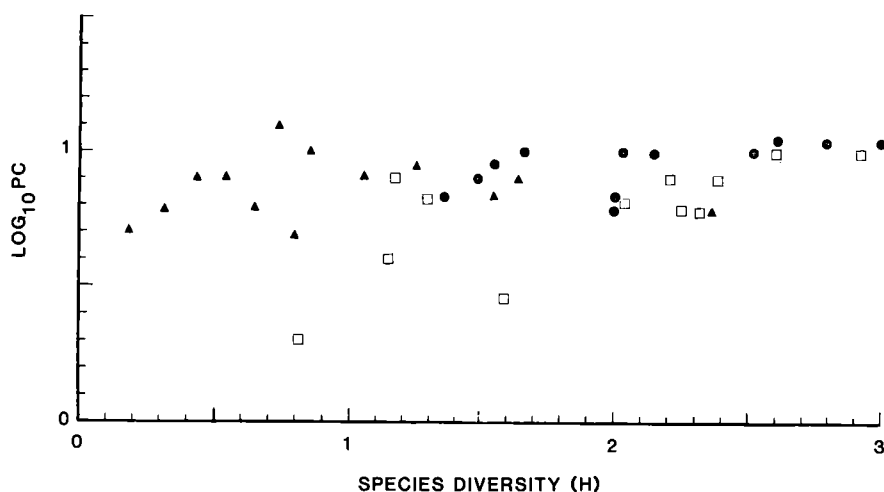
**Figure 9.** Shannon-Wiener Diversity Indices for prey categories (H) plotted against the log of prey categories in skink stomachs per monthly samples. Triangles, <u>Brachymeles boulengeri</u>; solid dots, <u>Mabuya multifasciata</u>; and hollow squares <u>Lamprolepis smaragdina</u>.

We must therefore conclude that prey diversity in nature determines the level of prey diversity in the stomachs. There is no strong evidence for selection of prey types other than in the proportion which these types occur in nature at the same time of year.

Our analyses show that the total number of prey categories per predator species per month varies from 1 to 13; Shannon-Wiener functions (H) ranged from 0.16 to 3.00, and equitability ratios from 0.12 to 1.00 (Table 8). A plot of the Shannon-Wiener values against the logarithm of the number of prey categories in each month per species (Fig. 9) shows that when the skinks of the open forested situations are considered, the prey categories fall on a logarithmic curve that is shifted to the Y axis in the fossorial *Brachymeles boulengeri* when compared to curves for the terrestrial *Mabuya multifasciata* and *Lamprolepis smaragdina*. In more dense forest habitats, the arboreal *Lipinia pulchella* exhibits a seasonal prey category diversity pattern that is more uniform throughout the year than the patterns of other local species.

**Food Location.--** The food eaten by the 11 scincid species studied suggests that much of the prey of most local lizards are foraged from leaf litter and similar small particle-sized surface debris. This is particularly true of the terrestrial skink species studied. Thus, the foraging tactics of these terrestrial Philippine forest species seem very similar to that of *Eumeces*

*laticeps* when searching for hidden prey, as studied by Vitt and Cooper (l986) in forests of southeastern United States. Most species of scincids outside the tropical forests probably fall into this category. However, even among the Caramoan leaf litter foragers there is much searching for prey on herbs and rocks. This is particularly true for lepidopteran prey (both larvae and adults), odonates, dipterans, jumping spiders, winged termites during swarming periods, and ants during mass movements on the forest floor. Prey found commonly in the leaf litter, or at the interface of the soil and litter, are isopods, termites, ants, some spiders, earthworms, blind snakes, centipedes, and scorpions. On Negros Island, Reyes (1960) presented evidence for occasional carrion feeding in *M. multifasciata*.

On the other hand, other local skinks find much of their food under the surface of the soil. *Emoia atrocostata* feeds extensively on marine crustaceans, most of which it finds by digging small holes in the sand; others are found running across the surface. Both local species of the fossorial *Brachymeles* are probably highly opportunistic and apparently find most of their food just under or at the interface of the soil and the surface. Such prey include termites, blind snakes, earthworms, centipedes, scorpions, and beetles.

The local arboreal species (*Lipinia pulchella, Dasia grisia*, and *Lamprolepis smaragdina*) find much of their prey by digging in pockets of leaf debris collected in crevices and hollows on the trunks and branches. However, all three predators also catch much prey on the bark or twigs. In fact, *L. smaragdina* is one of the most active foragers of the local skinks. All the arboreal species occasionally descend to the ground to forage; least of all *Dasia grisia*, which tends to live at the highest levels within the canopy of any of the local skinks.

The semiaquatic *Tropidophorus grayi* forages in leaf litter on the edges of small streams, as well as in the same substrate under a film of water. Depending on moisture, prey obtained in plant litter are mainly termites, ants, isopods, and some semiaquatic to aquatic crustaceans. Additionally, it will sometimes forage for free-moving prey in shallow water, such as freshwater shrimp and particularly small fishes. That they also will snap up small invertebrates that enter the short burrows and the crevices in which they are regularly found near the water-air interface is demonstrated by the fact that we regularly caught them with small baited hooks lowered into their hiding places.

All the skinks studied forage almost exclusively during daylight hours (but see below). However, there is good evidence from among the forest transect data that most individuals forage on the surface about 40 percent of the days in a week.

**Food Niche Breadth.--** On the basis that if over 40% of the food taken represents a single category, the species is to be considered a food specialist

on that food type, seven scincid species can be so designated in the Caramoan forests. *Emoia atrocostata* is the only one specializing on crustaceans (61.7%). It is also the only species found in the marine littoral zone of this area. The only scincid species specializing on beetles are both arboreal forms- -*Dasia grisia* (48.6%) and *Lamprolepis smaragdina* (47.2%).

Most food specialization in Caramoan scincids involves termites. The local termite specialists represent both terrestrial (*M. multifasciata* 45.5%, *M. multicarinata* 61.4%, and *S. jagori* 80.7%) and fossorial species (*B. boulengeri* 70.8% and *B. samarensis* 80.7%), but almost all local skinks feed on them from time to time. Standardized niche breadth for the Caramoan scincids is shown in Table 9.

**Food Niche Overlap.--** Of all the food categories taken by Caramoan skinks, Isoptera, Crustacea, Coleoptera, Lepidoptera, and Orthoptera are the most consistently common among the different species. Niche overlap values between pairs of skink species and for each of these major food categories are shown in Tables 10 to 15.

For Isoptera prey, food niche overlap is relatively minor among all species pairs (Table 10), varying from 0.0024 to 0.45. Species pairs showing the least overlap are *Sphenomorphus jagori-Lamprolepis smaragdina* and *Brachymeles boulengeri-L. smaragdina*. All these species live in very different microhabitats. Species pairs with the greatest overlap are *Mabuya multifasciata-L. smaragdina* and *M. multifasciata-Emoia atrocostata*. None of these species shares the same microhabitat, though both *M. multifasciata* and *L. smaragdina* live in rather open situations.

The data show that while many termites are eaten by local skinks, there is relatively little overlap between skink species when termites are used as the basis of the dietary comparison. In some cases where sympatric species do eat large numbers of termites (i.e. *M. multicarinata* and *S. jagori*), foraging for them occurs during different parts of the day. In both these species termites are found by rooting through leaf litter. Although *S. jagori*, as a morning feeder, would tend to disturb the termites and remove a small number, the subterranean galleries are left undisturbed. Since the litter is in a shaded, temperature-moderated environment, the termites probably reenter the litter in a few hours (see Johnson and Whitford 1975). Thus, even if individual home ranges of these two species do overlap in some areas and even if both lizard species search for the same food, their foraging at different times of the day, even in the same location, offers a tactic to harvest the obviously huge numbers of termites found in these forests

Both these skinks occur in fairly high densities in the local forests. Since their primary food is termites, one might expect considerable interspecific competition between them for this resource. Such interactions are deemed energetically expensive. We found very little evidence of agonistic behavior among these skink species, due perhaps mainly to the fact that their daily

foraging patterns differed significantly. Furthermore, our transect studies show that not every individual in the area was active every day (probably less than half the days of each week, see above). These results are similar to those of Creusere and Whitford (1982) for teiids, and to those of Simon and Middendorf (1976) for iguanids. Considering a pattern of surface activity less frequent than daily and the reduced and segregated diel activity patterns of the two species, temporal partitioning is probably very important in these two species

Niche overlap for coleopteran prey (Table 12) shows a different pattern. When compared to the patterns discussed above, niche overlap for coleopteran prey is, in general, greater among various species pairs; none of the values is as low as those above. This shows that beetle prey are regularly shared among these species. The lowest overlap value is found in the pair *D. grisia-M. multicarinata*. Both are found in forests, but one on the ground and the other in the trees. In general, *M. multicarinata* tends to have low overlap values with many other Caramoan skinks, and particularly with *L. smaragdina* (arboreal) and *S. jagori*. The latter is particularly interesting, for it is one of the few cases in which food niche overlap can be considered as related to possible food competition. The highest levels of overlap for coleopteran foods are in the species pairs *M. multicarinata-O. cumingii*, *T. grayi-O. cumingii*, and *T. grayi-B. boulengeri*. All live in different microhabitats.

For lepidopteran prey the overlap is generally low (Table 13). The least overlap is found in the pairs *L. smaragdina-L. pulchella*. Though both species are arboreal (in different microhabitats), the former feeds on many lepidopterans, and the latter on relatively few. Another low overlap pair is *O. cumingii-E. atrocostata*, where the latter feeds on very few lepidopterans in its beach habitat, while the former feeds on a fair number in the forest in which it lives. The greatest overlap is in the species pair *E. atrocostata-M. multicarinata*. Both feed on few lepidopterans.

The pattern of orthopteran feeding among the caramoan skinks is rather similar between species pairs, accounting for generally high overall values (Table 14). The lowest overlap is found in the pair *O. cumingii-E atrocostata*. The high values encountered in pair comparisons for orthopteran food are among the highest recorded in the entire series of analyses. The arboreal *L. pulchella* has remarkably high overlap with all skink species in the area, regardless of skink SVL or habitat. The pair *M. multifasciata-M. multicarinata*, and the former with *L. smaragdina* show high overlap values as well. Although inhabiting different microhabitats, they are often found close to one another spatially.

Table 15 shows the result of recalculating the same data, but combining all these major food categories to illustrate overall food niche overlap. This shows that of all the local skinks, *S. jagori* has the least overlap with other pair members, and this overlap is least with *M. multicarinata*, and *L. pulchella--*

species found in the same general habitat (but also with *L. smaragdina* found in more open situations). This suggests that food selection may play a role in the distribution of these species in dense forest habitats. The greatest overlap is seen between the pairs *E. atrocostata-L. pulchella, M. multifasciata-L. smaragdina, E. atrocostata-M. multicarinata,* and *M. multifasciata-O. cumingii.* All these pairs are composed of species that live in totally different environments, except the two species of *Mabuya,* which show some intermixture along the forest edge.

**Food Nutritional Value.--** None of the local invertebrates eaten by skinks was analyzed for nutritional content. However, adequate data are available in the literature for related prey types so that comparison and discussion is possible. These data are provided in Table 16.

With the exception of the earthworms, the difference between the mean water content of the various prey categories listed are not significantly different. Ash is significantly higher in both earthworms and termites, due to the fact that both these categories ingest much soil (Redford and Dorea 1984). In spite of the suggested differences in the means of percent nitrogen and fat in some taxa, none of those important as skink prey is significantly different at less than the 0.05 percent level; perhaps only because of small sample size in some cases. The only important exception is that the mean percentage fat of earthworms is significantly different than the means of all other taxa ($p$ varies from $< 0.01$ to $< 0.001$). Thus there seems little reason for believing that these food categories represent significantly different nutritional sources. There is thus no clear basis for suggesting that any of these foods are qualitatively more nutritious than others.

**Number of Food Items Per Stomach.--** Most Caramoan scincids have from 2 to 4 food items per stomach. Only 6 percent of all stomachs were empty, and there was no significant difference between skink species in this regard. The following sequence lists the species in order of increasing mean number of prey items per stomach (SD in parentheses): *E. atrocostata* 1.2 (0.6), *B. samarensis* 4.5 (3.1), *L. smaragdina* 2.0 (3.5), *D. grisia* 2.3 (2.1), *M. multifasciata* 2.6 (6.4), *T. grayi* 3.2 (12.9), *L. pulchella* 3.8 (11.7), *M. multicarinata* 4.3 (15.2), *O. cumingii* 4.4 (18.5), *S. jagori* 6.5 (19.1), and *B. boulengeri* 9.0 (21.3). The mean number of items per stomach is negatively related to mean prey size ingested. Additionally, those species with a greater prey range also have more prey items per stomach.

