The Marine Toad, *Bufo marinus:* A Natural History Resumé of Native Populations

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ABSTRACT

Zug, George R., and Patricia B. Zug. The Marine Toad, *Bufo marinus:* A Natural History Resumé of Native Populations. *Smithsonian Contributions to Zoology,* number 284, 58 pages, 20 figures, 22 tables, 1979.—*Bufo marinus* is one of the most common and widespread anurans of Central and South America, yet little is known of its natural history in native habitats. Through a survey of the literature and brief ecological studies in Panama, we attempted to summarize the natural history of the toads. Emphasis is placed on distribution, sexual maturity, reproductive cycles, body size and growth, population structure and size, food and feeding behavior, activity and movements, thermal physiology, and water balance.

In general, marine toads have one or two breeding seasons each year, apparently timed so metamorphosis occurs during periods of high humidity and prey abundance. Toadlets grow rapidly and reach the size of sexual maturity (approximately 90 mm snout-vent length) at about one year from metamorphosis, although they may not breed their first year. Populations in semi-natural habitats are of moderately high density, 50 to 150 late term juvenile to adult toads per hectare. One-year-old toads comprise at least 50 percent of total population with a progressive and rapid decline of the older year classes. Apparently two-thirds of the population turns over each year. The toads are opportunistic feeders with ants and beetles predominating in their diet. Most toads are quite mobile, changing feeding sites regularly within a forage area of roughly 160 sq m. A toad is generally active one evening out of every three or four; however, weather conditions do alter activity patterns. The toads have a broad temperature tolerance but have no or little control of water loss. The dry season and the resulting desiccation may be a major mortality factor.

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The Marine Toad, *Bufo marinus:* A Natural History Resumé of Native Populations

George R. Zug and Patricia B. Zug

Introduction

The marine toad, *Bufo marinus,* is the most widespread and common American amphibian. Yet in spite of its commonness, we know little of its life history in its native habitat. All major ecological studies (see Zug, et al., 1975, for literature review) have been undertaken in areas where it is an exotic. The goal of our study has been to correct this oversight and to obtain comparative ecological information from natural populations of the marine toad. Our approach has been purposely superficial, for we wished to survey a wide variety of the toad's life history aspects in a short time and hopefully stimulate other researchers with marine toads in their backyard to study them in detail. We also wished to bring together the scattered natural history notes on this toad in its native habitat and those physiological and behavioral studies that apply directly to the toad's ecology.

Acknowledgments.—Many people have helped and encouraged us throughout our study, and we wish to thank them all. The staff and associates of the Smithsonian Tropical Research Institute (STRI), especially Stan Rand and Cathy Toft, made our field work pleasant and successful. Wim Wolda's monthly collections of toads enhanced our reproductive samples. Blair Hedges and Joan Dudley helped greatly in the dietary analysis. Fran McCullough allowed us access to her growth data on captive toads, and Charles Myers lent us his size data on Darien toads. The reviewers, A. Bennett, R. Crombie, R. Heyer, and F. McCullough, tempered our excesses and improved the clarity of the text.

The fieldwork was sponsored by several Smithsonian Institution sources: Smithsonian Research Foundation, Environmental Science Program, Fluid Research Fund, and Department of Vertebrate Zoology. We gratefully acknowledge their suport.

Distribution, Habitats, and Systematics

The natural range of the marine toad extends from approximately 27° N latitude in southern Texas and western Mexico to 10° S latitude in central Brazil (Figure 1). The break or transition between *B. marinus* and its southern relatives—*arenarum, ictericus, paracnemis, poeppigii,* and *rufus* (Bertini and Cei, 1962)—lies between 10° and 14° S and remains to be accurately delineated. By and large, the toad is a lowland animal and

Dedicated with affection and appreciation to Dr. Charles F. Walker, University of Michigan.

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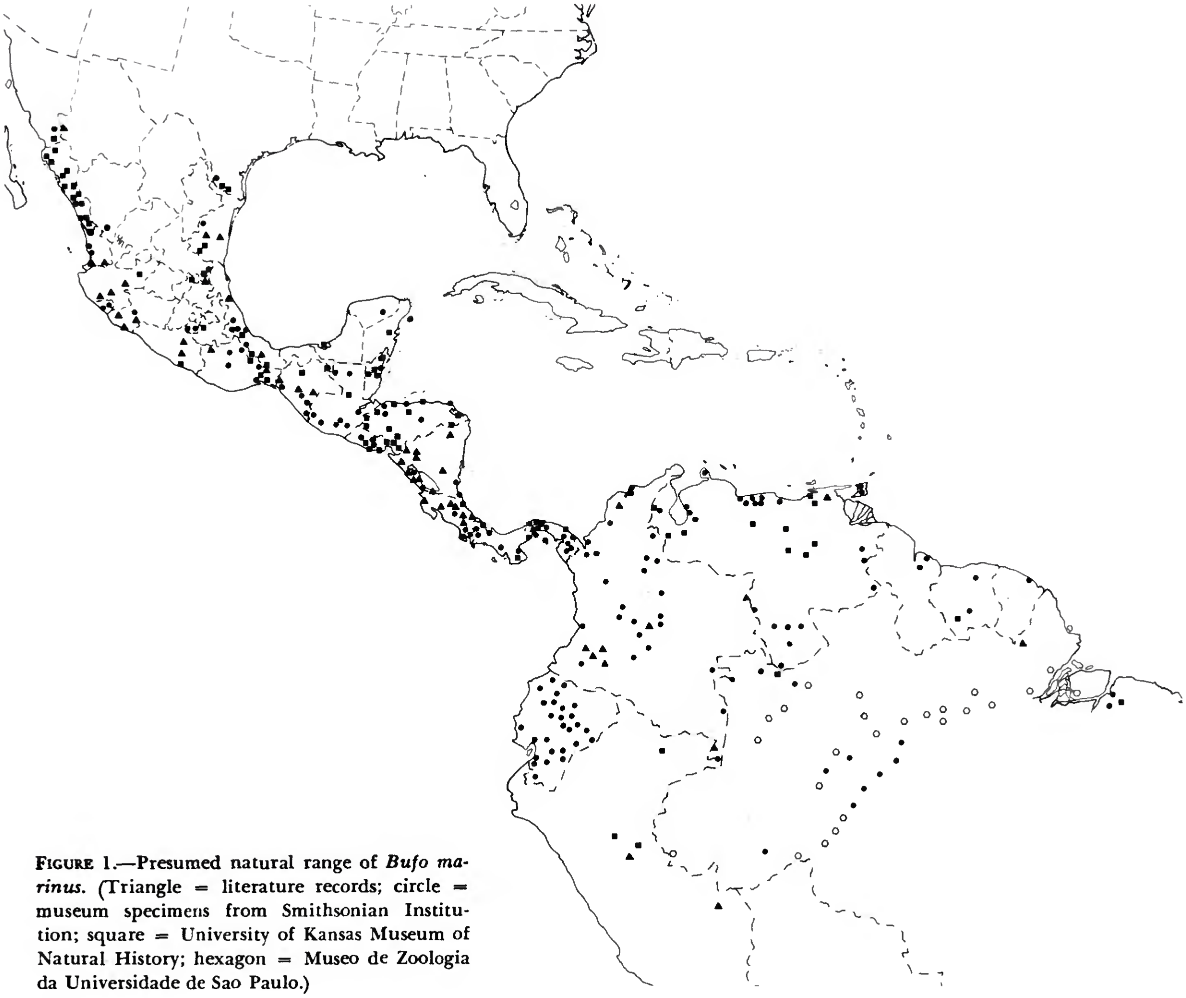


Figure 1.—Presumed natural range of *Bufo marinus.* (Triangle = literature records; circle = museum specimens from Smithsonian Institution; square = University of Kansas Museum of Natural History; hexagon = Museo de Zoologia da Universidade de Sao Paulo.)

generally occurs below 1000 m in elevation, although populations are known from above this elevation (Table 1). The maximum elevation for populational survival is apparently determined by the minimum thermal tolerance limits, so that the maximum elevation is lower at the higher latitudes, e.g., 500 m in Sinaloa, Mexico (Hardy and McDiarmid, 1969) compared to 1600 m in Venezuela (Rivero, 1961).

The toad occurs in a variety of habitats (Table 2), but nowhere is it more common than in open areas resulting from man's activity and in the grasslands. The most commonly cited habitat is in and around human settlements. As has been noted (Sexton, et al., 1964; Heatwole, 1966), *B. marinus* has become an associate or commensal of man and, in forested areas, is commonly in villages and small open areas but seldom seen elsewhere. Although not excluded from the forest, we suspect that the toads are largely marginal of open areas, and unbroken forest can and does act as a barrier to dispersal. Lescure (1975:66) notes the toad's absence in isolated Indian villages in Amazonia and also proposes unbroken forest as a barrier.

B. marinus is an old species. A fossil toad from the La Venta fauna of the late Miocene of Colom-

Table 1.—Selected examples of *Bufo marinus* occurrences above 1000 m in natural populations

Locality	Elevation (m)	Source
MEXICO		
Tamaulipas: Rancho del Cielo	1150	Martin, 1958
GUATEMALA		
Alta Verapas	<1300	Stuart, 1950
EL SALVADOR		
La Libertad: Santa Tecla	ca. 1200	Mertens, 1952
HONDURAS		
no specific locality given	1300	Meyer and Wilson, 1971
COSTA RICA		
Heredia: Volcán Poás	ca. 2100	Taylor, 1952
VENEZUELA		
Andes	1600	Rivero, 1961

Table 2.—Selected examples of habitats occupied by *Bufo marinus* populations (habitat descriptors unchanged from original sources)

Habitat	Locality	Source
sandy beach	Mexico	Hardy & McDiarmid, 1969
along streams	"	" " "
clearings in cloud forest	"	Martin, 1958
tropical scrub forest	"	Duellman, 1961
quasi-rainforest	"	Duellman, 1965
broad-leafed forest	"	" "
dense scrub forest	"	" "
coconut grove	"	" "
rainforest	Guatemala	Duellman, 1963
grasslands	"	Stuart, 1950
aquatic-riparian	"	" "
open broadleaf forest	"	" "
true savanna	"	" "
tropical moist forest	Honduras	Meyer & Wilson, 1971
tropical dry forest	"	" " "
tropical arid forest	"	" " "
subtropical wet forest	"	" " "
subtropical moist forest	"	" " "
subtropical dry forest	"	" " "
tropical rain forest	Guyana	Beebe, 1925
open cleared areas	Trinidad	Kenny, 1969

bia (Estes and Wassersug, 1963) is indistinguishable from modern *marinus* from northern South America. It was discovered in a floodplain deposit, which suggest that *marinus* habitat preferences have always been for open areas. When *marinus* originated is unknown, but we believe it arose as an adaptation to a seasonally xeric habitat, such as savanna or scrub forest. Cei (1972) postulates the Guiana shield as its ancestral home from which it radiated southward and speciated in the eastern Andean forest (*poeppigii*), Chaco (*paracnemis*), Brazilian planaltos (*rufus*), Atlantic coastal forest (*ictericus*) and Patagonia (*arenarum* complex); more recently (Plio-Pleistocene), it expanded northward across the Panamanian isthmus into Central America.

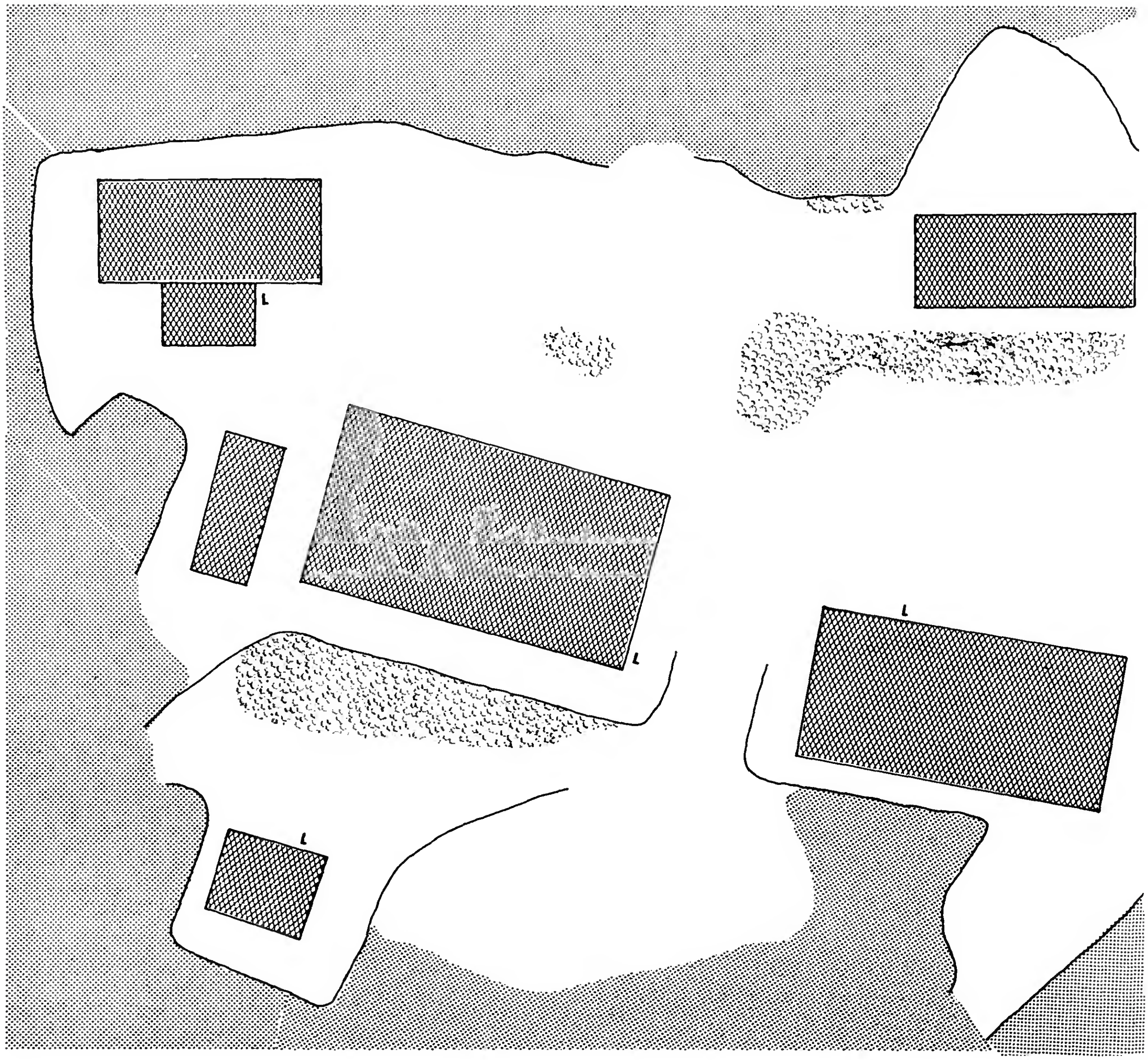
B. marinus and its relatives are considered to be one of the older or more structurally primitive groups of the broad-skulled toads (Martin, 1972). They share many similarities with the *valliceps* group of Central and North America. The latter has been interpreted as an Early Tertiary expansion of *marinus-valliceps* stock into Central America.

Since *B. marinus* is an old and widespread species, regional differentiation of populations is not unexpected. However, there are no strong morphological differences between populations (see Savage, 1960, for clinal variation in larvae characteristics) and apparently no differences in call. Differences in chromosome arm ratios and lengths do exist (Doyle and Beckert, 1969) between geographically distinct populations, so it is possible that more than one species is hiding under the name *marinus.*

General Materials and Methods

The toad populations of two areas were selected for ecological monitoring: Summit Gardens (SG) and Barro Colorado Island (BCI). Summit Gardens is a combined zoological and botanical garden in the Canal Zone, Panama, approximately 7 km southeast of Gamboa. In the center of the gardens there are two cement-enclosed ponds used for growing water lilies. The lily ponds are irregularly shaped with a circumference of approximately 110 m for the upper and 90 m for the lower pond. The upper pond is in a lawnlike setting with a few scattered trees and shrubs forming little apparent diurnal shelter for toads. The lower pond is encircled by a narrow belt (5–10 m) of grass and then a fairly complete ring of shrubs and trees. The grass along each pond is mowed and raked regularly so that there is little or no natural cover. The ponds are linked by a small cement-bottomed stream (approx. 100 m) that passes through a bamboo and tree gallery. A 10-meter-wide strip along the edge of the ponds and their connecting streams was designated as the study area. Nocturnal forays showed the toads to be concentrated around the ponds and seldom elsewhere except in the vicinity of the zoo.

Barro Colorado Island is a biological preserve in the Panama Canal, approximately 15 km northwest of Gamboa. The study sites were the laboratory/housing (Figure 2) grounds and dock/causeway area (Figure 3) of the Smithsonian Tropical Research Institute's biological station on BCI. The laboratory/housing site has an area of approxi-



mately 2812 sq. m, excluding the area of the various buildings; the area of the dock/causeway site is approximately 888 sq. m. The two sites are nearly 75 m apart, separated by a steep slope of secondary growth grasses and shrubs. The dock/causeway site is for the most part a bare or low grass habitat with numerous temporary stacks of lumber and equipment; only at its eastern end is the vegetation—grasses and cat-tails—continuous. This site is bounded on one side by water and on the other side by a sharp embankment on the western end that gradually slopes into a grassy area with buildings on the eastern end. The laboratory/housing site is bordered largely by seasonal rainforest. Within this site, there are numerous ornamental trees and shrubs; the open areas are cut infre-

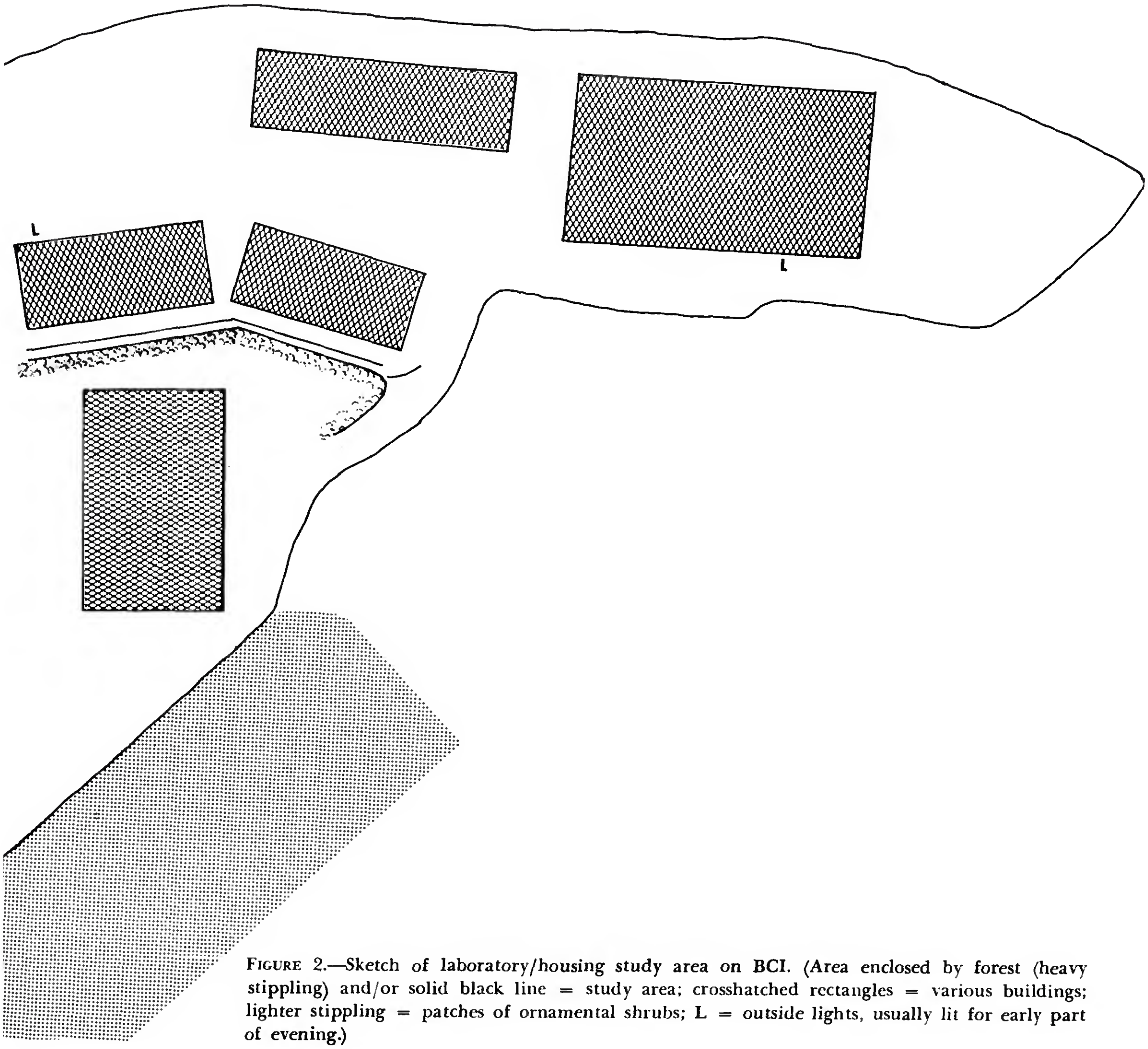
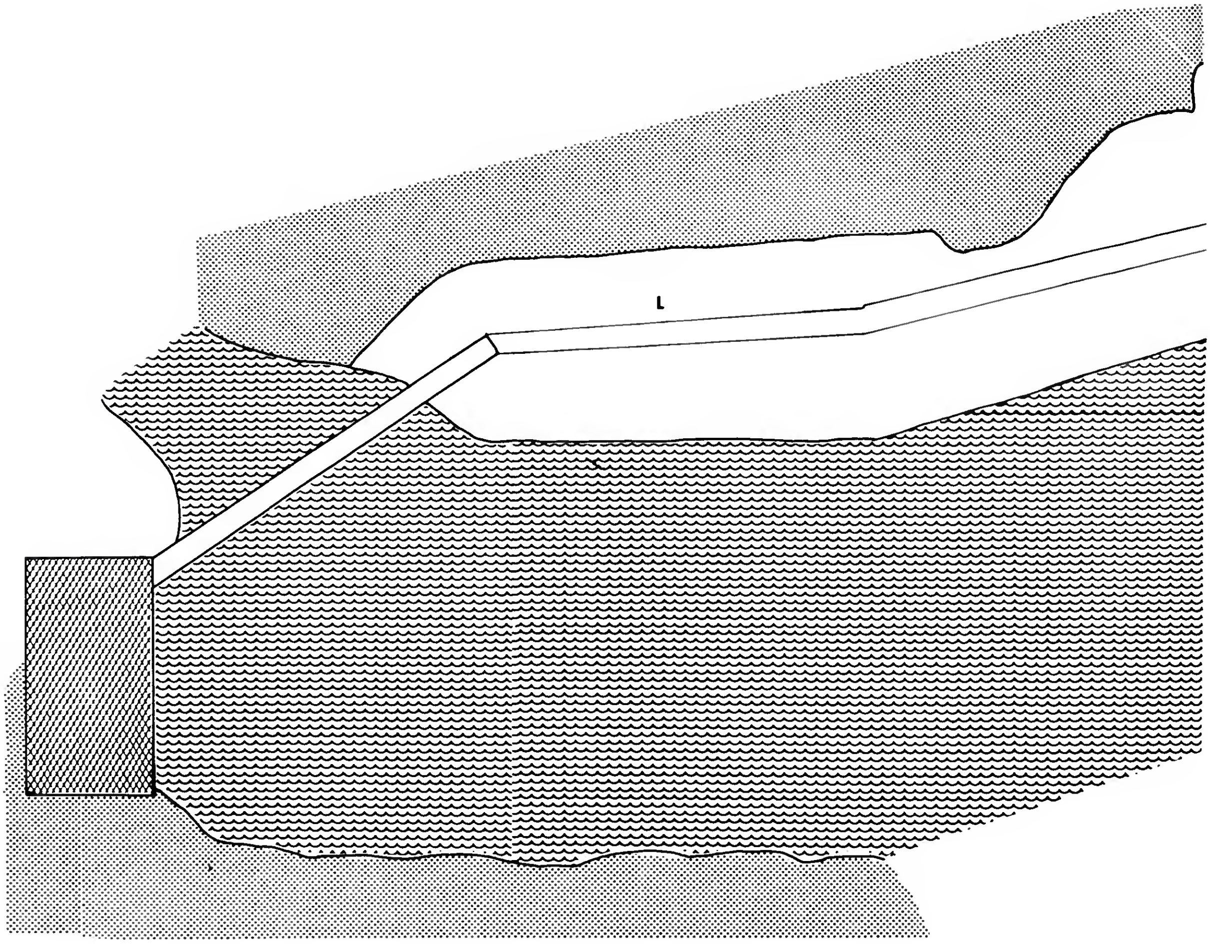


FIGURE 2.—Sketch of laboratory/housing study area on BCI. (Area enclosed by forest (heavy stippling) and/or solid black line = study area; crosshatched rectangles = various buildings; lighter stippling = patches of ornamental shrubs; L = outside lights, usually lit for early part of evening.)

quently so herbaceous ground cover varies from abundant to dense. Both sites were partially lighted from dusk (ca. 1830) to 2200 by the diffuse light from the interior of the buildings and by scattered outside lights. As will be seen later, the lights tend to concentrate the toads, but toads did not confine their activity to the brightly lighted areas.

