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REPRODUCTIVE PATTERNS IN SYMPATRIC PHILIPPINE SKINKS (SAURIA : SCINCIDAE)

Walter Auffenberg and Troy Auffenberg*

ABSTRACT

The reproductive biology of 11 species of geographically sympatric scincid lizards was studied in southern Luzon, Philippines. These are *Mabuya multicarinata, Mabuya multifasciata, Lipinia pulchella, Lamprolepis smaragdina, Sphenomorphus jagori, Dasia grisia, Otosaurus cumingii, Emoia atrocostata, Brachymeles samarensis, Brachymeles boulengeri*, and *Tropidophorus grayi*. Collectively they represent a broad range of local microhabitats, life styles (arboreal to fossorial), and sizes (among the smaller skink species of the world to some of the largest). Analyses were based on a total of 3252 adult individuals collected in more or less equal samples monthly over an entire year. Testis size, follicular development, oviductal eggs, body fat, skin color, and activity patterns were all investigated in the context of season, climate, sex, and size.

The results suggest that there is great diversity in reproductive strategies represented by the 11 species studied. This diversity in reproductive mode and timing is much greater than expected on the basis of published summaries, statements of general principal, or theoretical models of tropical lizard biocoenoses. It is clear that we are still far from understanding those factors that dictate clutch size and timing of cycles in tropical lizards. Cues triggering seasonal reproductive phases must either be numerous or reacted to in totally different ways by sympatric species. Many more data are needed on other tropical lizard communities before we can begin to unravel the complexity of the signals to which these lizards are responding and the physiological responses elicited by those cues. We found almost every conceivable type of annual reproductive strategy represented. Some species are egg-layers and others live bearers; some breed continuously throughout the year, whereas others are periodic. Those that are periodic have either one or two reproductive peaks, and these may fall at entirely different times of the year, despite their geographic and broad ecological sympatry. Even within specific microhabitats, patterns are remarkably variable among the resident species. There is no evidence for a single tropical forest reproductive pattern. There is, however, a tendency for reproduction to be collectively highest during and immediately after both the first (June-July) and second (September through December) monsoons. In general, reproduction is collectively lowest during the dry months preceding each of the monsoon periods.

There is no significant correlation between number of eggs (young)/clutch and habitat, female size, or reproductive mode. There are, however, two basic strategies represented in regard to number of eggs (young)/clutch. In one group, species lay consistently small clutches; in

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the other group, species lay significantly larger clutches. All oviparous species belong to the last group; viviparous species occur in both groups.

Several of the scincids studied show significant seasonal change in coloration of both males and females. These can be correlated with the reproductive period and are believed important in this context. The frequency of these color changes in members of the family Scincidae is somewhat surprising in view of the fact that these lizards are generally considered more scent- than sight-oriented. This may be a phenomenon of tropical Asian skink communities, where sympatric species are more numerous than in temperate forests, where most previous studies of skinks have occurred.

RESUMEN

Se estudió la biología reproductiva de once especies simpátricas geográficamente de lagartijas scíncidas en el sur de Luzón, Filipinas. Las especies son *Mabuya multicarinata, Mabuya multifasciata, Lipinia pulchella, Lamprolepis smaragdina, Sphenomorphus jagori, Dasia grisia, Otosaurus cumingii, Emoia atrocostata, Brachymeles samarensis, Brachymeles boulengeri,* y *Tropidophorus grayi.* En conjunto estas especies representan una amplia variación de microhabitats locales, hábitos (arborícolas a fosoriales), y tamaños (el grupo incluye desde algunas de las especies de scíncidos más pequeñas del mundo hasta algunas de las más grandes). El análisis se basó en un total de 3252 individuos adultos colectados en muestras más o menos iguales cada mes a lo largo de un año. Se registraron el tamaño de los testículos, desarrollo folicular, huevos en el oviducto, grasa corporal, color de la piel y patrones de actividad, en el contexto de época del año, clima, sexo, y tamaño.

Los resultados sugieren que hay una gran diversidad entre las estrategias reproductivas representadas por las once especies estudiadas. Esta diversidad en patrones y ciclos reproductivos es mucho mayor que la esperada sobre la base de reportes publicados, principios generales, o modelos teóricos de biocenosis de lagartijas tropicales. Es evidente que aún estamos lejos de comprender los factores que controlan el tamaño de nidada y los ciclos en lagartijas tropicales. Las señales ambientales que desencadenan las fases estacionales reproductivas deben ser numerosas, o tal vez las especies simpátricas reaccionan de maneras totalmente diferentes a señales similares. Se necesita aún mucha más información sobre otras comunidades de lagartijas tropicales para empezar a aclarar la complejidad de los factores a los que estos reptiles responden y las respuestas fisiológicas causadas por estas señales. Encontramos casi todos los tipos concebibles de estrategias anuales reproductivas. Algunas especies ponen huevos y otras son vivíparas; algunas se reproducen continuamente a lo largo del año, mientras otras lo hacen periódicamente. Estas últimas muestran uno o dos picos reproductivos, que pueden ocurrir en momentos totalmente diferentes en el año, a pesar de su amplia simpatría ecológica y geográfica. Aún dentro de microhabitats específicos, los patrones varían notablemente entre las especies residentes. No hay evidencia de que exista un solo patrón reproductivo para el bosque tropical. Sin embargo, hay una tendencia hacia una mayor incidencia reproductiva colectiva durante e inmediatamente después del primer (Junio-Julio) y segundo (Septiembre a Diciembre) monzones. En general, el punto más bajo de reproducción colectiva ocurre durante los meses secos que preceden a cada periodo de monzón.

No hay una correlación significativa entre el número de huevos (crías)/nidada y habitat, tamaño de la hembra, o tipo de reproducción. Sin embargo, hay dos estrategias básicas en relación con el número de huevos (crías)/nidada. En un grupo, las especies ponen nidadas pequeñas uniformemente; las especies en el otro grupo ponen nidadas significativamente mayores. Todas las especies ovíparas pertenecen al segundo grupo; las vivíparas ocurren en ambos grupos.

Varios de los scíncidos estudiados muestran un cambio significativo en la coloración tanto de machos como de hembras. Estos cambios pueden estar correlacionados con el periodo reproductivo y se cree que son importantes en ese contexto. La frecuencia de estos cambios de color en miembros de la familia Scincidae es relativamente sorprendente en vista del hecho de que se considera que estas lagartijas se orientan por el olfato, más que por la vista. Este puede ser un fenómeno particular de las comunidades de scíncidos de Asia tropical, donde las especies simpátricas son más numerosas que en bosques templados, donde se han realizado la mayoría de los estudios sobre scíncidos.

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INTRODUCTION

The present publication is the second part of a study of tropical forest scincids of Luzon Island, Philippines. The first (Auffenberg and Auffenberg 1988) dealt with feeding biology of sympatric species, whereas this one stresses their reproductive strategies. In the current study, we examined aspects of the reproductive biology of 11 geographically sympatric species in southern Luzon, in which the major goal was to obtain empirical quantitative data on their annual reproductive cycles. The most important question in this study was, "In what ways do these skinks vary in responses to annually changing environmental factors, even though these may be slight in this tropical area?". Most studies published on scincid reproduction are of single species; only a few compare sympatric forms, and none has explored broader patterns 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 reproductive biology.

Most of our knowledge of the reproductive patterns of lizards is based on studies of temperate iguanids and lacertids. Much less is known of these patterns in tropical lizards, and especially scincids. On the other hand, the annual reproductive activity of temperate scincids is understood in at least broad outline. All the temperate scincid species studied so far have restricted breeding seasons, though of varying length (Kehl 1944; Mount 1963; Guillette 1983). The testes of males have been shown to fluctuate cyclicly in size and in spermatogenic activity. Similarly, ovarian development is rhythmic, and all the females generally oviposit during the same several months.

Few investigations have been conducted on the annual breeding activity of tropical skinks (India, *Mabuya macularis*, McCann 1840; Africa, *M. spilogaster*, *M. occidentalis*, and *M. variegata*. Huey and Pianka 1977. *M. buettneri*, *M. maculilabris*, and *Panapsis nimbaensis*, Barbault 1974a, b; *Mabuya striata* and *M. quinquetaeniata*, Simbotwe 1980; Australia, Wilhoft and Reitter 1965; Philippines, *Emoia atrocostata*, Alcala and Brown 1967, the same species, plus *Lamprolepis smaragdina* and *Mabuya multifasciata*, Alcala 1966; South Pacific, *Emoia werneri* and *E. cyanura*. Baker 1947; Surinam, *M. mabouya*, Hoogmood, 1973; and Brazil, *Mabuya heathi*, Vitt and Blackburn 1983). Of these studies, the only ones that compare geographically sympatric species are those by Huey and Pianka, Baker, Wilhoft and Reiter, Alcala, and Barbault. Most tropical scincids studied live in savanna or thorn brush habitats. Only the studies of Baker (1947), Alcala (1966), Inger and Greenberg (1966), and Barbault (1974a, b) include tropical forest-dwelling species.

Fitch (1982) concluded that tropical reptiles possess a much wider variety of reproductive strategies than would be found in temperate species. Vitt (1986) reported nearly every known lizard reproductive strategy among sympatric lizards in a tropical semi-arid environment in Brazil. Barbault (1974a,b, 1983) believed there are two major reproductive patterns among tropical lizards. Those living in seasonal tropical environments tend to produce one, or at most only a few clutches during a limited part of the year, and their reproductive effort is proportional to average snout vent length of the females--a pattern typical of temperate lizards. The second tropical pattern he recognized was said to occur only in aseasonal environments. Here females tend to produce many small clutches throughout the year, and the number of eggs per clutch is not correlated with female snout vent length. Contrary to Barbault's findings (based mainly on African lizards), our results show that there is no single reproductive pattern among scincids living in wet tropical evergreen forests, but a number of patterns. This is in agreement with the conclusions of Fitch (1982) and Vitt (1986).

The present publication also addresses questions relating to the kind and degrees of seasonal changes in coloration of adult scincid males and females in a tropical forest setting. Normally scincids are believed to be largely scent-oriented, and coloration as either an intra- or interspecific discriminatory factor is not as generally associated with species in this family as with those of agamids and iguanids. Both seasonally and sexually correlated color patterns have been well demonstrated in many species of the last two families, as well as the teiids and the lacertids. In general, they have received little attention from ethologists and reproductive physiologists in the case of scincids. This is the first time that seasonal color changes have been studied in a community of tropical skinks.

To place the results in a proper comparison context, the general characteristics of the species with which we worked that are believed to have bearing on their reproductive strategies are summarized below. Unless otherwise stated, the latest review of the taxonomy and distribution of the skinks examined occurs in Brown and Alcala (1980).

Emoia atrocostata Lesson.-- A moderate-size species of the genus, with no Luzon congenerics. Caramoan females are larger than males ($P = 0.05$, X SVL females 88.2 ± 2.1 mm, X Wt. 12.6 ± 1.1g, N = 119; males 84.2 ± 3.3 mm, X Wt 10.9g, N = 60). Mean hatchling size is 35 mm (N = 6). 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.

Dasia grisia (Gray).-- A large member of the genus, with only one species on Luzon. In Caramoan the sexes are not significantly different in either length or weight (adult X SVL 105.0 ± 1.5 mm, X Wt 24.3 ± 4.1 g, N = 23). No hatchlings were found. It is widespread in the Philippines and has previously been reported from Luzon, though considered uncommon. Brown and Alcala (1980) reported finding individuals 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 sea level to 250 m, but always in relatively disturbed forest.

Lamprolepis smaragdina philippinica (Mertens).-- This is a relatively large species of the genus, with no congenerics on Luzon. In the Caramoan area the sexes are not significantly different in either length or weight (adult X SVL 92.0 ± 1.8 mm, X Wt. 18.6 ± 0.6 g, N = 151). The species is widespread in the Philippines and has previously been reported from Luzon. 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 Caramoan lizards.

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 X SVL 38.1 ± 0.8 mm, X Wt 0.6 g, N

= 106). Mean neonate SVL is 21.1 mm (N = 6). It has been reported from most northern Philippine islands south to Leyte, including the Caramoan area. We found it common on exposed tree trunks and 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 two congenerics on Luzon. There is no significant sexual difference in either length or weight. However, in the Caramoan area this species is somewhat smaller than reported elsewhere in the Philippine Islands (adult X SVL in study area 90.5 ± 2.0 mm, X Wt 22.6 ± 2.2 g, N = 135). 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 1200 m.