**Food Item Size.--** A total of 2672 prey items was measured (body length). These data and the distribution of size classes among the skinks studied are provided in Tables 17 and 18. They show that *Brachymeles boulengeri* and *Otosaurus cumingii* feed on the greatest range of prey size (some prey are longer that the predators own body length). The least range in prey size is found in the arboreal *Dasia grisia.* The mean prey length per skink species ranges from about 4 to 17 mm (Tables 17 and 18). Standard

deviations of the means reflect the overall range of prey sizes eaten by each skink species.

Many studies of lizard feeding have demonstrated a strong correlation between prey and predator body sizes. However, this relationship is not clear in the present analysis (Table 18). Prey size is not correlated with lizard size ($r_s$ = 0.43, Z = 1.35, $p$ < 0.05)

The data relating mean SVL to mean prey size per species poorly fits an exponential curve (Y = $4.23^{0.01}\overline{X}$, R = 0.57). The non-correspondence results largely from the tendency for the rather large *B. boulengeri* to eat many termites--small prey in proportion to predator SVL. In fact, were it not that this species often feeds on blind snakes, the mean prey size would be much smaller, further throwing this species out of what would otherwise be only a fair fit. *D. grisia* is another large skink that tends to feed on rather small prey. The remainder fall within the 95% confidence level of the curve. Thus the major exceptions are species living in somewhat extreme habitats (the most fossorial and the most arboreal of those examined).

The overall difference in mean food particle size among skinks studied (F = 8.63, $p$ < 0.001) was partitioned into separate sums of squares for testing the difference between pairs of skink species (Table 19). The results provide an indication of the relative separation of species on the niche dimension represented by food size. In this analysis, the magnitude of interspecific differences does not depend on the correlation between food and body size. A given difference in food size will reduce resource overlap and may enhance co-existence, whether one skink species is either larger or smaller than the second. Of the 55 pairwise contrasts, the pairs *M. multifasciata-S. jagori*, *M. multifasciata-B. boulengeri*, *L. pulchella-D. grisia*, *S. jagori-E. atrocostata*, and *S. jagori-T. grayi* are most similar in food size patterns. The pairs *M. multicarinata-O. cumingii*, *M. multicarinata-D. grisia*, *B. samarensis-O. cumingii*, and *M. multicarinata-L. pulchella* are most dissimilar in food size patterns. Each of the species comprising these species pairs, whether showing the least or the most similarity in food size selection, are found in the same habitat. The correlation may reflect the different feeding strategies of the lizard species, but more likely reflect the distribution of insect prey in each habitat.

**Food Item Volume.--** Another way of evaluating the importance of food in the total diet is to calculate the mean volume of prey acquired per prey category. These data are provided in Table 20. These volumes vary from 0.4 to 198.0 mm$^3$ for the smallest to largest prey types taken. Both mean and maximum prey volume are significantly correlated with SVL in almost all scincid species studied. The only important exception is *Brachymeles boulengeri*, which feeds on many prey at both the very small and the large ends of the total prey size spectrum. These data suggest that for almost all species studied, lizard size is the major determinant of prey size, even though

all of the lizard species studied could eat larger prey, and some regularly did (i.e. *B. brachymeles*). Regression analysis using lizard SVL and mean prey volume for all the species studied results in only poor coefficients of determination ($R^2$) (0.014 to 0.182, $p$ consistently greater than 0.05 in all cases).

Table 20 also makes it clear that the two most important prey categories eaten by local scincids from the standpoint of the total volume consumed, are termites and orthopterans, representing 42.1 and 27.7 percent respectively of the total food (in volume) eaten. No other prey categories come even close to comprising as much. Together they represent almost 70% of the total volume of food eaten by scincids in the Caramoan area. This is particularly significant in the case of termites, for the mean volume of local termites is only 7.2 mm³--a significantly small volume per food item when compared to the total spectrum of item volumes regularly taken. It is the number of termites taken, rather than their mass, that results in the high volumetric total for this prey category. Several local lizard species specialize on termites, which are represented by a diverse local fauna and a very common constituent of particularly the floor of open and closed canopied forests.

**Food Abundance.--** Diurnal insect abundance in the study area varies seasonally (Fig. 10). In general, diurnal insects are least common from
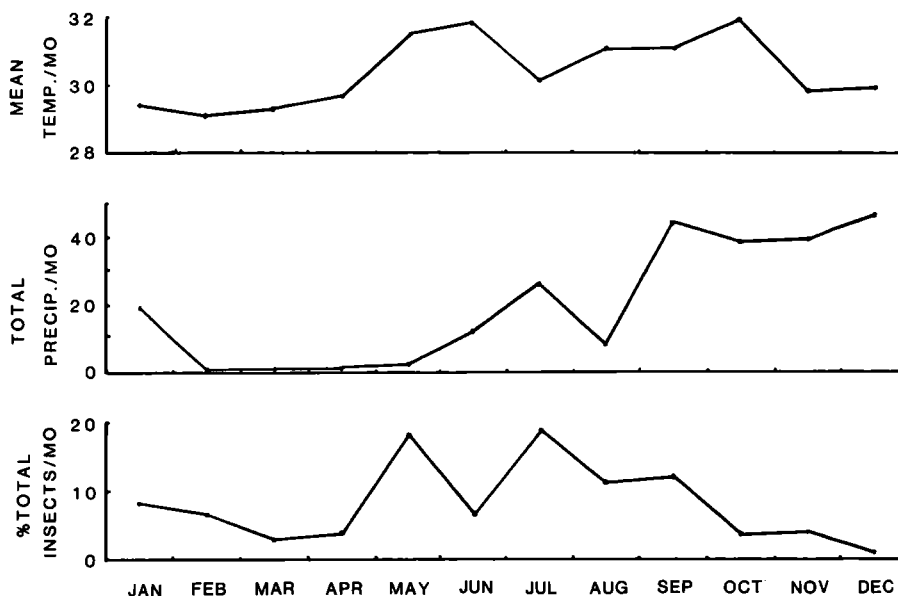


**Figure 10.** Monthly diurnal insect abundance (below), compared with total monthly precipitation and mean monthly temperature for the Caramoan area.

November through April, and much more common from May through July (with a dip in June). This pattern agrees fairly well with the rainfall pattern of the same area. Other studies of seasonal abundance in tropical forests show similar high peaks during early parts of the rainy season (Robinson and Robinson 1970, Fogden 1972, Janzen 1973, Smythe 1974). In the Caramoan area, the driest and wettest parts of the year have the least insects. The greatest number is found in May, just before the first (summer) monsoon, which occurs in July; August is a dry period between the two annual monsoons, and from this month through the stronger winter monsoon (September through January) insects become steadily less common. There is no correlation between insect abundance and seasonal temperature (Fig. 10).

Eight different microhabitats were regularly sampled for the seasonal abundance of diurnal insects (total insects trapped 4212, Table 21). These microhabitats are the trunks of trees in the forest and the more dispersed ones in the open, an overgrown field seasonally used for crops, a rocky exposure in the same field, the edge of the field adjacent to the forest, leaf litter in the primary forest, a rocky substrate in the same forest, and a series of deep rock crevices in the same forest.

Of these microhabitats, insects were most abundant at the ecotone of field and forest (Fig. 11)--the major habitat of *Mabuya multifasciata*. Insects were also common in the overgrown field and rock outcrops in them (also microhabitats of *M. multifasciata*, though less common there, perhaps because of seasonal disturbance related to agriculture) and in the forest leaf litter. The latter is the major microhabitat (with the forest-field ecotone) of *M. multicarinata*. Isolated trees in open situations have few insects when compared to the situations listed above, but are the major microhabitats of *L. smaragdina*. This is probably the major reason why *Lamprolepis smaragdina* feeds on more fruit (11.6% of total diet) than any other local species (Table
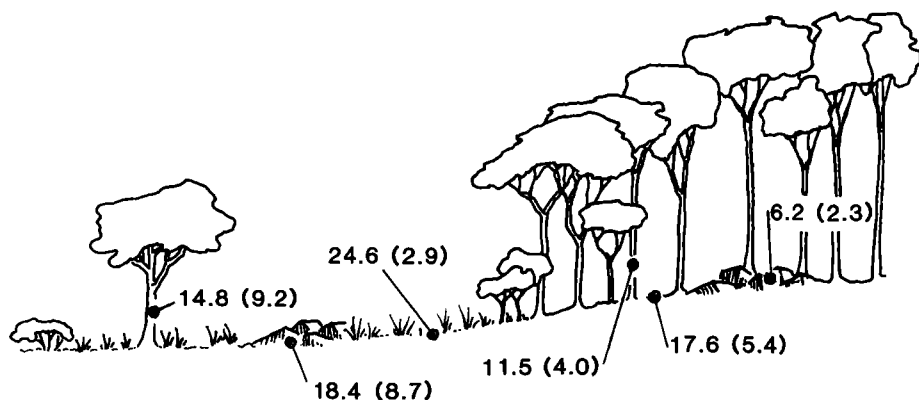


**Figure 11.** Percent (S. D.) of total insects in different microhabitats sampled (see text).

7). Forest trees also have fewer insects than most terrestrial microhabitats, but more than those inhabited by *L. smaragdina*. These forest trees are inhabited by two species of arboreal skinks. Of these, the larger *D. grisia* also feeds on many fruits (6.5% of total food eaten). The rocky substrate of the forest is the primary microhabitat of *S. jagori* and contains relatively few insects. This skink also feeds on more fruits (1.0%) than the remaining terrestrial skink species living in microhabitats of greater insect abundance (0.2-0.5%). Thus the extent of frugivory is related to the local prevalence of diurnal insects. In general, insect prey provides considerably more protein than fruits (see Auffenberg 1987 for details).

Lizard mean body size and insect abundance are not correlated in different microhabitats examined. However, on the basis of the number of lizards observed in different parts of the forest transect, the total number of lizards per microhabitat and the average amount of insect food available in each per month are almost perfectly correlated ($r = 0.98$). The relationship is that of a simple linear regression and is expressed by the formula $Y = 0.44 + 0.24X$. The grassy field is the only microhabitat out of line in an otherwise almost perfect positive regression. This is probably due to the fact that it is the only unstable environment of those studied, due to seasonal agricultural activity.

*Mabuya multifasciata* is the most common of the three terrestrial skinks along the transect studied and is most common in that part of the transect demonstrating the greatest insect abundance. *M. multicarinata* is found in all of the microhabitats of the transect except grassy fields, and tends to be associated with areas of moderate insect abundances. *S. jagori* is the most ecologically restricted of the three species and occurs in the microhabitat having the least insect abundance.

On the basis of insect abundance in the different microhabitats at different times of the year, the only microhabitat without seasonal insect shortages is field edge, where *M. multifasciata* is most common (Table 21). The microhabitat of *M. multicarinata* (mainly leaf litter in shaded forest) also has abundant food throughout the year, except for possibly April. The rocky forest substrate on which *S. jagori* is most commonly found has proportionately fewer insects throughout all the year, except during the first monsoon (June through August). The same pattern applies to the forest microhabitats of *L. pulchella* and *D. grisia*, both of which live in trees. While insect food resources seem low throughout the year for *L. smaragdina*, the potentially most stressful time for food seems to be during the dry season preceding the first monsoon. Though insect food is also low in December (probably due to the very heavy rain), *L. smaragdina* tends to be rather inactive during that time of the year.

In general our conclusion is that, while some microhabitats support more insect prey than others, there is in most of them a lower insect carrying
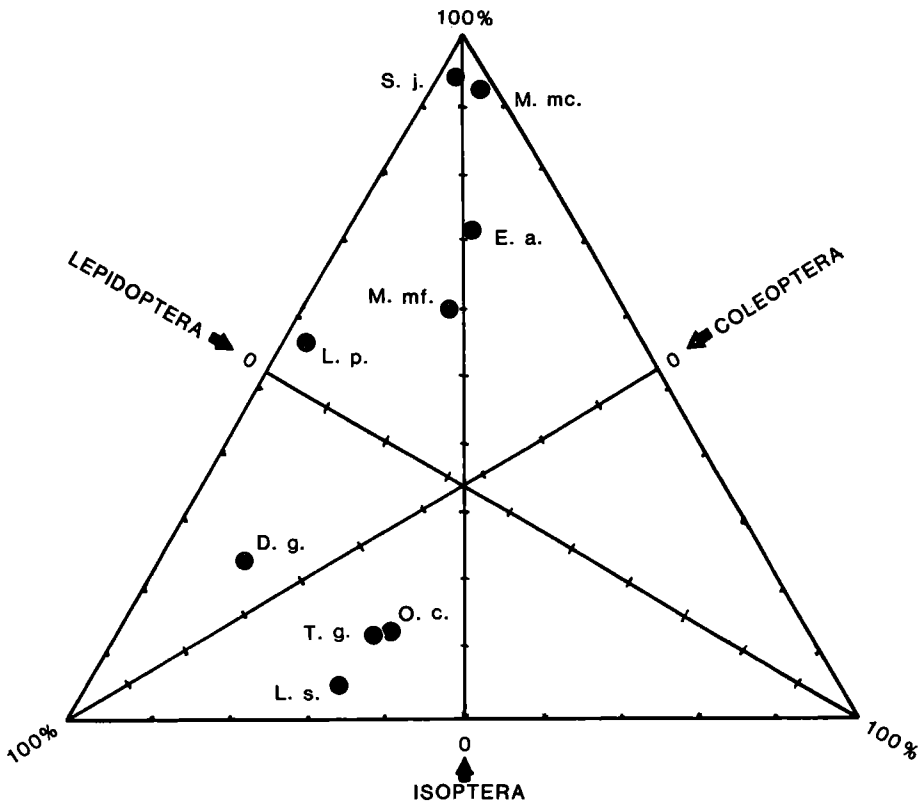
**Figure 12.** Summary of the utilization of the three most common prey categories eaten by Caramoan scincids--Lepidoptera, Coleoptera, and Isoptera.

capacity in the dry season preceding the first monsoon (Fig. 10). If competition for these resources is important, it is during this time of the year when it is probably operative. There is no evidence that food is a major factor in interspecific competition between these skink species in the local tropical microhabitats during most, if any at all, months of the year. Additional information and discussion regarding seasonal food use is provided below.