In both study areas (SG, BCI), the toads were hand caught and individually marked by toe clipping (only the terminal two phalanges) following the system of Nace et al. (1973). Snout–vent length, body weight, and sex were recorded upon the initial capture, and any succeeding ones at two-week intervals. Time and site of activity were recorded every time a toad was observed.

Samples were gathered from five other localities



in order to obtain information on feeding habits and the reproductive cycle. The Gamboa sample (G) came from a variety of locations within the town, viz., school ground, paddock, and canal maintenance yard; all locations were in close proximity to buildings, artifically lighted for most of the night, and with the grass and shrubs receiving frequent care. The Summit Hill (SH) sample (ca. 9 km SE of Gamboa) came from the edge of a golf course; the site is indirectly lighted for most of the night, and the grass is mowed frequently. The Las Cumbres (LC) sample (ca. 18 km E of Gamboa) came from a residential area supporting a variety of herbaceous ground cover and indirect and direct artificial lighting for much of the night. The Cocole (C) sample (ca. 18 km SSE of Gamboa) came from a shallow gravel pit; there is no artificial lighting and, except for an unpaved road, the site was covered with a dense stand of 1–1.5 m high grass. The Los Santos (LS) sample (from the Peninsula de Azuero, ca. 150 km SW of Gamboa) came from the border of a drying cattle tank; the tank was surrounded by small clumps of thorny scrub and patches of short grass and herbs; there was no artificial lighting. Appendix I summarizes the collecting data.

All the specimens from the preceding five samples were preserved in 10% formalin within three hours of capture. Stomach contents were removed later in the laboratory, air dried, weighed, sorted,

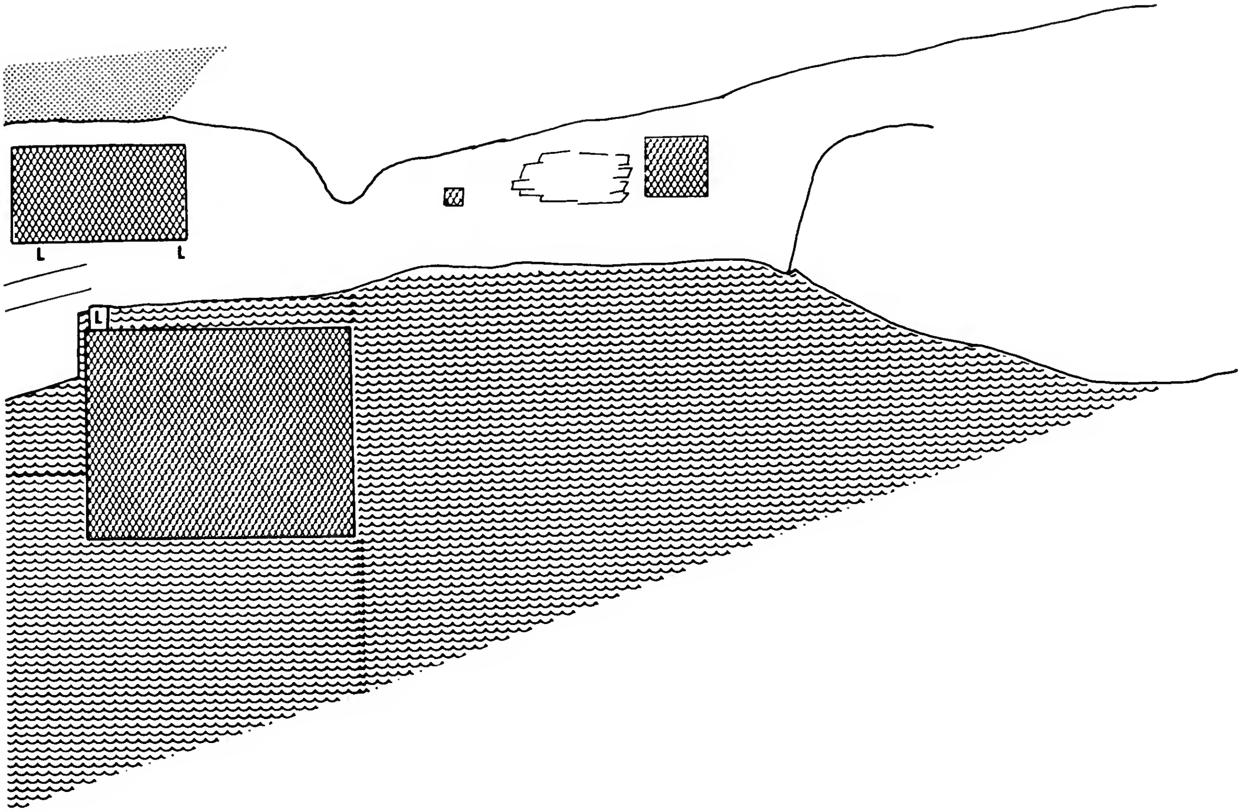


FIGURE 3.—Sketch of dock/causeway study area on BCI. (Wavy lines = water; other symbols same as Figure 2.)

counted, and identified to lowest reliable taxonomic level. Gonadal examination was also performed later in the laboratory.

All measurements (testes) or weights (ovaries and fat bodies) were taken from only one side, the right. Histological sections were made from several testes of each monthly sample. Further details on materials and methods are presented in the following sections, where appropriate.

Sex, Size, and Growth

PHYSICAL APPEARANCE

To pervert a phrase from Gertrude Stein, a toad is a toad is a toad—only more so for the marine toad. Marine toads have few admirers and are usually described in a derogatory manner, such as looking like mobile cow patties. Such epithets are, however, of little help in distinguishing them from their warty brethren. Although the recently metamorphosed toadlets may cause confusion, they are unique in bearing regular rows of paravertebral tubercles. Once the toads reach a snout-vent length of approximately 50 mm, they can be recognized by the following set of characters: a heavy-bodied toad with its maximum width nearly three-fourths of its body length; broad head with truncate snout; bony ridges (cranial crest) on the periphery of the head, i.e., canthal, preorbital, postorbital, and short temporal ridges; very large ovate to triangular parotoid gland extending from the temporal ridge to a level beyond the axillary region; the tympanum distinct, about half the diameter of the eye; skin on back and legs very warty; fingers free, toes distinctly webbed for at least half of their length; juveniles of both sexes and mature females with a mottled dorsal pattern, ground color a dusky brown covered with irregular blotches of beige and chocolate, large chocolate scapular blotches and usually a beige mid-dorsal stripe present; adult males unicolor cinnamon brown and spinose, each wart, no matter what its size, capped by one to many horny spines.

The tadpoles of *B. marinus* are small (approx. 10–25 mm in total length), round-bodied creatures. The body and tail are black or dark brown with a distinctive pale cream stripe along the lower edge of the caudal musculature. The tail fin is a uniform translucent gray. The mouthparts show the typical bufonid condition with wide oral disc laterally papillate and strong, keratinous jaws with serrate margins. Further details of tadpole morphology are in Altig (1970), Breder (1946), Kenny (1969), and Savage (1960).

Sexual Maturity and Reproductive Cycle

Maturity.—Female toads from Papua New Guinea reach sexual maturity at a snout-vent length of 70–80 mm (Zug et al., 1975). In the Canal Zone, Panama, females apparently do not reach maturity until they are 90–100 mm long. Only a single 93 mm toad showed oogenesis; all other gravid or actively oogenetic females were greater than 100 mm. The largest inactive oogenetic female was 102 mm, and there were several other presumably "immature" females in the 90–100 mm class.

Sexual maturity in males is more difficult to determine. The smallest male in the Canal Zone samples with well-developed secondary sex characteristics such as uniform brown dorsum and keratinous thumb patches was 103 mm. Several males in the 85–95 mm size class showed the transition pattern between the juvenile/female coloration and that of sexually mature males (captive males developed nuptial pads one to two weeks prior to juvenile pattern transition—F. McCullough, pers. comm.). On BCI, the smallest calling and amplexing male was 106 mm. Of the 31 BCI toads with distinct male characteristics, only 3 were less than 90 mm, and the smallest was 84 mm. Thus the circumstantial evidence suggests that male toads mature at a somewhat smaller body length (85–95 mm) than the females. Histological sections of the testes of several males (snout-vent lengths of 81, 84, 87, 88, and 90 mm) show heavy concentrations of spermatozoa and spermatids in the seminiferous tubules of the largest individual. The other males show active spermatogenesis with a predominance of primary spermatocytes in the smallest specimen and secondary spermatocytes and spermatids in the middle three specimens. On histological grounds,

Table 3.—Selected examples of sex ratios from anuran populations

Taxon	Sex ratio females:males		Situation	Author
	Raw	Calculated		
Bufo bufo	252:643	1:2.6	mixed biotopes (Mar-Oct)	Heusser, 1968
	275:545	1:2.0	" " "	" "
	130:262	1:2.0	" " "	" "
B. calamita	209:698	1:3.3	breeding pond (May-Jun)	Heusser, 1969
	120:647	1:5.4	" " "	" "
B. valliceps	34:66	1:1.9	breeding pond (Apr-Aug)	Blair, 1960
	20:80	1:4.0	" " "	" "
	36.64	1:1.8	" " "	" "
	7:93	1:13.3	" " "	" "
Gastrophryne carolinensis	80:148	1:1.8	breeding pond (Jun)	Anderson, 1954
	17:52	1:3.1	abandon field (Apr-May)	" "
	55:94	1:1.7	flooded field (Feb)	" "
Pseudacris triseriata	-	1:10	breeding pond (Feb-Apr)	Whitaker, 1971
Rana pretiosa	309:169	1.8:1	pond (summer)	Turner, 1960a

maturity (or more specifically reproductive ability) is attained at approximately 90 mm snout-vent length.

SEX RATIOS.—In anurans, there usually is a preponderance of one sex over the other (Table 3). Although the data are limited, males appear to outnumber females in terrestrial species, females outnumber males in semiaquatic species.

Even though our data for *B. marinus* are scanty, different sex ratios for populations in different habitats are apparent. Counting only the sexually mature individuals in our samples, males outnumber females at Cocole (males; females, total number—1:2.3, 10), Gamboa (1:6, 7), and Summit Garden (1:3.2, 38). Females outnumber males at Barro Colorado Island (2.4:1, 88), Las Cumbres (4.7:1, 17), Los Santos (1.5:1, 15), Summit Hill (2:1, 9), and El Real, Darien (4.1:1, 82; data from C. W. Myers). The most striking point of these data is the strong tendency for one sex to be at least twice as numerous as the other. Why the sexual imbalance should be so strong is unclear, and our knowledge of the different populations and their habitats is too sparse to draw definite conclusions. These data suggest, however, that the sex ratio is not species specific, but largely determined by environmental vagaries (abiotic as well as biotic) encountered by each population.

REPRODUCTION.—The inability to obtain large monthly samples from the Canal Zone leave this life history aspect unresolved. Our data are suggestive and nothing more.

A summary of the seasonality of oogenesis for Canal Zone toads is presented in Figure 4. Four oogenetic states were selected (Jorgensen, 1973): previtellogenesis, the ovaries are small and granular in appearance; early vitellogenesis, the ovaries are still small, although the oocytes become evident as discrete cells; late vitellogenesis, the ovaries are greatly enlarged and the oocytes are well yoked and beginning to pigment; gravid, the ova are mature and the ovaries fill the entire body cavity. These states are equivalent to the body weight/ovary weight proportions (Zug et al., 1975), except that the late vitellogenic state encompasses the values of 30 through 100.

The presence of gravid females in April and May suggests that reproduction occurs then, during the late dry season and the early wet season. The active vitellogenesis in these same samples further indicates that reproduction might continue into June and, possibly, July. Whether reproduction occurs at other times remains unanswered. Of the nine mature females from Los Santos, eight are in a previtellogenic or very early vitellogenic phase, the ninth in mid-vitellogenesis. From this we assume that the toads of this xeric area breed in the mid or late wet season, i.e., July or later, for there is

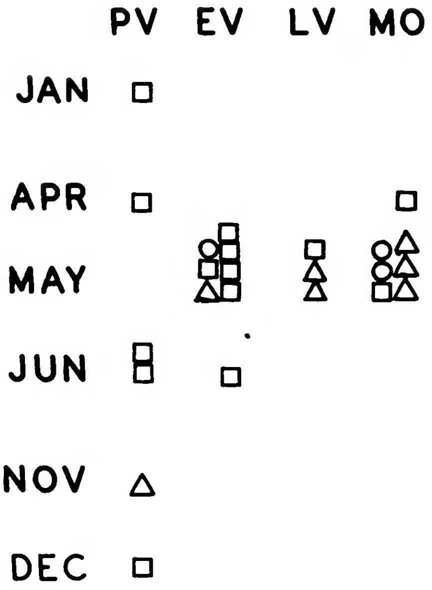


FIGURE 4.—Reproductive state of adult (>95 mm) toads in Canal Zone. (PV = previtellogenesis, EV = early vitellogenesis, LV = late vitellogenesis, MO = mature ova or gravid; square = LC sample, circle = C sample, triangle = G-SH sample.)

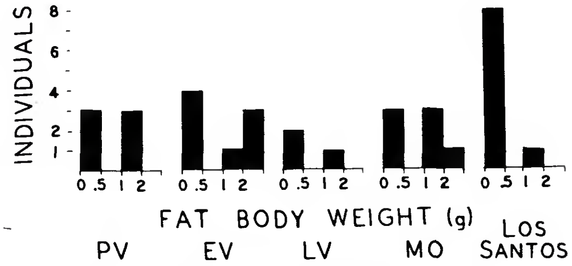


FIGURE 5.—Fat body weights of adult females in different phases of oogenesis. (Fat body weights, in grams, are divided into four classes: <0.5, 0.51–1.0, 1.01–2.0, > 2.0; Canal Zone sample—C, G, LC, SH—is segregated into four phases of oogenesis; see Figure 4 for explanation of abbreviations.)

FIGURE 6.—Monthly variation in fat body weights of adult (>90 mm) male toads from the Canal Zone. (Weight classes same as Figure 5.)

no evidence of May breeding (beginning of the wet season).

The fat body weights (Figure 5) suggest that the Los Santos female toads require a period of intense feeding in order to replenish their lipid stores before vitellogenesis can begin. The necessity of feeding at the beginning of the wet season may delay breeding until the mid or late wet season. A portion of the Canal Zone toads, in contrast, have more than adequate lipid reserves for vitellogenesis, because the fat bodies are not entirely depleted by the completion of vitellogenesis. The six mature males from Los Santos also have small to nonexistent fat bodies (≤ 0.5 g). The fat bodies of the majority of adult males and all immature females and males from the Canal Zone are small (Figure 6). Immature individuals would be expected to direct all their energy into growth, whereas adult males might be expected to use the fat bodies to store energy for periods of low food availability or for periods of nonfeeding during the breeding season. Although the data are meager, such storage is not indicated.

The testis length to snout-vent length ratio of adult male toads was examined to determine if this ratio reflected a spermatogenic cycle. For the samples from January, April, May, and November, the ratios in the adult males (≥ 90 mm) show no significant difference between the months, means of 6.6, 6.2, 6.4, and 6.5 mm, respectively. Comparison of immature to mature males show the testes of immatures to be proportionately smaller, although the ranges of the two groups strongly overlap. We can state only that testis length correlates well with body length ($N=27$; $Y=5.92+0.21X$; $r=0.73$), and upon maturity, the testes experience a growth surge. Changes in volume or weight might reflect periods of active spermatogenesis.

Testes from several adults were examined for spermatogenic activity by measuring the maximum diameter of 15 seminiferous tubules in the center of the testis (Figure 7). There is clearly an increase in tubule diameter from the beginning of the dry season (January) to the beginning of the wet season (May), possibly followed by a decline of testicular activity during the wet season. Although the number of sperm were not counted, the densest aggregations in the seminiferous tubules occurred in the April sample; the lightest aggregations in the January sample.

REMARKS.—The data on gonadic activity (Figures 4 and 7) suggest a seasonal reproductive cycle for the Canal Zone toads. The major reproductive effort appears to occur about the end of the dry and the beginning of the wet season. In contrast, the Los Santos toads are assumed to breed in the middle of the wet season (July or later). A series of 65 adult females collected in October from El Real, Darien, contained 53 individuals with enlarged ovarian eggs, suggesting a major breeding period in November or December (data from C. W. Myers). However, the data are so limited that they do not preclude sporadic breeding throughout the remainder of the year or, at least, another peak of breeding activity. Breder's data (1946) showed spawning

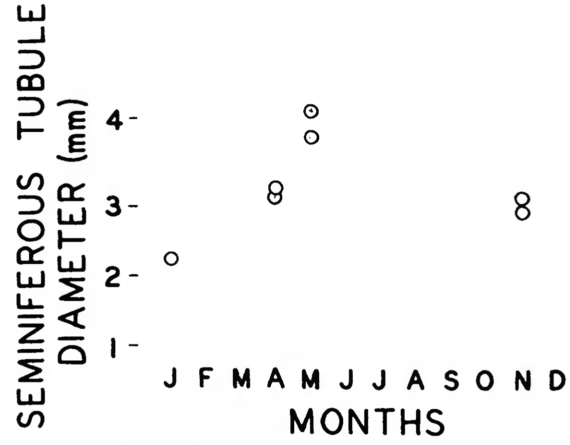


FIGURE 7.—Seasonal change in testicular activity of adult male toads from Canal Zone.

FIGURE 8.—Breeding activity of *B. marinus* within its natural range. Data, top to bottom, are from Hardy and McDiarmid (1969), Duellman (1963), M. Dix (pers. comm.), Breder (1946) and our samples, Breder (1946) and C. W. Myers (pers. comm.), Kenny (1969).

occurred in early January along the Rio Chagres, Canal Zone. Assuming that such breeding still occurs, we believe this represents a minor breeding peak, because of the reduced testicular activity. However, Breder's data demonstrate the major fault of our reproductive data, aside from its small size, is that we combined population that are separated by distances of 5 or more kilometers. We realize that adjacent but separate populations may have different breeding periodicity dependent upon their local climatic regime and their choice of breeding site. Hypothetically, stream breeding toad populations might have been selected for dry season reproduction, because of the low flow rate at that time (analogous to *Smilisca sila*); whereas temporary- or shallow-pond toad populations breed in the wet season when the ponds are full and stable.

Breder's data (1946) on tadpoles and reproduction choruses indicate an extended breeding season for the populations in the Rio Chucunaque drainage of Darien, Panama. Data from Latin America are summarized in Figure 8. The figure is based on actual spawning and/or presence of tadpoles, and not choruses for the latter can be misleading, e.g., Honegger's fig. 3 (1970). Most populations seem to have two peaks of breeding activity. In spite of statements to the contrary, e.g., breeding throughout the year in Nicaragua (Villa, 1972), we believe that this bimodal reproduction is typical of the majority of native *B. marinus* populations.

TABLE 4.—Development of *B. marinus* tadpoles from hatching to metamorphosis

Locality	Duration	Source
Oahu	30 days	Pemberton, 1934
Puerto Rico	60-70 days	Sein, 1937
Panama	4-6 weeks	Breder, 1946
Negros Island	7-8 weeks	Alcala, 1957
Queensland	75-80 days	Straughn, 1966
Trinidad	6 weeks	Kenny, 1969
Venezuela	29-32 days (experimental)	Durant, 1974
"	56 days (natural)	Durant, 1974

LARVAL DEVELOPMENT AND METAMORPHOSIS.—Like many aspects of the marine toad's life cycle, no thorough study of its larval biology has been done. Females deposit long strings of eggs, containing thousands of ova (Figure 9), in the shallow water of temporary or permanent streams and ponds. It is assumed that the female releases her entire clutch during a single amplexus, rather than mating with several males over several days or weeks. The eggs hatch in 36 hours (Kenny, 1969) to four days (Breder, 1946), and the larvae grow and metamorphose in one to two months (Table 4).

We have no data on development time for the Canal Zone toads. Mass metamorphosis was observed twice. In late March, 1974, large number of toadlets were metamorphosing from the few remaining pools in the drying streams of the Madden Forest Reserve; no metamorphosis was observed on BCI at that time. Mass metamorphosis occurred on BCI in mid May 1975 but not in May 1976. In addition to indicating an early dry season breeding period, these data suggest an irregular developmental time that may in some way be regulated by environmental conditions. The drying pools may have forced an earlier metamorphosis in the dry season to increase the likelihood of survival of the young. The ideal time of metamorphosis would seem to be at the beginning of the wet season, e.g., May 1975 sample. Insect abundance is rapidly increasing at this time and the high humidity permits rapid and distant dispersal.

BODY SIZE

Bufo marinus is purported to contain the "world's largest toad" (230 mm snout-vent length, Surinam; Reed and Browsky, 1970). Although this fact in and of itself has no biological significance, it does emphasize several points. Adult marine toads are generally large (100–150 mm) and, thus, poten-

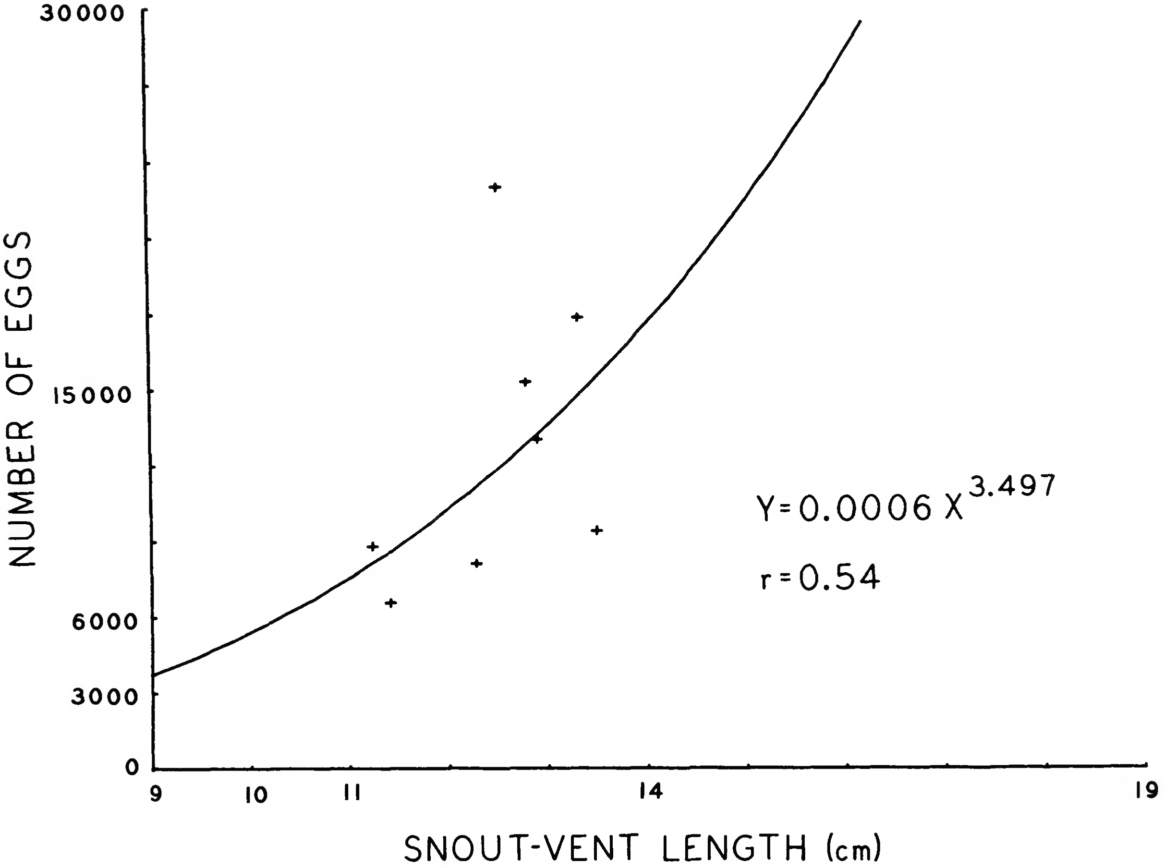


FIGURE 9.—Relationship between snout-vent length of gravid females and number of mature ova in both ovaries. (Total number of ova estimated by counting ova in 0.4 to 0.8 g sample of ovary and then extrapolating this value to total ovarian weight.)

tially one of the major nocturnal predators on small terrestrial animals. The large size of adults coupled with their large parotoid glands decrease the probability of predator attacks and suggest the likelihood of increased longevity once adulthood is reached. The large size of females increases their reproductive potential by enabling them to carry more eggs. A final point, which is not documented but a common impression held by many herpetologists, is that the marine toads of the Guiana shield area tend to average larger than anywhere else.

For our Panamanian data, we shall examine only two aspects of body size: the possibility of sexual and regional differences in body size.