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 X SVL 71.0 ± 2.5 mm, X Wt 11.5 ± 0.8 g, N=160). Mean neonate SVL locally is 28.5 mm (N = 8). 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 only 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 mean Wt of 1.9 ± 0.6 g, N=43. Neonates have a mean SVL of 28.0 mm (N = 3). Locally this species is found from sea level to 100 m, under leaves, vegetation mats on logs and rocks, and in rotten logs in both primary and secondary forests. It has been previously reported from southeastern Luzon. Two other species are reported from the same island, but only one other 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 X SVL 86.3 ± 3.0 mm, X Wt 13.9 ± 0.8 g, N = 97; male X SVL 77.0 ± 3.0 mm, X Wt 11.0 ± 1.0 g, N = 90). 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 X SVL 76.0 ± 6.1 mm, N = 162; adult females X SVL 75.0 ± 5.1 mm, X Wt 13.9 ± 0.9 g, N = 41; males X SVL 81.1 ± 4.1 mm, X Wt 15.8 ± 0.8 g, N = 121). Mean hatchling SVL = 29.4 mm (N = 5). It is widely distributed in the archipelago and has previously 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 also clambers actively 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 (*P* = < 0.05) in either SVL or Wt; adult X SVL 94.1 ± 8.1 mm, X Wt 18.9 ± 4.8 g, N = 121. Neonates have a X SVL of 28.3 mm (N = 5). It is widely distributed in the Philippines and has previously been reported from Luzon. Locally it is found mainly in holes in banks and under boulders 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 (*P* = < 0.05) 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). Two hatchlings had SVL's of 34.1 and 31.0 mm. Widely distributed in the Philippines, this species has previously been reported from Luzon. Locally it is found on rocks at the base of large boulders and cliffs, sometimes along 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.

A discussion of the relevance of mean body size distributions in this skink community is discussed in Auffenberg and Auffenberg (1988).

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Thanks are extended to the Philippine government for allowing this study to be conducted and to the citizens of the Caramoan Municipality for their cooperation during its tenure. Steve Alba, Forest Development Office, Naga District, obtained much of the data on densities and activity patterns of skinks. Sam Telford, Florida Museum of Natural History read an early draft and corrected many of our errors, for which we are very thankful. Finally, it is impossible to express our gratitude to Elinor and Garth Auffenberg. Without their massive assistance throughout all phases of the study in the field, the analyses and ideas expressed in the following pages would have been completely impossible. We extend to them both our deep appreciation for the countless hours they spent in behalf of the project.

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 1982-August 1983) 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*. Collection of most individuals was 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. The climatic year can be divided into four seasons. Though rain fall is relatively high all year (Fig. 1), some seasons have less than others, and this forms the basis for the four annual climatic phases recognized here: January through May has the least rainfall (= dry period I in the following pages); during June and July the southwest monsoon sweeps over the area (= monsoon I); August is an intermonsoon "dry" period (dry period II); September through December is the time of highest rainfall and most severe storms (monsoon II). Total annual rainfall is 2858 mm. Other details regarding the local vegetation, topography and climate are available in Auffenberg (1988) and Auffenberg and Auffenberg (1988).

Individuals utilized in the study were collected on a monthly basis. These were immediately killed by injecting a very small amount of alcohol into the brain. The specimens were then measured (hereafter snout-vent length = SVL, total length = TL) to the closest mm and weighed to the closest 0.1 g (= Wt hereafter). They were then preserved by fixing in 10% formalin. Several days after preservation the following data were recorded: gonadal state (testes diameter and weight); presence, number, diameter, state (yolked or not) of ovarian eggs; number, diameter, state (shelled or not) and weight of oviductal eggs (SVL of embryos if ovoviviparous), and any evidence of recent release of oviductal eggs were recorded; body fat was weighed to the closest 0.1 g, and, finally, certain colors and patterns of possible significance in indicating breeding readiness as well as sex and collection data were also recorded.

All similar data for each species per month were combined to obtain means and standard errors/deviations. One-way ANOVAs were performed to determine significant changes throughout the year (Sokal and Rohlf, 1981).

The total numbers of individuals of each species examined for reproductive state are: *E. atrocostata* 318, *L. smaragdina* 358, *B. samarensis* 43, *B. boulengeri* 350, *M. multifasciata* 378, *M.*

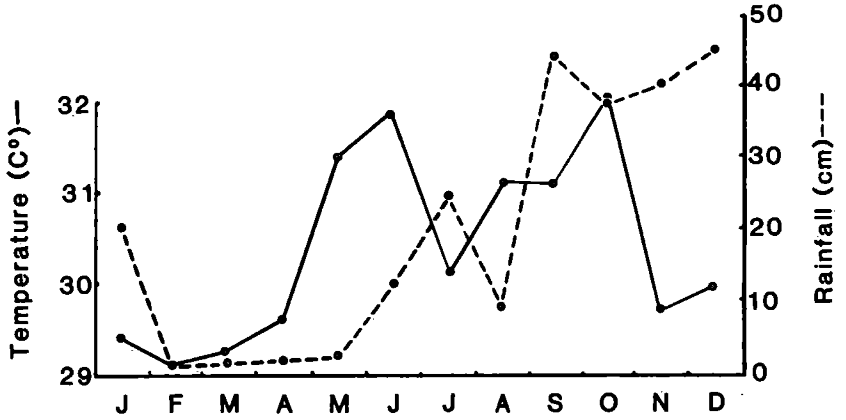

Figure 1. Annual temperature and precipitation cycles, Terogo, Caramoan, Luzon.

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.

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 several stations near the base camp. These were left for an entire day and collected in the late afternoon. The trapped insects were then 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 density.

Throughout the text, figures, and tables standard symbols are used for the mean (X), sample size (N), standard error of the mean (SE), standard deviation (SD), correlation coefficient (R^2), and Spearman rank correlation coefficient (R_s). If ± not defined, standard deviation is meant.

RESULTS

Female Reproductive Patterns

Female skink reproductive patterns in the Caramoan area are presented below. Figure 2 shows the percent of the monthly total of females of each species that possessed eggs/embryos in the oviducts.

Mabuya multifasciata.-- We measured 81 females (SVL 45.5-117.0 mm) and examined their ovaries and oviducts. The smallest lizard with yolking ovarian follicles was 72.7 mm SVL and the smallest with oviductal eggs was 101.0 mm; thus sexually mature females are > 72 mm. Follicles begin to accumulate yolk at a diameter of about 3.0 mm (as determined by macroscopic observation) and reach at least 7.0 mm before they are ovulated. The largest ovarian follicle was 10.3 mm and the smallest oviductal egg was 7.0 mm. The

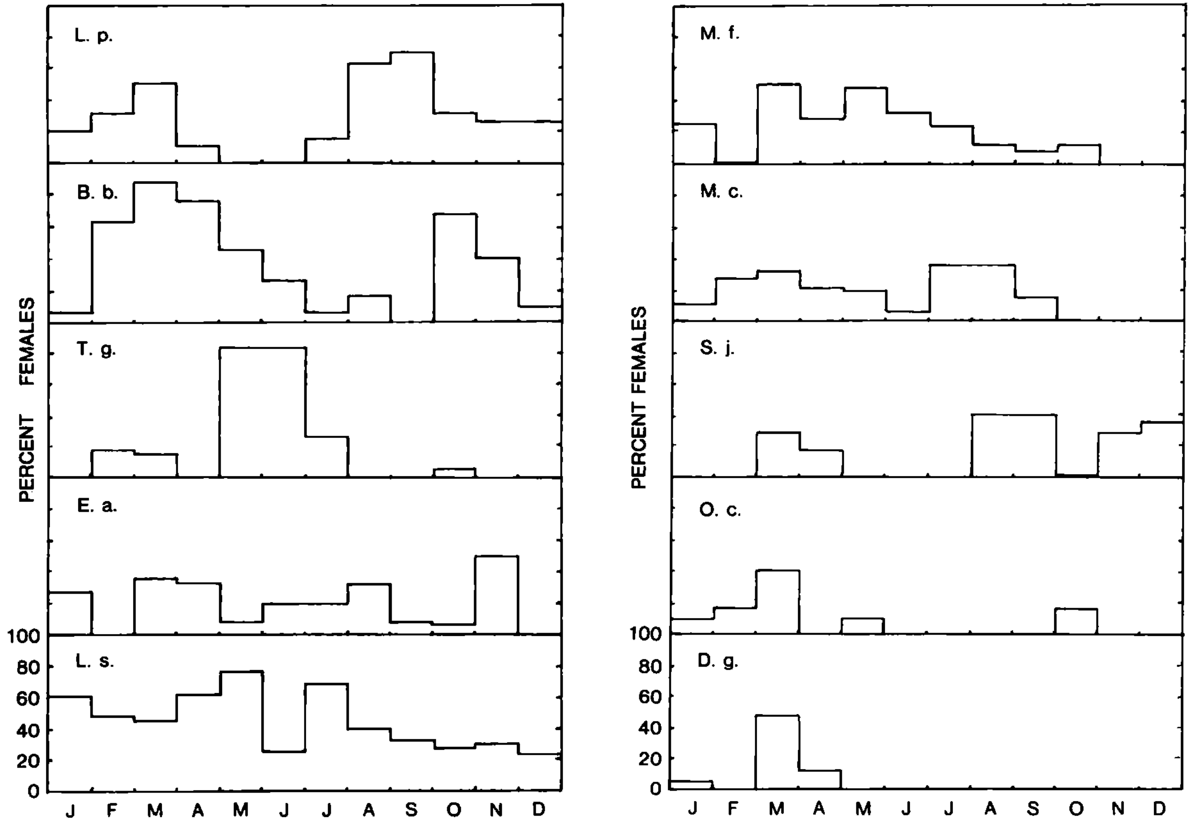

Figure 2. Seasonal variation (in %) of females taken each month with embryos/eggs in the oviducts. Abbreviations and numbers examined (N) are: B. b., *Brachymeles boulengeri* (N=52); D. g., *Dasia grisia* (N=13); E. a., *Emoia atrocostata* (N=52); L. p., *Lipinia pulchella* (N=57); L. s., *Lamprolepis smaragdina* (N=62); M. f., *Mabuya multifasciata* (N=81); M. c., *Mabuya multicarinata* (N=76); O. c., *Otosauria cumingii* (N=28); S. j., *Sphenomorphus jagori* (N=76); T. g., *Tropidophorus grayi* (N=73).

species is a live-bearer, producing from 1 to 8 young at a time (X = 4.2, SD 1.3), mode 4. (Alcala 1966 reported a range of 2-7 on Negros Island, Philippines.)

Females contain vitellogenic ovarian follicles all months except March, May, July, September, and October. Oviductal eggs/embryos were found during most months except November and December. These data suggest that mature females may have several broods each year. The number of mature females containing embryos per month comprised from 0 to 54.5 percent of the total monthly samples; highest values (50.0-54.4) occur during dry season I (March to May), and the lowest values during monsoon II (September through December). Whereas some young are produced throughout most of the year, the annual reproductive pattern is strongly modal (Fig. 2) in the sense that there is a clearly defined annual reproductive peak, followed by a resting phase. We found neonates only from early April through May, though some may be found later in the year.

Mabuya multicarinata.-- We measured 76 females (SVL 41.8-80.5 mm) and examined their ovaries and oviducts. The smallest lizard with oviductal eggs was 56.0 mm SVL, and the smallest with vitellogenic ovarian follicles was 53.9 mm. Sexually mature individuals are estimated > 56 mm. The species is oviparous, with the number of eggs per clutch varying from 1 to 3 (X = 2.0, SD 0.3), mode 2. It is likely that mature females lay several clutches annually. Vitellogenesis begins when follicles are about 3.0 mm. Vitellogenic ovarian follicles occur in all months except November through January. They are ovulated at a diameter of 9 to 10 mm; one was found loose in the coelom that measured 9.5 X 5.3 mm. Oviductal eggs (shelled or not) are found every month except November and December. The smallest oviductal eggs are 10 X 6 mm, and the shell is formed at a size of about 11 X 8 mm, or when the egg weighs about 0.7 g. They are laid when their length is 12.8 to 14.1 mm.

The percent of gravid females in the monthly samples varied from 0 to 36.3. The annual pattern (Fig. 2) is bimodal. A weak, flat pulse occurs during dry period I (February through May), but a stronger pulse occurs at the end of monsoon I (July) and through the following dry period II (August). No eggs are laid in November and December, or during the heaviest rains of monsoon II.

Newly hatched young are found in September and October, and May and June--the former during the early rains of monsoon II and the latter during dry period I. Thus one batch of young is born during a rainy period and the other during a dry one.

Sphenomorphus jagori.-- We measured 76 females (SVL 40.6-88.9 mm) and examined their ovaries and oviducts. The smallest lizard containing oviductal eggs was 70.2 mm SVL and the smallest having yolking ovarian follicles was 71.8 mm SVL. We have therefore used the SVL of > 70.2 mm as the approximate size of sexual maturity. Ovarian follicles begin to accumulate yolk at about 2.5 mm diameter and reach a diameter of at least 9 mm before being ovulated. The largest ovarian follicle measured 9.0 mm and the smallest oviductal egg 12.8 mm. Eggs are laid when about 18 X 8.6 mm and have a wet mass of 11.5 g. The new batch of ovarian follicles grow to about 8 to 9 mm before the oviductal eggs are laid, suggesting that this species has multiple annual clutches. Each clutch contains 1 to 4 eggs (X = 1.9 ± 0.3), mode 2.