Figure 12 shows the trophic relations between the species of Caramoan skinks in relation to the most common prey categories eaten. The illustration makes it clear that most species concentrate on coleopteran and isopteran prey; lepidopterans are not as common as these two categories. Terrestrial dense forest species are the most important skink predators of isopterans, and larger arboreal skinks the most important predators of beetles. Insofar as they can be compared, the stomach content data of Reyes (1957, 1960) for *Lamprolepis smaragdina* and *Mabuya multifasciata* on Negros Island,

Philippines, are nearly identical to those from Caramoan for the same two species, except that the relationship of lepidopteran to coleopteran prey is reversed in *L. smaragdina*.

**Seasonal Use of Food.--** Tables 22 and 23 provide data on the seasonal use of the more important prey of Caramoan skinks. Several patterns important in the feeding biology of this lizard community become apparent. In spite of the fact one might assume that most taxa would be available throughout the entire year in this tropical forest ecosystem, some prey are taken on a strong seasonal basis. The clearest pattern is found in oligochaete predation. These are taken during and particularly after the second monsoon. This is the coolest time of the year (Fig. 10). None is eaten during the warmer first monsoon. Mollusk feeding shows a similar pattern, though less distinct. The surprising thing in this food category is that land snails of all types are definitely very active and available during the first monsoon. The fact that they are not eaten in quantity during the first monsoon suggests that (l) mollusks are not preferred prey, and (2), when other prey types are available these are eaten in preference to snails.

The pattern for termite predation is clearly related to rain. The main utilization peak occurs during the early rains of the first monsoon, with a smaller peak during the second monsoon. Termite activity has often been shown to be related to rainfall patterns, and the utilization of termites by the local skinks is probably simply a reflection of the seasonal activity patterns of the termites on the ground. This is further suggested by the fact that over 90% of those termites eaten in May and June are alates, and that this is the time when swarming is most common. Termites are the only prey eaten in quantity during the earliest rains of the first monsoon.

Though eaten throughout the year, coleopterans are taken in greatest quantity during and particularly after the second monsoon. This can be related to the large number of seedlings and the new growth characteristic of January and February, as well as the heavy fruit loads during October and November (see Auffenberg 1987 for additional details). Fruit-eating also follows the phenology of plants, for there are three distinct peaks in the number of fruits found in the stomachs (March, July, and November-December). Most of the lepidopterans taken as food represent the caterpillar morph, and their abundance in the stomachs from February through April is undoubtedly related to the considerable plant growth at this time of year. Spiders are eaten throughout the year, though there are two peak periods. One occurs from July to August and is correlated with the lepidopteran peak of the same months; the second corresponds with the peaks in coleopteran and orthopteran abundance during the second monsoon.

Food preference indices (P = % *i*th prey taxon in stomach/% of *i*th taxon in wild) are calculated for all skink species living in microhabitats in which monthly insect abundances are available. These species are *Sphenomorphus*

*jagori, Lipinia pulchella, Mabuya multifasciata, Mabuya multicarinata, and Lamprolepis smaragdina.* In none of these species do the data suggest that specific insect taxa are consistently selected in proportions greater than they occur in nature (i.e. index greater than 1.0). However, variations in the number of high indices, the prey categories represented by them, and the months during which they occur do suggest several important patterns. *M. multifasciata* shows the least food preference of any species tested (11 of 72 possible cells in Table 24). In this species, spiders occur in significantly high proportion more often than any other prey. The same pattern occurs in M. *multicarinata.* During December prey preference indices are high in most food taxa. In *Sphenomorphus jagori* the preferred prey for over half of the year are orthopterans (June and August, through December). January shows high prey preference indices in almost all prey categories analyzed. *Lamprolepis smaragdina* has more high preference indices for more months for more prey categories than most local skink species; Diperta and Orthoptera are the most consistently taken in high proportion; November has the highest number of high indices for any month. Only *Lipinia pulchella* has a greater number of high preference indices (22 of 72 possible cells, see Table 24); ants, spiders, and flies all occur in high proportions during many months of the year; January is the month with the greatest number of high indices.

To summarize, it appears that high preference indices are (1) more typical of the period during the end and immediately following Monsoon II, (2) often found associated with spider and fly prey, and (3) found more often in arboreal than terrestrial skinks. Some of this can be explained by the apparent need for skinks to forage for hidden, inactive insects (1) during and after the heaviest rains of the year, and (2) in arboreal habitats. It is probably the inactivity of these prey, rather than their low actual abundances which explains this particular pattern of high prey preference indices. In the case of spiders and flies, we suspect that the higher proportion of both in the gut than in nature may actually be due to some selection on the part of the lizard predators.

When the patterns of seasonal insect utilization are compared to the seasonal abundance of insects in each of the preferred microhabitats of each skink species, a significant correspondence can be demonstrated (Table 25), except for the underrepresentation of both ants and flies in the stomachs when compared to their numbers in the local environments. This misrepresentation is probably related to the difficulty with which flies are captured and the fact that ants are rarely eaten by skinks, except by some of the arboreal species (see above). When Formicidae and Diptera are excluded from the analysis, a Spearman Rank Correlation Test suggests that there is a highly significant correlation between the abundance rankings of stomach and wild populations of insect prey (RS = 1.00, Z = 1.73). Thus we conclude that for almost all insect prey they are taken in direct relation to their abundance

in each of the microhabitats studied. It can be demonstrated that the occurrence of seasonal prey switching is related to local changes in prey densities and is probably not due to differential preferences or to interspecific competition.

The following section describes the seasonal utilization pattern of each of the Caramoan skinks studied. Details are provided in Tables 26-35.

*Brachymeles boulengeri* has a seasonal prey utilization pattern (Table 26), in spite of the fact that it is fossorial. The only prey taken continually throughout the entire year are coleopterans. However, the utilization pattern is erratic, with one month of high utilization followed by another of low utilization. Almost all the Coleoptera taken are larval morphs, and the pattern may reflect seasonal pulses of different developing beetle groups. In January there is major dependence on mollusks, beetles (larvae), and orthopterans. In February and March the diet changes to spiders and pillbugs, some beetle larvae, and particularly earwigs. This represents the highest utilization rate of earwigs for any Caramoan skink species at any time of the year. The following warm, dry period of April and May witnesses replacement of all these categories by termites, moth larvae, orthopterans, and some snakes. With the rain of the first monsoon in June, centipedes, isopods, and beetles join the categories heavily predated. The next major change occurs in the August dry period, between monsoon rains, when snakes, lizards, beetles, and moth larvae, as well as centipedes, continue to be well represented among the stomach contents. These are particularly common prey categories during the wet months of November and December.

The seasonal pattern is entirely different in the semiaquatic *Tropidophorus grayi* (Table 31). While termites are eaten during almost the entire year, over 40 percent of the yearly total are consumed during September. Lower peaks occur in January and June. This pattern occurs in no other species studied. With the exception of January, the peak termite feeding periods are probably related to changes in local rainfall. During wet periods, the low-lying areas in which *Tropidophorus grayi* live become water-logged, driving termites into the open. The seasonal pattern of feeding on lepidopterans also differs from that of most other local skinks. Fishes are eaten only during the dry seasons--presumably because the small streams along which this species most often occurs are represented by small scattered pools, in which fishes are evidently easily caught. Captives maintained in Gainesville, Florida, have frequently been noted to chase and capture live fish in shallow water.

*Lamprolepis smaragdina, Lipinia pulchella,* and *Dasia grisia* are all more or less arboreal, but the seasonal patterns of prey utilization are quite different in each species (Tables 31, 33, 34). Ants are eaten in rather high proportions throughout the year by *Lipinia pulchella,* but over 60% of those eaten by *Dasia grisia* are during July. *Lamprolepis smaragdina* feeds on them

extensively during the first half of the year and into the first monsoon. On the other hand, the seasonal pattern for Lepidoptera (mainly larvae) predation is essentially the same for all three species. All the mollusks eaten by Caramoan skinks are land snails. They are rarely eaten by *D. grisia*, but commonly by the other two species. The high level predation on snails by *L. smaragdina* from January to April, when these prey are generally not moving about but found under surface debris, suggests that this species regularly descends to the ground and scratches about in leaf litter at this time of year. This is also suggested by the high use of pill bugs and fruits. Ants are eaten throughout the dry period and are probably largely foraged on the tree trunks, for during this time of year huge streams of them are often seen moving up and down in very exposed places.

The seasonal feeding patterns of the three terrestrial and narrowly sympatric species *M. multicarinata*, *M. multifasciata*, and *S. jagori* are all somewhat dissimilar. Though some prey categories, such as orthopterans, are eaten by all three during more or less the same seasons, the patterns of prey category consumption for particularly *M. multicarinata* and *M. multifasciata* are interdigitating, with little overlap in many prey groups. This may be coincidence, but of the three terrestrial species in forested communities, these two species show the most prey overlap. With the exception of Coleoptera and Lepidoptera, *S. jagori* and *M. multicarinata* represent quite different seasonal feeding patterns.

Thus we conclude that the local skinks illustrate significant seasonal changes in prey utilization. While there is some overall correspondence in these changes that can be related to the absolute differences in abundance of certain insect groups at different times of the year, it is also clear that some changes reflect a need to change foraging tactics due to local shortages or abundances (e.g. *Lamprolepis smaragdina* does more foraging on the ground during certain seasons, and *Tropidophorus grayi* forages for fishes concentrated in drying pools, etc.). The only situation which might suggest that interspecific interactions are affecting seasonal prey choice would be in those similar species with similar feeding habits inhabiting overlapping microhabitats on the forest floor. Of the total Caramoan skink community, only about one-quarter can be said to fall in this category. Thus three-quarters of the local skink species seem to be free of competition over seasonal food resources.

## Abdominal Fat Bodies

**Female Abdominal Fat Cycle.--** The annual cycle in fat bodies of the female Caramoan skinks shows considerable interspecific variability (Table 36). Some of this variation can be explained; some cannot.

Of the 11 species in which abdominal fat bodies were weighed monthly, approximately one-half (55%) possess no appreciable amount of fat at any time of the year. These non-fat containing species are *Sphenomorphus jagori*, *Otosaurus cumingii*, *Lipinia pulchella*, *Brachymeles boulengeri*, *B. samarensis*, and *Tropidophorus grayi*. The list includes species characteristic of semiaquatic, terrestrial forest, arboreal, and fossorial microhabitats. Comparison of these microhabitats with insect seasonal abundances in each does not necessarily suggest that these habitats are blessed with high food resources throughout the entire year. In fact, some of these microhabitats (such as forest trees, or rocky forest substrates) have rather low food resources compared to other microhabitats in the immediate area in which other species of skinks live. Additionally, this species list includes skinks that represent a wide range of annual reproductive patterns (see below), so that the lack of abdominal fat cannot be related to a specific breeding pattern.

The remaining five skink species produce abdominal fat, and the amount produced in each varies seasonally. In general, the period of maximum fat production is during the second monsoon (October through December, see Table 36). *Emoia atrocostata* possesses the most fat from August to October and is thus the only species somewhat out of line with the remaining ones. In all five species the least fat is found during the period just before and into the first monsoon period.