SEXUAL DIFFERENCES.—Only three samples, Barro Colorado Island, Summit Garden, and El Real, are sufficiently large to analyze for size differences in sexually mature adults (see section on maturity, p. 8). The weight-length regressions (Figure 10 and Table 5) are very similar for males and females in the BCI and ER samples. At the larger body lengths, females tend to be slightly larger, i.e., higher slopes or allometric constants, than males but not greatly so. These slight differences result, at least in part, from the wider ranges of body lengths in the females, e.g., BCI males 90–130 mm, BCI females 95–160 mm. The narrow size range (90–110 mm) in the SG sample results in significantly different slopes for the male and female regression curves. Although it will become more

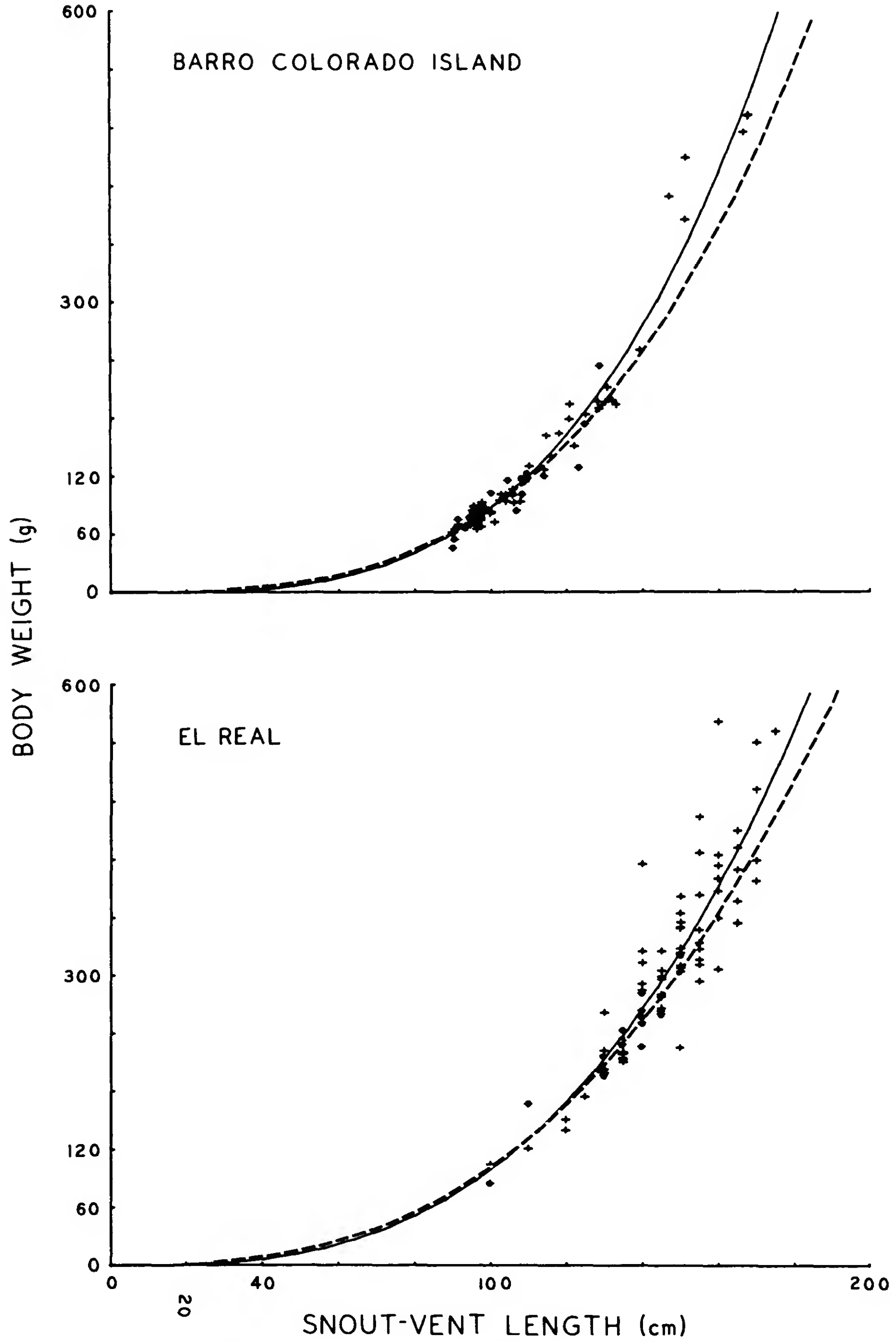


FIGURE 10.—Sexual differences in weight-length regression (power) of Barro Colorado Island and El Real toad samples. (Crosses and solid line = females; circles and broken line = males; data for power equations in Table 5.)

TABLE 5.—Summary of weight (Y, grams) and length (X, millimeters) regression relationships of *Bufo marinus* at six localities (A and B data derived from power regression $Y=AX^B$; r is correlation coefficient)

Locality	N	A	B	r
Barro Colorado Island	209	0.00008	3.019	0.99
female	54	0.00001	3.418	0.98
male	26	0.00004	3.137	0.93
Summit Garden	50	0.00010	2.965	0.96
female	7	0.00003	3.240	0.97
male	23	0.00187	2.340	0.82
Cocole	11	0.00013	2.906	0.98
Gamboa	12	0.00010	2.977	0.99
Summit Hill	19	0.00005	3.127	0.98
El Real	83	0.00010	3.030	0.94
female	65	0.00010	2.933	0.92
male	17	0.00040	2.722	0.95

apparent in the later discussion on age or size distribution, females average larger than males (see ER sample in Figure 10).

REGIONAL DIFFERENCES.—A comparison of six sampling localities (Table 5) demonstrates no major differences in the body weight-length regressions between any of the localities. In all the samples, the Y-axis intercept is nearly 0, and the slope is nearly 3. Although the habitats of the sampling localities may differ—strikingly so to our eyes—these differences have caused no apparent differences in the growth of the toads, such as were seen in the savanna and the rainforest margin toads in Papua New Guinea (Zug et al., 1975). This uniformity is somewhat surprising as we would expect populational adjustments in body dimensions relative to the harshness of its environment, particularly since such adjustments have been observed elsewhere.

GROWTH

The likelihood of death for a marine toad is probably greatest from metamorphosis to subadulthood. During this period, the toadlet is a juicy little morsel that has lost the toxicity of its larval stage (Licht, 1967; Wassersug, 1973) and has not yet gained the protection of large body size and well-developed parotoid glands. The dangers of juvenile life would place a high premium on rapid growth. The data from other species of toads (Turner, 1960b; Clarke, 1974; Labanick and Schlueter, 1976) show that they reach adult size within one full year of growth (not necessarily a calendar year) after metamorphosis. The marine toad has this capability or, at least the introduced toads in Hawaii (Pemberton, 1934) do. Our data for the Barro Colorado Island *marinus* indicate a similar rapid growth.

LARVAL GROWTH.—We have no data on larval growth and only a minuscule amount exists in the literature. The time available for growth is variable, ranging from one to nearly three months (Table 4). Presumably the shorter the larval period, the smaller is the metamorphosing toadlet; however, Durant's data (1974: fig. 4) show that weight of toadlets metamorphosing at 32 days is the same as those metamorphosing at 56 days. Straughn (1966) shows the tadpoles developing from approximately 5 mm at hatching to 15 mm at metamorphosis; this yields a growth rate of approximately 0.128 mm/day.

POSTMETAMORPHIC GROWTH.—The growth of the postmetamorphic marine toad is as poorly known as that of the larval stages. There are a few anecdotal reports. Pemberton (1934) reports toadlets in Hawaii grow from 6–12 mm to 60–75 mm in three months and reach 90–120 mm in six months; this would be a minimum growth rate of 0.434 mm/day. Australian toads reach approximately 76 mm by the beginning of their second summer and continue growing for another three years at roughly 25 mm/year (Straughan, 1966); these data yield growth rates of 0.139 and 0.068 mm/day, respectively. The controls in two growth hormone experiments (Zipser, Licht, and Bern, 1969) show growth rates of 0.287 g/day and 0.471 g/day during eight and six week runs, respectively; the initial weight of each sample was 20.1 g.

Our data on growth derive from the mark-recapture study on Barro Colorado Island; the Summit Garden study had too few recaptures to be reliable. Of the BCI toads, we had 47 recaptures; 20 of these are multiple recaptures. The intervals vary from five to 402 days; the maximum time between the initial marking and the last recapture is 760 days. Unfortunately, of the 75 postmetamorphics marked in May 1975, none were recovered the following May, so our growth data is largely confined to older juveniles (70–85 mm), subadults, and adults.

To examine the history of growth in BCI toads, we have been forced to make several assumptions

TABLE 6.—Growth in recently metamorphosed *Bufo marinus* from laboratory/housing study area on Barro Colorado Island in May 1975 (body length in mm, rate in mm per day)

Sampling period	Mean snout-vent length	Sample size	Growth rate
8 May	18.2	9	-
15 May	20.9	19	0.385
18 May	22.7	12	0.600
19 May	23.9	11	1.200
20 May	25.2	12	1.300
21 May	28.0	14	2.800
22 May	25.6	8	-2.400

TABLE 7.—Body length to age conversion table (conversion values based on growth rate of 0.65 mm/day for first five weeks and 0.37 mm/day thereafter; fuller explanation given in text)

Week	Snout-vent length (mm)	Week	Snout-vent length (mm)
0	11.0	25	85.5
1	15.5	30	98.5
2	20.0	35	111.5
5	33.5	40	124.5
6	36.1	45	137.5
10	46.5	50	150.5
15	59.5	55	163.5
20	72.5	60	176.5

and arbitrary decisions on the relationship between size and age, because a complete growth series was not obtained. Firstly, we do not know the size at metamorphosis of the May 1974 toadlets, or how old the toadlets were by the time they had reached our study site (a minimum of 150 m from the metamorphosis beach and probably considerably longer as the toad hops). By measuring a small sample (24) of metamorphosing toadlets, we determined the mean and modal snout-vent to be 11 mm. By averaging the growth rate of recently metamorphosed toadlets (Table 6), we obtained a rate of 0.647 mm/day, and by extrapolation, we can postulate that the toadlets measured on May 8 are 11 days old. If they were to continue to grow at this rate, they would reach 70 mm in 91 days (13 weeks), which is in complete agreement with Pemberton's findings; however, we believe this rate to be too high for the larger BCI toads.

In the absence of data for the 30–70 mm toads, we have two ways of estimating the growth rate: (1) determine growth rate in captive toads; (2) use the mean growth rate of mark/recapture BCI toads. The mean growth rate in four captive Jamaican toads (initial snout-vent lengths of 33, 34, 41, and 48 mm) is 0.369 mm/day; the toads were measured at weekly intervals over a period of 155 days (data from F. McCullough). The average growth rate from the 76 recapture determinations is 0.373 mm/day. These two estimates are surprisingly similar considering that the toads were derived from different populations and were subjected to quite different environments and, as such, we believe that 0.37 mm/day provides a reliable estimator to convert known body length to age (Table 7). In the table, we have carried the size to age conversion to extremes, for growth can be expected to slow down after sexual maturity and show occasional bursts during periods of high food abundance. However, these extremes are necessary as they provide us with an initial age to plot our growth data.

Figure 11 summarizes the growth data for the BCI sample. In spite of the arbitrariness of the age assignment, the overall pattern is clear. Growth is fairly rapid for several weeks, then it slows down, but not drastically so, until sexual maturity is reached. Sexually mature toads are still capable of rapid growth, e.g., one female grew from 87 to 133 mm in ten weeks, however most toads greater than 110 mm show slower growth rates. The larger toads tend to show a long periods of no or very slow growth.

The variability observed in Figure 11 results from at least three factors: (1) the arbitrariness of age assignment, (2) seasonal differences, and (3) sexual differences. Only the first is discussed here; the latter two factors are investigated in subsequent sections. Most of the individuals upon first capture were less than 100 mm long. On the basis of our age conversion, this would suggest that they are no more than 31 weeks old, which further suggests that they metamorphosed in November or later. We doubt this, because November is roughly the last strong pulse of the wet season, insect abundance is low, and conditions will continue to remain unfavorable for toads as the dry season advances, so a high and constant growth rate is

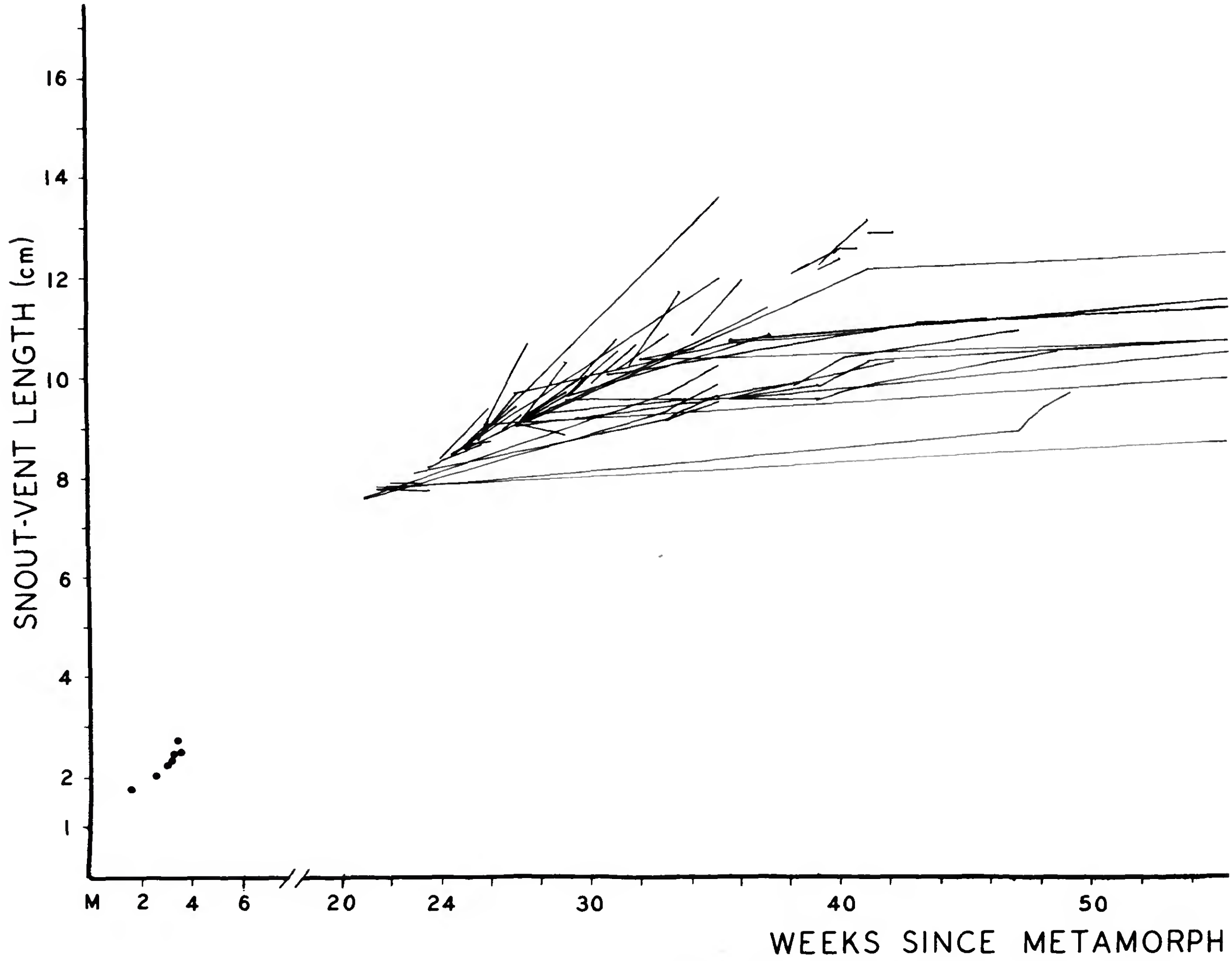
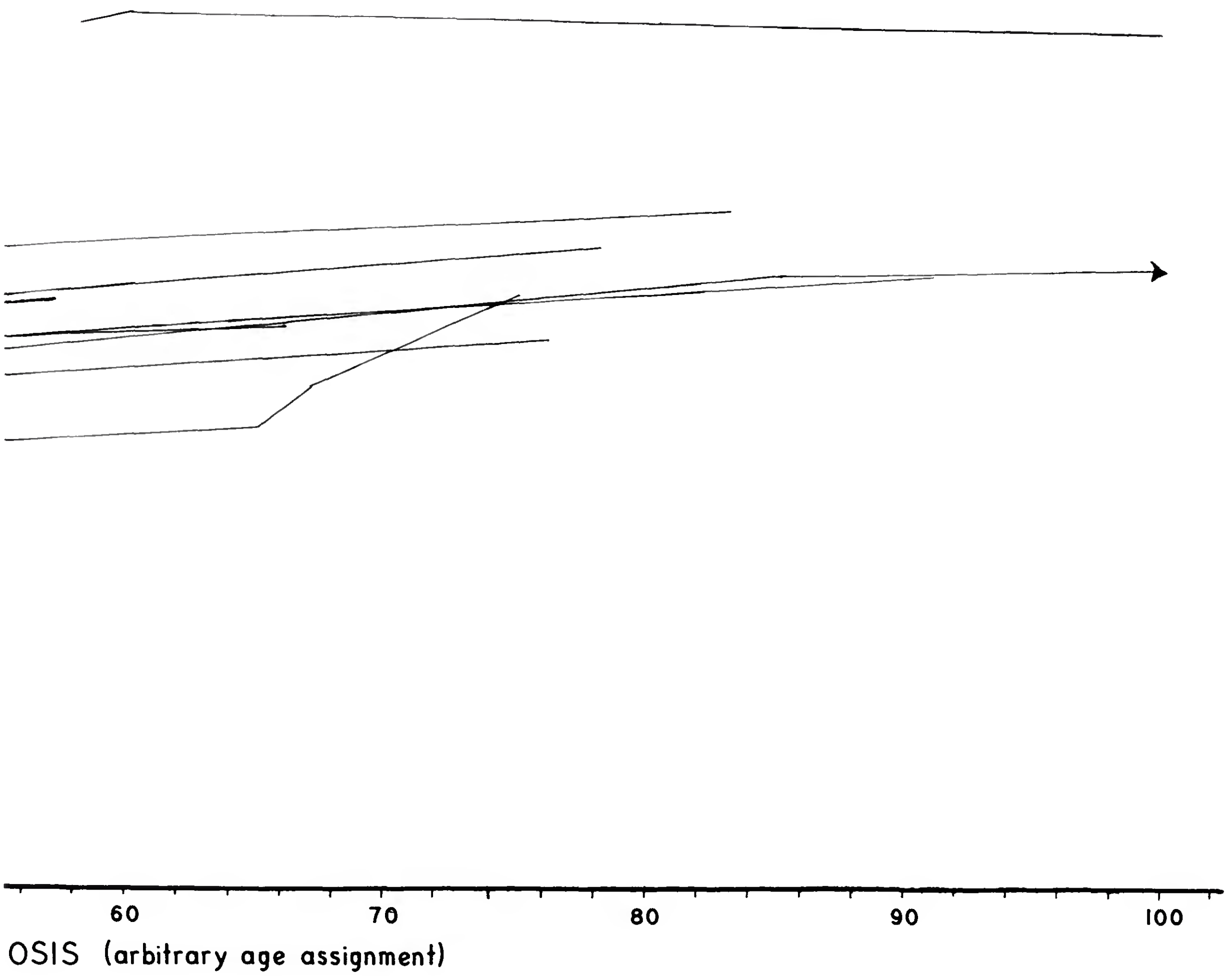


FIGURE 11.—Growth in Barro Colorado Island toads. (Assignment of age at first capture taken from Table 7; intervals thereafter are actual time to next capture; each solid circle = sample of recently metamorphosed toads (See Table 6), each line = different individual and its growth.)

unlikely. We are more inclined to believe that these late juvenile and young adult toads are approximately one year old, having metamorphosed at the beginning of the wet season (May or June) —this will become more apparent when we examine the age/size distributions in a subsequent section. This assumption leads to an interpretation that recently postmetamorphic toads grow rapidly for at least the first half of the wet season, growth slows or nearly halts for the remainder of the wet season and continues at this level through the dry season. At the beginning of the next wet season, the one-year-old toads have a burst of growth, which ends quickly. Subsequent energy intake is used either for maintenance or reproduction. Each year as the toad gets larger and older, the growth rate becomes lower until growth essentially stops. This hypothesis is consistent with the lack of growth of the 163 mm toad and the "2-year-old" 120 mm toad, and explains the bursts of growth in the 80–110 mm toads.

SEXUAL DIFFERENCES.—Since females tend to reach larger body sizes than males, the females may grow faster. The data in Table 8 do show a higher



growth rate for females, but not significantly so (F=1.38, df 6/19; t=0.330, df 25). The alternate for reaching larger size is to grow for a longer period of time. Our recapture data indirectly show this, for all longer recapture records (Figure 11) are females and, with the exception of the 163 mm toad, all show steady growth. The slightly higher growth rate and longer period of postmaturation growth can thus explain the presence of the large female size classes in marine toad populations.

Seasonality of Growth.—The BCI toads encounter two distinct seasons—wet and dry—and their activity patterns appear to change with the season. Toads are most common at the beginning of the wet season and abundances slowly decrease,

Table 8.—Sexual differences in growth rate of adult female (snout-vent length, 90–130 mm) and adult male (85–130 mm) toads during May 1975 on Barro Colorado Island

Sex	N	Mean	Standard deviation	Range
Females	20	0.570	0.318	0.000-1.000
Males	7	0.522	0.372	-0.133-1.067

TABLE 9.—Seasonal differences in growth rate of juveniles and adult females (snout-vent length, 75–130 mm) from Barro Colorado Island

Sample period	N	Mean	Standard deviation	Range
Nov-May	3	0.041	0.032	0.007-0.070
Feb-May	7	0.143	0.086	0.000-0.259
May-Jul	8	0.285	0.195	0.078-0.687

reaching the low point at the end of the dry season. Insect abundances seem to follow the same pattern, so we would expect maximum growth early in the wet season and minimum growth during the dry. The BCI toads do follow such a pattern of growth (Table 9). Although the differences are not statistically significant (F=3.71, df 2/15), the pattern is clear. The highest growth rate occurs at the peak of food abundance in the early wet season, lowest growth rate during low food abundance during the end of the wet season and the entire dry season.

Population Structure and Size

The close association of the marine toad with the man-made landscape has created the false impression that they are extremely abundant and ubiquitous animals. Although they may be very abundant, this abundance seems to occur only where they are exotics (Pemberton, 1934; Zug et al., 1975) and/or in close association with man (Heatwole, 1966). We were constantly informed throughout our study of the toad's superabundance, in spite of their low visibility to us. The data in this section and the activity section demonstrate that they are not nearly as abundant or ubiquitous as supposed. In both sections, our discussion will be confined largely to the seminatural populations of Barro Colorado Island and Summit Gardens.

AGE/SIZE DISTRIBUTION

While it is possible to estimate the age of toads (Table 7), these estimates are assumed to be accurate only for toads less than 100 mm snout-vent length, and the accuracy of prediction for these size classes is less than desirable. Thus, our following comments on age must be viewed as speculative.

The three censuses of the Summit Garden's population show that it is composed predominantly of young adults, one to two years old (Figure 12). Of the adults, males form the majority. The population is composed of moderate-sized individuals, roughly half of which are late term juveniles and half adults. Only during the May 1975 census did we observe a very large male and female. Reproductive activity was not observed, and only one recent postmetamorphic toadlet was discovered. There is a slight upward shift of the male size/age classes between November 1974 and May 1975 and a downward shift between May 1975 and May 1976. The upward shift may reflect growth of a single metamorphic cohort and the downward shift as the appearance of a new metamorphic cohort; however, the samples are too small and too widely spaced to add much credibility to this suggestion.

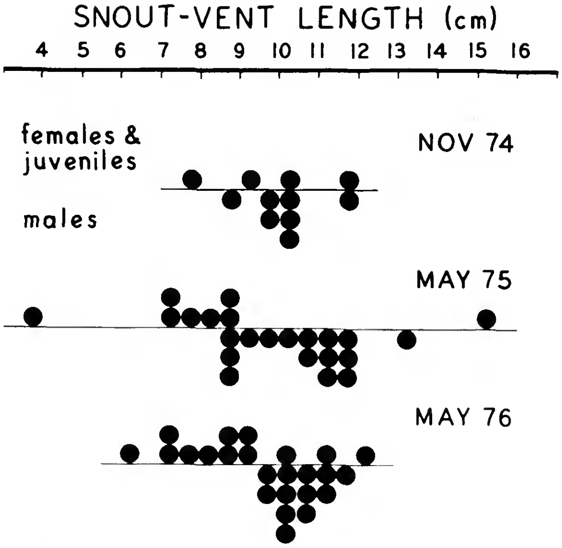


FIGURE 12.—Size distributions of Summit Gardens toad population. (Each class encompasses snout-vent length range of 5 mm; class limits 0.0–0.49, 0.50–0.99; juveniles and adult females plotted above axis, adult males below.)