The annual reproductive pattern is similar to that of *Mabuya multicarinata* in being mainly bimodal, although the peaks are more clearly defined (Fig. 2). The annual resting periods are January through February, and May through July. Except for October, gravid females are common throughout the year. March and April represent a second, less important peak period of gravid females before the resting phase during dry period I and monsoon I. Gravid females represent from 0 to 40 percent of the total monthly samples during the year (Fig. 2). Unlike the local *Mabuya* species, *S. jagori* produces no abdominal fat bodies.

Hatchlings were collected from the middle of October to January, and from the middle of May to near the end of June. Thus the early clutches produce young during a dry season and the late clutches during a wet season.

Lipinia pulchella.-- We measured 57 females (SVL 21.3-43.2 mm) and examined their ovaries and oviducts. The smallest lizard with oviductal eggs was 35.2 mm SVL, and the smallest with yolking follicles was the same length. Sexually mature individuals are estimated to be > 35 mm SVL.

The species is oviparous, with from 1 to 2 eggs per clutch (X = 1.8 ± 0.4), mode 2. Yolking follicles (> 2 mm diameter) are found every month. They are ovulated at a diameter of about 7.5 mm. The smallest oviductal eggs are 7.2 mm. Oviductal eggs occur all months except April, June, and July. The size of shelled oviductal eggs varies from 8.5 mm to 10.5 mm, with a mean wet mass of 0.04. Laid eggs are about 10.5 mm long, with an overall range within a single clutch of about 1 mm.

Gravid females constitute from 0 to 72.7 percent of the monthly mature females collected (Fig. 2). The greatest number of gravid females occurs in August and September (after monsoon I). A second, lower peak occurs in the early part of dry period I (February, March). There is no fat accumulation in the abdominal cavity at any time of the year. In the Caramoan area neonates are seen from October through May.

Brachymeles boulengeri and *B. samarensis*.-- Based on an examination of 52 female *B. boulengeri* and 21 female *B. samarensis*, we conclude that these species have nearly identical reproductive patterns (Fig. 2), and only the former will be described in detail. Both produce living young, in *B. boulengeri* from 1 to 5 (X = 3.1 ± 0.9), mode 4, and in *B. samarensis* from 1 to 2. In *B. boulengeri* yolking follicles are recorded for all months except May and June and are ovulated at a diameter of about 8.5 mm. Embryos have absorbed almost all their yolk when SVL is about 34 mm and therefore assumed to be near-term.

Percent of gravid females per month varied from 0 to 88.2 of the total monthly female sample individuals collected (Fig. 2). The pattern is distinctly bimodal, with the most important peak for gravid females occurring from February through June (entire dry period I). The second peak occurs during monsoon II. Thus young are produced during one dry and one wet period per year.

There is no fat accumulation in the abdominal cavity of either species during any time of the year. Neonates are seen in all months except July through September.

Tropidophorus grayi.-- We measured 73 females and examined their ovaries and oviducts. The smallest lizard with oviductal eggs was 85.0 mm, and the smallest with yolking ovarian follicles was 85.2 mm SVL. Sexually mature individuals are estimated > 85 mm SVL. The species bears living young, having from 1 to 8 (X = 3.8 ± 1.1), mode 4. Vitellogenic ovarian follicles occur during all months except September through November and are ovulated at a diameter of about 11 mm. Embryos, believed to be near-term, have absorbed most of their yolk when they attain an SVL of about 31 mm.

From 0 to 85.7 percent of the monthly total female sample are gravid each month (Fig. 2). The annual female reproductive pattern is essentially unimodal, with the high peak in May and June (end dry period I and beginning of monsoon I, Fig. 2). A much lower pulse occurs in dry period I. The non-reproductive period is long, about one half year, from August through January . In this species young are produced chiefly during the dry periods, probably because it lives along small mountain streams that become torrents during the wet periods. Neonates are seen from March through June. Abdominal fat is not accumulated at any time.

Otosaurus cumingii.-- We measured 28 mature females (SVL 91.1-142.0 mm) and examined their ovaries and oviducts. The species is oviparous, laying from 2 to 3 eggs per clutch (X = 2.1 ± 0.3), mode 2. SVL at sexual maturity is > 110 mm. Yolking follicles are about 3.0 mm in diameter and occur January through May, and in October. Ovarian follicles are 11 to 14 mm when ovulated. The largest is 14.1 mm and the smallest oviductal egg 11.9 mm. Oviductal eggs are completely shelled at about 21 mm diameter. Eggs are laid when longer than 29.5 mm.

The percent of gravid females per month varies from 0 to 41.7 (Fig. 2). The annual female reproductive pattern appears to be weakly bimodal. Most females are gravid during dry period I (February and particularly March). A second, low peak of gravidity occurs during October (early monsoon II). There is a long resting period for almost all females from April (June ?) through September and a short one during November and December. Thus, most production of young occurs during the cool, dry season. Neonates are seen during April and May. There are no abdominal fat bodies.

Dasia grisia.-- Only 13 females were available for measurement and examinations of ovaries and oviducts. The species is an egg layer, with clutch size varying from 2 to 5 (X = 3.3 ± 1.5, mode 3).

Relatively few gravid females (8) were found, almost all in February through April (Fig. 2). Although many more data are needed for confirmation, we believe that breeding in this species is seasonal, probably with a short reproductive peak during the cool, dry period. There is apparently a very long resting phase of at least 8 months for most females. The species clearly needs additional study.

Young of the year were seen only in May. Fat accumulation is not well documented, but seems erratic, occurring throughout the year except during April and May, when it is depleted to a certain extent. This suggests that the fat cycle may be related to the reproductive cycle (see below), but this requires additional study.

Emoia atrocostata.-- We measured 52 mature females and examined their ovaries and oviducts. The reproductive cycle of this species in the Philippines has been studied by Alcala (1966) on Negros Island, and the Caramoan pattern is very similar.

The species is oviparous, with clutches varying from 1 to 3 at Caramoan (X = 2.0 ± 0.4), mode 2. The smallest female with vitellogenic ovarian follicles is 71.3 mm SVL, suggesting that females are sexually mature at SVL > 71 mm. Gravid females are found in almost every month of the year (Fig. 2), with the percent gravid of the total varying from 0 in December and February to 50.0 in November. The annual cycle is possibly weakly modal; the highest peak occurs in November. It is clearly an almost continuous breeder in the Caramoan area.

Yolking follicles are found every month except November. They are ovulated at about 10.2 mm diameter. The smallest shelled eggs in the oviduct are 13 mm and have a mass of 0.8 g. Neonates are seen from April through November, or two thirds of the year.

Most abdominal fat is accumulated after the low-peaked spring breeding season, with the highest values in May and June (Table 2). The least fat occurs in December, following the peak reproductive period in November. Thus, abdominal fat is lowest following one peak and highest just below another.

Lamprolepis smaragdina.-- The reproductive cycle of this species also was studied by Alcala (1966) on Negros Island. Its cycle in Caramoan is similar. We measured 52 mature females and examined their ovaries and oviducts during the present study. The smallest lizard with yolking follicles was 83.0 mm, and the smallest with oviductal eggs was 82.5 mm SVL. One to two eggs are laid in a single clutch (X = 1.9 ± 0.3), mode 2. Yolking follicles were found every month and are ovulated at a diameter of about 12.7 mm (N = 2). Oviductal eggs are completely shelled at a length of about 16.2 mm and are laid when about 22.7 X 10.5 mm.

Gravid females are found every month of the year, representing from 2.2 to 77.8 percent of the total monthly female samples (Fig. 2). The annual pattern represents a case of relatively high, sustained monthly production, with a low, broad reproductive peak lasting from January to July . Abdominal fat bodies are present, with accumulation highest during the peak reproductive period and lowest during the lowest reproductive period (Table 2).

During this study, neonates were seen in September and October, but most occurred over a longer time period on the basis of oviductal data. Alcala (1966) reported young in every month.

Male Reproductive Cycles

Generalities.-- In males of the species studied the right testis is almost always located anterior to the left (in *Mabuya multicarinata* the testis of both sides may be in the same position, or the left may be slightly anterior). In almost all species, the right testis has a greater diameter than the left, though this is not true in all *Mabuya multifasciata* examined. Species mean testis size is not significantly correlated with species mean SVL (R^2 = 0.14). Though *Otosaurus cumingii* is the largest of all the local skink species, its mean testis diameter is the second smallest--only the diminutive *Lipinia pulchella* has smaller ones. To a certain extent, testis shape varies seasonally in all species except *Lipinia pulchella*. In most they are distinctly ovoid, but more spherical in *Sphenomorphus jagori* and often decidedly spindle-shaped in both *Dasia grisia* and *O. cumingii*. The testes in *Lipinia pulchella* are a deep black color. Melanin-covered testes have been reported in other reptiles. Those of the remaining species are white to yellow, sometimes tan in *Dasia grisia*. Examination of sectioned testes shows that those that are white in color are usually inactive, and those yellow, orange, or tan are involved in spermatogenesis, when they also become turgid with a greater volume. Figures 3 and 4 show the close approximation of testis size and mature and/or maturing sperm (stages II, III, and/or IV) in *M. multifasciata* and *S. jagori*. Similar data are available for the other species studied, and the relationship

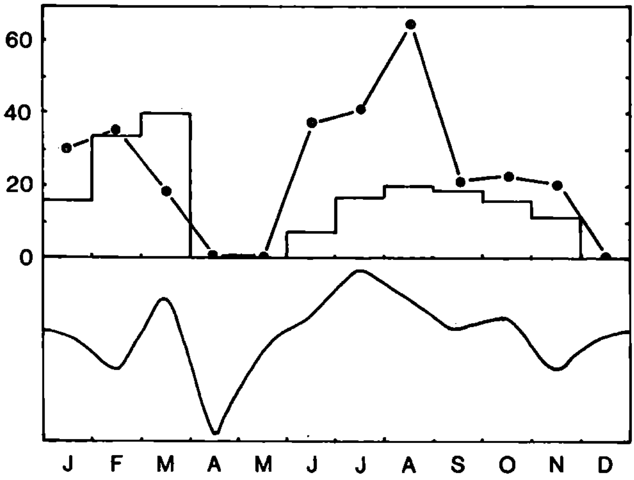

Figure 3. Above, mean monthly percent of sectioned testes of *Mabuya multifasciata* with mature/maturing sperm (stages II-IV, dotted line), compared with testes diameter (histogram). Below, solid line, diagrammatic, see Figure 6.

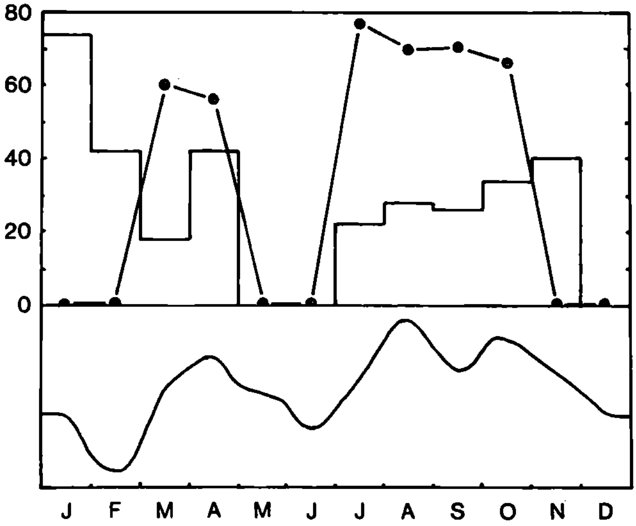

Figure 4. Above, mean monthly percent of sectioned testes of *Sphenomorphus jagori* with mature/maturing sperm (stages II-IV, dotted line), compared with testes diameter (histogram). Below, solid lines, diagrammatic, see Figure 6.

has been repeatedly demonstrated in other reptiles (Fitch 1970). We thus feel justified in using testis diameter as an indication of sperm production, and in assuming that these diameters are indicative of the annual breeding cycles of male skinks in the Caramoan area.

Seasonal Cycles.-- In most temperate lizards, seasonal testicular growth exhibits relatively short-lived, spring-peaked patterns (e. g. *Sceloporus formosus*, Guillette and Sullivan 1985; see Fitch 1970 for review). In the tropics, reproductive patterns are much more varied, and many variations of continuous and discontinuous reproductive activity occur (Fitch 1982). Study of the seasonal variation in testis diameter in Caramoan skinks shows that interspecific patterns are highly variable, even within a small area of tropical rainforest.