When this general pattern is compared with the annual reproductive patterns of the skink species involved, we find that there is no correlation, for the five species demonstrate a variety of annual breeding cycles (see below). The annual cycle of abdominal fat deposition and depletion shows the best correlation with annual fluctuation in insect abundance (see Fig. 10). Fat reserves are accumulated during the first monsoon, when insect abundance is high. Maximum fat loads are accumulated by the beginning of the major rainfall in the second monsoon (November and December), when insect food resources are generally rather low. The fat reserves are then steadily depleted through the spring dry season and reach their lowest levels at the end of that season and the beginning of the first monsoon. Thus the fat accumulated during the first monsoon and the period following it (about four months) is used during the remaining seven to eight months--the utilization rate undoubtedly dependent on food abundance as well as the energetics of the skink species involved.

Male Abdominal Fat Cycle.-- The same species that lacked abdominal fat in females also lacks it in males. Of those species in which the males do contain abdominal fat, it is also seasonally variable, as in the females of the same species (Table 36).

In general, the seasonal pattern is very similar to that of the females, i.e. the greatest fat accumulation occurs during the second monsoon and the least during the early part of the first monsoon and the dry period immediately preceding it. In *Lamprolepis smaragdina* the period of high fat reserves is longer than in males (or females) of any other species studied, beginning in September, with the peak in October. This is also the only local skink species in which the males contain significantly more abdominal fat than the females ($t = 24.3$, df = 20, $p < 0.001$). In the remaining species, females have greater amounts of mean monthly fat, but the differences are not statistically significant in any sex related comparisons.

The variation of the abdominal fat weight in males and females in the monthly samples of each species shows significant values that can be related to seasonal food supply. Coefficients of variation (= CV) for mean monthly abdominal fat weight were calculated for males and females. Such coefficients negate size differences between the species and allow direct comparison of the resulting percentage values. There is no significant difference between the annual mean CV values of the males and females of *Mabuya multicarinata* and *Emoia atrocostata*, whereas the males of *M. multifasciata* and *Lamprolepis smaragdina* have significantly less variation in fat weight throughout the year than females of the same species. The reasons for this are not clear.

The seasonal pattern of the degree of variation in fat weight shows that the greatest variation in fat weight occurs during the end of the dry season and the earliest part of the first monsoon. This has been shown above to be the period when fat reserves are usually the lowest of the entire year in all species that have fat reserves. The fact that variation is greatest during this period suggests that some individuals are probably able to continue to find food during this high stress time, while others are not and are thus more dependent on their abdominal fat reserves. On the other hand, in all species studied, the time of year when fat reserves show the least variation in both males and females of all species studied is during the heavy rains of the second monsoon and the beginning of the dry season immediately following them. This is the time when food resources begin to get slim. The fact that all individuals of both sexes of all species have built up a fat supply in more equal amounts suggests that the accumulation of fat during the preceding first monsoon must be a very important strategy for all species. This is particularly cogent when one realizes that there are a variety of reproductive strategies operative among these species, and that they cannot be directly related to the

fat accumulation and utilization patterns in the different species (data currently being analyzed by W. and T. Auffenberg ).

## CONCLUSIONS

The data presented above show that (1) the Caramoan peninsula of southern Luzon contains a number of habitats and no species of skink studied ranges through all of them; (2) dense forest types are the richest local communities in number of species, and evidence suggests that this is due to their greater structural complexity; (3) the distribution of the terrestrial species *Mabuya multifasciata, M. multicarinata,* and *Sphenomorphus jagori* are about the same size and replace one another ecologically. A fourth terrestrial forest species, *Otosaurus cumingii,* that is syntopic with these is much larger. The fossorial species pair *Brachymeles boulengeri-B. samarensis* is significantly different in size and replace one another ecologically. The arboreal forest species *Lipinia pulchella* and *Dasia grisia* are dissimilar in size and replace one another vertically in the forest vegetational strata; (4) the dense and open forest skink community seems to comprise two distinct ecological units; and (5) in general, these conclusions for a Philippine skink community are similar to those for a complete lizard community of several different families in Brazilian forests (Rand and Humphrey 1968).

We would now like to return to the questions posed in the introductory section. Some of these, such as evidence of seasonal prey switching, have been answered adequately in the body of the text. However, others more important and wide reaching require additional comment.

**Food as a Limiting Resource.--** Information obtained during this study of the skink community of southern Luzon, Philippines, does not provide adequate data to prove that food is a limiting resource for the species found in the local environments. Data needed for such analyses are currently lacking and include (1) the amount of food skinks need to survive and reproduce, and (2) the length of time they can go without food (or subsist on a minimal amount of it) before either survival or reproduction is affected.

However, our data do show that there is, at least within the insect prey eaten by the species studied, little segregation of prey size by most of these skinks. Some are limited to only the smaller insects as food, but even the largest species, which can feed on very large insects and smaller vertebrates, also consume a great number of prey items well within the range of the smallest local skink species. There is no evidence of prey selection depending on predator size, nor is there any evidence of prey selection on the basis of nutritional factors. Almost all the evidence of seasonal prey shifting documented here can be explained as being due to demonstrated changes in

prey abundances at different seasons. The only suggestion of shifts in prey selection caused by possible interspecific interactions is among three terrestrial species inhabiting secondary and primary forests and the ecotonal zones between them. These are, additionally, the most narrowly sympatric skink species among those studied. The remaining species of the local skink community are apparently not significantly affected by food competition from other local species.

**Availability of Prey.--** Huffaker (1966) has suggested that food could be in short supply whenever the predator lacks the capacity to locate or utilize it efficiently. While some references to tropical forest ecosystems suggest that insect prey are equally abundant throughout the year, our study shows that this is certainly not the case in southern Luzon. In general, the period of lowest insect abundance in the study area is from November through April. However, our data also show that food abundances vary from habitat to habitat--even within the same geographic area. Some areas suffer less variation in food abundance through the year than others. There is, for example, no evidence that *Emoia atrocostata*, living in a marine littoral environment, ever suffers food scarcity. Casual observation on the local beaches suggests that the crustaceans forming the major prey of this skink are available in more or less equal numbers throughout the year. In spite of this stable and relatively abundant food supply, only this species of the 11 found in the entire area feeds on this consistent and abundant food resource. However, to search for and excavate the beach crustaceans must subject *E. atrocostata* to relatively high predation pressures, since the habitat is devoid of much cover. Additionally, the habitual feeding on marine forms, as well as the habitat itself may subject this lizard to salt loads which the other species may find intolerable.

Within the adjacent forests there are 10 additional skink species. Most of these are found in somewhat different microhabitats. Thus food shortages, if they occur at all, probably do not result in food competition between them. If competition does occur, and if it is important in their survival, it must be during the months of November through April, when food resources tend to be at their lowest annual levels.

**Food Niche Overlap.--** The most important ecological differences we have documented for the Caramoan skinks are in habitat utilization. Species that live in different places are expectedly exposed to different prey types and seasonal schedules of microclimate and food availability. For the most part, almost all of the differences in diet between these geographically sympatric species can be attributed to differences in habitat. At the same time, those few species that do live in close proximity in nearly the same microhabitat show the greatest evidence for low food niche overlap values and differences in foraging periodicity and thus represent the only evidence for possible competition among any of the local species.

Food niche overlap values are not, of course, proportional to intensity of competition; nor does high food niche overlap necessarily imply strong competition. However, given the relative magnitudes of food niche overlap in particularly the terrestrial forest skink community, the chances of competition are greater here than in any other habitat in the entire area. As in the two broadly sympatric *Mabuya* species of southern Africa studied by Huey and Pianka (1977), niche overlap values must be concluded to be simply consistent with a hypothesis that relatively strong interspecific competition between the terrestrial forest species of southern Luzon may help restrict the zone of coexistence. It is possibly for these reasons that *Mabuya multifasciata, Mabuya multicarinata,* and *Sphenomorphus jagori* inhabit slightly different microhabitats in the same general area, eat slightly different foods and forage at different times of the day.

Several authors have suggested that narrowly sympatric species are often interspecifically territorial or aggressive (Brown 1971, Cody 1974, Nevo et al. 1975). Though no evidence of aggression was noted between *M. multicarinata* and *S. jagori, M. multifasciata* was regularly seen chasing individuals of *M. multicarinata.* This is consistent with the fact that the stomachs of *M. multifasciata* often contain entire lizards or their tails (see Tables 26-35).

To summarize, our evidence supports two explanations for local distributional patterns of scincids in southern Luzon. First, the separation of the distributions in a number of local microhabitats probably reflects morphological, physiological, and behavioral adaptations of seven of the local species to specific microecological discontinuities of the local forest ecosystems. Given the variety of microhabitats in a tropical moist forest, such as that at Caramoan, and the number of niches represented in each of the microhabitats, we conclude that there are probably many more niches available for skinks than species able to fill them. Of course, many such niches are probably filled with non-skink predators in the local forests. Secondly, within the terrestrial forest floor niche, at least some competition between three local species falling into this category may restrict their zones of sympatry. The most aggressive and largest species (*Mabuya multifasciata*) lives in that part of the local habitat that contains the greatest food abundance.

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Table 1. Summary of meristic data relating to the scincid species studied at Caramoan, Luzon.

| Species | SVL (mm) at Maturity | X̄ Female | | X̄ Male | | Total Examined |
|---------|---------------------|-----------|-----|---------|-----|----------------|
| | | SVL | Wt | SVL | Wt | |
| *L. pulchella* | 35 | 39 | 0.6 | 38 | 0.5 | 355 |
| *M. multifasciata* | 72 | 90 | 22.6 | 91 | 23.1 | 378 |
| *M. multicarinata* | 60 | 71 | 11.5 | 71 | 11.3 | 353 |
| *T. grayi* | 79 | 94 | 18.9 | 94 | 19.1 | 368 |
| *S. jagori* | 61 | 75 | 13.9 | 81 | 17.8 | 363 |
| *L. smaragdina* | 70 | 92 | 18.6 | 90 | 15.8 | 358 |
| *B. boulengeri* | 71 | 86 | 14.5 | 77 | 11.9 | 350 |
| *B. samarensis* | 55 | 59 | 1.9 | 61 | 2.0 | 43 |
| *O. cumingii* | 110 | 121 | 43.5 | 113 | 38.8 | 305 |
| *D. grisia* | 65 | 107 | 27.3 | 104 | 26.8 | 61 |
| *E. atrocostata* | 71 | 84 | 12.6 | 89 | 14.8 | 318 |

Table 2. Body size gradation ratios in Caramoan skinks and general habitat.

| Species | SVL (mm) | Ratios | General Habitat |
|---------|----------|--------|-----------------|
| *S. steerei* | 27.0 | ---- | Terrestrial, forest |
| *L. pulchella* | 38.1 | 1.41 | Arboreal, forest |
| *B. samarensis* | 60.0 | 2.22 | Fossorial, forest |
| *M. multicarinata* | 71.0 | 2.63 | Terrestrial, forest |
| *S. jagori* | 78.1 | 2.89 | Terrestrial, forest |
| *B. boulengeri* | 81.5 | 3.02 | Fossorial, open |
| *E. atrocostata* | 86.2 | 3.19 | Marine littoral |
| *M. multifasciata* | 90.5 | 3.35 | Terrestrial, open |
| *L. smaragdina* | 92.0 | 3.41 | Arboreal, open |
| *T. grayi* | 94.1 | 3.49 | Semiaquatic |
| *D. grisia* | 105.0 | 3.89 | Arboreal, forest |
| *O. cumingii* | 117.0 | 4.33 | Terrestrial, open |

Table 3. Habitat use by three sympatric Caramoan scincids.

| Species | Fields | Ecotonal | | Forest | |
|---|---|---|---|---|---|
| | | River Bed | Forest Edge | Dense Shrub | Rocky Floor |
| *M. multifasciata* | 16 | 56 | 33 | 5 | 1 |
| *M. multicarinata* | 0 | 0 | 10 | 44 | 7 |
| *S. jagori* | 0 | 0 | 2 | 15 | 34 |
| Totals | 16 | 56 | 45 | 64 | 25 |

Table 4. Mean body lengths (SVL, in mm) for skinks living in different habitats. Number of skink species/category in parentheses.

| | Terrestrial | Fossorial | Arboreal | Total Sp. |
|---|---|---|---|---|
| Dense Situations | 58.7 (3) | 60.0 (1) | 71.5 (2) | 6 |
| Open Situations | 97.8 (3) | 81.5 (1) | 92.0 (1) | 5 |
| Total Species | 6 | 2 | 3 | 3 |

Table 5. Basis of food analyses for species examined.

| Species | Total with Food in Stomach | Percent with Food of Total Examined |
|---|---|---|
| *D. grisia* | 46 | 75 |
| *L. smaragdina* | 251 | 70 |
| *L. pulchella* | 206 | 58 |
| *M. multifasciata* | 235 | 85 |
| *M. multicarinata* | 230 | 65 |
| *B. boulengeri* | 280 | 80 |
| *B. samarensis* | 35 | 81 |
| *S. jagori* | 182 | 69 |
| *T. grayi* | 221 | 60 |
| *O. cumingii* | 163 | 59 |
| *E. atrocostata* | 244 | 77 |
| Total | 2093 | 779 |