The census data for the Barro Colorado Island population is somewhat more complete. Like the SG population, this population is composed primarily of moderate-sized toads (late term juveniles and young adults) for most of the censuses (Figure 13); however, in May 1975 a large metamorphic cohort had joined the population. Also the BCI population contains more large individuals, probably two or more years old. Of the sexually mature

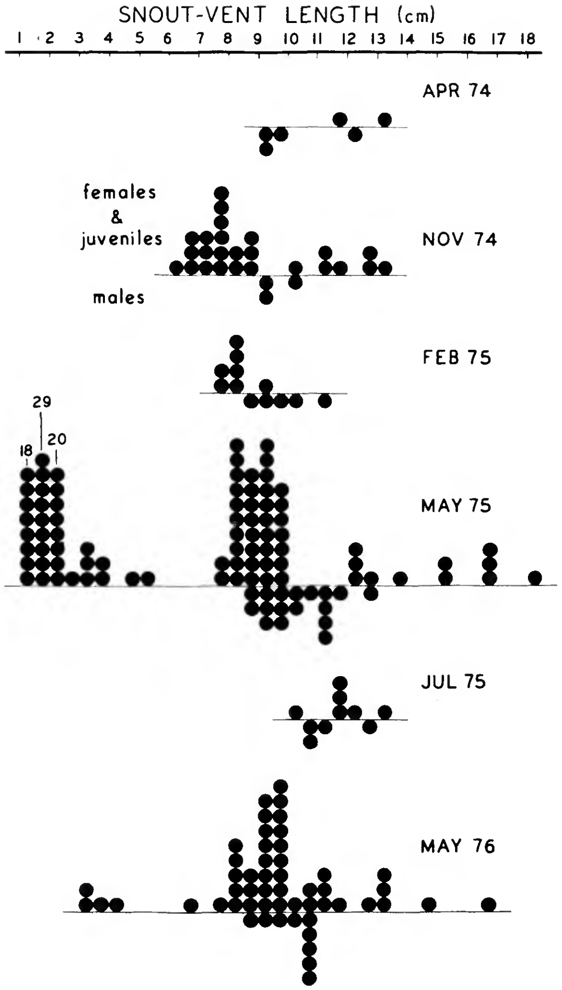


FIGURE 13.—Size distributions of Barro Colorado Island toad population. (Additional explanation in legend of Figure 12.)

toads, females predominate, nearly two and half times as many females as males. Females also dominate, nearly exclusively so, in the large size classes; comparing the two main censuses, one male was greater than 120 mm in 1975 and none in 1976, in contrast to 11 females in 1975 and six in 1976. The growth of males appears to halt or proceed very slowly after sexual maturity, whereas the females continue to grow at a moderate to fast rate.

The most noteworthy features of Figure 13 concern the recruitment and growth of single-aged cohorts through the population. From November 1974 through July 1975, a cohort can be seen to gradually increase in size from 65–90 mm in November, to 75–95 mm in February, to 80–105 mm in May, and finally to 100–120 mm in July. In May 1975, a metamorphic cohort joins the population. This cohort is very numerous relative to the metamorphic cohort of May 1976. The larger size of the 1976 cohort members suggests that they had metamorphosed three to four weeks earlier than their sister cohort members had in the preceding year. Also their low numbers suggest a higher mortality, either of larval stages or recently metamorphosed toadlets. These data tend to support our conjecture in the section on postmetamorphic growth that the BCI toads take one full year to reach sexual maturity. It is possible that some of these one-year-old individuals participate in the population's reproductive activity; however, we expect that their contribution is minimal until their second year. The major reproductive effort would appear to be confined to the relatively small group of females larger than 110 mm and males larger than 105 mm, but like many of our comments, this is speculative.

ABUNDANCE

Population size is estimated by three different methods: (1) Lincoln index and index with Bailey modification, (2) Schumacher-Eschmeyer regression method (1943), and (3) Zippin removal method (1958). All estimates of population size from mark/recapture studies are known to have biological errors in their assumptions as well as sampling errors, which often cause incorrect estimates of the population size. We will not discuss these errors here, since analyses of these difficulties have been published by others, e.g., Eisenberg (1972), Ettershank and Ettershank (1973), and Turner (1978). The use of three techniques provides a somewhat independent means for the comparison of the estimates (Table 10). Only the Zippin method requires a brief explanation, since we did not remove individuals from the population. We treated the new or unmarked toads caught each evening as the sample that was removed for that sampling period. In all estimates, the recent postmetamorphs are analyzed separately from the late-term juveniles, subadults, and adults.

POSTMETAMORPHS.—During the May 1975 monitoring period 76 postmetamorphic toadlets were captured on the BCI study site. As mentioned previously, the toadlets were migrating from the metamorphosis beach approximately 150 m away; presumably after reaching the study area, many were staying. The estimates (Table 10) suggest a population of approximately 200 toadlets. Although this may be the case, our search was quite thorough, yet we found no more than 20 individuals in any evening, so 200 resident postmetamorphs may be an overestimate. Since the toadlets were actively dispersing, it seems more likely that many of them were passing through the study site.

In May 1976, only four postmetamorphic toadlets were captured on the BCI site. They were also older individuals than those captured the preceding year, and thus, many represent the resident remnants of an April 1976 dispersal. The data are insufficient to estimate the density of this particular cohort.

Old Juveniles to Adults.—The SG population consisted solely of late-term juveniles, subadults, and adults. The November sample reflects low activity more than number of toads present. Both May samples should be better estimates of population size, since this is a period of high activity. All three methods (Table 10) yield similar estimates of density, approximately 54 toads per hectare in 1975 and 84 toads per hectare in 1976. The differences do support our impression that the toads were more abundant in 1976 than in 1975. While these densities seem to be an accurate estimate of toad abundance around the lily ponds of the study area, they are misleading for the botanical garden of Summit Gardens as a whole. The toads were concentrated around the ponds. Elsewhere in the garden, they were absent or density was extremely low. No toads were ever observed during the 0.5 kilometer walk to the lower pond and the 0.1 km walk between ponds, or in the areas adjacent to the pond clearings. Apparently the ponds attracted more insects, which in turn attracted the toads.

Table 10.—Summary of toad population estimates of Summit Gardens and Barro Colorado Island study sites (estimates determined by Schumacher-Eschmeyer (1943) regression method, Lincoln index, and Zippin (1958) removal method; raw data for all calculations listed in Appendix I, Table B)

Samples	Sch-Esch	Lincoln	Zippin
Summit Gardens			
Nov 74	16	16	11
May 75	27	28 (22-33)	24
May 76	42	42	38
Barro Colorado			
Apr 74	6	6	8
Nov 74	56	64 (60-67)	30
Feb 75	27	27	-
May 75	68	70 (68-71)	68
May 76	51	54 (52-56)	53 (53-53)
BCI toadlets			
May 75	218	182 (81-300)	79 (79-79)

The variable abundance (Table 10) of the BCI toads reflects the levels of toad activity during the various sampling periods. While we will discuss toad activity patterns later, it must be noted that we found toads most active in May at the beginning of the wet season, thus we will use only the May estimates in the following discussion. Furthermore, the high similarity of the estimates from the three different methods and the lack of or low numbers of unmarked toads on the last few survey evenings indicate that we had censused nearly all members of the population. These data yield an estimate of 184 toads per hectare in 1975 and 138 toads per hectare in 1976. Although these data are of interest for comparative purposes, the actual number of toads living on the study site is the important number, for it is this number of individuals upon which the continued survival of the BCI population depends. Toads occur elsewhere on the island, but in very low numbers. Toads are rarely seen in the forest, and tree-fall clearings are usually small (approximately 100 sq. m) and shortlived. We would hazard an estimate that marine toad density is no more than 1 toad per hectare for the remainder of the island. Even at the biological station, the distribution of toads is not uniform.

The BCI study site consists of the laboratory-housing area separated (approximately 100 m) from the dock area by a steep slope covered by low grasses, herbs, shrubs, and a few buildings. This area was thoroughly searched several times during each monitoring period; no toads were ever found, so it was excluded from the regular nightly censuses and from the density determinations. Toads must occur on this slope, at least temporarily, for we have recorded switches in feeding sites of toads from the dock to the lab and vice versa. On the study sites, toads tended to congregate in lighted areas to feed on the attracted insects; however not all regularly lighted areas were used and preferences shifted from visit to visit.

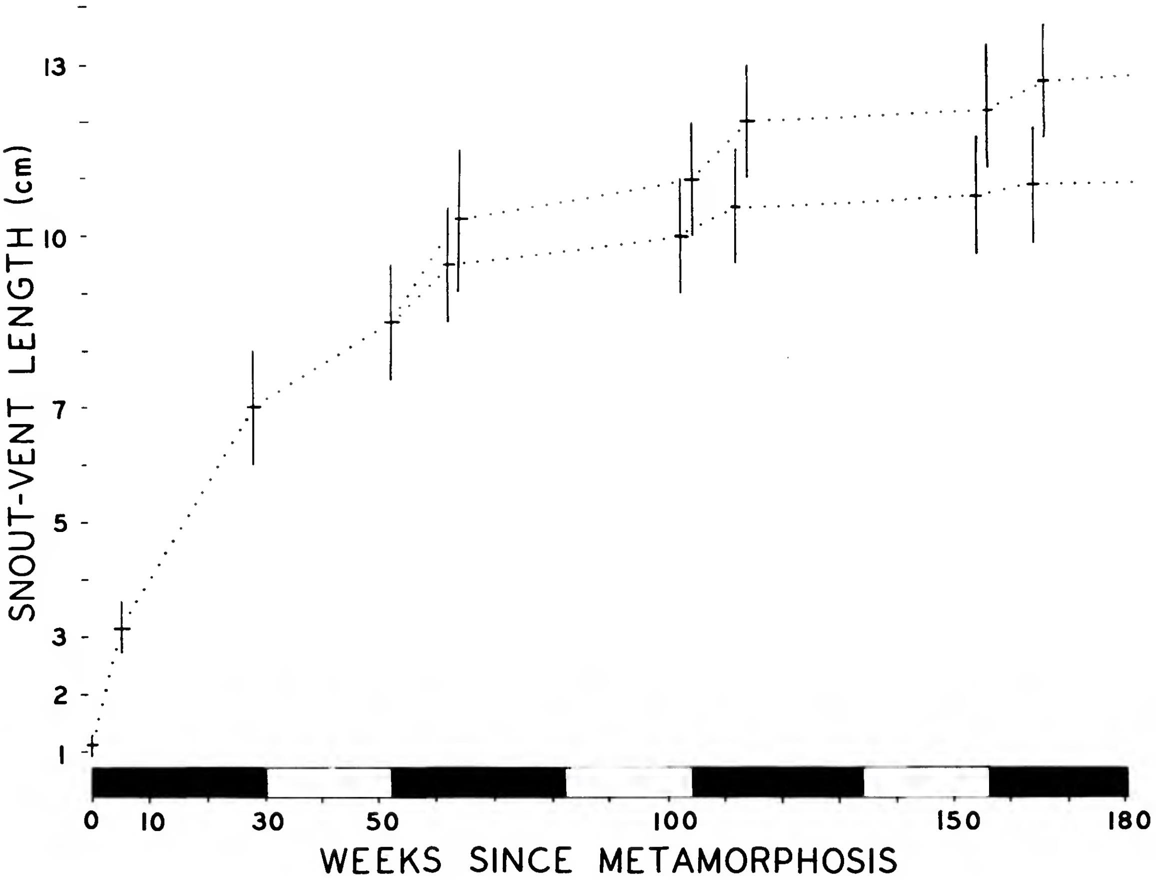


FIGURE 14.—Hypothetical growth curve for a cohort of Barro Colorado toads metamorphosing early in the wet season. (Closed bar = wet season; open bar = dry season; upper curve = female growth; lower curve = male growth; point of convergence = sexual maturation; further details provided in text.)

Abundance for the laboratory area was nearly identical in May 1975 and May 1976, 34 and 33 individuals, respectively. In the dock area, 34 toads were captured in 1975 and 20 in 1976. Thus, the larger population of 1975 resulted entirely from an increased abundance at the dock area. Even though there is movement between the two areas, the data suggest a higher stability of the laboratory area subpopulation. This suggestion is reinforced further by the recapture data of November 1974 taken during a period of low activity; 18 toads were found in the laboratory area and 10 in the dock area. Perhaps the stability of abundance in the laboratory reflects the carrying capacity of this area. In fact, the narrow range of the November 1974, May 1975, and May 1976 estimates (51–68) suggests a stability for the BCI population. By combining the areas of the study sites and the slope, the entire clearing of the biological station is estimated to occupy nearly a full hectare, which results in a density of 51–68 toads per hectare. So the marine toads may be considered abundant now on BCI, certainly much more so than in 1928–30, when Dunn (1931) saw only three toads during his 57 days on the island.

SPECULATION ON DEMOGRAPHY

Our data are too incomplete to yield an accurate picture of *marinus* demography. Nonetheless, we wish to extract as much demographic information from our data as possible in order to provide future workers with a bit of comparative data and, more importantly, to expose the numerous gaps in the knowledge of marine toad population dynamics. Firstly we wish to remind researchers of Cagle's (1956) and Turner's (1962) summaries of the population parameters that must be measured in order to gain a full understanding of amphibian population dynamics.

AGE DISTRIBUTION.—In Table 7, we developed a hypothetical conversion table for estimating a toad's age from its body length. The conversion values are based on the assumption of constancy of growth rate once the postmetamorphic growth surge is passed. As we have shown, growth rate is not constant; there are seasonal changes, sexual differences, and age (or body size) differences. We earlier speculated on how these differences might modify the relationship of body length to age and wish to carry this speculation one step further and suggest ages for the various size classes.

At metamorphosis, the toadlets will range in body length from 9–13 mm. Growth will be rapid for the first five weeks, assuming that metamorphosis occurs near the beginning of the wet season; the toadlets should triple their size (27–36 mm). With increasing size and decreasing food abundance as the wet season advances, the juveniles grow slowly and reach a length of 60–80 mm by the beginning of the dry season. During the dry season, the growth rate is reduced further, so by the end of their first year, the cohort's size range is 75–95 mm. A few of the cohort have reached the size of sexual maturity, but probably not the hormonal state of maturity. The same pattern of growth, although not the same rate, is shown during their second year, at the end of which the females are 100–120 mm long and the males 90–110 mm, because the latter's growth rate is sharply reduced with the attainment of sexual maturity. This is the first year when all surviving members of the cohort should be able to reproduce. The third year shows the same pattern as the preceding years with an additional reduction of growth, particularly in the males. Males at the end of three years are 97–117 mm long, females 112–132. Beyond this point, male growth essentially stops, and, if Straughan's (1966) data can be applied to BCI toads, the females have two more years of active, albeit reduced, growth. (See Figure 14 for diagramatic illustration of cohort growth.)

This hypothetical growth sequence converts the May 1975 size distribution (Figure 13) to the following age distribution: a postmetamorphic cohort (73 individuals), approximately one month old; two individuals, approximately three months old, which may represent a cohort that metamorphosed early in the dry season or very rapidly growing toadlets of the postmetamorphic cohort; a one-year-old cohort of 49 members; a two-year-old cohort of six female and five males; two females of a three-year-old cohort and two males of three- or more year-old cohort; a four- or more year-old cohort of six females. The May 1976 age distribution is similar but much reduced in number of individuals: postmetamorphic cohort (4 individuals), one-year-old cohort (32), two-year-old cohort (6 males, 6 females), three-year-old cohort (4 females), four-year-old cohort (2 females).

FERTILITY.—Once again our data are incomplete for determining the frequency of reproduction and the age-specific fertility. A rough estimate of clutch size can be obtained from the egg number-body length regression curve (Figure 9) when a female's body length is known. However, the curve is based on too few data points to indicate if there is peak in the fertility or reproductive potential. Furthermore, the use of a size to age conversion table assumes that individuals of the same body length are also of the same age; this is certainly not true.

We have assumed that the BCI toads have a single breeding season each year and that a female breeds every year. Marine toads are opportunistic elsewhere (Figure 8; Honegger, 1970: fig. 3), and they also may be so on BCI, although this is doubtful. If the population has more than one breeding season each year, an individual female might also. If the population possesses a single breeding season, this does not necessarily imply that a female breeds every year.

RECRUITMENT AND SURVIVORSHIP.—There is absolutely no data on the survivorship in the larval stage of the marine toad. We have assumed it to be reduced as compared to other anuran species, owing to the toxicity of the egg coat, distastefulness, and schooling behavior of the tadpoles. Data on the fertility of an egg mass, egg predators, and hatching success are required as well as data on tadpole survivorship.

TABLE 11.—Survivorship matrix for Barro Colorado Island toad population (right diagonal side of matrix contains number of newly caught and marked individuals and number subsequently recaptured; left diagonal side shows percent survival)

Sample period	1974		1975		1976
	Apr	Nov	Feb	May	May
Apr	6	0	0	4	1
Nov		30	0	4	0
Feb			13	10	1
May	67%	13%	77%	52	4
May	17%	0%	8%	8%	44

We continue to postulate that the highest mortality or, at least, the highest mortality per unit time occurs during and immediately following metamorphosis. In addition to death due to drowning and embryological abnormalities, the toadlets tend to form large aggregations near the site of metamorphosis and this probably results in a high incidence of predation. Another source of mortality may be dehydration and starvation if metamorphosis occurs during a dry spell.

As the toadlets continue to grow, mortality by predation should decrease. Environmental mortality would also decrease if these early growth stages coincide with the favorable conditions of the early wet season. The next period of major mortality is probably the toads' first dry season. Lack of adequate shelter would result in death by desiccation, and an extended dry season with its associated low food abundance could lead to starvation of those individuals with low energy reserves at the beginning of the dry season. After reaching maturity the toads should experience low mortality, although they might die from the same environmental stresses they experienced as juveniles.

In order to test these assumptions, we need a more detailed monitoring of marine toad populations. Of the eggs laid, what percentage hatch? How great or small is larval mortality? Is this mortality due primarily to predation or environmental stress? What is the rate of successful metamorphosis and what is the daily or weekly survival rate of the postmetamorphic toadlets? How many toadlets survive their first year? What is the year-to-year survival rate of adults and is there a sexual difference?

We can provide only estimates for the latter few questions. Our estimates must be considered recruitment values rather than survivorship, since we have no concrete estimate of the egg or larval population. Seventy-six postmetamorphic toads joined the population in 1975; none were recaptured in 1976. In 1976, only four toadlets were seen to enter the population. Table 11 provides an estimate of late-term juvenile and adult survivorship. The annual survivorship of this age or size class is surprisingly low, less than 17 percent in most cases. Only the April 1974 group show a significantly higher survivorship, probably because of the small sample size. It is also interesting to note that the four survivors in 1975 appeared to be just terminating their reproductive activity in 1974. The longest-lived individual of this group was a male with a 92 mm snout-vent length at first capture and two years later was only 114 mm; this suggests a minimum age of three years for the toad in 1976 and adds a credibility to our hypothetical growth curve (Figure 14). Because of the disparity in sample sizes, an averaging of the survival rates would be meaningless; we can only postulate that annual survivorship of the adult toads is about 10 percent. Whether 90 percent of the toads actually die remains unanswered. Some may be moving into the surrounding forest and still may contribute reproductively to the population.

The BCI population gained 52 and 44 new "adult" members in 1975 and 1976 respectively, or a recruitment rate of 74 and 85 percent. These values will also act as an estimate of the annual turn-over rate. They are rather high for an animal with a potential life span of 16 years (Pemberton, 1949).

An estimate of survival rate for marine toads from egg to adulthood can be made by assuming an initial deposition of 10,000 eggs and 50 individuals surviving to sexual maturity. This yields an estimate of 0.5% survival, which must be considered a maximum survival rate since a reproductive effort of only 10,000 eggs is low for a single *marinus* female.

GENERAL REMARKS

Bufo marinus is an extremely adaptable anuran, as its extensive natural distribution and occurrence in a wide range of tropical and subtropical habitats demonstrate. This adaptability will undoubtedly be reflected in many divergent population structures and sizes, each an adaptation to environmental constraints of a particular habitat. A brief comparison of the BCI and SG populations show such differences. The SG population is substantially smaller in abundance (28 in 1975; 42 in 1976) and density (54/hectare; 84/hectare) as compared to the BCI abundance (70; 54) and density (184; 138). The BCI population was larger in 1975 than 1976, whereas SG population showed the reverse trend. The population structure of both population is relatively stable from year to year but quite different in organization. On BCI, at least four age classes are present. The SG population appears to contain only one, or at the most two age classes, thereby suggesting the SG population is a migrant one that recruits new individuals each year from an unknown source area. We observed no reproductive activity in the lily ponds, and the density of crocodilians in the pond may prevent successful reproduction there. In contrast, the BCI toads breed in Gatun Lake adjacent to their year-round home and their young move into the area occupied by their parents.

Food and Feeding Behavior

The marine toad is an opportunist and will apparently eat almost every animate object it can catch. Its diet has been analyzed numerous times (e.g., Dexter, 1932; Hinckley, 1963; Illingworth, 1941; Pippet, 1975; Wolcott, 1937; Zug et al., 1975) in exotic areas, and although terrestrial arthropods form the bulk of its diet, snails, earthworms, and small vertebrates are also engulfed. They tend to be sloppy eaters, since rocks, bits of plants, etc. are frequently found in their digestive tracts. At least in one population (Zug et al., 1975), plant matter appears to have been intentionally ingested. They also have adapted well to urban life and will eat the canned food set outside for dogs and cats (Alexander, 1965).

The feeding habits of the marine toads are herein based on an examination of stomach contents, except for the fecal samples of BCI toads. The toads were preserved in 10% formalin within three hours of capture. Later in the laboratory, the stomach was slit open and the contents removed and stored separately. The contents were air dried and weighed in toto; plant matter and miscellaneous objects (stones, pieces of glass, hair, etc.) were removed and weighed individually. The weight of these two classes of items usually accounted for less than 5% of the stomach content and, as such, are considered as accidentally ingested items. The animal matter was sorted and identified to familial level or higher. The number of items of each group were counted and an estimate of body length of each item was made.

The feeding success of an animal is usually determined by the actual weight (wet or dry) and/or volume of its stomach contents or the number of prey items present. Although these values are useful, we believe that an animal's feeding success can be more accurately portrayed by determining the actual biomass of the prey items in its stomach. We determined the weight-to-length power regression equations for the common prey items (Appendix II) and then used these equations to calculate the biomass of the ingested prey in each toad. Although this method is more laborious, it provides a more accurate estimate of the various prey groups' contribution to the toad's energy budget. The weight or volume of the ingested prey is greatly distorted by differential digestion rates of the different prey, e.g., several hours after ingestion, most of a soft-bodied prey item will be digested whereas much of a hard-shelled prey item will remain. Similarly, number of prey is misleading; energetically one cicada may equal a dozen ants. It is for these reasons that we have chosen to use biomass of ingested prey rather than the other parameters. We also wish to encourage other researchers to do likewise and have, therefore, included our arthropod weight-length data in Appendix 3.