Table 1 provides data on seasonal changes in testes diameter for those Caramoan species for which sufficient material is available for analyses. Figures 5 and 6 illustrate seasonal changes for each species. From these data we conclude that none of the reproductive cycles of any Caramoan skink species are as sharply pulsed as those of most temperate male lizards that have been studied. Rather, the pulses representing periods of maximum testicular activity are less clearly defined, and often occur at different times of the year in different local species.

Males of some Caramoan species exhibit significant variability in testes size throughout the year, whereas others show less seasonal size variation. The former is represented by *Mabuya multicarinata*, *Lipinia pulchella*, *Lamprolepis smaragdina*, *Tropidophorus grayi*, and *Otosaurus cumingii*. Coefficients of variation (CV = SD/X, facilitating comparisons of variability about different-sized means) in this group range from 13.8 (*O. cumingii*) to 22.9 (*T. grayi*). Those species with the least seasonal variation in testis size are *Mabuya multifasciata*, *Brachymeles boulengeri*, and *Sphenomorphus jagori* (CV ranges from 5.7 in *B. boulengeri* to 9.3 in *M. multifasciata*). *Lipinia pulchella* is intermediate (CV = 11.8). The degree of annual variation in testis size is a continuum, with no clear separation into groups.

We do not mean to imply that males exhibiting less seasonal variability are equally sexually active during all months of the year. That this is not the case is clearly shown in Figure 5, in which plots of mean monthly deviation on mean annual testis size demonstrate a weak seasonal pattern of mean testis size in even those species showing least annual size variation. The figure shows even more clearly the great differences in annual testicular cycles among Caramoan skink species. In the case of *B. boulengeri*, sperm maturation takes place in most males during January, though at least some testes are still active until June. In July, a majority of individuals experience testicular collapse. Recrudescence occurs quickly during January. Thus only one period of spermatogenesis, almost five months, is suggested for this species. The pattern

Table 1. Seasonal variation in testis diameter (X/mo, in mm) in Caramoan skinks. SE = standard error.

	CV	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov	Dec.
Mfs	9.3	4.2	4.0	4.7	3.4	4.2	4.6	4.9	4.8	4.5	4.6	4.0	4.4
	(SE)	0.2	0.1	0.5	0.1	0.2	0.1	0.1	0.1	0.2	0.2	0.2	0.2
Mmc	15.4	4.0	3.8	4.7	4.4	4.6	4.4	4.4	4.5	3.5	2.7	3.2	3.3
	(SE)	0.2	0.1	0.2	0.1	0.1	0.1	0.2	0.3	0.5	0.2	0.1	1.1
Ea	7.1	4.6	4.3	4.2	4.4	4.0	3.7	3.7	4.4	4.4	4.4	4.1	4.4
	(SE)	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.3	0.3	0.3
Lp	13.3	1.5	1.3	1.3	1.0	1.3	1.7	1.3	1.5	1.7	1.7	1.5	1.8
	(SE)	0.1	0.1	0.1	0.1	0.5	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Bb	5.7	3.9	3.6	3.7	3.7	3.6	3.5	3.2	3.2	3.2	3.3	3.4	3.3
	(SE)	0.2	0.2	0.1	0.1	0.1	0.2	0.2	0.2	0.1	0.1	0.1	0.2
Ls	15.1	3.0	3.2	3.2	4.5	2.8	2.8	3.5	4.0	3.3	3.5	2.6	3.0
	(SE)	0.1	0.1	0.1	0.6	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Tg	22.9	3.5	4.1	3.8	3.0	2.1	2.3	2.8	3.7	3.8	3.9	4.1	4.6
	(SE)	0.3	0.1	0.2	0.1	0.1	0.1	0.3	0.3	0.2	0.3	0.1	0.2
Oc	13.8	2.7	3.3	3.0	2.7	3.0	3.1	3.1	2.2	2.4	3.5	3.8	2.8
	(SE)	0.2	0.1	0.2	0.4	0.2	0.2	0.1	0.2	0.3	0.2	0.1	0.2
Sj	8.9	4.3	3.8	4.6	4.9	4.2	4.2	4.7	5.1	4.6	5.0	4.5	4.2
	(SE)	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.3	0.2	0.2	0.1	0.1

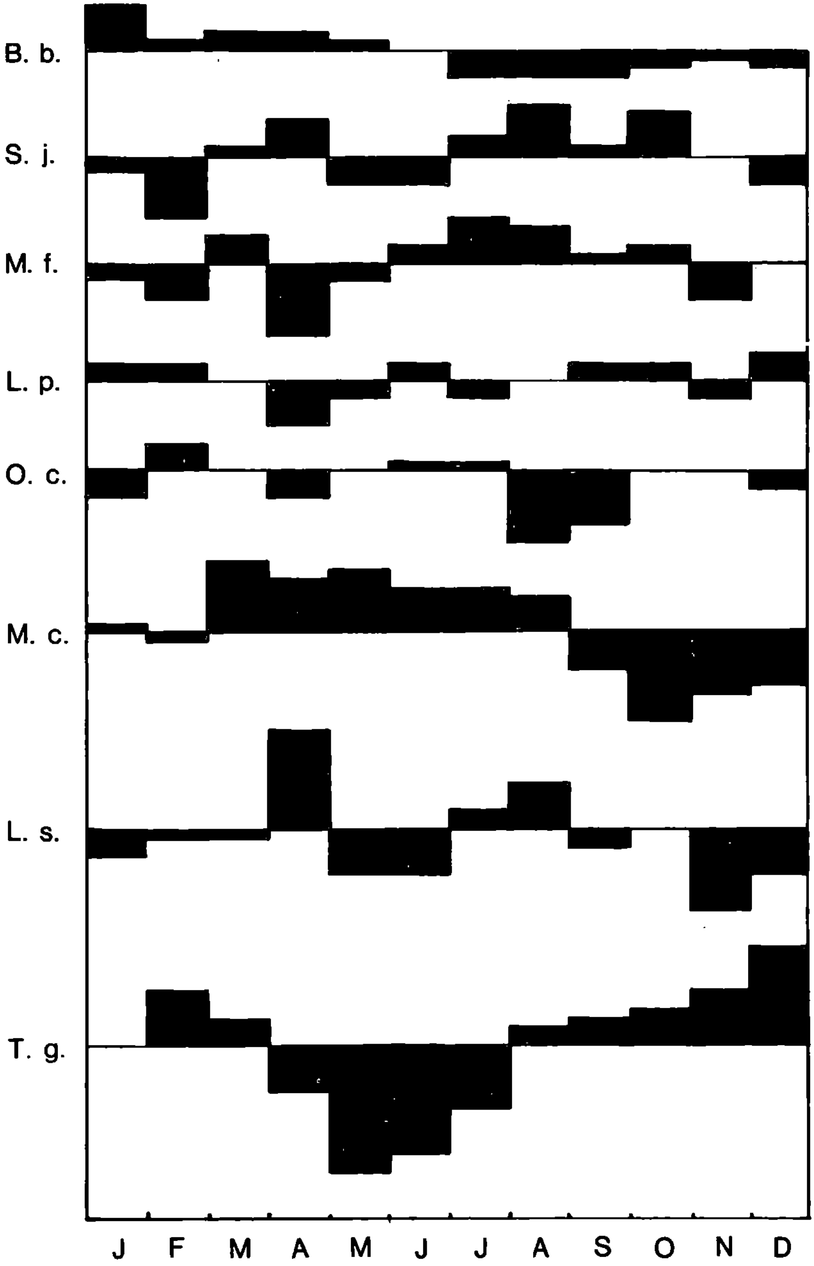

Figure 5. Deviation in mean monthly testes diameter (in mm) from mean annual diameter (in mm) in male Caramoan skinks, arranged in increasing levels of seasonal variation.

for *Sphenomorphus jagori* is clearly quite different, for there appear to be two major periods of quiescence and two of spermatogenic activity. Mature sperm are apparently available throughout much of the year, though the major periods are the end of dry period I and early monsoon II. Testicular quiescence occurs during the early part of dry season I and monsoon I. The pattern in *Emoia atrocostata* is similar, as is that of *Mabuya multifasciata*. *Lipinia pulchella* apparently produces sperm for most of the second half of the year, with testicular quiescence occurring from February through May. In *Otosaurus cumingii* the major quiescence and activity periods are more sharply pulsed and both occur late in the year. Some males probably produce sperm in February as well. *Mabuya multicarinata* has a much longer, but more distinct, sperm maturation cycle, with the long active phase occurring from March through August, followed by four months of rest. The pattern in this species is most like that known to occur in most temperate species (see Fitch 1970). The maturation cycle of *Lamprolepis smaragdina* is sharply pulsed in what appears to be two decreasingly active periods, starting in April and separated by two resting phases. *Tropidophorus grayi* possesses a testicular maturation pattern similar to that of M. *multicarinata* in having both long and distinct active and resting periods, though each is during opposite times of the year, as those of *M. multicarinata*.

Figure 6 summarizes and diagrams the main features of these spermatogenic patterns in Caramoan skinks for comparison with the local rainfall pattern. The variety in sperm maturation cycles is evident, as well as the fact that peak and lowest phases occur under all possible weather conditions. However, whereas peak activity periods are scattered through most of the year, only in December are the spermatogenic activity peaks of any two local species coincident. No peaks occur in May-June (late dry I period and early monsoon I period), or September-October (early monsoon II). All other months have one peak each. Thus, spermatogenesis among the resident species is rather remarkably spread evenly through most of the year. We conclude that each species is responding to different environmental cues, or responding differently to some of the same cues. There is no single, or even dominant pattern of sperm maturation for the skink species in this tropical evergreen forest.

Cycle Type and Ecological or Behavioral Factors

Annual reproductive patterns in tropical lizards are categorized as either continuous or exclusively periodic. Continuous breeders may be intraspecifically asynchronous as an aseasonal sustained reproductive species pattern, or continuous breeding may exhibit some form of seasonal pulsation in

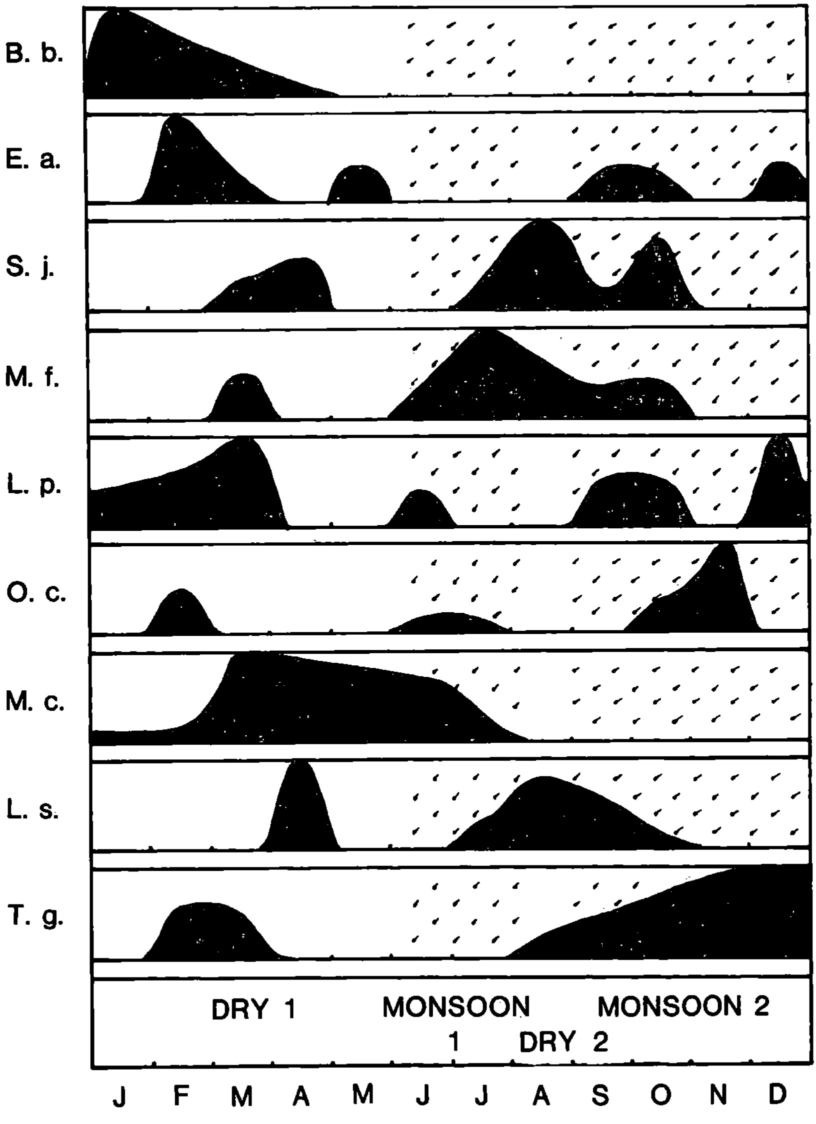

Figure 6. Diagrammatic representation of those periods of the year (black) when male testes size is distinctly enlarged (i.e. spermatogenesis proceeding). Abbreviations as in Figure 2. The two major periods of rainfall are shown as crosshatching.

the reproductive pattern. Periodic breeders have periods of reproductive activity interspersed with reproductive resting periods. Peak production of young in this case is often related to precipitation patterns (Fitch 1982). In the Caramoan area the reproductive year is further divisible into first and second wet seasons (monsoons I and II). All permutations of these factors are represented in the Caramoan skink biocoenosis.