Table 6. Prey utilization of scincids in the Caramoan area.

| Prey Taxa | Total Items Taken | Percent of Total | Remarks |
|---|---|---|---|
| Mollusca | 79 | 0.74 | |
| Arthropoda | | | |
| Crustacea | | | |
| Isopoda | 409 | 3.81 | Including littorals |
| Decapoda | 152 | 1.42 | Littorals only |
| Chilopoda | 34 | 0.36 | |
| Arachnida | | | |
| Chelonethida | 1 | 0.01 | |
| Phalangida | 2 | 0.02 | |
| Scorpionida | 12 | 0.11 | |
| Araneida | 299 | 2.73 | |
| Insecta (eggs only) | 61 | 0.57 | |
| Collembola | 14 | 0.13 | |
| Odonata | 7 | 0.08 | |
| Isoptera | 6735 | 62.65 | |
| Dermaptera | 16 | 0.15 | |
| Hemiptera | 30 | 0.28 | |
| Homoptera | 9 | 0.08 | |
| Formicidae | 348 | 3.24 | Including 6 eggs |
| Coleoptera | 1142 | 10.63 | Adults and larvae |
| Lepidoptera | 465 | 4.33 | Adults and larvae |
| Diptera | 201 | 1.87 | Including 6 larvae |
| Orthoptera | 615 | 5.73 | |
| Annelida | | | |
| Oligochaeta | 11 | 0.10 | |
| Polychaeta | 1 | 0.01 | |
| Chordata | | | |
| Pisces | 12 | 0.13 | |
| Amphibia | 1 | 0.01 | Adult |
| Reptilia | | | |
| Sauria | 32 | 0.30 | Including 1 egg |
| Serpentes | 15 | 0.14 | Including 1 egg |
| Aves | 2 | 0.02 | Including 1 egg |
| Plants | 46 | 0.43 | Angiosperm fruits |
| Total | 10,739 | | |

Table 7.  Comparative major dietary items in Caramoan skinks.  For SVL size ratios, *Lipinia pulchella* is used as the base.

| Species | Size Ratio | Major Food Categories (%) | | |
|---|---|---|---|---|
| | | First | Second | Third |
| *L. pulchella* | ---- | Isoptera(33) | Coleoptera(26) | Formicidae(26) |
| *B. samarensis* | 1.57 | Isoptera(78) | Formicidae(12) | Oligochaeta(05) |
| *S. jagori* | 1.74 | Isoptera(81) | Coleoptera(04) | Isopoda(03) |
| *D. grisia* | 1.86 | Coleoptera(49) | Isoptera(16) | Formicidae(08) |
| *L. smaraagdina* | 2.00 | Coleoptera(42) | Lepidotera(23) | Fruits(11) |
| *E. atrocostata* | 2.02 | Decapoda(68) | Isoptera(12) | Isopoda(09) |
| *B. boulengeri* | 2.03 | Isoptera(70) | Coleoptera(23) | Araneida(02) |
| *M. multifasciata* | 2.14 | Isoptera(43) | Orthoptera(19) | Coleoptera(14) |
| *T. grayi* | 2.17 | Isopoda(62) | Coleoptera(14) | Isoptera(08) |
| *O. cumingii* | 3.14 | Oligochaeta(24) | Orthoptera(24) | Coleoptera(20) |

Table 8. Seasonal Shannon-Wiener Diversity Indices (D), equitability (E), and number food categories (PC) for those Caramoan skinks with sufficient data for analysis.

| Species | | Months | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. |
| B. boulengeri | D | 1.64 | 1.56 | 1.06 | 0.54 | 0.31 | 0.64 | 0.44 | 0.73 | 2.36 | 0.85 | 1.00 | 0.17 |
| | E | 0.55 | 0.55 | 0.35 | 0.18 | 0.12 | 0.21 | 0.15 | 0.20 | 0.91 | 0.26 | 1.00 | 0.07 |
| | PC | 8 | 7 | 8 | 8 | 6 | 6 | 8 | 12 | 6 | 10 | 2 | 5 |
| E. atrocostata | D | 1.73 | 0.61 | 0.43 | 0.70 | 0.86 | 0 | 1.15 | 1.32 | 1.00 | 1.67 | 1.00 | 1.30 |
| | E | 0.62 | 0.39 | 0.27 | 0.44 | 0.86 | 0 | 0.72 | 0.83 | 1.00 | 0.72 | 1.00 | 0.82 |
| | PC | 7 | 3 | 3 | 3 | 2 | 1 | 3 | 3 | 2 | 5 | 2 | 3 |
| S. jagori | D | 1.69 | 1.79 | 1.99 | 0.75 | 0.76 | 0.54 | 0.67 | 1.83 | 1.74 | 1.35 | 1.39 | 1.30 |
| | E | 0.53 | 0.57 | 0.63 | 0.25 | 0.25 | 0.19 | 0.29 | 0.65 | 0.58 | 0.45 | 0.40 | 0.41 |
| | PC | 9 | 5 | 9 | 8 | 8 | 7 | 5 | 7 | 8 | 8 | 11 | 9 |
| T. grayi | D | 1.41 | 2.88 | 1.75 | 2.28 | 2.23 | 1.14 | 1.58 | 1.0 | 0.16 | 1.71 | 2.35 | 2.28 |
| | E | 0.54 | 0.87 | 0.88 | 0 | 0.89 | 0.49 | 1.00 | 1.00 | 0.08 | 0.66 | 0.91 | 0.76 |
| | PC | 6 | 10 | 4 | 6 | 6 | 5 | 3 | 2 | 4 | 6 | 6 | 8 |
| L. pulchella | D | 1.82 | 1.72 | 0.95 | 1.61 | 2.05 | 1.76 | 2.35 | 0.99 | 1.72 | 1.87 | 2.07 | 2.27 |
| | E | 0.78 | 0.74 | 0.47 | 0.62 | 0.65 | 0.58 | 0.74 | 0.62 | 0.67 | 0.72 | 0.69 | 0.72 |
| | PC | 5 | 5 | 4 | 6 | 9 | 8 | 9 | 3 | 6 | 6 | 8 | 9 |
| M. multifasciata | D | 1.55 | 2.15 | 1.67 | 1.36 | 1.48 | 2.03 | 2.01 | 2.52 | 2.80 | 2.60 | 1.99 | 3.00 |
| | E | 0.49 | 0.65 | 0.50 | 0.48 | 0.49 | 0.61 | 0.78 | 0.76 | 0.81 | 0.75 | 0.71 | 0.87 |
| | PC | 9 | 10 | 10 | 7 | 8 | 10 | 6 | 10 | 11 | 11 | 7 | 11 |
| M. multicarinata | D | 2.53 | 1.00 | 2.28 | 2.09 | 1.09 | 0.79 | 2.63 | 2.79 | 2.49 | 1.85 | 1.52 | 2.54 |
| | E | 0.84 | 0.32 | 0.76 | 0.66 | 0.36 | 0.26 | 0.71 | 0.78 | 0.69 | 0.58 | 0.45 | 0.85 |
| | PC | 8 | 9 | 8 | 9 | 8 | 13 | 12 | 12 | 9 | 10 | 8 |
| L. smaragdina | D | 1.16 | 2.21 | 2.34 | 2.92 | 2.25 | 2.05 | 1.14 | 0.81 | 1.58 | 2.33 | 2.63 | 1.30 |
| | E | 0.39 | 0.74 | 0.78 | 0.88 | 0.87 | 0.79 | 0.57 | 0.81 | 1.00 | 0.90 | 0.79 | 0.46 |
| | PC | 8 | 8 | 8 | 10 | 6 | 6 | 4 | 2 | 3 | 6 | 10 | 7 |

Table 9. Standardized food (category) niche breadth ($B_{st}$) in Caramoan skinks.

| Species | N Food Items | Standard Food Niche | N Prey States |
|---------|--------------|---------------------|---------------|
| *D. grisia* | 146 | 0.219 | 10 |
| *T. grayi* | 148 | 0.009 | 13 |
| *E. atrocostata* | 178 | 11.130 | 11 |
| *B. samarensis* | 46 | 3.331 | 5 |
| *B. boulengeri* | 195 | 0.013 | 13 |
| *L. smaragdina* | 280 | 0.003 | 16 |
| *S. jagori* | 240 | 0.006 | 15 |
| *M. multifasciata* | 390 | 0.012 | 15 |
| *M. multicarinata* | 383 | 0.007 | 15 |
| *L. pulchella* | 288 | 0.042 | 11 |

Table 10. Niche overlap ($C_{ih}$, X 100) among Caramoan skinks for Isoptera prey.

|                   | L. p. | M. f. | M. c. | L. s. | S. j. | D. g. | T. g. | E. a. | B. b. |
|-------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| L. pulchella      |       |       |       |       |       |       |       |       |       |
| M. multifasciata  | 0.12  |       |       |       |       |       |       |       |       |
| M. multicarinata  | 0.10  | 0.10  |       |       |       |       |       |       |       |
| L. smaragdina     | 0.13  | 0.45  | 0.25  |       |       |       |       |       |       |
| S. jagori         | 0.03  | 0.09  | 0.02  | 0.01  |       |       |       |       |       |
| D. grisia         | 0.10  | 0.09  | 0.11  | 0.03  | 0.06  |       |       |       |       |
| T. grayi          | 0.10  | 0.10  | 0.12  | 0.03  | 0.06  | 0.12  |       |       |       |
| E. atrocostata    | 0.13  | 0.33  | 0.23  | 0.24  | 0.07  | 0.21  | 0.22  |       |       |
| B. boulengeri     | 0.04  | 0.01  | 0.02  | 0.01  | 0.04  | 0.02  | 0.02  | 0.01  |       |
| O. cumingii       | 0.12  | 0.27  | 0.21  | 0.15  | 0.06  | 0.19  | 0.20  | 0.27  | 0.08  |

Table 11. Niche overlap ($C_{ih}$, X 100) among Caramoan skinks for Crustacea prey.

|                   | L. p. | M. f. | M. c. | L. s. | S. j. | D. g. | T. g. | E. a. | B. b. |
|-------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| L. pulchella      |       |       |       |       |       |       |       |       |       |
| M. multifasciata  | 0.07  |       |       |       |       |       |       |       |       |
| M. multicarinata  | 0.01  | 0.07  |       |       |       |       |       |       |       |
| L. smaragdina     | 0.26  | 0.28  | 0.16  |       |       |       |       |       |       |
| S. jagori         | 0.01  | 0.03  | 0.04  | 0.01  |       |       |       |       |       |
| D. grisia         | 0.38  | 0.30  | 0.16  | 0.44  | 0.10  |       |       |       |       |
| T. grayi          | 0.01  | 0.05  | 0.07  | 0.03  | 0.07  | 0.02  |       |       |       |
| E. atrocostata    | 0.00  | 0.00  | 0.00  | 0.00  | 0.01  | 0.00  | 0.00  |       |       |
| B. boulengeri     | 0.02  | 0.08  | 0.10  | 0.05  | 0.08  | 0.04  | 0.09  | 0.02  |       |
| O. cumingii       | 0.24  | 0.27  | 0.16  | 0.34  | 0.10  | 0.33  | 0.13  | 0.02  | 0.18  |

Table 12. Niche overlap ($C_{ih}$, X 100) among Caramoan skinks for Coleoptera prey.

|                   | L. p. | M. f. | M. c. | L. s. | S. j. | D. g. | T. g. | E. a. | B. b. |
|-------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| L. pulchella      |       |       |       |       |       |       |       |       |       |
| M. multifasciata  | 0.06  |       |       |       |       |       |       |       |       |
| M. multicarinata  | 0.07  | 0.07  |       |       |       |       |       |       |       |
| L. smaragdina     | 0.05  | 0.02  | 0.01  |       |       |       |       |       |       |
| S. jagori         | 0.05  | 0.03  | 0.02  | 0.03  |       |       |       |       |       |
| D. grisia         | 0.04  | 0.02  | 0.01  | 0.02  | 0.02  |       |       |       |       |
| T. grayi          | 0.06  | 0.04  | 0.02  | 0.04  | 0.04  | 0.03  |       |       |       |
| E. atrocostata    | 0.07  | 0.09  | 0.05  | 0.06  | 0.06  | 0.04  | 0.07  |       |       |
| B. boulengeri     | 0.10  | 0.05  | 0.03  | 0.04  | 0.17  | 0.08  | 0.04  | 0.13  |       |
| O. cumingii       | 0.10  | 0.05  | 0.36  | 0.12  | 0.17  | 0.08  | 0.37  | 0.13  | 1.05  |

Table 13. Niche overlap ($C_{ih}$, X 100) among Caramoan skinks for Lepidoptera prey.