PREY PREFERENCE

The occurrence of prey types for our samples are summarized in Appendix I, Table A. As noted earlier for the introduced populations, marine toads feed primarily on terrestrial arthropods. Ants and beetles are the most numerous remains in the stomach. Of the ants, *Atta*, the leaf-cutting ants, are common. The presence of these spiny ants, as well as other distasteful and toxic arthropods, demonstrates a lack of prey discrimination by the toads and a high level of diet flexibility to adjust their ingestion

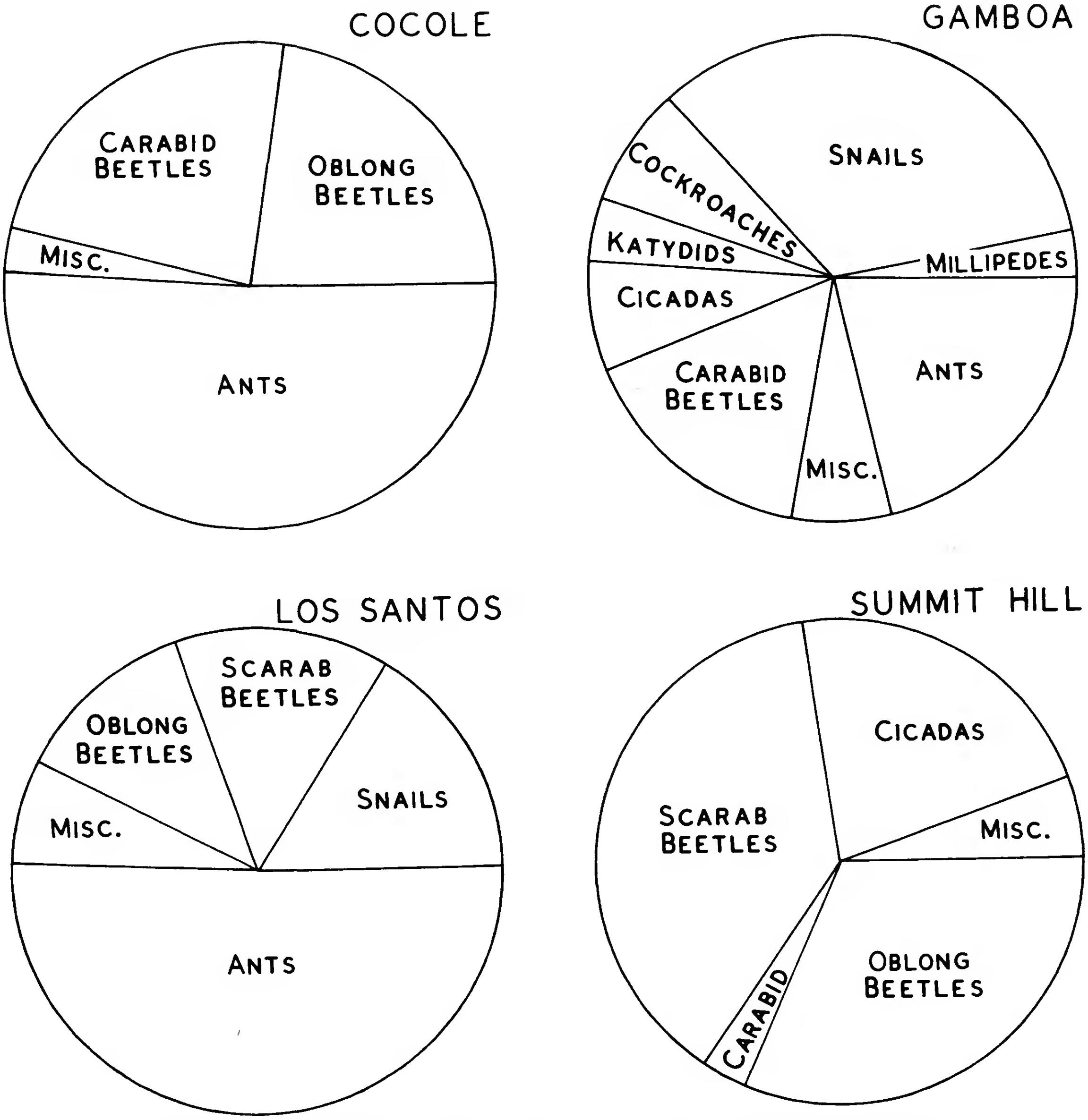


FIGURE 15.—Prey preference of marine toads from four localities. (Proportions calculated from prey biomasses and only those prey representing more than 2.7%—10 or more degrees of circle—are plotted separately.)

to any prey that is available. Grant (1948) also noted the utter disregard of this species for noxious, biting, or stinging prey.

REGIONAL AND SEASONAL DIFFERENCES.—Since toads are opportunists, their diets reflect the regional and seasonal abundance of prey. Our data are insufficient to recognize any seasonal trends, but do provide us with the impression that in most localities (excluding the urban sample from Gamboa) ants are the staple items for most of the year and only with the increase in prey abundance early in the wet season do other prey become dominant dietary items.

The diagrams of prey occurrences (Figure 15) are based largely on samples collected in May, except for the Gamboa sample, which was collected in November. Ants dominate in both of the savanna samples (Cocole and Los Santos) with beetles the next common prey items. These two localities are the most "natural" sites and, thus, the most accurate indicators of the toad's diet before becoming a commensal of man. The Summit Hill sample demonstrates the dietary habits of toads depending exclusively on the insect attraction ability of street or parking-lot lights. The Gamboa sample shows greater dietary diversity and reflects the diversity of feeding sites in an urban environment. The greatest diversity occurs in the BCI toads, which use the lighted areas as their major feeding stations; these areas attract insects from the surrounding rainforest, secondary growth, buildings, and the lake.

SIZE SELECTION.—Marine toads appear to be as non-selective in their choice of prey size as they are in their choice of prey items. They show no tendency to increase prey size with an increase in their snout-vent length (Table 12). The absence of such a trend was tested further by examining the linear regression of modal prey size to toad head width in the four samples. Even though the slopes of all regressions are positive, they are low, as are the linear correlation coefficients (Cocole, 0.49; Gamboa, 0.13; Los Santos, 0.03; Summit Hill, 0.25). If selectivity exists for late-term juveniles, subadults, and adults, it is for them to select prey in the 5.1–10.0 mm (0.01–0.1 g) size class. Combining all sample localities, 70% of toads had their modal prey length fall in this size class, and the percentage is slightly higher if mean prey length is used. We suspect that this results from the interaction of two factors: (1) large toads tend to ignore prey less than 2.0 mm long; and (2) the most abundant prey items are in the 5.1–10.0 mm range.

Heatwole and Heatwole (1968) showed that the degree of physiological satiation modifies a Fowler's toad (*Bufo fowleri*) choice of prey size. The upper size-threshold of acceptable prey decreases as the toad becomes increasingly satiated. The marine toad may show a similar feeding response.

FEEDING BEHAVIOR

In spite of the marine toads' commonness, tolerance of human observers, and adaptability to laboratory conditions, there are few studies of its feeding behavior and physiology. Observations and experiments on aspects of feeding, such as consumption or ingestion rates, digestion rates, and prey selection, are relatively easy to perform, and we had planned to include them in our study. However, largely through the lack of sufficient time we were forced to abandon these experiments. The following sections summarize a few of our casual observations, the published observations on feeding, and, as usual, our speculative impressions.

CONSUMPTION RATES.—The rate of ingestion can be expected to be a function of food availability. If given an opportunity, marine toads are first-rate gluttons. On BCI during periods of high prey abundance, the toads would glut themselves on insects, so much so that they would crackle when picked up from the insect exoskeletons in their stomachs. Such satiation is apparently not a rare event, for 40% of the toads examined contained over 50 prey items in their stomachs. Usually one prey species (either an ant or a beetle) formed the

TABLE 12.—Frequency of different sized prey in different sized marine toads from Gamboa (prey size classes selected to portray relative live weight; using equation $W = 0.0001L^3$, length classes approximately equivalent to <0.0001, 0.0001–0.001, 0.001–0.01, 0.01–0.1, 0.1–1.0, and >1.0 in grams, respectively)

Snout-vent length (mm)	Head width (mm)	Prey classes					
		<1.0 mm	1.1-2.0	2.1-5.0	5.1-10.0	10.1-22.0	>22.0 mm
64	26	0	0	1	0	1	0
86	33	0	0	29	15	11	0
92	34	0	0	0	18	18	0
105	37	2	3	0	48	2	0
110	40	0	0	5	101	2	0

majority of the prey items. Another 10% of the toads had empty stomachs. Since they were taken concurrently with the toads with high prey counts, it is obvious that they had not fed on the evening of capture and perhaps not for several preceding evenings. As we will show later, an individual is not active every evening even during periods of optimal prey abundance, suggesting that toads feed maximally when active and then retire for several days to assimilate their food.

Prey abundance is likely reflected in the biomass estimates of the stomach contents. The Cocole sample had an average of 1.1961 g of prey per toad (range, 0.1359–2.3661), the Gamboa sample 2.3222 g (0.3472–6.7532), the Los Santos sample 0.8955 g (.0418–3.5533), and the Summit Hill sample 8.8589 g (0.1533–35.3671). The two "natural" populations (Cocole and Los Santos) possess the lowest stomach content biomass and are the only ones with members with empty stomachs; two and three individuals, respectively. The toads of these two populations occur in savanna-like habitats and depend upon the natural movement and distribution of prey in their feeding territories, whereas the Gamboa and Summit Hill toads utilize the artificial aggregation of prey around lights, thereby elevating the number of prey available to them. Although we have no data on frequency of feeding, it seems likely that toads of the "artificial" populations ingest more prey per unit time than those of the "natural" populations. Thus, the consumption rate of the former would be greater than that of the latter. It would be of interest to discover if the latter populations compensate for a lower consumption rate by increasing the duration of their feeding activity.

The closest we can estimate consumption rate is to use the daily intake value proposed by Heatwole and Heatwole (1968). This value is simply the number of prey items in a toad's stomach, and is based on the assumption that toads only feed once a day and that food completes its passage through the stomach before the next feeding session begins. Based on this assumption, the May samples from Cocole, Los Santos, and Summit Hill and the November sample from Gamboa have mean daily prey intake rate of 45.6, 30.0, 50.6, and 50.3, respectively, or combined 43.2 prey/toad. Although numerous objections can be enumerated against the validity of these estimates, until someone actually records the prey capture rates of wild toads, this estimate provides a rough index to a marine toad's consumption rate and a measure of feeding activity/energetics during each feeding bout.

Locating and Catching Prey.—Vision appears to be the primary sense for the detection and capture of prey by toads (Heatwole and Heatwole, 1968). Marine toads certainly seem to rely heavily on moving prey; however, the presence of snails in their diet suggests that they require only slight movement for detection. In addition, some marine toads feed on stationary food (Alexander, 1965). The latter is clearly a learned behavior, possibly originating from the presence of moving prey on the stationary food. If olfaction is used, its role remains undiscovered.

Hearing has definitely been shown to be utilized by the marine toad in prey location (Jaeger, 1976). Jaeger observed an adult toad locate a pool by following the calls of male *Physalaemus pustulosus* and later eating two of the *pustulosus*. We observed a similar event that suggests marine toads recognize the various sounds made by their prey. Some BCI students were dissecting an ant nest in an area usually inhabited by at most a single active toad. As soon as the students left, toads beban to arrive at this site of high insect activity. Eventually four toads were feeding on the ants, apparently attracted to the site by the noise of the ants attempting to repair their nest.

Ingle (1971, 1976) used marine toads in his experiments on spatial vision in anurans. Like most frogs, the marine toad possesses a snap zone that is essentially a circular zone with the toad on the edge of the circle, and any moving object within the circle causes either an orientation movement and/or a snap response. When tested with stimulus pairs, the marine toad will (1) immediately snap at one of the retreating stimuli, (2) follow with its head directed at the leading stimuli, and (3) duck approaching paired stimuli whether large or small but ignore a single small stimulus.

Interactions.—We did not observe any antagonistic interactions between toads using the same feeding sources. Tht toads seemed to distribute themselves so they had non-overlapping snap zones. In this way, they equally shared the resource area, but not to the extreme of a ring of five toads alternately feeding on emerging termites (Fellows, 1969). In laboratory experiments, R. Boice and C. Boice (1970) discovered that marine toads established intraspecific feeding heirarchies; heirarchial position was positively correlated to body length and was established by tongue striking (see C. Boice and R. Boice, 1970, for *Bufo* feeding and aggressive postures).

Activity and Movements

With the exception of tadpoles and recently metamorphosed toadlets, marine toads are predominantly nocturnal. They appear shortly after dusk and feed for a few hours before retiring. Usually several nights will pass before a toad reappears again at its feeding station (Brattstrom, 1962:176), thus periods of inactivity exceed those of activity.

In the following discussion, "activity" is divided into two discrete categories, activity and movement. Activity is the presence of a toad above ground and engaged in an overt behavior, e.g., feeding, calling, locomotion. We will examine activity patterns of individuals and the population as a whole. Movement is the presence of an active toad in different locations. Our data on movement examine the nightly, weekly, and seasonal shifts in the centers of activity of individuals.

MATERIALS AND METHODS

The data on activity and movements are derived from the Barro Colorado Islands site and primarily from the May 1975 and May 1976 monitoring periods. However from the beginning of our study, we recorded the individuals active each evening and their locations. Beginning in May 1975, we attempted to make hourly surveys and record which toads were active and where. An evening survey was begun at dusk, approximately 1850, and concluded at 2330. The survey of the entire laboratory site took 45 minutes and the dock site 20 minutes under normal circumstances. When toad activity was high or when new toads had to be measured and marked or other projects required attention, the survey became irregular so that the census hours were not sampled equally. Usually the laboratory site was surveyed three times each evening and the dock site two times.

During the April 1974, November 1974, and May 1975 surveys each toad had to be captured to identify it by its clipped toes. We were unsuccessful in marking the toads with nail polish and butyrate dope paint in April and November. The markings either rubbed off or stimulated the toad to shed its skin. In May 1975, the toads were marked with silver nitrate branding (Thomas, 1975), but this technique proved inadequate for marine toads. The brands did not take well on the toad's skin, the dark brand was difficult to decipher on the dark background coloration of adult females and juveniles, and the marks disappeared when the skin was shed. In 1976, we used colored waistbands (Emlen, 1968) with good success. The bands nearly eliminated our handling of toads once the bands were fitted. Aside from the occasional loss of a band, the disadvantage of bands is an obscuring of the colored marking by mud from the toad's rest burrow or shed skin. We recommend the bands for short term use only, because approximately 25 percent of the toads were developing skin ulcers from waistband abrasion when we removed the bands at the conclusion of our study.

For analysis of toad activity, we have used the presence/absence data from all four monitoring periods, with a heavy reliance on the May 1975 and May 1976 censuses. The movement data are derived largely from the May 1976 census. Foraging area or home range is calculated only for those toads that were seen at locations at least 3 m apart. After each hourly survey, the position of each toad was plotted on a site map similar to those in Figures 2 and 3. To determine forage area, an overlay was placed on an accurately scaled site map and the toads' locations during the different censuses were plotted. All points were arbitrarily enclosed in an irregular polygon. The area of this polygon, excluding the area of enclosed buildings, is our estimate of the toad's forage area. We believe that in all cases it is an underestimate. The length of the forage area is the maximum length of the polygon. The maximum distance moved is the longest distance moved during a single evening, not successive evenings.

ACTIVITY

Bufo activity in the temperate zone is affected by many factors; temperature, light intensity, moon

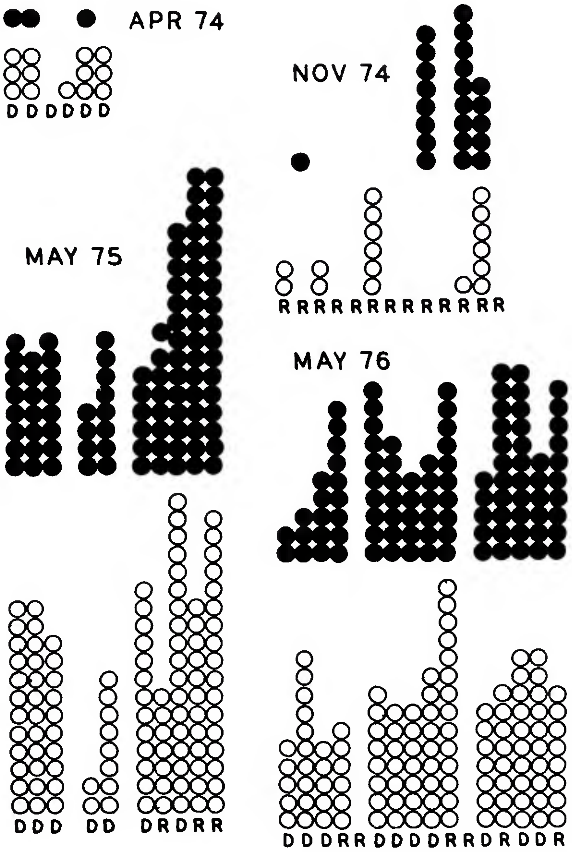


FIGURE 16.—Daily activity patterns of Barro Colorado Island toads during four monitoring periods from 1974 to 1976. (Open circle = dock site toads; closed circle = laboratory site toads; each circle represents one toad, each column one day; D = sampling day with no rain, R = sampling day with rain; blank columns in 1975 and 1976 histograms = no census days.)

phase, weather, age, and season (for examples, see Martof, 1962; Fitzgerald and Bider, 1974a, b, c). Marine toad activity is presumably also modified by similar factors; however few studies have been made to identify the factors and their effects. Zug, et al. (1975) showed activity was greatly depressed during the Papuan dry season, and Brattstrom (1962) noted an approximate three-day activity cycle for BCI marine toads in the middle of the wet season.

DAILY ACTIVITY.—Only a fraction of the total toad population is active, even under the most ideal conditions. During the May 1975 and May 1976 censuses, the wet season had begun; rain fell frequently—on approximately 25 percent of the census days—relative humidity was always 75 percent after sunset, and insect abundance was high. Yet on the average, only 31 percent of the population was active each evening, and 50 percent was the highest level of activity observed. The relative level of activity is summarized in Figure 16 for the dock and laboratory sites. The activity of the toads in the two areas, while similar, does not show an identical pattern. During periods of alternating dry and rainy days, rain tends to stimulate activity on the day of the rain and the following day. As the number of consecutive dry days increases, the activity of the population declines. While there is no stability of activity levels, the dock population seems to have less extreme fluctuation in number of toads active. This may be due, in part, to lower human activity and constancy of light at the dock in the evening.

The activity patterns of individual toads are quite variable. Only one individual, the largest adult female in 1976, was active almost every night. The majority show either a pattern of activity for two to three nights in succession followed by several nights of absence; others show a single evening activity alternating with irregular periods of inactivity and an occasional bout of activity on two or three successive nights. A few toads were active for only one or two nights during an entire two-week observation period. The toads of the labora-

TABLE 13.—Summary of mean number of evenings a toad is active on Barro Colorado Island (sample size is enclosed in parentheses; juveniles are toads less than 90 mm and greater than 60 mm snout-vent length)

Locality	Apr 74	Nov 74	May 75	May 76
Laboratory				
Juveniles	0	1.3(11)	2.2(11)	2.2(8)
Females	1.5(2)	1.0(5)	3.4(16)	4.3(14)
Males	0	1.0(2)	2.8(6)	4.2(4)
All	1.5(2)	1.2(18)	2.8(33)	3.6(26)
Dock				
Juveniles	0	1.5(6)	3.3(6)	5.0(2)
Females	0	4.0(1)	3.9(14)	5.5(15)
Males	3.2(4)	1.5(2)	2.9(12)	5.5(4)
All	3.2(4)	1.7(9)	3.2(32)	5.2(21)
Number of survey days	6	12	10	14

TABLE 14.—Mean number of subadult and adult toads active per hour in Barro Colorado Island study site (first number in each column is mean number of toads, number in parentheses is number of sampling periods)

Sampling period	1900-2000	2000-2100	2100-2200	2200-2300	2300-2400
Laboratory					
May 1975	6.1(7)	7.2(5)	4(4)	2.7(4)	-
May 1976	4.5(13)	3.2(8)	2.5(14)	2(8)	0.8(4)
Dock					
May 1975	-	-	12.3(6)	5.7(3)	-
May 1976	5(1)	7(11)	5.7(6)	5.3(8)	3.2(3)

tory site are active on the average about one day out of every four, those from the dock site about one day out of every three (Table 13). This general pattern is probably characteristic of all populations.

When active, a toad is seldom active for the entire night. Most toads appear and stay at a feeding site for one to two hours and then disappear for the night and usually for several successive nights. The short duration of each night's activity of the BCI toads is probably shared only with other populations that depend upon lights as insect attractants. Presumably toads from more "natural" areas are active longer in order to catch sufficient prey. Furthermore, toads from such areas may also have to be active more frequently.

The greatest number of active toads occurs one to two hours after dusk (Table 14). From 2000 on, there is a steady decline in numbers, and by 2400 (midnight), few if any toads are found. This pattern conforms to that of most other nocturnal ectotherms, and the few mornings we checked for predawn activity showed none. It is important to note that the early evening activity peak coincides with an increase in oxygen consumption and locomotor activity during photoperiod experiments (figs. 1–3 and 12 in Hutchison and Kohl, 1971). Is the toad's metabolic rate increasing in preparation for feeding or simply a reflection of increased locomotor activity?

TABLE 15.—Summary of mean number of toads active each evening and frequency of wet days on Barro Colorado Island during four monitoring periods

Locality	Apr 74	Nov 74	May 75	May 76
Laboratory	0.5	1.8	9.7	6.9
Dock	2.2	1.4	11.1	8.2
Total	2.7	3.2	20.8	15.1
Percent of days with rain	0	100	20	29

Park et al. (1940) provide an enigmatic report of exclusively diurnal activity in BCI marine toads. Both their field observations and experimental data show a preponderance of diurnal activity. We suspect that they confused *Bufo typhonius* with *B. marinus*, because they state that the toads were abundant along the forest trail during the day. *B. typhonius* is a forest toad, generally very abundant, and exclusively diurnal; *B. marinus* is not.

SEXUAL AND AGE ACTIVITY PATTERNS.—Adult females show a slight tendency to be active more frequently than either juveniles or adult males (Table 13). The differences are slight. Since adult males grow more slowly than either females or juveniles, they might be expected to feed less frequently, and thus show less activity. The converse would be expected of juveniles, because they possess the highest growth rate. The only time when male activity exceeded that of females was in April when the males were half-heartedly calling by the lake, while the females high on the hillside ignored them.

SEASONAL ACTIVITY PATTERNS.—The first two surveys—one at the height of the dry season and the other at the height of the wet season—demonstrated that toad activity was strongly influenced by seasonal weather conditions. At both times, an average of only three toads were present each evening (Table 15 and Figure 16). Toad activity at the dock site was four times that of the laboratory site in the dry season, probably in part because of the greater humidity at the lake margin. At the height of the wet season, the activity at the two sites was nearly identical. The same situation occurred at the beginning of the wet season (May 1975 and May 1976), although the number of active toads was five to ten times greater. In addition to more toads being active each evening during the wet season, each toad tended to be active during more evenings (Table 13).

These activity patterns are predictable considering the marine toad's moisture and energy requirements. In the dry season, prey abundance is low to moderate, but the aridity of air and soil imposes rigid restraints on the length and frequency of activity in order to avoid excess water loss. At the height of the wet season, water loss is inconsequential, but prey abundance and activity are low. So the toads must await short dry spells with increased prey activity, if they are to balance energy expenditure of feeding with energy intake. Maximum activity at the beginning of the wet seasons correlates well with the high humidity and high prey abundance and activity. It is at this time that the toads can maximize their feeding efforts to grow and lay in energy stores for the much leaner periods of the wet and dry seasons.

MOVEMENT

The marine toad's wide distribution in tropical America indicates a propensity for long distance dispersal, hence a well-developed colonizing ability. Our observations suggest an initial dispersal of the postmetamorphic toadlets. They travel several hundred meters before they are consistently found in a single location. Whether the subadults and adults have another dispersal phase and what percentage of the population participates in such a dispersal remains unknown.

FORAGING AREA.—There is no evidence of territories (defended areas) for marine toads in the wild. However, when they share a feeding site, they do not form closely packed aggregations, but rather maintain a regular spacing between each other. R. Boice and C. Boice (1970) report the establishment of feeding hierarchies in a laboratory situation, so it is not unlikely that in the wild the spacing results from similar interactions with the larger toads obtaining the better feeding stations.

TABLE 16.—Summary of forage area/home range dimensions and maximum observed movement during a single evening in Barro Colorado toads (sample sizes in parentheses)

Locality	Forage area (m^2)	Maximum length of area (m)	Maximum length of movement (m)
Laboratory			
Juveniles (2)	95.1	32.5	16.4(2)
Females (10)	169.2	41.5	22.5(7)
Males (3)	167.8	46.7	-
All (15)	159.1	41.4	21.2(9)
Dock			
Juveniles (1)	213.4	30.5	-
Females (11)	155.4	31.5	9.4(4)
Males (3)	166.3	29.7	11.9(3)
All (15)	161.4	31.1	10.5(7)

Most toads (80% of our recapture sample) changed their feeding sites either during a single evening or during successive evenings of activity. The area encompassing these different feeding sites can be labeled a foraging area or a home range. We prefer to use forage area for our data since it is based on the distribution of feeding sites.

The foraging area for the BCI toads is approximately 160 square meters (Table 16). There are no apparent area differences between the dock and laboratory toads or between adult males and females; the juvenile sample is too small to be conclusive. The maximum length of the forage area (Table 16) does show a pronounced difference between dock and laboratory toads. At the dock, the length of the forage area is shorter than that at the laboratory site. We doubt that this difference is biologically significant and probably results from topography of the site and our method of delineating forage areas. The topography of the sites and greater irregularity of lighting at the laboratory may also account for the greater distances traveled in a single evening.

HOMING.—In 1959, Brattstrom (1962) tested the "homing" ability of 15 marine toads at the BCI laboratory site. Seventy-three percent of his experimental toads return to their feeding stations within seven days at which time the experiment was terminated. He concluded that of those that were recovered they had 100 percent accuracy in locating the correct feeding station and that homing was probably due to use of visual cues and retention of previously learned topographic cues. Although we do not fault his results or conclusions, we do not believe that the experiment was a true test of homing ability. Foremost, Brattstrom was assuming that the toads had a single feeding station and that seven days was sufficiently long for all the toads of his sample to be active again. As we demonstrated earlier, marine toads are not site specific, but occupy a large forage area (mean area of 160 sq. m). Furthermore, he noted that a toad is active on the average of every 3.6 nights, which is similar to our findings, but we have also shown that it may be absent from a specific site for more than seven days. Most of Brattstrom's toads were released within their foraging area and were simply returning to a preferred feeding site within that area. Some of the toads were probably outside of their current foraging area, but probably not outside of an area with which they were familiar.

During our study, we observed movement of toads between the dock and laboratory sites and changes in forage areas. Two toads moved from the laboratory site to the dock between monitoring periods and one moved the opposite direction. During monitoring periods, we recorded three movements from dock to laboratory and one complete round trip. Even though these movements are in the minority, they do show that the BCI toads do have larger "home" ranges than that implied by a foraging area determined by a few nights of research.