Of the skinks in the Caramoan area, 64 percent produce young "continuously" through the year (eight months or more). These include *L. smaragdina*, *L. pulchella*, *M. multifasciata*, and *E. atrocostata* (Fig. 2). Of these, only *L. smaragdina* is known to produce eggs/embryos every month. *E. atrocostata*, both species of *Brachymeles* and *M. multifasciata* may do so. *S. jagori*, *O. cumingii*, *T. grayi*,, and *D. grisia* are discontinuous "periodic" breeders.

Of the presumed "continuous" breeders, two species are semi-arboreal, two are terrestrial, and two are semifossorial. Each species represents a different microhabitat, though most live in rather open situations. With the exception of *L. smaragdina*, the annual patterns of all of them are distinctly modal, in spite of nearly continuous reproduction. *E. atrocostata*, L. *pulchella*, *B. boulengeri*, and *M. multicarinata* are all weakly bimodal. Typically in these species a high percentage of the females are gravid during many months of the year. Three species are viviparous. Viviparity also occurs in the discontinuous breeding *T. grayi*. The peak reproductive period for *E. atrocostata* is January through March; for *M. multicarinata* it is March through June; for *L. smaragdina* it is May through July, and for *L. pulchella* it is August and September. Thus the peak reproductive period of each species in the "continuous" breeder category falls at a different time of year. All but *L. pulchella* accumulate fat seasonally, though there is no consistent pattern in the season of fat accumulation in respect to the reproductive peaks.

Figure 7 diagrams the second major reproductive pattern in female Caramoan skinks. When the peak period for percent of gravid females is considered for each species we see that none falls during January to February (early dry period I), October, or December (both monsoon II). Most species have the highest proportion of gravid females in March (late dry period I). By the time the eggs are laid and then hatched, the young would be active during the early part of monsoon I (when food resources are high, see below). Two of the three species with peak periods of gravidity in May (*T. grayi* and *M. multifasciata*) are viviparous, so that the young would be born during the same early part of monsoon I. The remaining species (*E. atrocostata*) lives in the equitable marine littoral, and the May peak is barely discernible from several others during the year. Several species (both *Brachymeles* species, *S. jagori*, *L. pulchella*, and *M. multicarinata*) have one peak falling during a dry period and the second during a wet period. Reproductive quiescent periods for females

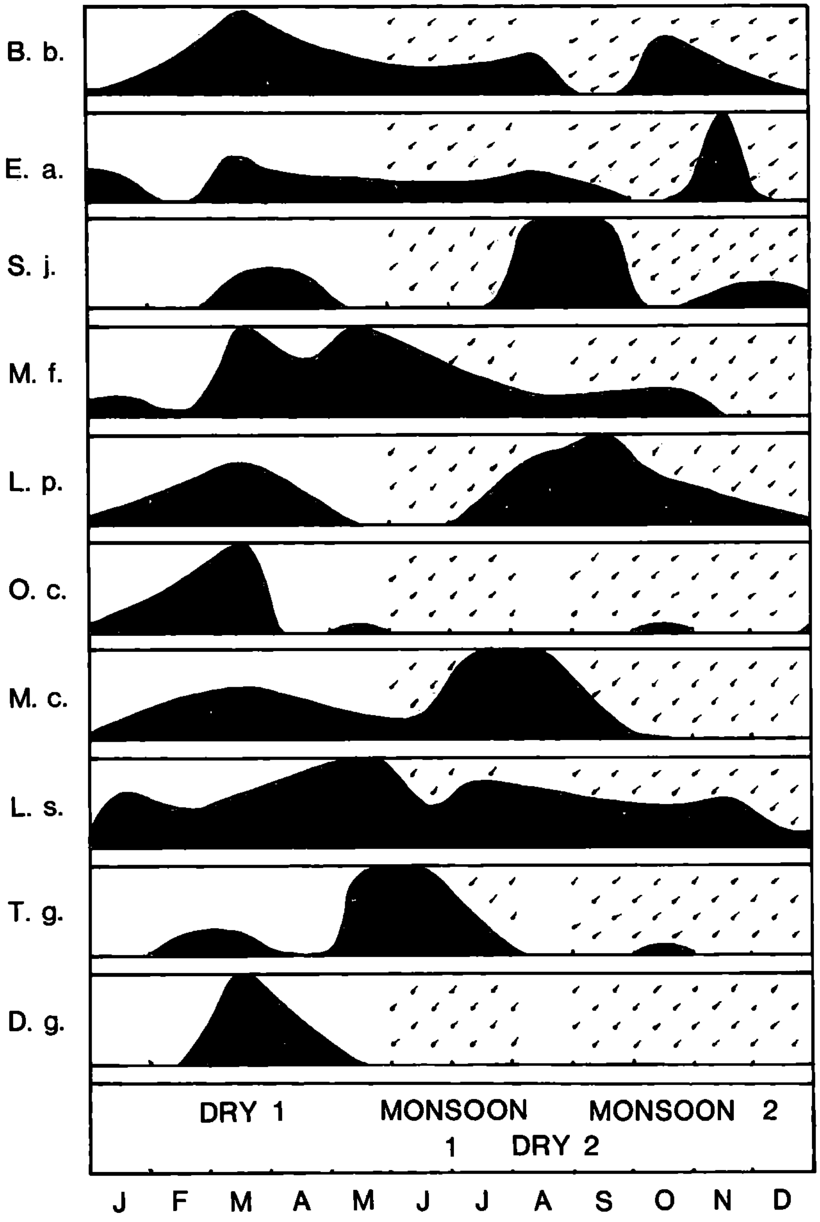

Figure 7. Generalized diagram of proportion of gravid females per month in major Caramoan species studied. The two major rainfall periods are shown as crosshatching.

are most common in November and December (late monsoon II) when rainfall is particularly heavy. No species is completely inactive in March.

The above descriptions of breeding cycles for these skinks demonstrates that almost every conceivable annual pattern occurs among them. Some are egg-layers and others live-bearers; some breed continuously throughout the year, others are periodic. Those that are periodic have either one or two reproductive peaks, and these may fall at entirely different times of the year, despite their geographic and often ecological sympatry. Patterns even vary among the resident species of the same microhabitats. We conclude that these species must depend on either different cues for their reproductive cycling or use the same cues (such as the first or second rainy season) in different ways to initiate or stop breeding activity. Mendez de la Cruz et al. (1988) have suggested that a multiplicity of cues probably determine the reproductive cycles of not only different species of Neotropical iguanids, but of the different sexes as well. We find no evidence for "tropical forest" or "tropical woodland" reproductive patterns among the skinks we studied (savannas do not occur naturally in the Philippine Islands). However, there is a tendency for maximum reproduction to occur during and immediately after the first monsoon, as well as after the second monsoon, regardless of type of annual reproductive cycle. Even among some of the continuous breeders, there is an increase in percent of gravid females during these seasons. Reproduction often reaches annual lows during the dry months preceding the first monsoon and particularly during the wettest parts of the second monsoon.

Fecundity.-- About half of the local skink species have small clutches of 1 to 3 (means range from 1.8 to 2.1), usually 2 eggs. Within these species, clutch size is consistent (standard deviations range from ± 0.1 to 0.4) and all are oviparous. None of these species has been proven to have multiple annual egg clutches/litters, though this is highly likely. The species comprising the small clutch group are *O. cumingii*, *M. multicarinata*,*E. atrocostata*, *L. pulchella*, and *L. smaragdina*.

The remaining five species (1) have more eggs per clutch (ranges in mean clutch size vary from 2.1 to 4.0), and (2) exhibit less consistency in clutch number (1-8; standard deviations range from 1.3 to 1.9). Of this group, two species are oviparous (*S. jagori* and *D. grisia*). The remaining three species are all viviparous (*T. grayi*, *M. multifasciata*, and *B. boulengeri*). The live-bearing species occur in a variety of habitats (semiaquatic, *T. grayi*; fossorial, *B. boulengeri*; and terrestrial, *M. multifasciata*). None is arboreal.

There is no significant correlation between number of eggs/clutch and microhabitat. Those species with the largest clutches live in a variety of microhabitats (semiaquatic *T. grayi*, terrestrial *M. multifasciata*, and arboreal *D. grisia*). Regression of number of eggs (or young)/ clutch against mean SVL of females shows a poor correlation ($R^2 = 0.13$). Vitt and Cooper (1986) also found no significant correlation between female SVL and clutch size in a species of skink, though Guillette (1983) did for the viviparous *Eumeces copei*. The common association between clutch size and SVL found in lizards (iguanids, lacertids, agamids) may be less frequent in scincids than generally assumed.

In summary, we find no significant pattern between number of eggs (young)/clutch and habitat, female size, or reproductive mode. There are, however, apparently two strategies in number of young(eggs)/clutch , in which one group of species lays consistently small clutches and the other group lays larger clutches. Except that all local viviparous species belong to the last group (through there are some egg-layers in it as well), no general principal(s) can be deduced from the distribution.

Abdominal Fat Bodies

Female Abdominal Fat Cycle.-- The annual cycle in fat bodies of female Caramoan skinks exhibits considerable interspecific variability (Table 2). Some of this variation can be explained; some cannot.

Of the 11 species studied, 6 (55%) possess no appreciable amount of abdominal fat at any time of the year. These are *S. jagori*, *O. cumingii*, *L. pulchella*, *B. boulengeri*, *B. samarensis*, and *T. grayi*. These include taxa found in semiaquatic, terrestrial forest, terrestrial arboreal, and fossorial microhabitats. Comparison of these microhabitats with insect seasonal abundances in each (see below) suggests that these habitats do not have high food resources throughout the year. In fact, some of these microhabitats (such as forest trees and rocky forest substrates) have rather low food resources compared to other microhabitats in the immediate area in which other species of skinks live. Additionally, the list includes species representing 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 species produce a seasonally variable amount of abdominal fat. In *M. multifasciata* the most abdominal fat is usually present from about August through January. Though females are gravid throughout most of the year, the peak reproductive period is from about March through May. Thus, abdominal fat depletion more or less coincides with the period of vitellogenesis. *M. multicarinata* has approximately the same fat accumulation and depletion pattern, followed by a period of high proportion of gravid females. Abdominal fat accumulation may be an important factor in the reproductive cycle of this species as well. The relationship of fat loss and reproductive cycle is not as clear in *E. atrocostata* and *L. smaragdina*, for they

Table 2. Seasonal variation in abdominal fat (in g) of Caramoan skink species by sex. Species missing do not produce any abdominal fat. t= trace only.

Species [a]	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

[a] Only those species with abdominal fat bodies.

both tend to produce eggs over much of the year, and fat is mainly accumulated during the second monsoon (September through December).

Thus, while the abdominal fat accumulation and degradation cycle of some local skink species can be correlated with vitellogenesis, others produce no major abdominal fat bodies at all, yet are obviously able to produce clutches or young without it. In some other lizards Hahn and Tinkle (1965) have shown that as long as the female has an adequate diet, abdominal fat bodies are not needed for vitellogenesis. Some of those Caramoan skink species that do accumulate abdominal fat bodies tend to produce the greatest quantity of fat during the second monsoon (October through December, see Table 2), and utilize it at about the time when vitellogenesis takes place. However, the best correlation for all species seems to be with annual fluctuation in insect abundance (see Fig. 8). The accumulation cycle of abdominal fat always begins during monsoon I (a period of high insect abundance). The rate is increased over the ensuing months, and the process is generally completed by the beginning of the heaviest rains (November and December) of monsoon II (when insect food resources become low). Fat reserves are then steadily depleted through dry season I, reaching their lowest levels during the end of that season and the beginning of monsoon I. Thus, the fat accumulated during monsoon I and the period following it (about four months) is used during the remaining seven to eight months. Some may be used for reproductive activities, but its increased rate of use is also correlated with generally low food resources at the same time.

Male Abdominal Fat Cycle.-- The species that lack abdominal fat in females also lack it in males. Of those species in which the males do contain abdominal fat, it is also seasonally variable, as in conspecific females.