|  | L. p. | M. f. | M. c. | L. s. | S. j. | D. g. | T. g. | E. a. | B. b. |
|---|---|---|---|---|---|---|---|---|---|
| L. pulchella |  |  |  |  |  |  |  |  |  |
| M. multifasciata | 0.01 |  |  |  |  |  |  |  |  |
| M. multicarinata | 0.16 | 0.09 |  |  |  |  |  |  |  |
| L. smaragdina | 0.00 | 0.02 | 0.01 |  |  |  |  |  |  |
| S. jagori | 0.04 | 0.07 | 0.06 | 0.04 |  |  |  |  |  |
| D. grisia | 0.05 | 0.07 | 0.07 | 0.04 | 0.09 |  |  |  |  |
| T. grayi | 0.06 | 0.08 | 0.08 | 0.04 | 0.10 | 0.10 |  |  |  |
| E. atrocostata | 0.06 | 0.09 | 0.36 | 0.05 | 0.16 | 0.18 | 0.20 |  |  |
| B. boulengeri | 0.12 | 0.08 | 0.00 | 0.05 | 0.12 | 0.13 | 0.14 | 0.02 |  |
| O. cumingii | 0.04 | 0.07 | 0.05 | 0.04 | 0.07 | 0.07 | 0.07 | 0.01 | 0.06 |

Table 14. Niche overlap ($C_{ih}$, X 100) among Caramoan Skinks for Orthoptera prey.

|  | L. p. | M. f. | M. c. | L. s. | S. j. | D. g. | T. g. | E. a. | B. b. |
|---|---|---|---|---|---|---|---|---|---|
| L. pulchella |  |  |  |  |  |  |  |  |  |
| M. multifasciata | 1.00 |  |  |  |  |  |  |  |  |
| M. multicarinata | 0.90 | 0.91 |  |  |  |  |  |  |  |
| L. smaragdina | 0.98 | 0.99 | 0.14 |  |  |  |  |  |  |
| S. jagori | 0.92 | 0.18 | 0.27 | 0.20 |  |  |  |  |  |
| D. grisia | 0.99 | 1.65 | 0.12 | 4.17 | 0.16 |  |  |  |  |
| T. grayi | 0.93 | 0.20 | 0.53 | 0.25 | 2.86 | 0.18 |  |  |  |
| E. atrocostata | 0.97 | 0.70 | 0.10 | 0.44 | 0.10 | 0.18 | 0.08 | 0.10 |  |
| O. cumingii | 0.99 | 1.03 | 0.12 | 8.00 | 0.17 | 0.10 | 0.08 | 0.02 | 0.08 |

Table 15. Overall niche overlap (all major prey taxa added together, X 100)

|  | L. p. | M. f. | M. c. | L. s. | S. j. | D. g. | T. g. | E. a. | B. b. |
|---|---|---|---|---|---|---|---|---|---|
| L. pulchella |  |  |  |  |  |  |  |  |  |
| M. multifasciata | 35.15 |  |  |  |  |  |  |  |  |
| M. multicarinata | 35.87 | 35.20 |  |  |  |  |  |  |  |
| L. smaragdina | 52.12 | 88.63 | 49.10 |  |  |  |  |  |  |
| S. jagori | 14.12 | 24.37 | 18.48 | 12.42 |  |  |  |  |  |
| D. grisia | 68.42 | 59.23 | 43.15 | 64.67 | 34.70 |  |  |  |  |
| T. grayi | 25.91 | 29.60 | 34.10 | 17.31 | 30.73 | 30.56 |  |  |  |
| E. atrocostata | 103.68 | 72.78 | 78.16 | 52.21 | 37.41 | 65.88 | 54.53 |  |  |
| B. boulengeri | 44.49 | 40.41 | 22.14 | 29.56 | 32.73 | 31.18 | 39.16 | 16.26 |  |
| O. cumingii | 56.99 | 77.13 | 51.40 | 68.89 | 23.99 | 74.20 | 53.92 | 32.98 | 45.37 |

Table 16.  The nutritional quality of terrestrial invertebrates, shown as percent of dry weight, means in parentheses.

| Taxa | Water | Ash | Nitrogen | Fat | Source |
|------|-------|-----|----------|-----|--------|
| Annelida | | | | | |
| Oligochaeta | 82-85(83) | 9-23(16) | 9-11(10) | 4-8 (6) | 1, 7, 8 |
| Arthropoda | | | | | |
| Orthoptera | 57-76(69) | 4-9 (7) | 7-12(10) | 4-50(17) | 1, 2, 4, 5 |
| Coleoptera | 52-80(66) | 5-10(7) | 9-19(11) | 5-33(16) | 1, 6 |
| Lepidoptera | 56-82(73) | 5-10(7) | 5-9 (8) | 4-61(29) | 1, 3, 4, 6 |
| Diptera | -------- | 5-12(9) | 10   (10) | 9-15(12) | 5 |
| Hymenoptera | 44-70(59) | ------- | 1-10(5) | 3-51(25) | 2, 3, 6, 9 |
| Isoptera | 34-81(66) | 2-71(17) | 6-11(8) | 8-53(30) | 2, 9, 10, 11, 12, 13 |

Sources: 1, Oftsal unpubl. in 9; 2; Leung 1968; 3, Leung 1972; 4, Gohl 1975; 5, DeFolliart 1975; 6, Taylor 1975; 7, Lawrence and Miller 1945; 8, French et al. 1957; 9, Redford and Dorea 1984; 10, Ketelhodt 1966; 11, Matsumoto 1976; 12, Phelps et al. 1975; 13, Hladik 1977.

Table 17.  Frequency of food size classes (total measured food items 2585).

| Species | Frequency Food Size Classes (mm) | | | | | | | | | | |
|---------|-----|------|-------|-------|-------|-------|-------|-------|-------|----|----|
| | 1-5 | 6-10 | 11-15 | 16-20 | 21-25 | 26-30 | 31-40 | 41-50 | 51-80 | Other | |
| M. multifasciata | 60 | 238 | 63 | 19 | 1 | 1 | | | | | |
| M. multicarinata | 29 | 189 | 111 | 25 | 12 | 11 | 7 | 5 | | | |
| L. pulchella | 249 | 45 | 1 | | | | | | | | |
| L. smaragdina | 34 | 118 | 60 | 29 | 16 | 7 | 6 | 2 | 2 | | |
| S. jagori | 102 | 216 | 57 | 17 | 2 | 4 | 3 | | | | |
| D. grisia | 6 | 48 | 29 | 9 | 3 | 1 | | | | | |
| T. grayi | 13 | 65 | 43 | 9 | 10 | 2 | 2 | | | | |
| E. atrocostata | 2 | 81 | 61 | 3 | 3 | 3 | 1 | 1 | | | |
| B. brachymeles | 20 | 91 | 24 | 16 | 3 | 2 | 16 | 5 | 1 | 73 | 2 |
| B. samarensis | 43 | 38 | | | | | | | | 83 | 2 |
| | | | | | | | | | | 91 | 1 |
| | | | | | | | | | | 111 | 1 |
| O. cumingii | 12 | 115 | 46 | 23 | 11 | 8 | 23 | 16 | 5 | 62 | 3 |
| | | | | | | | | | | 200 | 1 |
| | | | | | | | | | | 151 | 1 |
| Totals | 570 | 1244 | 495 | 150 | 61 | 39 | 58 | 29 | 9 | 17 | |

Table 18.  Mean particle size and SVL (mm) of Caramoan skinks.

| Species | Prey | | | Skinks | | |
|---|---|---|---|---|---|---|
| | Mean | SD | N Items | SVL | SD | N |
| *M. multifasciata* | 9.64 | 5.34 | 388 | 90.5 | 2.0 | 135 |
| *M. multicarinata* | 11.83 | 7.06 | 387 | 71.0 | 2.5 | 160 |
| *L. pulchella* | 3.79 | 1.25 | 295 | 38.1 | 0.8 | 106 |
| *L. smaragdina* | 11.33 | 6.89 | 274 | 92.0 | 1.8 | 151 |
| *S. jagori* | 8.26 | 4.82 | 401 | 78.0 | 6.1 | 162 |
| *D. grisia* | 10.66 | 4.40 | 96 | 105.0 | 1.5 | 23 |
| *T. grayi* | 11.29 | 5.96 | 144 | 94.1 | 8.1 | 121 |
| *E. atrocostata* | 10.63 | 3.69 | 155 | 86.7 | 3.4 | 139 |
| *B. boulengeri* | 15.20 | 15.99 | 186 | 81.3 | 4.8 | 87 |
| *B. samarensis* | 5.62 | 2.01 | 81 | 50.7 | 2.3 | 43 |
| *O. cumingii* | 16.18 | 12.60 | 265 | 118.9 | 12.0 | 63 |

Table 19. Differences in insect mean food particle size between skink species pairs by analysis of variance [a] (F values).

| | M. m | M. c | L. p. | S. s. | S. j. | D. g. | T. g. | E. a. | B. b. |
|---|---|---|---|---|---|---|---|---|---|
| M. multifasciata | | 0.16 | **12.07** | 3.18 | 0.41 | 0.60 | 2.12 | **5.31** | 0.01 |
| M. multicarinata | | | 36.46 | 0.52 | 3.38 | **40.33** | 2.86 | 3.22 | 1.86 |
| L. pulchella | | | | **23.68** | 9.23 | 0.02 | **18.53** | **10.81** | **18.55** |
| S. smaragdina | | | | | 3.53 | 3.89 | 2.24 | 1.48 | 0.78 |
| S. jagori | | | | | | 0.68 | 0.05 | 0.05 | 1.80 |
| D. grisia | | | | | | | 0.34 | 0.51 | 1.57 |
| T. grayi | | | | | | | | 0.25 | 1.86 |
| E. atrocostata | | | | | | | | | 6.38 |
| B. boulengeri | | | | | | | | | |
| B. samarensis | | | | | | | | | |

[a] Sums of squares, simultaneous test procedure. Bold F values significantly different at a level less than .001.

Table 20. Mean volume of ingested food items by prey categories and percent of total volume of all foods eaten.

| Prey Category | Mean Prey Vol. $(mm^3$ per item) | Total Food Recorded $(mm^3)$ | Percent of Total Food |
|---|---|---|---|
| Mollusca | 41.3 | 326.3 | 2.8 |
| Isopoda | 6.8 | 27.81 | 2.4 |
| Chilopoda | 18.8 | 6.39 | 0.6 |
| Araneida | 3.5 | 10.46 | 0.9 |
| Insect Eggs | 0.4 | 0.24 | trace |
| Isoptera | 7.2 | 484.92 | 42.1 |
| Formicidae | 3.2 | 11.14 | 1.0 |
| Coleoptera | 9.6 | 22.84 | 2.0 |
| Lepidoptera | | | |
| larvae | 23.2 | 86.54 | 7.5 |
| adults | 20.1 | 18.49 | 1.6 |
| Diptera | 2.0 | 4.02 | 0.3 |
| Orthoptera | 51.8 | 318.57 | 27.7 |
| Sauria | 198.0 | 63.36 | 5.5 |
| Serpentes | 140.0 | 21.03 | 1.8 |
| Fruits | 55.9 | 42.48 | 3.7 |

Table 21. Seasonal insect abundance in local skink microhabitats.

| | Microhabitats | | | | | | | |
| | Field | | | Forest | | | | |
| Months | Open | Edge | Rocks | Trees | Crevices | Rocks | Litter | Trees |
|---|---|---|---|---|---|---|---|---|
| Jan. | 12.3 | 20.9 | 25.6 | 4.8 | 10.2 | 7.3 | 13.1 | 7.3 |
| Feb. | 8.9 | 22.1 | 8.9 | 5.3 | 9.6 | 8.2 | 25.1 | 8.2 |
| Mar. | 8.3 | 12.4 | 31.4 | 7.4 | 5.0 | 4.1 | 24.0 | 4.1 |
| Apr. | 13.6 | 54.0 | 4.0 | 1.7 | 5.1 | 9.1 | 9.1 | 9.1 |
| May | 31.6 | 27.9 | 5.8 | 2.7 | 2.3 | 5.1 | 15.3 | 5.1 |
| Jun. | 16.6 | 40.2 | 12.6 | 3.4 | 11.0 | 25.1 | 11.7 | 25.1 |
| Jul. | 14.0 | 14.2 | 19.7 | 6.2 | 3.0 | 13.8 | 19.7 | 13.8 |
| Aug. | 16.1 | 23.4 | 15.8 | 6.0 | 4.2 | 10.1 | 18.1 | 10.1 |
| Sep. | 26.8 | 21.3 | 12.4 | 6.5 | 4.5 | 6.3 | 18.5 | 6.3 |
| Oct. | 18.3 | 21.8 | 13.4 | 9.5 | 5.6 | 5.6 | 20.4 | 5.6 |
| Nov. | 17.2 | 20.1 | 20.0 | 7.8 | 6.0 | 6.2 | 17.5 | 6.2 |
| Dec. | 29.0 | 18.0 | 34.5 | 3.7 | 6.0 | 6.1 | 10.3 | 6.1 |
| Means | 17.7 | 24.7 | 15.3 | 5.4 | 6.0 | 8.9 | 16.9 | 8.9 |
| SD | 7.6 | 7.3 | 9.7 | 3.3 | 2.8 | 2.7 | 5.1 | 4.9 |