Preferred feeding station shifts were common during the May 1975 and May 1976 monitoring periods. For example, the largest female in 1976 spent the first ten days with its activity center around the *Physalaemus* pond with occasional mid-evening excursions to the dining room bug light. It then shifted its feeding station exclusively to the dining room. Other toads showed similar shifts in feeding station, frequently from one end of the laboratory or dock sites to the other.

These movements strongly indicate that the toads are familiar with most of the open (nonforested) area around the STRI facility. Whether they could return to this area if moved a half kilometer or more into the forest remains an unknown. Within the open area, we agree with Brattstrom that visual recognition of landmarks serves as the main orientation cues. However, Williams (1967) has shown that marine toads can use spatial cues (muscular imprinting) to compensate for incorrect visual cues in determining their direction of travel. Thus, there is no reason to assume that they use a single set of cues in moving about their foraging areas.

Physiology: Heat and Water

The geographic distribution, habitat selection, and activity pattern of *B. marinus* appear to be influenced by the toad's temperature tolerance or preference and water economy. In this section, we summarize the published data on *B. marinus* thermal and water balance physiology and report on a few physiological tests that we performed.

THERMAL PHYSIOLOGY

The marine toad has a wide temperature tolerance range. Native juvenile and adult toads have a critical thermal minimum (CTMin) of 10°–12° C and a critical thermal maxium (CTMax) of 41°–42° C (Table 17). Tadpoles have a CTMax of 41.5°–42.5° C. The CTMin has not been determined for tadpoles, but Stuart (1951) reported tadpoles and egg masses in mountain streams and pools at 13.5° C. The CTMax and CTMin temperatures reported here are ecological-behavioral death points and not actual death points. At these temperatures, the toads have lost the ability to use coordinated movements to escape the adverse temperatures (see Brattstrom (1968) for a discussion of behavioral death versus lethal temperature).

Postmetamorphic toads are primarily nocturnal animals that seek shelter in burrows or semiburrows during the day. Thus, they seldom, if ever, encounter temperatures that would exceed their CTMax, and it seems unlikely that their geographic distribution, choice of habitat, or activity patterns are regulated by high temperatures. However, these traits may be influenced by low temperatures. Stuart (1951) found Guatemalan toads only below elevations of less than 1500 m, which coincides with the isopleth for the mean minimum temperature of 15° C. Similarly, the northern limit of the toad's range in Texas coincides with the 15° C isopleth for the January mean minimum daily temperature. These mean minimum temperatures are 3 to 5 degrees higher than those of the CTMin. This should not be unexpected, for the former measures population survival over a

TABLE 17.—Summary of temperature tolerance of *Bufo marinus*

CTMin	CTMax	Acclimation		Locality	Source
(°C)		Temp	Time (days)		
Adults					
10-12		10-12	NA	Guatemala	Stuart, 1951
	41-42	41-42	NA	Guatemala	Stuart, 1951
	35.0	7	1	Panama	Brattstrom & Lawrence, 1962
	30.5	7	2	Panama	Brattstrom & Lawrence, 1962
	39.5	27	7	Panama	Brattstrom & Lawrence, 1962
11				Panama	Brattstrom, 1968
	36.5?	15	14+	Panama	Brattstrom, 1968
	39.3	26	14+	Panama	Brattstrom, 1968
	41.8	38	14+	Panama	Brattstrom, 1968
	40.0	27	4	Florida	Krakauer, 1970
	40.8	37	4	Florida	Krakauer, 1970
10		10	4+	Florida	Krakauer, 1970
	38.9	25	7	Queensland	Johnson, 1972
6.1		NA	0	Queensland	Johnson, 1972
	40.0	26-29	3+	St. Croix	McManus & Nellis, 1976
Tadpoles					
13.5		13.5	30+	Guatemala	Stuart, 1951
	41.5	21	7	Puerto Rico	Heatwole et al., 1968
	41.6	23	NA	Florida	Krakauer, 1970
	42.5	25.6	NA	Florida	Krakauer, 1970

long period of the time, and the latter measures individual survival for a brief moment under artificial conditions. Toads from the periphery of the species range should be more hardy or low temperature tolerant, since they are from a stock that has evolved under wider temperature fluctuation and periodic freezing temperatures and are also acclimated to lower temperatures during the cold part of the year. A comparison of low temperature survival in Floridian toads (Krakauer, 1970; acclimated at 27° C for 4 days) and Panamanian toads (Brattstrom, 1961; acclimated at 27° C for 3 days) supports this point. All Panamanian toads were dead after 48 hours at 7° C, yet the Floridian toads were normal after 72 hours at 7° C and only after 96 hours was half of the sample dead.

In contrast to the postmetamorphic individuals, the CTMin is of little importance to the eggs and larvae. Admittedly, low temperature can be just as hazardous to the premetamorphic stage as to the postmetamorphic stage; however, the premetamorphic stage exists for a brief period of time—seldom more than two months—so that their presence can be scheduled to avoid low temperature. Thus, the CTMax may determine where the premetamorphic stages can live, particularly so since they are deposited and grow in shallow, commonly unshaded bodies of water. The CTMax of tadpoles is a degree higher than that of postmetamorphic individuals (Table 17). Even though this difference may not be significant due to differences in experimental techniques, tadpoles probably encounter higher temperature more frequently because of their diurnal habits and the shallowness and openness of their habitat, although they will tend to aggregate in cooler areas of a pond rather than the hot water at its margin (Mares, 1972). High temperatures, as long as they are not too high, are advantageous for the tadpoles, since the rate of development and growth is directly proportional to temperature. In many cases, *B. marinus* lays its eggs in temporary pools and tadpoles must complete their growth and development before the pool dries. It seems likely that the eggs or embryos of the marine toad are less temperature tolerant than the tadpoles, since this occurs in other frogs (Zweifel, 1977). Three species of Sonoran desert toads have a maximum tolerance of 33°–34° C for the survival and growth of their embryos (Zweifel, 1968). *B. marinus* embryos probably do not exceed this tolerance limit.

Brattstrom's (1968) summary of thermal acclimation in anurans shows that *B. marinus* requires three days to completely acclimate to higher temperatures. We question the biological significance of such data for a tropical anuran such as the marine toad. The survival value of complete acclimation seems minimal or non-existent for a toad living in a relatively stable thermal environment of the lowland tropics. Even toads in fluctuating thermal environments experience temperature change gradually and, thus, are probably constantly acclimatizing to their environment. The latter is certainly indicated by Johnson's (1972) observations on daily variation in *B. marinus*' CTMax. We are of the opinion that thermal acclimation is of less importance for survival of a toad at temperature extremes than it is for the toad to constantly adjust its biochemical and physiological processes in order to optimize these processes.

Several aspects of the marine toad's thermal physiology remain undetermined, e.g., temperature preference of pre- and postmetamorphic stages, developmental and growth rates under different temperature regimes, thermoregulation and daily temperature regimes. The following experiment is our attempt to provide a partial answer for the last physiological parameter.

MATERIALS AND METHODS.—The body temperatures of three toads from Summit Hill, Canal Zone, Panama, were monitored for 24 hours. The toads were not fed for five days prior to testing and were fully hydrated by sitting in 1–2 cm of water for 24 hr prior to testing. Each toad was tested individually on consecutive days in a glass aquarium (150×37×31 cm) in an open air, screen-enclosed laboratory. Core body temperature (T_b), air temperature (T_a), and substrate temperature (T_s) were recorded hourly, except for the period 0100–0500, by a YSI tele-thermometer. T_b was obtained by a small flexible vinyl probe (#402) inserted into the cloaca and rectum for approximately one quarter of the toad's body length; the probe was held in place by bands of dermicel tape around the inguinal and the axillary regions. T_a was obtained from an air temperature probe (#405) suspended in the middle of the aquarium, 10 cm from the bottom. T_s was obtained from a surface probe (#409) taped to the bottom of the aquarium. Air could freely circulate through the aquarium and half of the aquarium received sunlight from approximately 1415 to 1530. Relative humidity fluctuated between 65 and 85 percent (see Figure 18 for average daily regime).

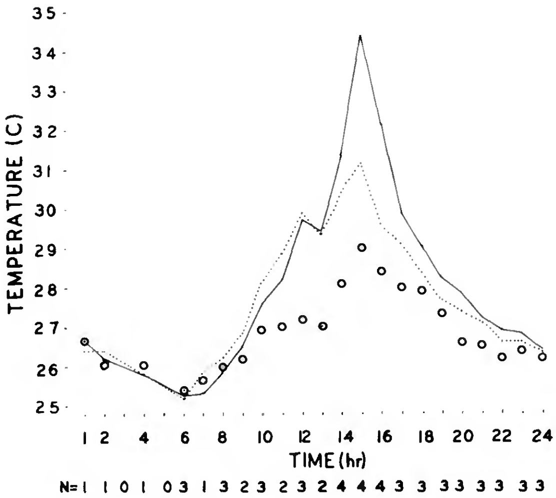


FIGURE 17.—Daily temperature regime of unrestrained *Bufo marinus*. (Circle = mean body temperature; broken line = mean air temperature; solid line = mean substrate temperature; bottom row along abcissa lists sample size by hour.)

RESULTS AND DISCUSSION.—As expected, the marine toad's body temperature are closely tied to the fluctuation in ambient temperatures (Figure 17); however, the daily fluctuation of body temperature is less than that of ambient temperatures (T_a and T_s). Body temperatures ranged from 25° to 30° C with a daily mean of 26.4° C. Whether this mean should be called the preferred body temperature (Brattstrom, 1970) and whether the greater stability of T_b as compared to T_a and T_s should be called thermoregulation are debatable. Nonetheless the toads' body temperature fluctuations are less than those of the environment. During the night, T_b is nearly equivalent to T_a and T_s, but during the day, T_b stays below T_a and T_s. The lower temperature is obtained through evaporative cooling from the body surface. Since evaporative water loss can be controlled only to a limited degree, the cooling is a passive physiological process. Even though it is passive, it is continually experienced by the toad and has probably been combined with active physiological and behavioral aspects to dampen T_b fluctuation. The actual fluctuation of T_b is presumably even less than portrayed by this simple test. The toad is buried or semiburied during the day so the daytime temperatures of its shelter do not become as high. We would postulate that only during the dry season in open habitats could the temperature of the shelter become high enough to endanger the toad, and it is likely that by that point the toad would be subjected to near lethal dehydration.

WATER ECONOMY

Approximately 76 percent of the marine toad's body weight is water (78.0%—Shoemaker, 1965; 74.1%—Thorson, 1964; 77.2%—Krakauer, 1970). The difference between Thorson's value and those of Shoemaker and Krakauer may indicate a difference in experimental method or a relationship between total body water and size and/or sex. Thorson's sample certainly contained larger individuals (137–450 g) than those of the latter two researchers (100–200 g and 63–129 g, respectively), and this size difference may reflect sexual difference, i.e., females tend to be heavier. Certainly, the robustness and, hence, the weight of the skeleton is directly proportional to size. However, the effect of increasing skeleton weight on total body weight may be small in comparison to the influence of lipid concentration on body weight (Krakauer, 1970).

Of this total body water (= standard body weight minus body weight when dried to a constant weight; $W_S - W_D$), a toad can lose approximately 52 percent (Krakauer, 1970) before it reaches its lethal limits and dies (Figure 18). Relative to the toad's standard body weight (W_S), the toad can lose nearly 40 percent of its W_S before death occurs. No matter whether the lethal limit for total body water or for W_S is used, the actual amount of water lost can be somewhat higher under natural conditions than in the laboratory, since the urinary bladders are emptied prior to the laboratory tests. It has been known (Steen, 1929) that the urinary bladders of frogs act as a water reservoir from which water can be resorbed during dehydration stress. Although the storage capacity of the marine toad's bladder is unknown, the capacity is probably near 30 percent of gross body weight (W_G) like that reported for *Bufo cognatus* (Ruibal, 1962). If only 10 percent of this bladder water (relative to gross body weight) is available for resorption, this will enable the toad to tolerate a 45 percent W_S loss before the lethal limit is reached (Figure 18). Although the lethal limits are high and indicate a definite adaption to xeric habitats, other toads possess greater tolerance to desiccation (fig. 4 in Krakauer, 1970), and we suspect that desiccation is an important mortality factor for marine toad populations in the seasonal tropics.

In addition to the high tolerance to dehydration, marine toads have other physiological and behavioral means for reducing water loss and regaining water. Presumably the main water loss occurs across the skin. Toads reduce this loss by retreating to sheltered areas during the day or other periods of low relative humidity, and by assuming a crouched posture that reduces the amount of skin surface area exposed to the air. Further reduction is obtained by decreasing the evaporative gradient at the skin-air interface. This does not appear to be an active physiological process, but a physical one in which the skin loses moisture faster by evaporation than it can be replaced by passive diffusion from the inside. This diffusion lag creates a drier skin and an associated reduction of the evaporative gradient, thereby reducing the rate of water loss (Machin, 1969). Another physical barrier to water loss is the layer of mucopolysaccharides in the external part of the dermis. This layer of ground substance is thicker in *B. marinus* than any other amphibian studied (Elkan, 1968). Physiologically, the marine toad shares the "water balance response" with other frogs. As a frog or toad dehydrates, the increasing concentration of plasma stimulates the release of neurohypophyseal hormones that, in turn, stimulate the resorption of water from the bladder and increases the cutaneous absorption of water from the surrounding water or soil (see Bentley, 1971 for a summary of the "water balance response;" Shoemaker, 1964; and Shoemaker and Waring, 1968, for its specific action in *B. marinus*). In addition to the active absorption of free water, the external sculpturing of the toad's skin provides a series of interconnecting channels that move water from the venter upward along the sides to the back thereby reducing cutaneous dehydration (Lillywhite and Licht, 1974).

The marine toad absorbs water through its skin (Shoemaker, 1964) when partially immersed in

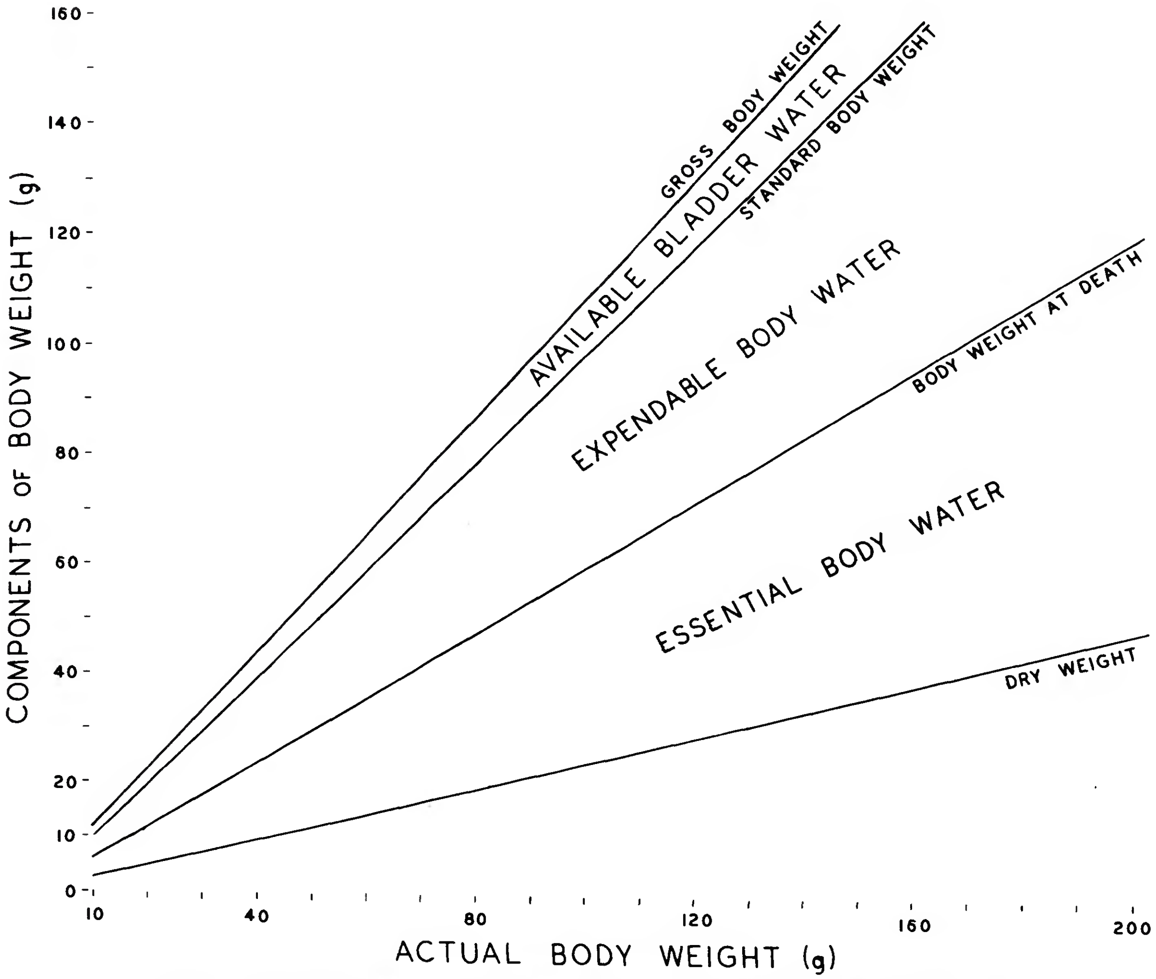


FIGURE 18.—Influence of body weight on water economy in marine toad. (Lines based on total water content of 76 percent of standard body weight (W_S), lethal limit (W_D) of 52% of total water content, gross body weight (W_G) with bladder water (10% of W_S) and dry weight (W_d) of toad.)

water. It is likely that it also possesses the ability to absorb water from damp soil like other *Bufo* (Fair, 1970; Walker and Whitford, 1970). Although it is often stated (e.g., Fair, 1970) that a water balance deficit is required to initiate cutaneous absorption, Shoemaker's data (fig. 1) indicates that, at least for *B. marinus,* water exchange can occur with no deficit. The rate of water uptake does increase as the deficit increases, to about 15 percent, at which time the rate levels off. The maximum rate is about 1 ml/(100 g × hr). Presumably the marine toad absorbs most of the water through a ventral pelvic patch of highly vascularized skin (surface area of this patch, $y=0.13x+5.65$; $y=\text{cm}^2$, $x=$standard weight in g; Fair, 1970). This patch shows the greatest change in osmotic permeability in response to the water response hormone, vasotocin (Bentley and Main, 1972) and has the most extensive vascularization in the marine toad of all frogs studied (Roth, 1973). Hydration occurs faster in free water than in saturated soil (Walker and Whitford, 1970).

For information on salinity tolerance, which is inappropriate to our discussion here, Ely (1944) and Krakauer (1970) are recommended.

Since we believe dehydration to be a significant mortality factor in marine toad populations, we wished to determine rates of dehydration under more natural conditions, as suggested by Seymour and Lee (1974). The following experiments provide such data.

Materials and Methods.—The dehydration experiments were performed in a screen-enclosed laboratory so that the test animals were subjected to the same temperature and humidity fluctuations as those toads outside the laboratory. Each toad was placed in a separate hardware-cloth cage, and the cage was then placed on a dry sand platform. This permits the toad to adpress its entire ventral surface to the substrate, yet does not allow absorption of water. Body weight and relative humidity were recorded every two hours, except for the period from 0100–0500, for one day for each toad. The relative humidity was measured by a sling psychrometer swung one meter from the sand platform. The average daily temperature regime is illustrated in Figure 17. The toads were not fed for at least three days and were fully hydrated by placement in 1–2 cm of water for a minimum of 12 hours prior to testing. All toads were tested with full urinary bladders.

An attempt to test the dehydration rates of the resident Barro Colorado Island toads in a manner similar to that proposed by Seymour and Lee (1974) was unsuccessful. Toads weighed and released upon emergence could not be located the following morning. The toads caught immediately upon emergence and placed in hardware-cloth cages were extremely excitable and would release copious amounts of bladder water during the initial capture and with each subsequent weigh-in. Also, they repeatedly defecated during the test period so that this test of dehydration had to be abandoned.

Results and Discussion.—As the relative humidity decreases and temperature increases the rate of water loss (here, as in previous physiological studies, we are assuming that weight loss is equivalent to water loss) increases. This is strictly a physical event, for any such increase in the evaporation gradient increases evaporation rate. However, Figure 19 also shows that toads can modify the rate of water loss. While toads B and C were inactive and maintained a crouched or low sitting posture throughout most of the test, toad A showed bursts of activity and was often found sitting upright, both of which actions would increase water loss by exposing more skin surface and elevating respiratory water loss.

The rate of water loss is clearly related to body size (Figures 19 and 20; Table 18). Larger toads lose more water and at a faster rate. However, presenting the rate as g/hr or ml/hr is misleading as far as an individual toad's survival is concerned, for the standard formula ml/(100g × hr) or percent body weight loss shows an inverse relationship between water loss and size. It is this relationship that is important to the survival of the toad in nature. By referring to Figure 18 and using the rate loss of Table 18, a 22 g toad has only 22 hours before it reaches its lethal water loss, a 110 g toad 48 hours, and a 228 g toad 70 hours.

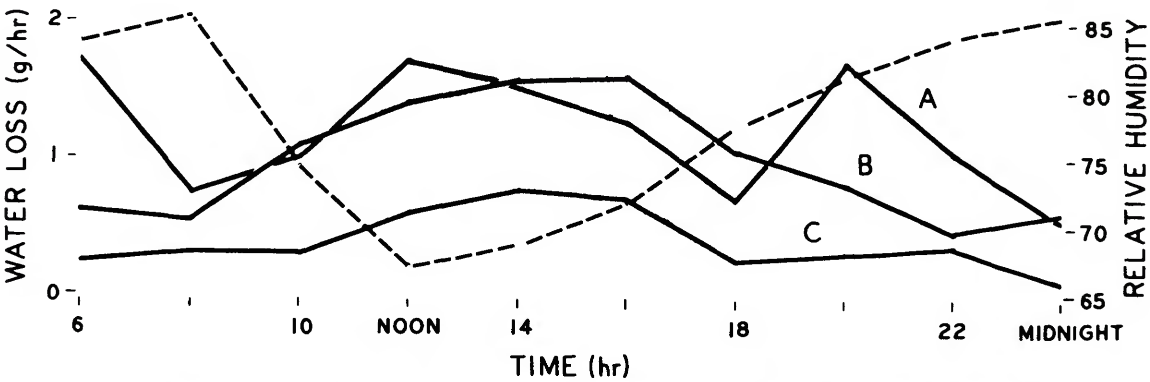


Figure 19.—Daily water loss in marine toads of different body sizes. (Initial body weights: A = 228 g, B = 110 g, C = 22 g; broken line = bihourly averages of relative humidity for four days of testing.)

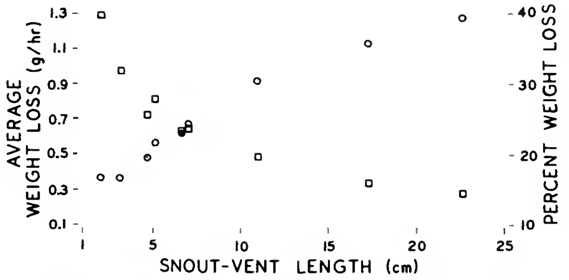


FIGURE 20.—Rate of water loss relative to body size during one day, with toads subjected to natural fluctuations of temperature and humidity. (Circle = g/hr, $Y = 0.057 X^{0.575}$; square = percent loss, $Y = 136.71 X^{-0.425}$, $r = 0.99$.)

The presence of bladder water is particularly critical for the survival of the toads. In addition to increasing the survival time of a dehydrating toad by increasing the amount of expendable body water, it enables the toad to maintain a more normal ionic balance of its plasma. During dehydration, toads with empty bladders have the sodium concentration of their plasma increased, while toads with filled bladders resorb bladder water and maintain a normal sodium concentration (Shoemaker, 1964). Presumably those toads with increased sodium concentration will be less resistant to parasite load, starvation, etc., and might die from these other causes in conjunction with dehydration.

As mentioned previously, we believe the dry season to be the time and dehydration the major cause of mortality in the Barro Colorado toad population. This is based largely on the negative evidence of low annual recapture rate and reduced population activity during the dry season. The BCI season usually extends from late December to late April, with March being the driest month (usually less than 5 cm of rainfall). The forest floor is completely dried out and cracked; the soil of the clearing is likely even drier and would provide few moist, sheltered retreats. Since the juveniles possess less tolerance to dehydration, they should show the highest mortality, like that found in *Bufo debilis* (Creusere and Whitford, 1976). Subadults and adults probably compete for sheltered retreats, with those in marginal shelters subject to mortality if the dry season is extended or particularly severe. Even for those toads not subjected to near lethal dehydration, the dry season may restrict activity so that the toads are incapable of catching sufficient food to permit survival through the dry season.