In general, the seasonal pattern of males is similar to that of females, i.e. the fat is accumulated from monsoon I through monsoon II. In *L. smaragdina* males the season of high fat resource is longer than in either sex of any other species studied; it begins in September, with the peak occurring in October. This is also the only local species in which the males contain a significantly greater mass of abdominal fat than females ($t = 24.3$, df = 20, $P < 0.001$). In the remaining species females have higher amounts of mean monthly fat, but the differences in means are not statistically significant in any sex-related comparisons.

The variation of 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 abdominal fat weight were calculated for the male and female data for each species for each month. Such coefficients negate the size differences among the species and allow direct comparison of the percentage values. There is no significant difference between the annual mean CV values of the males and females of *M.*

multicarinata and *E. atrocostata*, whereas the males of *M. multifasciata* and *L. smaragdina* have a significantly lower variation in abdominal fat weight throughout the year than females of the same species. The reasons for this are not clear.

The seasonal pattern in abdominal fat weight indicates that the greatest variation occurs during the end of dry season I and the very earliest part of monsoon I. This has been shown above to be the period when abdominal fat reserves are usually the lowest of the entire year in all species that have such reserves. The fact that variation is greatest during this period may be due to reproductive dynamics. 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 is during the heavy rains of monsoon II and the beginning of the period immediately following dry season I. This is the time when food resources begin to drop significantly after a period of previous high food levels. The fact that all individuals of both sexes in all species with abdominal fat accumulate it in more equal amounts at the same time suggests that fat deposition during monsoon I is an important strategy for all these species. This similar seasonal pattern occurs in spite of the fact that among these species fat accumulation and utilization cannot be directly related to the reproductive pattern in the same way (see below and Fig. 8).

Most authorities believe abdominal fat is critical for vitellogenesis. This view is based mainly on the work of Hahn and Tinkle (1965), who demonstrated that abdominal fat body lipid is mobilized for vitellogenesis in *Uta stansburiana* (Iguanidae), though it is not essential. Some Philippine scincid species are here shown to lack abdominal fat at any time of the year. One then wonders about the source of lipids for vitellogenesis in these species. For these Philippine skinks it seems likely that this lipid is derived from some other as yet unidentified fat storage area(s)--perhaps the tail, in which fat is known to vary seasonally in several lizard families, including Scincidae , or the body wall, as has been demonstrated in an American skink species (Vitt and Cooper 1985). These data suggest that the dependence of vitellogenesis on abdominal fat bodies as demonstrated for many temperate Iguanidae, Lacertidae, and Agamidae is less clear for other lizard families, such as Scincidae (this study, Vitt and Cooper 1985) and Varanidae (Auffenberg 1988). That stored lipids are required for vitellogenesis seems definite. The question raised here is whether the abdominal fat bodies of at least tropical scincids are the source of these lipids. Our results suggest that they are probably not--at least not in all Luzon species. Vitt and Cooper (1985) provide a clue to a potentially important source of lipid for vitellogenesis in their study of lipid cycling in the skink *Eumeces laticeps*. They show that fat in the tail alone comprises nearly one half of the standing lipids in individuals of this scincid species. It seems that the matter of lipid sources for vitellogenesis in tropical lizards requires additional study before we can generalize about lizard reproduction and lipid cycling.

Seasonal Insect Abundance

Diurnal insect abundance varies seasonally (Fig. 8). In general, diurnal insects are least common from 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 demonstrate similar high peaks during early parts of the rainy season (Robinson and Robinson 1970, Fogden 1972, Janzen 1973, Smythe 1974). In the Caramoan area, both the driest and wettest parts of the year have the least insects. The greatest number is found in May, just before monsoon I. From dry season II (August) through monsoon II insects become steadily less common. There is no correlation between insect abundance and seasonal temperature (Fig. 8).

Eight different microhabitats were regularly sampled for the seasonal abundance of diurnal insects (total insects trapped 4212, Table 3). 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 rock crevices on the surface of the same forest.

Of these microhabitats insects were most abundant at the ecotone of field and forest--the major habitat of *M. multifasciata*. Insects were also common in the overgrown field and rock outcrops in them (also microhabitats of the same species), 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 above microhabitats, but are the major microhabitats of *L. smaragdina*. Forest trees also have fewer insects than terrestrial habitats, but more than those trees inhabited by *L. smaragdina*. These forest trees are inhabited by two species of semi-arboreal skinks--*D. grisia* and *L. pulchella*. The rocky forest substrate is the primary microhabitat of *S. jagori* and contains relatively few insects. Those skinks living in microhabitats with lower insect abundance tend to feed on a greater proportion of small fruits (see Auffenberg and Auffenberg 1988 for details).

On the basis of seasonal differences in insect abundance in different microhabitats, the only microhabitat without seasonal insect shortages is field edge--the major habitat of *M. multifasciata*. The microhabitat of *M. multicarinata* (mainly leaf litter in shaded forest) also has abundant insect food

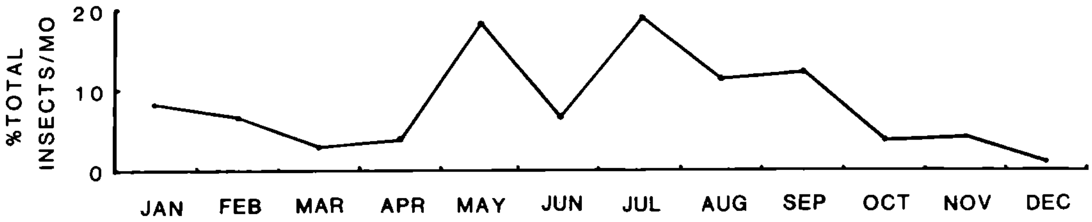

Figure 8. Insect abundance compared with annual rainfall pattern and fat abundance curves for each species.

Table 3. Seasonal insect abundance in local skink microhabitats.

	Field				Forest			
	Open	Edge	Rocks	Trees	Crevices	Rocks	Litter	Trees
Jan.	12.3	20.9	24.1	4.8	10.2	7.3	13.1	7.3
Feb.	8.9	22.1	12.6	5.3	9.6	8.2	25.1	8.2
Mar.	8.3	15.7	31.4	7.4	5.0	4.1	24.0	4.1
Apr.	13.6	48.3	4.0	1.7	5.1	9.1	9.1	9.1
May	31.6	32.1	5.8	2.7	2.3	5.1	15.3	5.1
Jun.	16.6	28.9	12.4	6.5	4.5	6.3	18.5	6.3
Jul.	14.0	14.2	19.7	6.2	3.0	13.8	15.3	13.8
Aug.	16.1	23.4	12.4	6.5	4.5	10.1	16.9	10.1
Sep.	26.8	21.3	12.4	6.5	4.5	6.3	16.0	6.2
Oct.	18.3	21.8	13.4	9.5	5.6	5.6	20.2	5.6
Nov.	19.0	18.0	30.8	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

throughout most of the year. The same is true of the microhabitats of the semiarboreal *L. pulchella* and *D. grisia*. While insect food is generally low throughout the year for *L. smaragdina*, the most stressful time seems to be during dry season I.

We conclude that, in general, while some microhabitats support more insect prey than others, the lowest insect abundance in most of them occurs during dry season I, and it is probably this time of the year that is most important from the standpoint of food availability. Comparison of Table 3 and Figure 14 shows that there is no strong correlation between the time when young are injected into the microhabitat and seasonal variation in insect abundance; except that neonates of none of the scincid species but L. pulchella hatch during periods of lowest local insect abundances.

Differential Seasonal Representation of Sexes

Among skinks, adult females are often disproportionately represented in collections made at different seasons of the year, due largely to factors associated with reproduction (egg brooding, differences in feeding habits, etc.). Males may be poorly represented in some species because they may be spending much time "guarding" females during the reproductive period (Vitt and Cooper 1985). Some Caramoan skinks show very significant shifts in number of females during some months, and these can be shown to be related to reproduction.

Figure 9 demonstrates that female *T. grayi* are more common than males for most months. The high proportion of females in June and July is actually due to the fact that fewer males were taken, rather than more females. The two months of fewest females (February and September) are associated with breeding periods (Fig. 7).

Mabuya multifasciata is represented by fewer females than males during much of the year (Fig. 9). Two periods of high male representation are noted--one in April (following the March breeding peak), and the other in October, when (on the basis of color changes) another breeding season is believed to occur. The few females in November-December is clearly caused by an unexplained increase in males, rather than a decrease in females.

Brachymeles boulengeri is represented by more or less the same number of females throughout the year (Fig. 9). However, March is apparently a peak month of activity for females, and this is correlated with the high proportion of gravid females during the same time. This high female representation in March is probably associated with courtship activity. The large number of females in June is, however, not correlated with any increase in number of

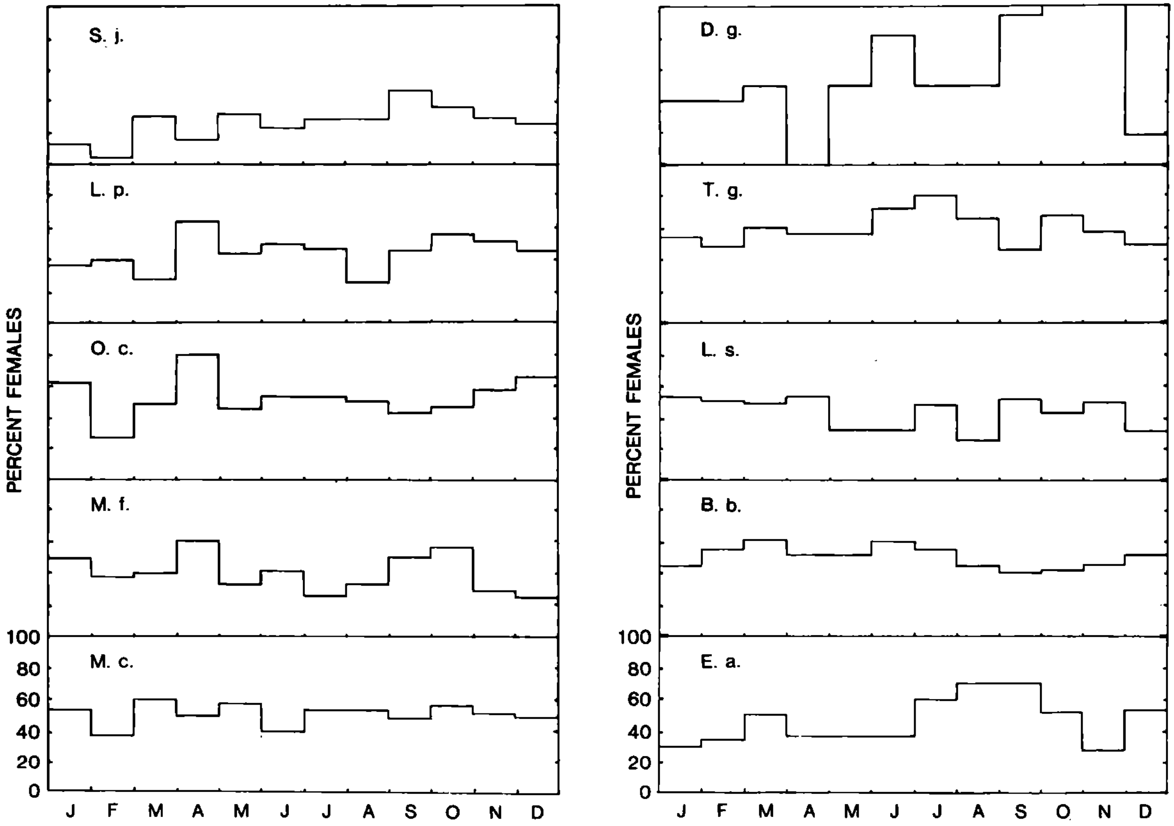

Figure 9. Percent females of each species collected each month. Species abbreviations as in Figure 2.

gravid females. The lowest monthly representation of females (September) is associated with that time of year when no females are gravid.

Otosaurus cumingii females are particularly common from December to January and during April (Fig. 9). The lowest numbers occur in February. This is the month of the greatest number of gravid females. Thus it is possible that *Otosaurus* broods its eggs. The highest number of females per month (April) is associated with the second, lower breeding peak. The increase in female number in December and January is probably related to an increase in female activity prior to the February breeding peak. The low number of females during February also is partly due to not only a reduction in females caught, but an increase in males during the same period. The latter may be related to territorial or courtship behaviors.

Sphenomorphus jagori (Fig. 9) is peculiar in that there are relatively few females active during the entire year. The monthly number of females approaches one half of the total monthly specimens only during September. The lowest number of females is found during the time of highest proportion of gravid individuals (January-February). This is followed by a significant increase in number of females per month, and this may be associated with increased feeding of the females. The month with the highest number of females per year (September) also follows a breeding period (July), suggesting post-laying increase in female activity. These data sets suggest the possibility of egg brooding in this species as well.