Table 22. Seasonal use of major food categories (all skink species combined)

| | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | 5 | 4 | 5 | 5 | | 1 | 1 | 3 | 3 | 13 | 1 | 8 |
| Araneida | 26 | 27 | 33 | 27 | 10 | 12 | 19 | 37 | 18 | 19 | 66 | 49 |
| Isoptera | 281 | 406 | 487 | 527 | 818 | 1059 | 525 | 384 | 130 | 365 | 671 | 470 |
| Coleoptera | 174 | 90 | 81 | 51 | 86 | 124 | 82 | 69 | 79 | 104 | 101 | 81 |
| Lepidoptera | 20 | 114 | 65 | 68 | 18 | 23 | 59 | 20 | 11 | 11 | 40 | 33 |
| Orthoptera | 33 | 62 | 51 | 185 | 37 | 64 | 23 | 46 | 36 | 44 | 75 | 61 |
| Oligochaeta | 2 | 3 | | | | | | 1 | 1 | 1 | 1 | 1 |
| Fruits | 7 | 7 | 13 | 3 | 9 | 1 | 10 | | 6 | 13 | 37 | 2 |

Table 23. Seasonal use of major food resources (by whole percent of category total).

| | Dry Cool | | Dry Warm | | Wet Warm | | Dry | Wet Warm | | Wet Cool | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
| Mollusca | 13 | 11 | 13 | 13 | | 3 | 3 | 8 | 8 | 34 | 3 | 21 |
| Araneida | 9 | 9 | 11 | 9 | 3 | 4 | 6 | 13 | 6 | 6 | 22 | 17 |
| Isoptera | 4 | 6 | 8 | 8 | 13 | 16 | 8 | 6 | 2 | 6 | 10 | 7 |
| Coleoptera | 15 | 8 | 7 | 4 | 7 | 11 | 7 | 6 | 7 | 9 | 9 | 7 |
| Lepidoptera | 4 | 24 | 14 | 14 | 4 | 5 | 13 | 4 | 2 | 2 | 8 | 7 |
| Orthoptera | 5 | 9 | 7 | 26 | 5 | 9 | 3 | 6 | 5 | 6 | 10 | 8 |
| Oligochaeta | 20 | 30 | | | | | | | 10 | 10 | 10 | 10 |
| Fruits | 8 | 8 | 15 | 3 | 10 | 1 | 12 | | 7 | 15 | 43 | 2 |

Table 24. Preference indices per month for selected prey categories of skinks living in secondary and primary Caramoan forests. Boldface values suggest prey selection; empy cells = 0.0.

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *S. jagori* | | | | | | | | | | | | |
| Araneida | **1.0** | | | | 0.15 | 0.13 | | **1.0** | 0.35 | 0.50 | | **1.5** |
| Formicidae | | **1.0** | **1.4** | 0.1 | | **1.4** | | 0.5 | 0.5 | 0.6 | | **1.9** |
| Coleoptera | **1.5** | 0.4 | | **1.2** | 0.8 | 0.9 | | 0.3 | 0.4 | | | 0.7 |
| Lepidoptera | **1.8** | 0.8 | | | 0.2 | | 0.5 | | | | | |
| Diptera | **1.6** | | **19.5** | | | | | | | **1.7** | **3.9** | |
| Orthoptera | **8.1** | 0.9 | **1.1** | | 0.6 | **1.3** | | **1.5** | **1.5** | **1.0** | **8.2** | **12.0** |
| *L. pulchella* | | | | | | | | | | | | |
| Araneida | **1.8** | 0.8 | | **1.6** | | **1.8** | **1.6** | **1.8** | | | | **1.6** |
| Formicidae | **1.1** | | | **1.3** | **2.3** | **2.9** | **1.3** | | **2.7** | **2.2** | 0.3 | **1.1** |
| Coleoptera | **1.8** | 0.3 | 0.1 | **2.2** | **1.7** | 0.8 | 0.4 | 0.1 | 0 7 | 0.1 | 0.1 | 0.7 |
| Lepidoptera | | **1.0** | | | 0.3 | | | | | **1.3** | **2.3** | **1.0** |
| Diptera | | | | **2.2** | | **2.7** | **1.6** | | **3.3** | **3.5** | | **1.1** |
| Orthoptera | **1.2** | 0.6 | | | 0.4 | 0.4 | **1.1** | | 0.2 | 0.6 | 0.8 | **1.2** |
| *M. multifasciata* | | | | | | | | | | | | |
| Araneida | **1.5** | **2.5** | | | **2.2** | 0.1 | | **1.0** | **1.9** | 0.4 | **1.4** | **1.4** |
| Formicidae | | | **4.0** | | | | | **2.3** | **1.0** | | | |
| Coleoptera | 0.6 | 0.4 | 0.4 | 0.1 | 0.5 | **1.4** | 0.9 | 0.3 | 0.2 | 0.4 | 0.3 | 0.1 |
| Lepidoptera | **1.7** | **3.9** | **1.0** | 0.7 | | 0.4 | **1.7** | 0.8 | 0.1 | 0.1 | 0.1 | 0.5 |
| Diptera | 0.1 | 0.8 | 0.2 | | 0.4 | 0.3 | 0.7 | 0.8 | | 0.2 | 0.2 | 0.3 |
| Orthoptera | | 0.1 | | **1.6** | 0.1 | | 0.1 | 0.2 | 0.3 | | 0.2 | 0.2 |
| *M. multicarinata* | | | | | | | | | | | | |
| Araneida | **1.0** | 0.2 | 0.4 | 0.5 | | **1.4** | **1.0** | **1.5** | **1.7** | 0.3 | **1.7** | 0.9 |
| Formicidae | | | | | | | | **2.3** | | **1.3** | **1.5** | |
| Coleoptera | 0.6 | 0.3 | 0.3 | 0.4 | | 0.2 | 0.5 | **1.0** | **1.0** | 0.4 | 0.5 | 0.2 |
| Lepidoptera | | 0.4 | 0.5 | 0.1 | 0.1 | 0.2 | 0.3 | **1.5** | | 0.6 | 0.7 | **1.8** |
| Diptera | **1.1** | 0.4 | **1.1** | | 0.3 | 0.4 | 0.2 | 0.1 | 0.1 | 0.5 | **1.0** | **1.7** |
| Orthoptera | | 0.3 | 0.2 | **1.0** | 0.1 | 0.3 | 0.2 | 0.8 | 0.4 | 0.3 | 0.1 | **1.2** |
| *L. smaragdina* | | | | | | | | | | | | |
| Araneida | **1.3** | | | | | | | | | | **1.7** | **1.3** |
| Formicidae | | 0.7 | 0.6 | 0.4 | 0.4 | **3.0** | | | 0.4 | | **2.9** | |
| Coleoptera | **1.5** | **1.0** | **1.4** | 0.2 | 0.2 | 0.3 | | 0.3 | | **1.0** | | 0.6 |
| Lepidoptera | | | **2.5** | 0.1 | 0.3 | **3.0** | | | | | | 0.3 |
| Diptera | **1.0** | 0.6 | 0.4 | **1.0** | | 0.6 | 0.2 | **1.7** | | **1.3** | **1.2** | |
| Orthoptera | | **3.7** | **1.5** | 0.2 | 0.2 | **1.0** | | | | **1.0** | **1.2** | 0.4 |

Table 25.  Percent of total major food categories found in all scincids examined*, compared with relative abundance (in %) if insects in the Caramoan area.

| Prey Taxa | Percent of Total in Stomachs | Percent of Total in Nature |
|---|---|---|
| Coleoptera | 10.7 | 12.3 |
| Orthoptera | 5.8 | 4.4 |
| Lepidoptera | 4.3 | 3.1 |
| Formicidae | 3.2 | 33.7 |
| Araneida | 2.8 | 2.7 |
| Diptera | 1.9 | 41.7 |

* Isoptera excluded because trapping technique seriously underestimates these organisms locally.

Table 26. Seasonal prey of *Brachymeles boulengeri* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | 2 | 1 | 1 | | | | | 1 | | 2 | | | 7 |
| Chilopoda | | | | 1 | | 3 | 4 | 7 | 3 | 3 | 1 | 1 | 23 |
| Araneida | | 2 | 2 | | 1 | 1 | | 1 | | 1 | | 1 | 9 |
| Isopoda | 7 | 11 | 21 | 2 | | 7 | 7 | 3 | 1 | | | 3 | 62 |
| Isoptera | 49 | 40 | 158 | 192 | 203 | 30l | 359 | 241 | | 144 | 10 | 261 | 1958 |
| Dermaptera | | | 4 | | | | | | 2 | 1 | | | 7 |
| Formicidae | | | | | | | 1 | 2 | | | | | 3 |
| Coleoptera | 6 | 4 | 7 | 2 | 4 | 8 | 5 | 9 | | 8 | | 2 | 55 |
| Lepidoptera | | | 1 | 3 | 1 | | 1 | 2 | 5 | | | | 13 |
| Diptera | 1 | 1 | | | | | | | | 1 | | | 3 |
| Orthoptera | 4 | | 1 | 4 | 1 | 8 | 1 | 1 | | | | | 20 |
| Oligochaeta | 1 | 1 | | | | | | 1 | | 1 | | | 4 |
| Sauria | 1 | 1 | | 1 | 1 | 1 | | 5 | 1 | 4 | | | 15 |
| Serpentes | | | | 2ᵃ | | 1 | 2 | 3 | 3 | 4 | | | 15 |
| Totals | 7l | 6l | 196 | 206 | 211 | 330 | 380 | 276 | 15 | 169 | 11 | 268 | 2194 |

ᵃ Including an egg.

Table 27. Seasonal prey of *Brachymeles samarensis* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | | | | | | | | | | 2 | | | 2 |
| Isoptera | 2 | 2 | 5 | | | 3 | 4 | 7 | 5 | 10 | 5 | 3 | 46 |
| Formicidae | | | 1 | 3 | 1 | 1 | | 1 | | | | | 7 |
| Coleoptera [a] | | | | | 1 | | | | | | | | 1 |
| Oligochaeta | 1 | 1 | | | | | | | | | 1 | | 3 |
| Total | 3 | 3 | 6 | 3 | 2 | 4 | 4 | 8 | 5 | 12 | 6 | 3 | 59 |

ᵃ larva.

Table 28.  Seasonal prey of *Emoia atrocostata* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Isopoda | 4 | | 1 | | 6 | | 1 | .3 | | .3 | | 2 | 20 |
| Decapoda | 19 | 18 | 27 | 13 | 15 | 20 | | 11 | 7 | 17 | 4 | 1 | 152 |
| Isoptera | | 1 | | | | | 5 | 18 | | | 4 | | 28 |
| Formicidae | | | | | | | | | | 5 | | | 5 |
| Coleoptera | 2 | | 1 | | | | 1 | | | | | | 4 |
| Lepidoptera | 1 | | | | | | | | | | | | 1 |
| Diptera | 1 | 1 | | | | | | | 1 | 2 | | 5 | 10 |
| Orthoptera | | | | 1 | | | | | | 1 | | | 2 |
| Polychaeta | 1 | | | | | | | | | | | | 1 |
| Pisces | | | | 1 | | | | | | | | | 1 |
| Sauria | 1 | | | | | | | | | | | | 1 |
| Totals | 29 | 20 | 29 | 15 | 21 | 20 | 7 | 32 | 8 | 28 | 8 | 8 | 225 |

Table 29.  Seasonal prey of *Sphenomorphus jagori* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | | | | 27[a] | | | | | | | | 5 | 32 |
| Isopoda | 12 | | 4 | 2 | 3 | 7 | 4 | 10 | 10 | 5 | 17 | 4 | 78 |
| Chilopoda | | | | | | | | | | | | 1 | 1 |
| Scorpionidae | | | | | 1 | | | 1 | | | 1 | | 3 |
| Araneida | 7 | | 13 | 1 | 1 | 2 | | 9 | 4 | 1 | 20 | 3 | 61 |
| Isoptera | 89 | 27 | 98 | 372 | 196 | 516 | 58 | 43 | 59 | 112 | 435 | 142 | 2147 |
| Hemiptera | | | 1 | | | | | | 2 | | | | 3 |
| Homoptera | | | | | | | | | | | 1 | | 1 |
| Formicidae | | 4 | 4 | 1 | | 4 | | 2 | 2 | 9 | 20 | 9 | 55 |
| Coleoptera | 6 | 6 | 12 | 12 | 8 | 13 | 1 | 3 | 8 | 10 | 31 | 7 | 117 |
| Lepidoptera | 3 | 5 | 11 | 6 | 1 | 4 | 1 | | 1 | | 6 | | 38 |
| Diptera | 1 | | 7 | | | | | | | 3 | 7 | | 18 |
| Orthoptera | 6 | 4 | 7 | 1 | 4 | 10 | 1 | 3 | 3 | 6 | 7 | 7 | 59 |
| Salientia | 1 | | | | | | | | | | | | 1 |
| Fruits | 3 | | | | 6 | | | | | 5 | 12 | 1 | 27 |
| Totals | 128 | 46 | 157 | 246 | 396 | 556 | 65 | 71 | 89 | 151 | 557 | 179 | 2641 |

[a] including eggs.