TABLE 18.—Data summary of dehydration experiments on Panamanian *Bufo marinus* (results for a 24-hour period)

Initial body weight	Weight loss	Percent body weight loss (24 hr)	Weight loss per hour (g/hr)	Origin of toad
21.8	8.6	39.4	0.358	Summit Hill
27.6	8.7	31.5	0.363	*Summit Hill
47.6	11.6	24.4	0.483	Summit Hill
50.7	13.4	26.4	0.558	Summit Hill
66.8	15.1	22.6	0.629	Summit Hill
70.4	16.1	22.9	0.671	*Summit Hill
109.0	21.8	19.8	0.908	Gamboa
173.9	25.9	14.9	1.079	Summit Hill
227.6	30.8	13.5	1.283	Gamboa

* The weight loss for these toads was obtained during the thermal physiology test.

Mortality Factors

Mortality usually results from the interaction of both abiotic and biotic factors. While we are here concerned with the major biotic factors, diseases, parasites, and predators, we wish to emphasize our belief that climate, particularly the dry season may be a strong mortality factor in the post-larval stages. The effect of climate is, at least, two pronged: (1) dehydration owing to low moisture levels in air and soil; (2) starvation owing to low prey abundance and activity. Prey availability also appears to be low in the latter part of the wet season with a slight increase at the beginning of the dry season followed by the lowest levels.

The following discussion deals exclusively with postmetamorphic stages. There are no data on the intensity of predation on marine toad egg masses and tadpoles. It is generally assumed to be low because of the toxicity of the egg jelly coat (Licht, 1967 and 1968) and the distastefulness of the tadpoles (Wassersug, 1971); however, predation during these life stages may be quite high owing to the abundance of invertebrate and vertebrate predators in and around tropical ponds (Durant, 1974; Heyer, et al., 1975).

PREDATORS

Predators of introduced marine toads have been summarized in Zug et al. (1975) and Covacevich and Archer (1975). Reports on natural predators are limited. Pope (1955) mentions *Caiman latirostris*, and Allen and Neill (1956) list a *Helicops*. We observed a *Leptodeira annulata* eating a 20 mm toadlet.

We suspect a large variety of mammals, birds, reptiles, and amphibians, including adult *B. marinus,* eat the recently metamorphosed toadlets and juveniles. It is our contention that few predators eat the subadult and adult toads. In addition to their large size, the toxic skin secretion, particularly from the parotoid gland, acts as an effective predator deterrent. The structure and histochemistry of the parotoid gland is analyzed by Hostetler and Cannon (1974). Allen and Neill (1956) describe the clinical effects of the toxin on man and provide a short bibliography on this topic. Low (1972) summarizes parotoid gland secretions stressing their diversity and use in *Bufo* systematics. Licht and Low (1968) tested the effects of *marinus* parotoid secretions on the cardiac response of several snakes and discovered that the secretions caused lethal cardiac tetany in nontoad-eating species and no cardiac disturbances in toad-eating species. Presumably some birds and mammals could turn over the adult toads and eat the viscera, thereby avoiding the toxic skin secretions.

DISEASE AND PARASITES

Some of the parasitic or disease organisms of *B. marinus* are listed in Table 19. Presently, there are no data on whether they act as significant mortality factors in the toads. During the dry season, almost every BCI toad has ticks, *Amblyomma.* Although the ticks occur widely on the body, they appear to be concentrated on the head, particularly on or adjacent to the parotoid glands. When a tick falls off, it leaves behind a small lesion. We never observed any of these lesions to become infected or to retard the normal activities of the toad.

TABLE 19.—Parasites of *Bufo marinus*

Parasites	Source
Bacteria	
Salmonella (7 species)	Kourany, et al., 1970
Protozoans	
Cytoamoeba bactipera	Lehmann, 1966
Ochoterenella cf. *digicauda*	Marinkelle, 1970
Tritrichomonas batrachorum	Marinkelle, 1968
Helminths	
Creptotrema lynchi	Brooks, 1976
Cyclindrotaenia americana	Brooks, 1976
Glypthelmins robustus	Brooks, 1976
Gorgoderina diaster	Brooks, 1976
Ophiotaenia bonariensis	Brooks, 1976
Rhabdias fuelleborni	Kloss, 1971
R. sphaerocephala	Kloss, 1971
Arthropods	
Amblyomma dissimile	Jakowska, 1972
A. humerale	Marinkelle, 1970
A. rotundum	Marinkelle, 1970
A. testudinis	Lehmann, et al., 1969

We observed no heavy helminth infestations in any of the toads we dissected for food and reproductive data. In fact, we were surprised at the low incidence of intestinal nematodes, and only in one toad, did we observe a large hepatic infection. In this Los Santos toad, the liver was composed largely of cysts containing egg-laden trematodes.

Rather than being a primary mortality factor parasitic infections, we suspect, reduce the toad's resistance and make it more susceptible to death by starvation or dehydration.

Summary

While this report is an attempt at a synthesis of the marine toad's natural history, we are well aware of the inadequacy of our present and previously published data. Nonetheless, we believe a survey is needed at this time to encourage others to study the biology of the marine toad. The main reason we chose to build so many windmills of conjecture on feeble bases of facts is the hope that our readers will be tempted to topple these windmills.

In Panama, male marine toads reach sexual maturity at a snout-vent length of 85–95 mm, females at 90–100 mm. Most toads appear to reach 80–90 mm one year from metamorphosis, although it seems doubtful that the one year olds are capable of breeding at this time. Growth is rapid during the first year, approximately 0.37 mm per day and slows down at sexual maturity, much more so in the males than in females. The females appear to grow for at least three years after maturity, the males for one year and during this year their growth rate is less than the females. As a consequence females attain larger body sizes than males.

In all adult populations studied, there is a preponderance of one sex over the other, usually at least two times as many of one sex as the opposite. In half of the samples females outnumbered males, the reverse situation in the other half. Reproduction appears to be cyclic with one or two egg laying periods each year. The male's spermatogenic cycle peaks in April and declines to a low in January. Breeding period appears to be timed so that metamorphosis occurs during periods of high humidity and prey abundance, primarily at the beginning of the wet season.

Marine toad populations consist largely of young adults (one- to two-year-olds), with a small minority of the older individuals. Approximately two-thirds of the population is new each year; whether this turnover is due to emigration or mortality is unknown. The density of subadults and adults is variable: 50 to 70 toads per hectare at Summit Gardens, 140–180 at Barro Colorado Island. The actual population size is certainly much smaller, about 60 toads at the BCI site, and fairly constant from year to year.

The toads are feeding opportunists and will eat almost any animate object they can catch, particularly those prey in the 5.1–10.0 mm size class for all adult-sized toads. Ants and beetles tend to be the most numerous prey items and also the prey contributing the most biomass to the toad's diet.

During high humidity and prey abundance, a toad is active one out of every three or four evenings. About a fourth of the population will be active during a single evening. Peak activity occurs from one to three hours after dusk. Most toads are active for only a couple of hours before disappearing from their feeding sites.

Toads have several feeding sites within a larger forage area (average of 160 sq m) and regularly move from one to another. The change of feeding site usually occurs with the beginning of a new activity period, rather than during a single evening. Both activity and movement are influenced by weather conditions. Long periods of dry or rainy weather suppress activity.

Marine toads are eurythermal and apparently do not thermoregulate. Their temperatures follow the fluctuation of the ambient temperatures; the two are nearly equivalent at night, but during the day, body temperature is lower than ambient. Water balance seems to be a more critical factor for survival in Panamanian toads. While they can tolerate a 53% loss in total body water before dying, they are not physiologically efficient in slowing or reducing water loss. A recently metamorphosed toadlet will reach its lethal limit within one day if moisture is not available, an adult toad within two to three days. This indicates that the dry season may be a critical period for survival.

Mortality is, however, probably highest owing to predation. Although no data are available, the period from metamorphosis to maturity seems to be the time of highest mortality. Vertebrates are likely the major predators.

Appendix I

Sample Data

TABLE A.—Research use of marine toad samples examined in this study

Locality and date	N	Ecological monitoring	Food habits	Reproduction	Physiological test
CANAL ZONE					
Barro Colorado Island					
2-8 Apr. 1974	6	+			
20 Nov.-1 Dec. 1974	29	+			
6-22 May 1975	141	+			
10-25 May 1976	55	+			
Cocole					
26 Nov. 1974	1		+	+	
10 May 1975	10		+	+	
Gamboa					
28 Nov. 1974	10		+	+	
11 May 1976	2			+	+
Summit Gardens					
26-29 Nov. 1974	11	+			
9-14 May 1975	23	+			
14 & 20 May 1976	24	+			
Summit Hill					
28 Nov. 1974	2		+	+	
9 May 1975	9		+	+	
14 May 1976	8			+	+
LOS SANTOS					
Los Santos					
12 May 1975	15		+	+	
PANAMA					
Las Cumbres					
17 Dec. 1974	2			+	
17 Jan. 1975	2			+	
17-19 Apr. 1975	4			+	
17-19 May 1975	7			+	
17-19 Jun. 1975	3			+	

TABLE B.—Mark/recapture data from Barro Colorado Island and Summit Gardens sites used to estimate population size (U = unmarked, R = recapture of marked, T = total individuals captured—used in Schumacher-Eschmeyer estimate; 1st = marked and released in first sampling period, 2nd = total capture in second sample, MR = marked in first and recaptured in second period—data used for Lincoln index population estimate; position in date row indicates level at which summation of column U stopped; C = consecutive number of new individuals caught—data used for Zippin method of population estimate; MT = recently metamorphosed toadlets, less than 35 mm; where column is incomplete, data row again designates level of summation; all but last column of data based on old juveniles, subadults, and adults, i.e., toads greater than 60 mm)

Date	U	R	T	1st	2nd	MR	C	MT
Summit Gardens								
26 Nov 74	4	0	4				4	
27	3	1	4				3	
28	1	1	2				1	
29	3	3	6	8	6	3	3	
9 May 75	15	0	15				15	
10	5	10	15	15	15	10	5	
14	4	6	10	20	10	6	4	
14 May 76	15	0	15				15	
	9	5	14	15	14	5	9	
Barro Colorado								
3 Apr 74	4	0	4				4	
4	2	2	4				2	
5	0	0	0					
6	0	1	1					
7	0	4	4	6	4	4		
8	0	3	3					
20 Nov 74	2	0	2					
21	0	0	0					
22	3	0	3					
23	0	0	0					
24	3	3	6					
25	0	0	0					
28	7	0	7				17	
29	0	1	1					
30	12	4	16	15	16	4	12	
1 Dec 74	3	2	5	27	5	2	3	
13 Feb 75	9	0	9				9	
26	4	2	6	9	6	2	4	
6 May 75	21	0	21					
7	8	11	19					
8	8	10	18					
9 May 75	2	3	5				39	
14	2	3	5					
15	7	10	17					
18	6	13	19					
19	3	11	14	54	14	11	18	
20	6	26	32	57	32	26		
21	2	27	29	63	29	27		
22	3	32	35	65	35	32	11	
10 May 76	7	0	7					
11	9	4	13				16	
12	4	6	10					
13	10	5	15				14	30
15	5	12	17					
16	5	9	14				10	
17	2	11	13					
18	1	13	14				3	
19	3	20	23					16
21	1	12	13				4	
22	2	18	20	47	20	18		
23	3	22	25	49	25	22	5	
24	1	15	16	52	16	15		
25	0	16	16	53	16	16	1	7
BCI toadlets								
8 May 75	9	0	8				9	
15	19	0	19				19	
18	16	4	12	27	12	4	16	
19	11	0	11				11	
20	10	2	12	50	12	2	10	
21	11	3	14	62	14	3	11	
22	3	5	8	76	8	5	3	

TABLE C.—Identity of prey and their frequency in stomach contents of Panamanian marine toads (first four localities based on stomach contents only; numbers in parentheses are numbers of empty stomachs and number of stomachs with prey, respectively; Barro Colorado Island data based on stomach contents and on eight fecal samples, three of which are aggregates; because fecal samples were included, precise numbers of prey are not listed for BCI

Prey	Cocole (2/9)	Gamboa (0/10)	Summit Hill (0/11)	Los Santos (3/12)	BCI (1/1)
Arthropoda					
Diplopoda (millipedes)		5			+
Arachnida					
Phalangida (daddy-longlegs)					+
Araneida (spiders)	1	2	2	1	
Insecta					
Odonata (dragonflies)				1	
Orthoptera					
Acrididae (grasshoppers)					+
Tettigoniidae (katydids)		2			
Gryllidae (crickets)		1	1		+
Blattidae (roaches)		3			+
Isoptera (termites)			1		+
Dermaptera (earwigs)		4	1		
Hemiptera					
oblong bugs (e.g., reduviids)			1		+
obovate bugs (e.g., pentatomids)		1	1		
Homoptera					
Cicadidae (cicadas)		1	3		
Neuroptera (lacewings)					+
Coleoptera					
Carabidae (ground beetles)	6	7	5		+
Curculionidae (weevils)	1	3	3	1	+
Scarabaeidae (scarabs)			9	3	+
oblong beetles (e.g., elaterids)	5	4	8	3	+
round beetles (e.g., chrysomelids)	2	1	2	1	
Lepidoptera (moths)			1	1	
Hymenoptera					
Formicidae (ants)	9	8	6	10	+
winged hymenopterans			8	2	+
Annelida (earthworms)			1		
Mollusca					
Gastropoda (snails)		5		1	+

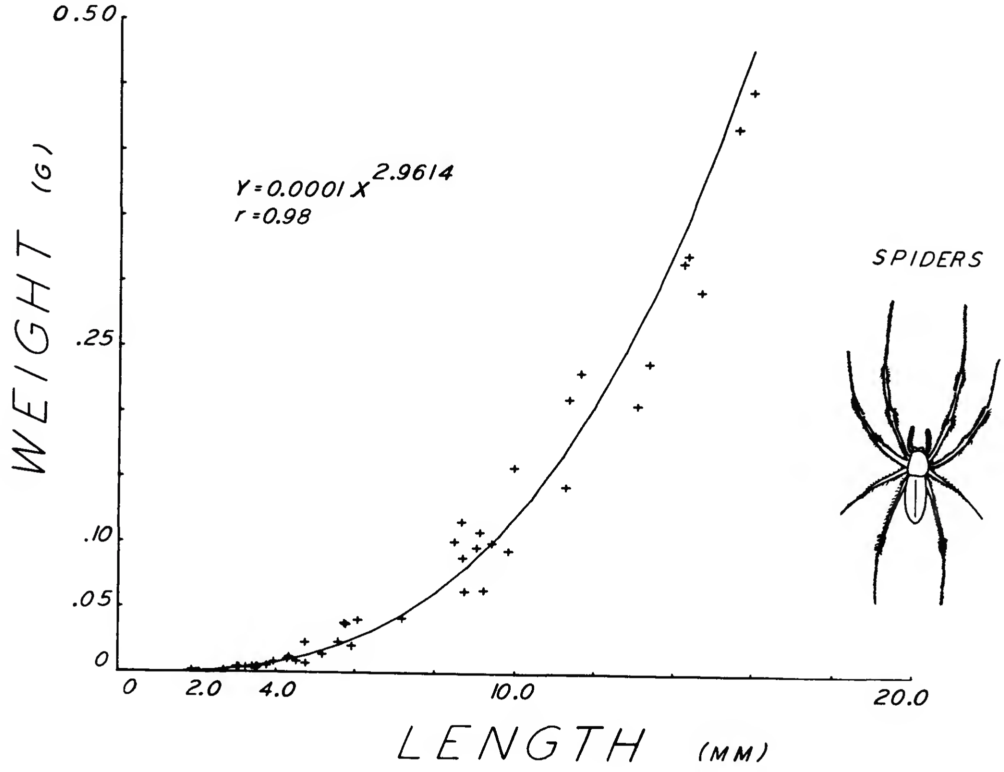
Appendix II

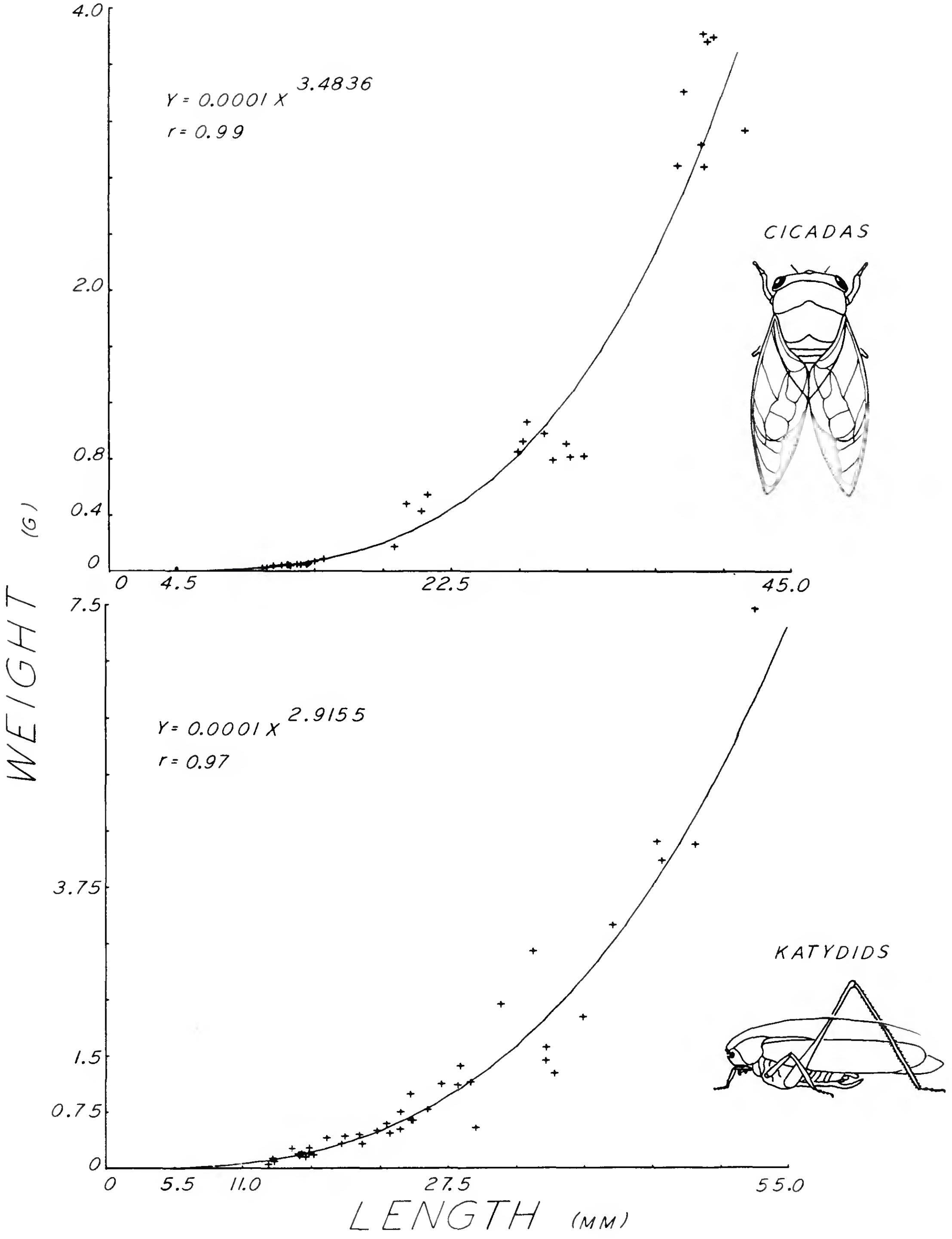
Weight-Length Relationships of Arthropods

After examining the stomach contents of a small sample of Panamanian marine toads and identifying the arthropod remains, we made an effort to obtain the lengths and weights of living individuals from each group of arthropods represented in the stomachs. The groups presented here and identified from the stomach contents are identified to the familial level or to a higher taxonomic level. In a few cases, such as beetles and bugs, members of the same order may be analyzed in different groups, if they have different body shapes, because shape greatly influences the weight-length relationships. Although the constituents of each group may appear to be somewhat arbitrary, they represent the highest level of determination that can be accurately made from the bolus found in a toad's stomach. Unless an animal is clearly a specialized feeder, it seems wasteful of a researcher's time to attempt specific determination and leads to a false sense of accuracy.

The regression lines were calculated and plotted on an HP 98 calculator/plotter with the "Family Regression" program. Each graph contains a power equation for the plotted curve and its correlation coefficient (r). Although the correlation coefficient of the parabolic curve was occasionally higher than that of the power curve, the former overestimates the weights of the smaller size class so we consistently used the power equation in order to obtain the greatest accuracy throughout our calculations of arthropod live weight or biomass in each toad's stomach.

The illustration and common name on each graph is sufficient to identify the arthropods represented, except for the subdivisions of the beetles and bugs. The obovate bug sample is composed largely of pentatomids, the oblong bug of pyrrhocorids and reduviids. The round beetles are principally chrysomelids, but include other beetles that have a circular outline. The oblong beetles include mainly cerambycids, elaterids, and lampyrids. The scarab beetles are exclusively of that family, and predominantly of a broad elliptical outline. The winged hymenopterans include both bee- and wasp-shaped insects. All the arthropods were collected in the vicinity of the STRI compound on Barro Colorado Island, Panama.




4.0
2.0
0.8
0.4
0
0
4.5
22.5
45.0
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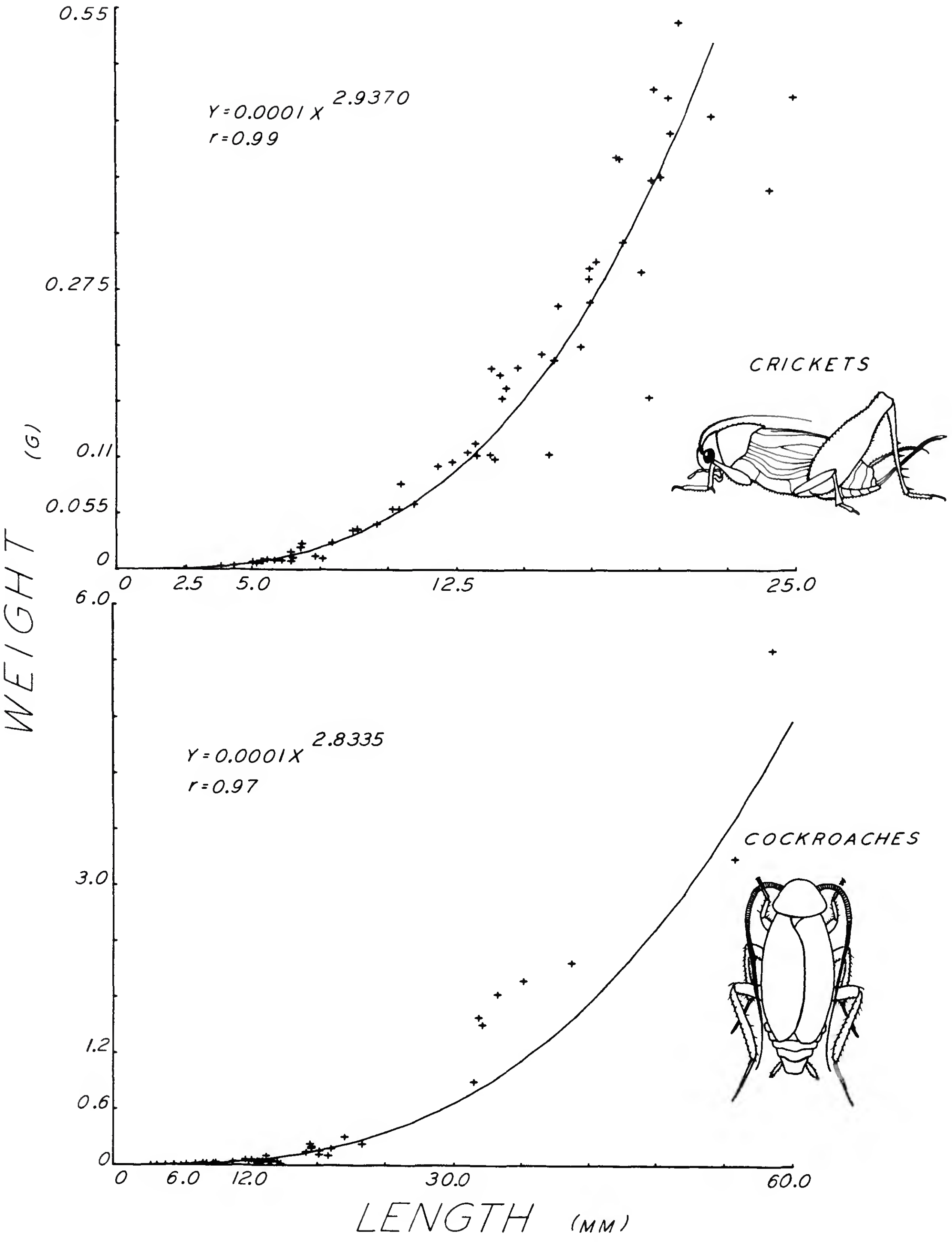
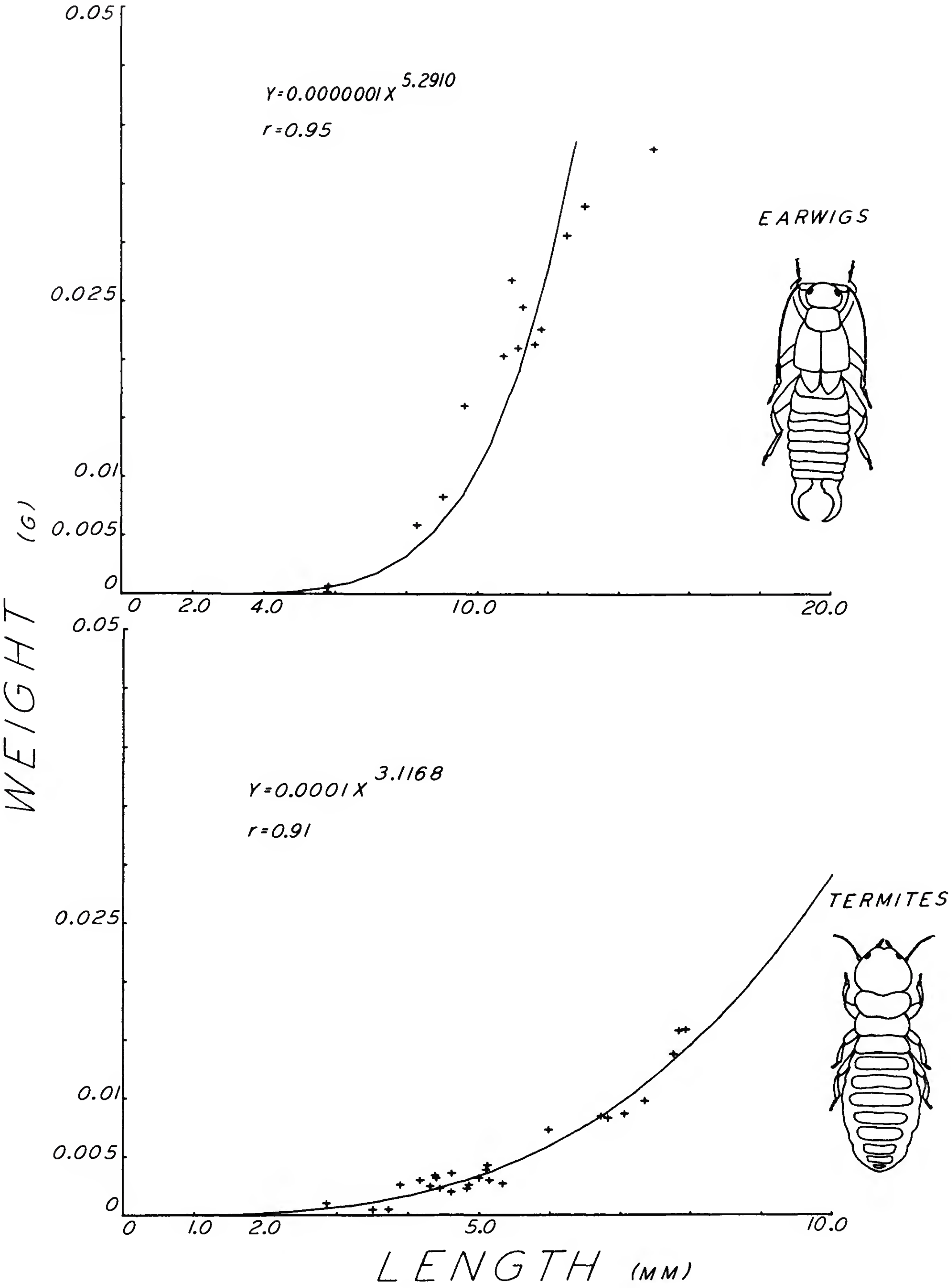
r = 0.99
CICADAS
WEIGHT (G)
7.5
3.75
1.5
0.75
0
0
5.5
11.0
27.5
55.0
Y = 0.0001 X^2.9155
r = 0.97
KATYDIDS
LENGTH (MM)