Mabuya multicarinata (Fig. 9) exhibits a female monthly frequency pattern similar to that of *Otosaurus cumingii* and *S. jagori*, i.e., the period of fewest females is the period of most gravid females (February). This is followed by a period of increased female activity. The low number of females in June is unexplained, and there is no significant change in number of females per month during the secondary breeding peak of July and August.

Lipinia pulchella (Fig. 9) has a similar pattern, i.e. the periods of highest gravid females are periods of lowest number of active females (March and August). There is a significant increase in females after both inactive periods--particularly during April.

Lamprolepis smaragdina (Fig. 9) males and females are more or less equally represented during most months. However, after both the major breeding peak in April and the lesser breeding peak in July, the following two months have a significant decrease in female activity.

Emoia atrocostata (Fig. 9) exhibits remarkable changes in monthly proportion of females in view of the nearly uniformly sustained breeding throughout the year. The fewest females are recorded in January and November. Most gravid females occur in February, after which the number decreases in March. The long, low breeding pulse from July through September is similarly associated with a high representation of females (September).

To summarize these data, there seem to be two major patterns regarding the relationship of major breeding and activity peaks in females. In one, female activity seems to decrease following the seasonal breeding peak(s). Among Caramoan skinks this is illustrated by *Lamprolepis smaragdina* and *Brachymeles boulengeri*. Both live in totally different microhabitats, the former being arboreal and the latter fossorial. The remaining skinks illustrate the second pattern, in which female activity increases after the major breeding peak(s). The numbers of females available per month for most of these species show that the fewest females are found during the peak breeding period, suggesting that females are particularly inactive at this time. This may be related to brooding of parturient females. No data are available on brooding in any Philippine skink species. *Emoia atrocostata* is slightly set apart because the breeding seems to occur at the same time that females are becoming more active. In this case, the part of the year in which females are least active would have preceded the peak breeding period. *M. multifasciata* is similar to *E. atrocostata*, but the pattern is more or less intermediate.

Seasonal Color Changes

Changes in lizard body color, particularly males, is known to be associated with the breeding season. Hadley and Goldman (1969) and Bagnara and Hadley (1973) have shown that in at least some iguanids, male breeding colors are under hormonal control and directly associated with testosterone levels in mature males during certain times of the year. However, seasonal color changes in those skinks previously studied suggest they occur only in males and that they serve in agonistic encounters during the breeding season. We were thus surprised to find that in our study area seasonal color changes also occur in females, and one wonders how this might be correlated with those changes in the males and how they might be important in intra- and intersexual behavioral contexts. To determine the level of correspondence between such color changes and season and reproductive condition, we noted the coloration of all mature specimens dissected during the study with the hope that such color changes might be found useful in further defining breeding readiness by individuals of different species at different times of the year.

Our studies show that not all Caramoan skink species exhibit seasonal color changes. But of those that do, similar changes can be demonstrated in both males and females in almost all the local species, though the seasonal colors of the males are always more intense. There are no color changes in mature individuals of either sex of either *Brachymeles* or *T. grayi*. *Dasia grisia* may not have seasonal color changes, but our sample is too small to be certain. Excluding *Dasia*, these three species are all semi- or nearly completely fossorial--*Brachymeles* lives in mesic situations and *Tropidophorus* in nearly hydric ones. Thus seasonal color changes are completely absent in those local skinks that spend most of their time under the surface and evidently court and breed there as well. All the other species show some form of seasonal color change which can be related to breeding periodicity.

Only in *Lipinia pulchella* does this seasonal color change occur in only one of the sexes (males). Color changes occur in both sexes in all other local skink species. At least some mature *Lipinia pulchella* males have a large bright yellow to orange blotch on the chin and throat. The same color is occasionally seen around the cloaca and the inferior surface of the hindlimbs. These males are evidently in breeding condition, and the color appears in some individuals in all months of the year, except April and May, when the same areas are white. The chins of immature females and juveniles are always white. These months correspond with periods of increased testicular size (Fig. 6), and with increased percentages of gravid females in the local population (Fig. 7). These data suggest that mature males are ready to breed during all months except April and May. The highest percentage of males with this color occur in March and September (Fig. 10). The yellow chin in male *Lipinia pulchella* suggests very strongly that combat occurs at this time and that courtship is also occurring.

Both mature male and female *Lamprolepis smaragdina* often have a deep yellow cloacal area . Only the males have a yellow glandular heel patch during the breeding season (also noted by Alcala 1966). At least some individuals of both sexes have yellow cloacal areas every month of the year, though the percentage varies seasonally (Fig. 10). The monthly proportion of males and females having this color is concordant, though males consistently have more individuals per month with this color than females. The lowest percentage of both sexes with yellow cloacal color occurs from just before to just after monsoon I (May through August) and in December (monsoon II). The highest proportions of colored males occur in the early part of dry period I (January through April) and in the early part of monsoon II (September through November). However, the proportion of *L. smaragdina* males "ready" to breed is higher during all months of the year than in any other local species. Testicular size is greatest during April and August.

The seasonal curve for yellow-colored females is more distinctly pulsed than that for males, with the highest peaks in March and October. The highest peak for colored females does not correspond with the peak for monthly proportion of gravid females (May and July). The July peak for gravid females corresponds with a sharp rise in colored males as well as females. However, the Caramoan data presently available suggest that the period of courtship during dry season I is much longer than that during monsoon I, and that while both males and females may have been ready to breed during monsoon II, they did not do so (see Fig. 2). Dissections reveal that yellow cloacal color occurs in

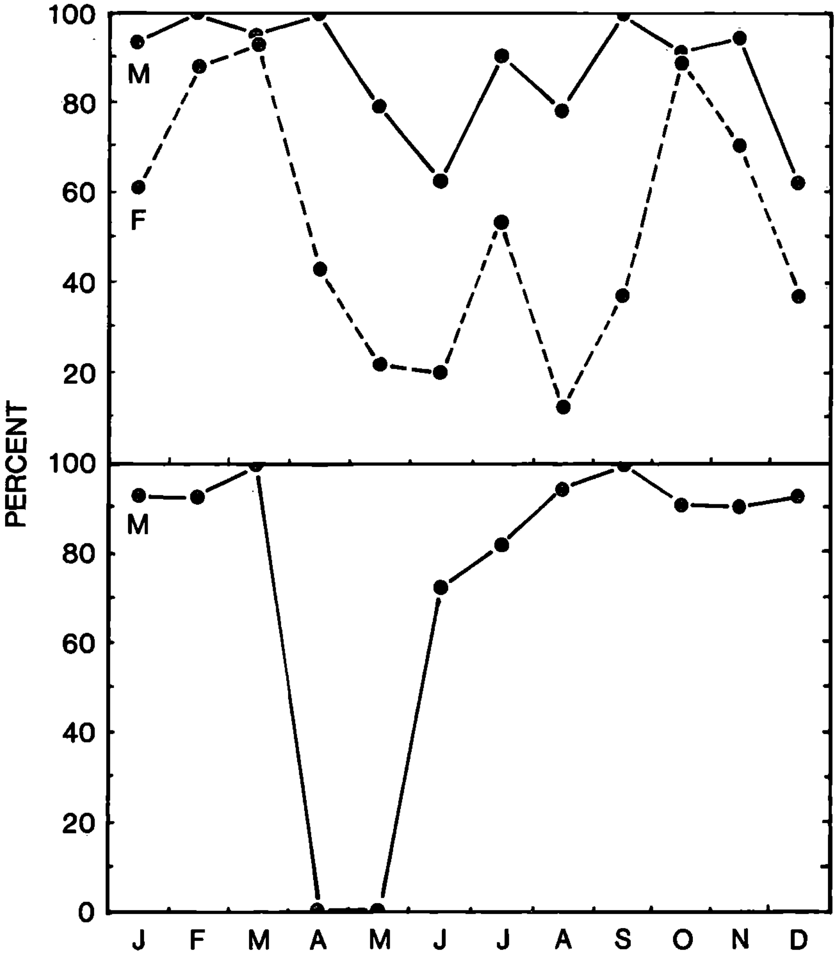

Figure 10. Above, percent of males (M) and females (F) of *Lamprolepis smaragdina* in which the cloaca is yellow. Below, the same for *Lipinia pulchella* males with yellow or orange on the chin.

females with both yolking ovarian and developing oviductal eggs. Immatures of both sexes lack the yellow cloacal color.

Some mature male and female *O. cumingii* have gray chins. The belly is additionally washed with yellow in those individuals with the darkest chins. Immatures of both sexes have white chins. Gray-chinned individuals are found during every month of the year, varying from 50 to 100 percent in the total monthly male sample, and 62.5 to 100 percent in the monthly female samples. This is the only local skink species in which females sometimes possess more intense color than males during the breeding season. The curves of monthly proportion of individuals with dark chins are highly coincident in both sexes (Fig. 11), with the highest proportions for both sexes from December through March and the lowest in April and May. The curves for both sexes fit those curves for both testis size (Fig. 6) and proportion of gravid females per month (Fig. 7), though the highest peaks in the two latter curves are reversed.

Some mature *E. atrocostata* are also seasonally colored. In this species the chin of both males and females is medium gray and the belly often yellow to peach. Immature individuals of both sexes have a white chin and belly. The proportion of colored to non-colored mature individuals per month is shown in Figure 11; both male and female curves are concordant. In both, the variation is from 0 to 100 percent of the total monthly sample. Males are more commonly colored than females and have the highest number of colored individuals from December through March and July through September. This curve is almost opposite that for testis size in males of the same species for the months of July through September, but coincides with the high February peak (Fig. 6). The curve for the proportion of gravid females per month (Fig. 7) illustrates that the fewest colored females occur during the peak period of gravidity (November) and the highest number of colored females at the lowest point of the annual gravidity cycle (February).

Immature *S. jagori* of both sexes have a white belly. In some mature individuals it becomes bright yellow, and this varies seasonally and coincidently in both sexes (Fig. 12). Monthly variation in colored individuals of both sexes is from 0 to 100 percent, with colored males only slightly more common than colored females, and then only for some months. No colored individuals of either sex are found from April through May. This corresponds with one period of testicular degradation (May through June). The reduction in number of colored males in November also corresponds with a second decrease in testicular size during the same month. The highest proportions of gravid females (Fig. 7) occur during March and April, just after the January-February high proportion of colored females, and the two curves are coincident during the respective peaks in August-September. The increasing proportion of gravid females during December is correlated with an increase in number of colored females at the same time.

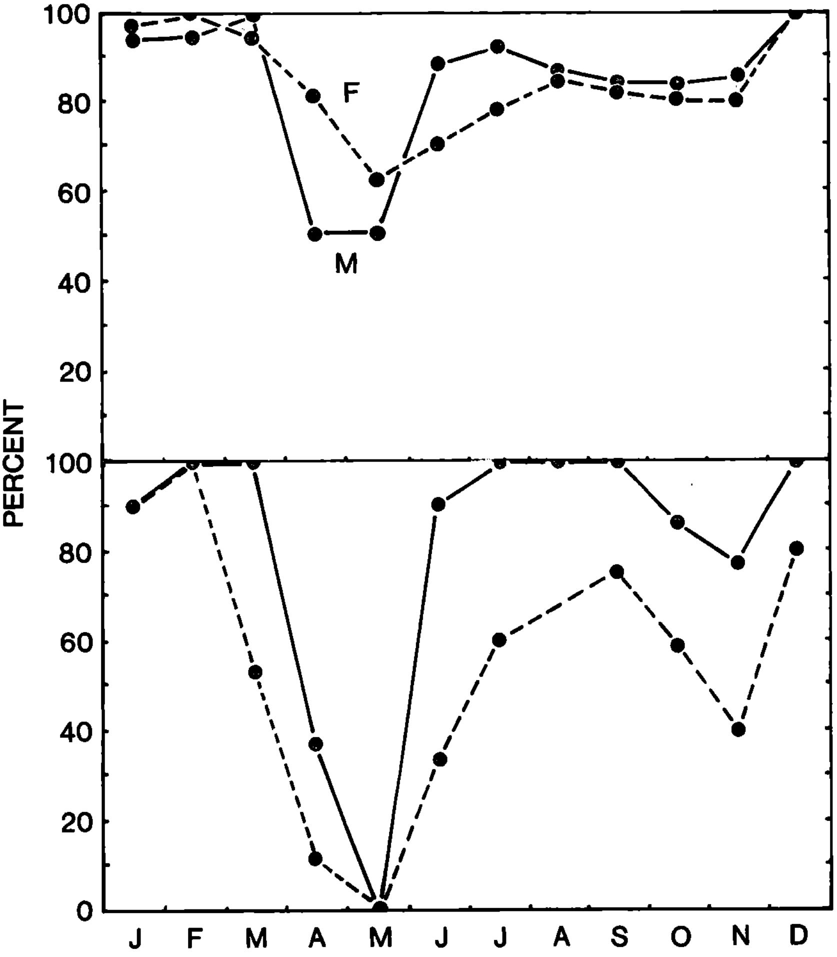

Figure 11. Above, percent males (M) and females (F) of *Otosaurus cumingii* in which the chin is gray. Below, the same for males and females of *Emoia atrocostata* with gray chin and yellow to peach belly.