Table 30.  Seasonal Prey of *Tropidophorus grayi* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | 2 | | | | | | | | | 7 | | 1 | 10 |
| Isopoda | 3 | 5 | 3 | 1 | 6 | 2 | | | | | 4 | 14 | 38 |
| Chilopoda | | 1 | | | | | 1 | | 1 | 1 | 1 | 1 | 6 |
| Scorpionidae | | 5 | | | | | | | | | | | 5 |
| Araneida | | | | | 1 | | | | | | | | 1 |
| Isoptera | 38 | 4 | | | | 72 | | | 160 | | 3 | 3 | 280 |
| Formicidae | | 1 | | 2 | | | | | | 1 | 2 | | 6 |
| Coleoptera | 9 | 9 | | 1 | | 17 | 1 | 1 | | 17 | 1 | 3 | 59 |
| Lepidoptera | | 4 | 3 | 5 | 1 | | | | | | | 1 | 14 |
| Diptera | 1 | | | | | | | | 1 | | | 1 | 3 |
| Orthoptera | 1 | 5 | 4 | 4 | 3 | 2 | 1 | 1 | 1 | 2 | 1 | 4 | 29 |
| Oligochaeta | | 1 | | | | | | | | | | | 1 |
| Sauria | | | | | 1 | | | | | | | | 1 |
| Pisces | | 1 | 1 | 2 | 4 | 3 | | | | | | | 11 |
| Fruits | | | | | | | | | | 1 | | | 1 |
| Total | 54 | 36 | 11 | 15 | 16 | 96 | 3 | 2 | 163 | 29 | 12 | 28 | 465 |

Table 31.  Seasonal prey of *Lipinia pulchella* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | | | | | | | | | 3 | | | 1 | 4 |
| Scorpionida | | | 1 | | | 1 | | | | | | | 2 |
| Araneida | 1 | 1 | | 2 | 1 | 1 | 2 | 1 | | | 2 | 2 | 13 |
| Isopoda | | | | | 4 | 1 | 1 | | | | | | 6 |
| Insect eggs (sp?) | | | | | 61 | | | | | | | | 61 |
| Isoptera | 28 | 13 | 34 | 42 | 9 | 17 | 16 | | 6 | 10 | 11 | 31 | 217 |
| Dermaptera | | | | | | | | | | | 1 | | 1 |
| Hemiptera | | | | 1 | | 3 | 2 | | | | | 1 | 7 |
| Formicidae | 23 | | 1 | 7 | 14 | 73 | 21 | 1 | 23 | 28 | 2 | 18 | 211 |
| Coleoptera | 16 | 11 | 7 | 24 | 15 | 15 | 10 | 7 | 31 | 30 | 32 | 15 | 213 |
| Lepidoptera | | 1 | | | 1 | | | | | 1 | 3 | 1 | 14 |
| Diptera | | | | 1 | | 5 | 3 | | 2 | 3 | 3 | 4 | 21 |
| Orthoptera | 3 | 3 | | | 2 | 2 | 1 | | 3 | 5 | 4 | 3 | 26 |
| Fruit | | | | | 2 | | | | | | | | 2 |
| Total | 72 | 29 | 43 | 77 | 109 | 116 | 58 | 41 | 68 | 77 | 58 | 76 | 824 |

Table 32. Seasonal prey of *Mabuya multifasciata* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | | 2 | 1 | | | 1 | | 1 | 2 | 1 | 1 | 2 | 11 |
| Isopoda | 5 | 3 | | 7 | 1 | 5 | 5 | 8 | 25 | 36 | | | 95 |
| Chilopoda | | | | | | | | | 2 | 1 | .1 | | 4 |
| Araneida | 2 | 11 | | 1 | 4 | 1 | | 2 | 2 | 9 | 6 | 6 | 44 |
| Insect eggs | | | | | | | | | | 1 | | | 1 |
| Odonota | | | 1 | | | | | | | | | | 1 |
| Isoptera | 100 | 2 | 126 | 41 | 166 | 81 | 38 | 31 | 7 | | | 3 | 899 |
| Dermaptera | | | | 1 | | | | | | | | | 1 |
| Hemiptera | 1 | 1 | | | | | | 1 | 1 | 1 | 2 | 1 | 8 |
| Formicidae | | | 5[a] | | | | | 4 | 5 | | | 3 | 17 |
| Coleoptera | 27 | 24 | 34 | 14 | 47 | 49 | 52 | 26 | 10 | 16 | 21 | 3 | 323 |
| Lepidoptera | 16 | 85 | 21 | 4 | 6 | 27 | 16 | 4 | 4 | 21 | 4 | 10 | 218 |
| Diptera | 1 | 15 | 2 | 1 | 5 | 3 | 3 | 2 | | 1 | 3 | 10 | 46 |
| Orthoptera | 4 | 14 | 1 | 164 | 14 | 6 | 8 | 13 | 12 | 10 | 34 | 11 | 291 |
| Oligochaeta | | | | | | | | | 1 | | | 1 | 2 |
| Sauria | 1 | 1 | 2[a] | | | 1 | | | | | | | 5 |
| Fruits | | | 3 | | | 1 | | | | 5 | | | 9 |
| Total | 157 | 158 | 285 | 232 | 244 | 297 | 215 | 92 | 71 | 102 | 71 | 51 | 1975 |

[a] eggs

Table 33. Seasonal prey of *Mabuya multicarinata* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | | | | 1 | | | 1 | 1 | 1 | | | | 4 |
| Isopoda | 16 | 8 | 9 | 4 | | 2 | 6 | 35 | 18 | 10 | 5 | 16 | 129 |
| Phalangida | 2 | | | | | | | | | | | | 2 |
| Chelonethida | | 1 | | | | | | | 1 | | | | 2 |
| Scorpionida | | | | | | | | | 1 | | | | 1 |
| Araneida | 16 | 11 | 15 | 23 | 1 | 6 | 17 | 24 | 12 | 5 | 28 | 15 | 163 |
| Insect egg | | | | | 1 | | | | | | | | 1 |
| Collembola | | | | | | | 1 | 12 | 2 | | | | 14 |
| Odonata | | | | 1 | | | 1 | | | | 1 | | 3 |
| Isoptera | 10 | 316 | 63 | 50 | 58 | 133 | 44 | 45 | 51 | 89 | 199 | 36 | 1094 |
| Dermaptera | | 1 | | | | | 2 | 3 | 1 | | 1 | | 8 |
| Hemiptera | | | 2 | | 1 | 1 | 1 | | 1 | 1 | 2 | | 9 |
| Homoptera | 3 | | | 1 | | | 1 | 2 | | | | | 7 |
| Formicidae | | | | | | | | 1 | | 2 | 4 | | 7 |
| Coleoptera | 2 | 6 | 11 | 6 | 1 | 4 | 7 | 18 | 12 | 12 | 5 | 3 | 87 |
| Lepidoptera | | 6 | 11 | 1 | 1 | 1 | 7 | 2 | | 1 | 1 | 7 | 38 |
| Diptera | 5 | 4 | 6 | | 4 | 2 | 2 | 1 | 2 | 4 | 8 | 8 | 46 |
| Orthoptera | 2 | 20 | 6 | 17 | 3 | 11 | 10 | 28 | 17 | 15 | 22 | 16 | 167 |
| Total | 56 | 496 | 123 | 104 | 70 | 160 | 100 | 171 | 119 | 139 | 275 | 82 | 1782 |

Table 34. Seasonal prey of *Lamprolepis smaragdina* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | 1 | 1 | 3 | 1 | | | | | | 1 | | 1 | 8 |
| Isopoda | 1 | | | | | | | | | 5 | 1 | 1 | 8 |
| Chelonethida | | | | | | 1 | | | | | | | 1 |
| Scorpionida | | | | 1 | | | | | | | | | 1 |
| Araneida | 1 | | | | | | | | | | 6 | 1 | 8 |
| Odonata | | 1 | | 1 | | | | | | | | 1 | 3 |
| Isoptera | | | | | | | 1 | | | | 2 | | 3 |
| Hemiptera | | | | 1 | | | | | | | | | 1 |
| Homoptera | 1 | | | | | | | | | | | | 1 |
| Formicidae | | 4 | 3 | 2 | 5 | 2 | | | 1 | | 6 | | 21 |
| Coleoptera | 106 | 30 | 9 | 7 | 5 | 6 | 1 | 3 | | 7 | 9 | 47 | 230 |
| Lepidoptera | 13 | 16 | 32 | 5 | 10 | 23 | | | | 5 | 6 | 19 | 129 |
| Diptera | 5 | 4 | 4 | 6 | | 3 | 1 | 6 | | 9 | 12 | | 50 |
| Orthoptera | | 3 | 3 | 2 | 1 | 2 | | | | 2 | 4 | 3 | 20 |
| Sauria | | | 3 | | 1 | | | | 1 | 1 | 1 | | 7 |
| Fruits | 5 | 6 | 8 | 2 | 3 | | 10 | | 1 | 7 | 23 | | 65 |
| Total | 132 | 65 | 65 | 28 | 25 | 37 | 13 | 9 | 3 | 37 | 71 | 72 | 558 |

Table 35. Seasonal prey of *Dasia grisia* (total items/month).

| Prey | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Isopoda | | | | | .1 | | | | | | | | 1 |
| Araneida | | | | | | | | | | 2 | 2 | | 4 |
| Isoptera | | | | 9 | | 6 | | | 2 | | | | 17 |
| Hemiptera | | | | | 2 | | | | | | | | 2 |
| Formicidae | | | | | | | .9 | | | | | | 9 |
| Coleoptera | | | | 4 | 6 | 12 | 4 | 2 | 18 | 4 | 1 | 1 | 52 |
| Lepidoptera | | | 2 | | | 2 | | | 1 | 1 | | 2 | 4 |
| Orthoptera | | | | | | | | | | 1 | | | 1 |
| Sauria | | | | | | 1 | 1 | | | | | 1 | 3 |
| Fruits | 2 | 1 | | 1 | | | | | | 2 | 1 | | 7 |
| Total | 2 | 1 | 2 | 14 | 9 | 19 | 14 | 2 | 22 | 10 | 7 | 5 | 107 |

Table 36. Seasonal variation in abdominal fat (in g) of Caramoan skink species, by sex. Those species missing produce no abdominal fat accumulations. t = trace only.

| Species | Sex | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *E. atrocostata* | F | 0.2 | 0.1 | 0.2 | t | t | t | 0 | 0.4 | 0.2 | 0.5 | 0.3 | 0.3 |
| | M | 0.4 | t | 0.1 | 0 | t | t | 0 | 0.4 | t | 0.5 | 0.3 | 0.6 |
| *M. multicarinata* | F | 0.5 | 0.5 | 0.4 | 0.1 | t | t | .3 | t | 0.5 | 0.2 | 1.2 | 0.7 |
| | M | 0.2 | 0.3 | 0.1 | 0.1 | t | 0 | 0 | 0.2 | 0.6 | 0.3 | 0.9 | 0.4 |
| *M. multifasciata* | F | 0.7 | 0.5 | 0.8 | 0.3 | 0.2 | t | t | 0.8 | 0 | 1.0 | 0.9 | 0.7 |
| | M | 0.1 | 0.3 | 0.3 | 0. | t | 0 | .2 | 0.6 | 0.6 | 0.5 | 0.6 | 0.5 |
| *L. smaragdina* | F | 0.2 | 0.3 | 0.2 | t | 0.1 | t | 0 | 0.2 | 0.1 | 0.3 | 0.3 | 0.3 |
| | M | 0.4 | 0.2 | 0.1 | 0.1 | 0.5 | 0.2 | 0.3 | 0.2 | 0.4 | 1.0 | 0.4 | 0.8 |
| *D. grisia* | F | 1.5 | 0.5 | t | 0.2 | 0.4 | 0.9 | 2.5 | 1.0 | 0.3 | 0.9 | 2.5 | 1.6 |
| | M | 0.9 | 0.1 | t | 0.2 | 0.3 | 0.1 | t | 0.9 | t | 0.5 | 1.6 | 1.6 |

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