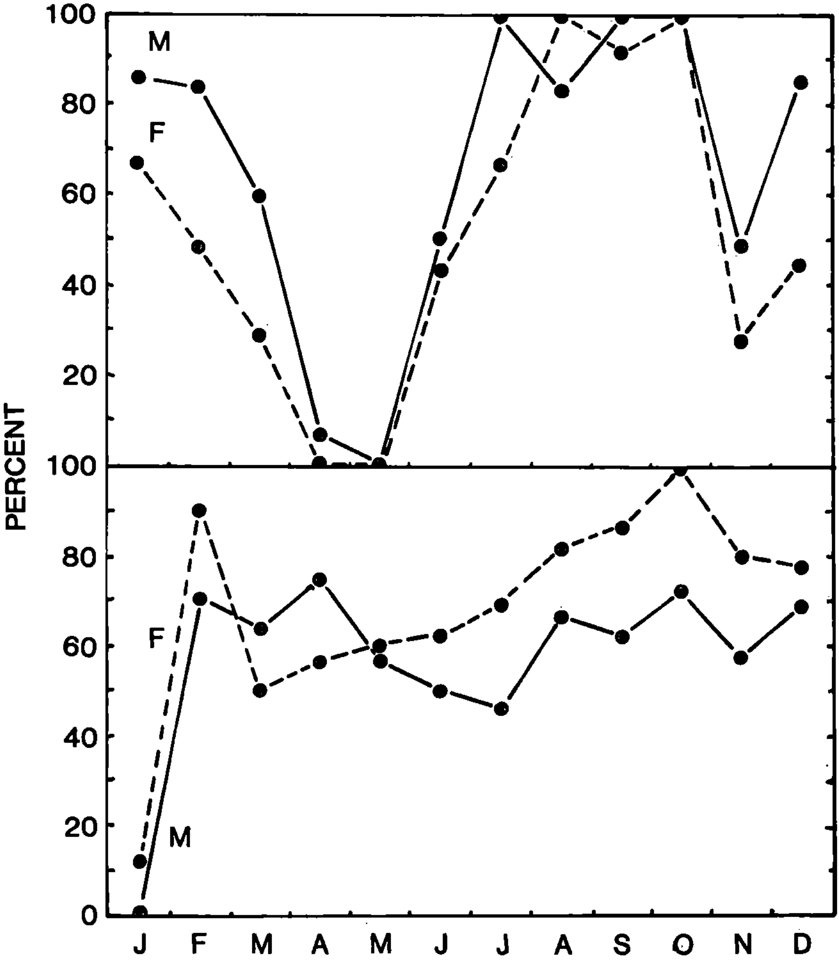

Figure 12. Above, percent males (M) and females (F) of *Sphenomorphus jagori* with yellow belly. Below, the same for males and females of *Mabuya multicarinata* with brassy green or blue belly.

Immature males and females of *M. multicarinata* have white bellies. Some mature males and females have a distinct metallic brassy tint on their bellies that can be either greenish or bluish. The seasonal proportion of colored males and females are coincidental (Fig. 12), with generally more females having this color during most months than males. The color is present in 46 to 75 percent of all males during most months, except January when the proportion sharply falls to 0. Females have a similar seasonal pattern, with the proportion of colored individuals ranging from 50 to 100 percent, except for January, when it drops to 12 percent. Though the proportion of colored males remains generally high throughout the year, peak values occur during April and October. There is no correspondence with the curve for testis size (Fig. 6), except for the rapid rise in both curves during the early part of the year. The remaining parts of each curve are, in general, opposite. Breeding colors are usually associated with plasma testosterone, but the latter is not directly associated with testes size. Therefore, testicular mass is not a valid measurement of testosterone level in the individual. Apparently the operant system in breeding color development of *M. multicarinata* is different from that in the other Caramoan skinks studied. However, the female seasonal color curve does correspond with monthly percent gravid females, though the peaks do not coincide.

Mabuya multifasciata is known to be quite variable in regard to color over its extensive geographic range. Some individuals have a red to yellow stripe, running for varying distances down the sides of the neck and body behind the axilla. Mertens (1927) was the first to point out that both sexes have such stripes. Auffenberg (1980) showed that the intensity of these colors was related to the timing of the breeding season. No immature individuals of either sex have the stripes, though some mature individuals do so seasonally. In the Caramoan area the stripes are absent during June, July, and August. The monthly pattern in proportion of individuals having such stripes is rather concordant in both sexes (Fig. 13), though more males have the stripes than females. Our dissections show that in females the yellow stripe may be found in individuals with either yolking follicles late in their development or with oviductal eggs early in their development. Females with well-developed embryos usually have only faint stripes, while those with large yolking follicles usually have brilliant red stripes. The highest peak of the male color curve matches the period of increased testicular size in March (Fig. 6), and the second somewhat lower peak coincides with the broad-pulsed period of testicular size increase during monsoon II. The curve for proportion of colored females shows two monthly peaks in place of the single early peak of the males. These two peaks are nearly completely coincident with the two peaks during the same time for percent of gravid females (Fig. 7). However, while the color of both males and females suggests they were in a state of reproductive readiness during monsoon II, very few females became gravid.

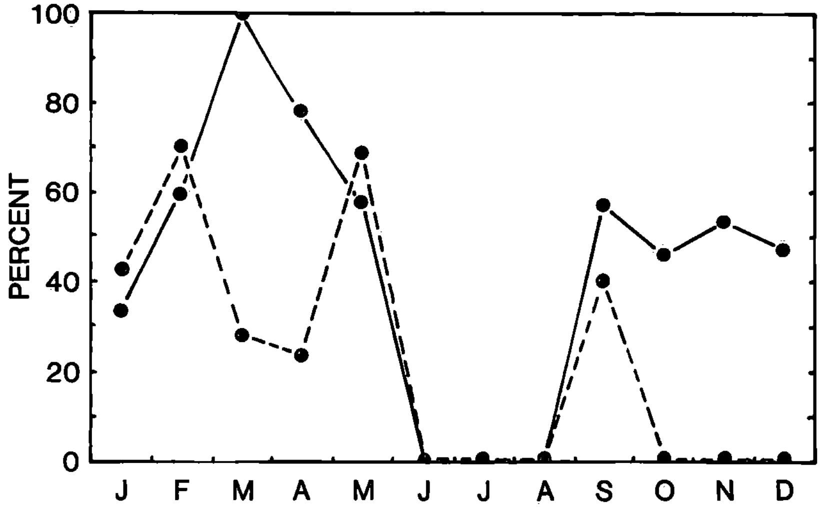

Figure 13. Percent males (solid line) and females (dashed lines) of *Mabuya multifasciata* with anterolateral yellow to red stripes.

CONCLUSIONS

Table 4 is a composite of all data available relating to reproduction in those skinks studied for which adequate information is available. What is immediately obvious is that though all these species were sympatric, there is great diversity of reproductive patterns represented in the species studied. This suggests that the local environment is not the only determining factor of lizard life history patterns, in spite of the fact that other workers (Tinkle et al. 1970; Barbault 1974a, b) have repeatedly suggested that it is. Vitt (1986) drew this same conclusion for lizards of Brazilian forests. Furthermore, he demonstrated that the reproductive patterns of the Brazilian forest lizards are more similar to those of species within the same family than to species in other families. In the current study we show that within even one family (Scincidae), reproductive patterns show considerable pattern diversity, in spite of the fact that all live in the same tropical forest area in the Philippine Islands.

All the factors shown in Table 4 for each species are seasonally variable, but undoubtedly linked to one another physiologically. Of these factors, the seasonal injection of young into the local ecosystem is ultimately the most important; and all other reproductive events are coupled to this in a necessarily sequential array.

Taken as a whole, the Caramoan skink biocoenosis introduces young into the system every month of the year, in both dry and wet periods. However, when the species are individually examined, only *Lamprolepis smaragdina* does so the entire year (11 % of total species in area). Of the remaining species, four (50%; *Emoia atrocostata*, *Lipinia pulchella*, *Brachymeles boulengeri*, and *B. samarensis*.) are long-pulsed breeding types (i.e., produce young over a period of 6 months or more, see Table 4). None are found in the same habitat, and none share even their microhabitat with any other skink species (see Auffenberg and Auffenberg 1988 for details). In the last three listed species, the annual non-productive phase is during monsoon I and the short dry period between it and the beginning of monsoon II. *Emoia atrocostata* has its rest period from the end of monsoon II through the early dry period (Ia), i.e. the coolest time of the year.

Collectively the short-pulsed species (55%) also produce young during almost every month of the year, but each species in one or two major bursts (Table 4). The only "cool-wet" producer in this category is *Sphenomorphus jagori*, most young appearing from October through January (heaviest rainfall period of monsoon II). It probably also injects neonates into the system during monsoon I, but none were noted (Table 4). In the same dense forest habitat (but slightly different microhabitat, see Auffenberg and Auffenberg 1988), *Mabuya multicarinata* produces young during two short-pulsed periods, one near the beginning of monsoon I and the second at the beginning of monsoon II. *Mabuya multifasciata* injects its young into the system over a single long pulse of four months, spanning both the driest time of the year (April-May) and the entire first monsoon (June-July).

Tropidophorus grayi has a similar strategy, but with a cycle beginning and ending one month earlier. This pattern evidently avoids injecting the young into the system when torrents are produced in the mountain streams along which the species occurs.

Otosaurus cumingii has one of the most restricted reproductive periods of all. Neonates are found in the Caramoan area only in April and May; gravid females mainly during a a short time in February and March (with another very low peak in October). Thus this species is mainly an early dry season I breeder, with most of the young emerging before the rain and the concomittant increase in insect biomass associated with monsoon I.

The most significant conclusion regarding our study of reproduction in sympatric Philippine skinks is that we are still far from understanding the factors that dictate relative clutch mass, individual egg size, total clutch number and timing of cycles in tropical scincids. However, our study does suggest a much greater diversity within a single tropical lizard biocoenosis than expected on the basis of published summaries, statements of general principal(s), or

Table 4. Composite of the seasonal representation for those reproductive factors studied in the Caramoan skink biocoenosis.[a]

```
      Jan   Feb   Mar   Apr   May   Jun   Jul   Aug   Sep   Oct   Nov   Dec
      ______DRY I__________   MONSOON I   DRY II ______MONSOON II________
        Cool       Warm                                     Early    Late           Condition

Mfs   |-----------#####-------------###############----------|                      Sperm
                  #####                         #####                               Courtship
      |------------###############----------------------------|                     Gravid
                            |--LOW--|                                               Fat

Mmc                     ##############################                              Sperm
            - - -------------------------------------------- - -                    Courtship
      |-----------#####--------------------###########--------|                     Gravid
                            |--LOW--|                                               Fat

Sj                |##########             |#####################                    Sperm
      ###########----|                    ######################--------#####       Courtship
                  ##########                    #########         ###########       Gravid
                                    (No Abdominal Fat)                              Fat

Lp    |-----------#####             #####             #########         #####       Sperm
      ################              |-----------#############################       Courtship
      ----------#####----|                |----##########--------------------       Gravid
                                    (No Abdominal Fat)                              Fat
```

Table 4 Continued.

```
Bb      #######################------|                                            Sperm
                                      (No Breeding Color)                         Courtship
        -----------#####--------------------------#####       #####------------   Gravid
                                      (No Abdominal Fat)                          Fat

Tg            ###########                         |-----------------###########   Sperm
                                      (No Breeding Color)                         Courtship
              ###########       ##########-----|              |---|               Gravid
                                      (No Abdominal Fat)                          Fat

Oc      ----#####                     |--------|              |-----------#####   Sperm
        ###############               #########################################   Courtship
        |---------#####         |---|                         |---|               Gravid
                                      (No Abdominal Fat)                          Fat

Ea            #####-------------#####                   ##########        #####   Sperm
        #################             ######################--------------#####   Courtship
        |--|        #####-------------------------------------------#####         Gravid
                              |--LOW--|                                           Fat

Ls                        #####----|        |---#####------|                      Sperm
        ----##################--------------------------#################         Courtship
        ----------------------#####---------#####-----------------------------    Gravid
                              |--LOW--|                                           Fat
```

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[a] Dashed months represent periods during which reproductive activity was noted; #'s are the period(s) of most intense activity.

theoretical models. Clearly more data are needed on reproductive output and annual patterns within sympatric tropical species where those climatic constraints known to be of great importance in temperate scincid breeding patterns are reduced or even lacking.

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