0.55
0.275
0.11
0.055
0
$Y = 0.0001 X^{2.9370}$
$r = 0.99$
CRICKETS
0
2.5
5.0
12.5
25.0
6.0
$Y = 0.0001 X^{2.8335}$
$r = 0.97$
COCKROACHES
3.0
1.2
0.6
0
0
6.0
12.0
30.0
60.0
WEIGHT (G)
LENGTH (MM)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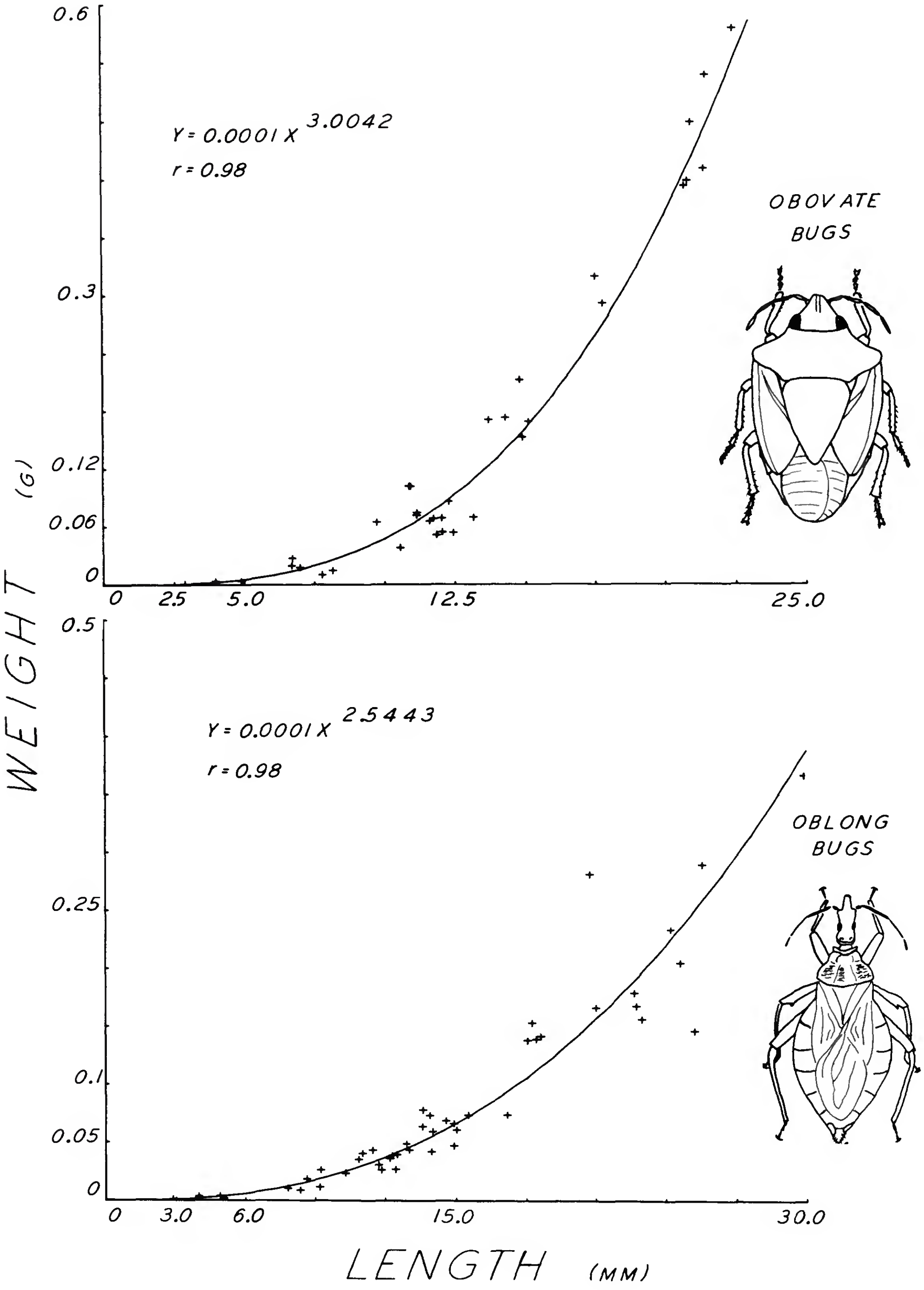
Y=0.0000001X^5.2910
r=0.95
EARWIGS
0.025
0.01
0.005
0
0
2.0
4.0
10.0
20.0
WEIGHT (G)
0.05
Y=0.0001X^3.1168
r=0.91
TERMITES
0.025
0.01
0.005
0
0
1.0
2.0
5.0
10.0
LENGTH (MM)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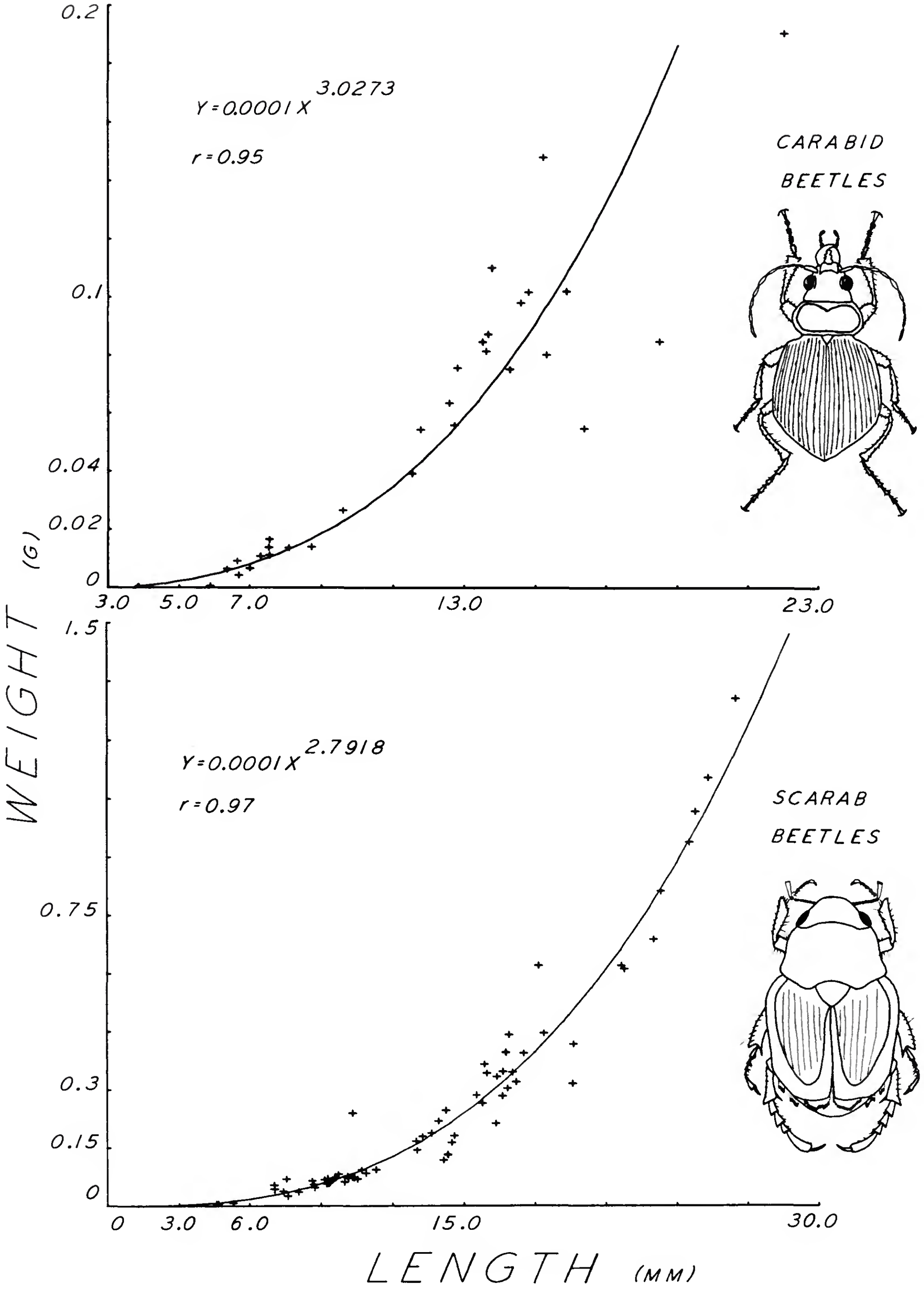
0.3
0.12
0.06
0
Y = 0.0001 X 3.0042
r = 0.98
OBOVATE BUGS
0
2.5
5.0
12.5
25.0
0.5
0.25
0.1
0.05
0
Y = 0.0001 X 2.5443
r = 0.98
OBLONG BUGS
0
3.0
6.0
15.0
30.0
WEIGHT (G)
LENGTH (MM)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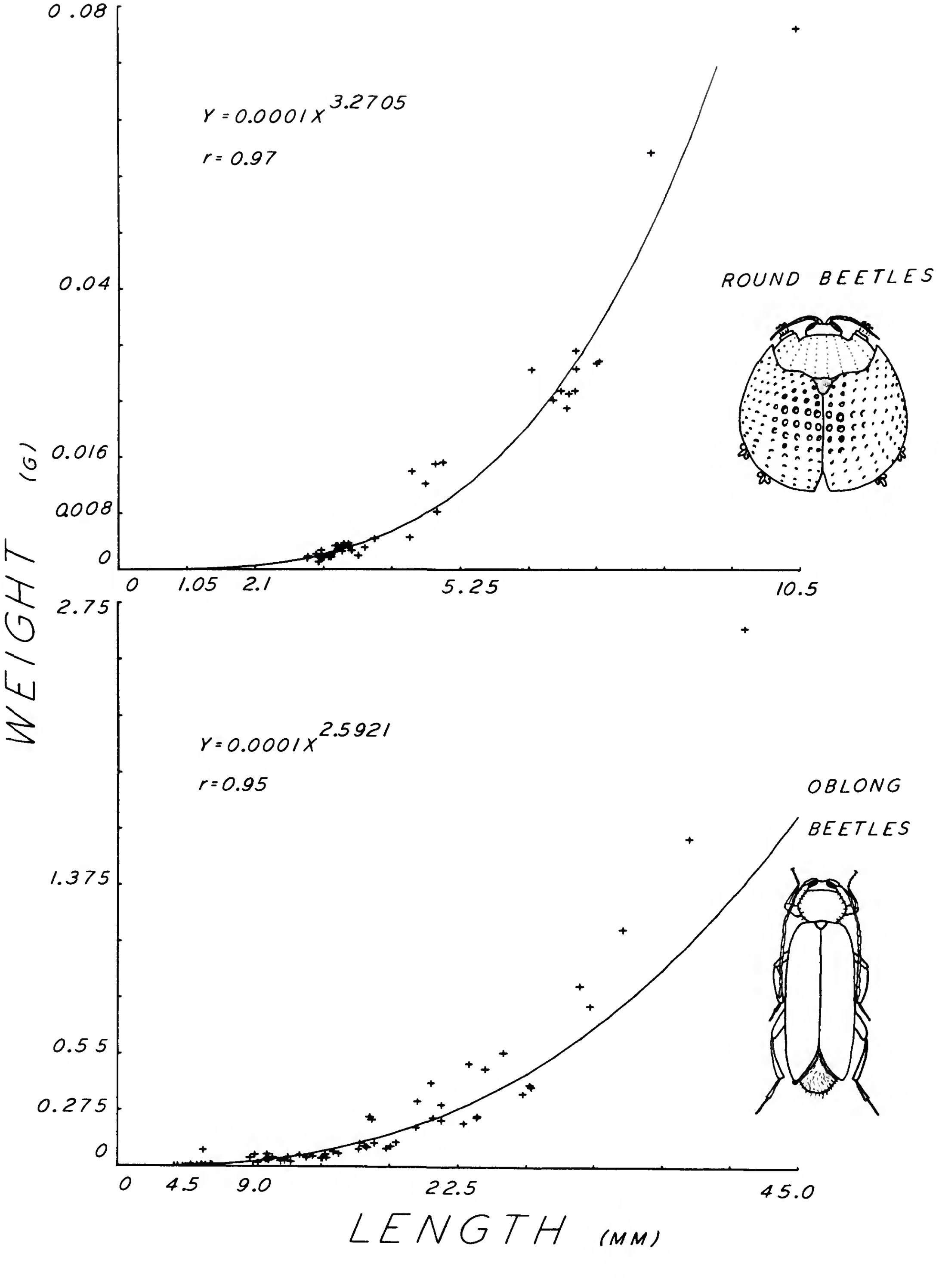
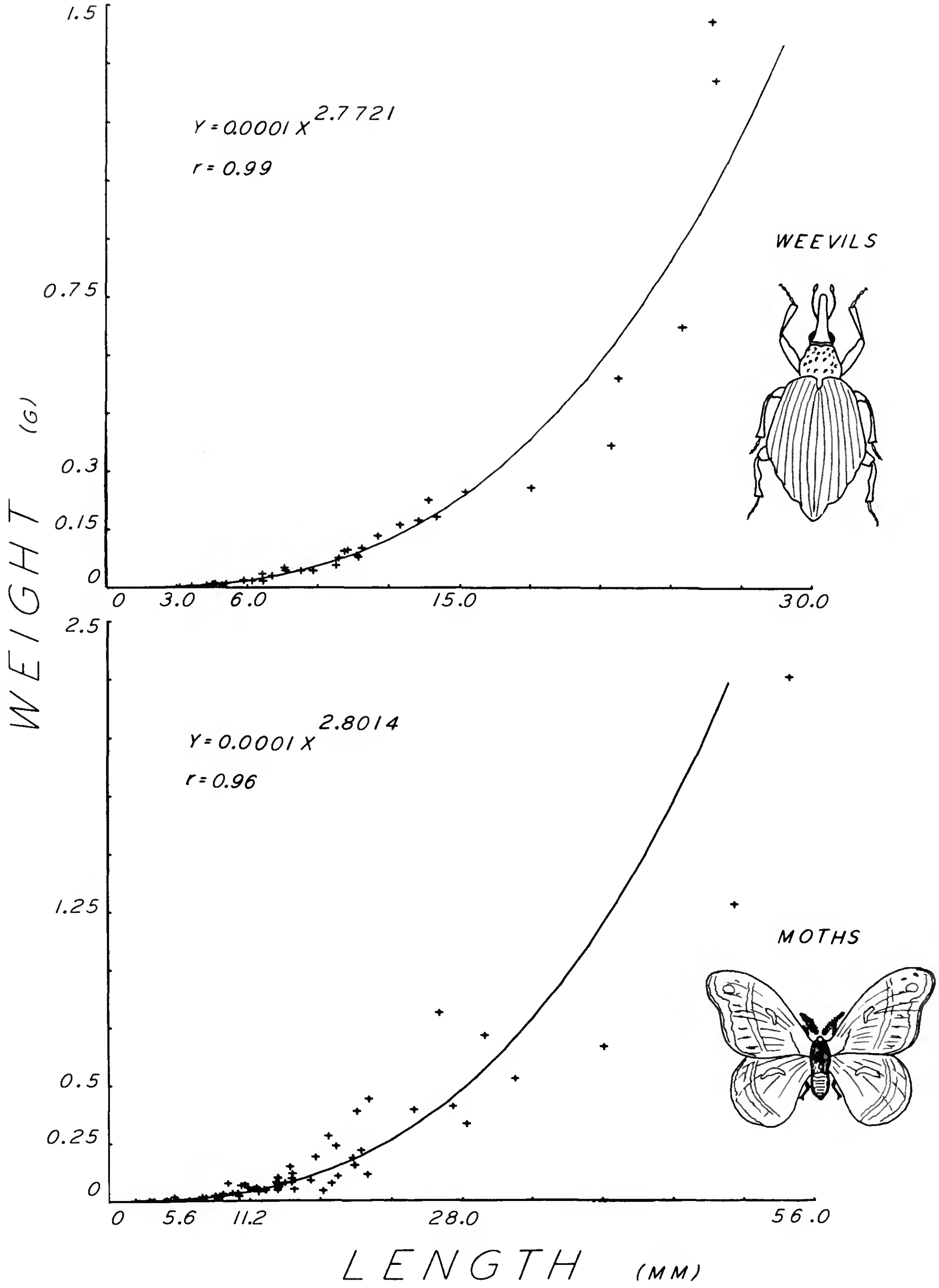
0.1
0.04
0.02
0
$Y = 0.0001 X^{3.0273}$
r = 0.95
CARABID
BEETLES
3.0
5.0
7.0
13.0
23.0
1.5
0.75
0.3
0.15
0
$Y = 0.0001 X^{2.7918}$
r = 0.97
SCARAB
BEETLES
0
3.0
6.0
15.0
30.0
WEIGHT (G)
LENGTH (MM)


0 .08
0.04
0.016
0.008
0
$Y = 0.0001X^{3.2705}$
$r = 0.97$
ROUND BEETLES
0
1.05
2.1
5.25
10.5
2.75
1.375
0.5 5
0.275
0
$Y = 0.0001X^{2.5921}$
$r = 0.95$
OBLONG BEETLES
0
4.5
9.0
22.5
45.0
WEIGHT (G)
LENGTH (MM)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0.75
0.3
0.15
0
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$r = 0.99$
WEEVILS
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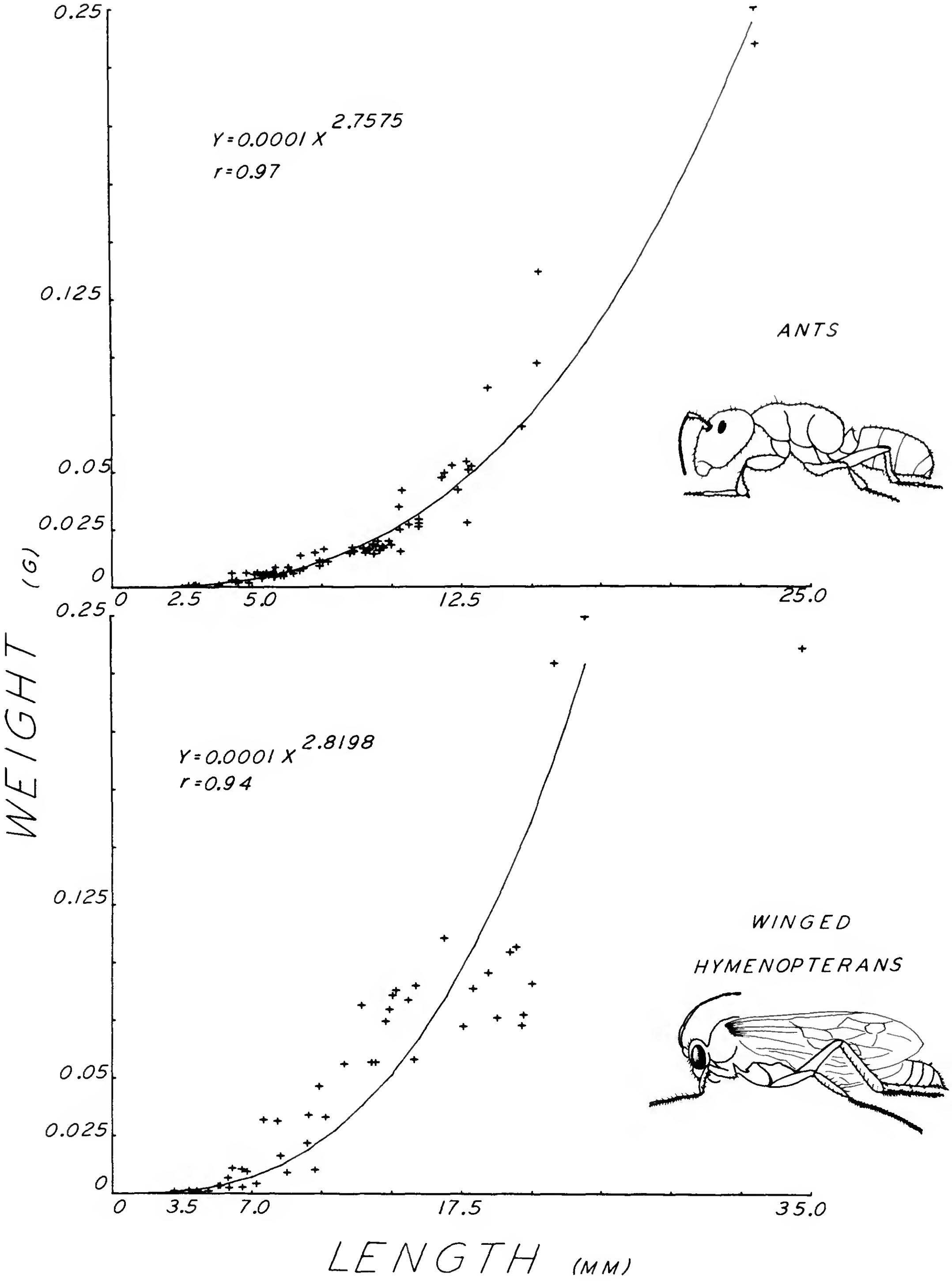
3.0
6.0
15.0
30.0
2.5
1.25
0.5
0.25
0
$Y = 0.0001\,X^{2.8014}$
$r = 0.96$
MOTHS
0
5.6
11.2
28.0
56.0
WEIGHT (G)
LENGTH (MM)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0.125
0.05
0.025
0
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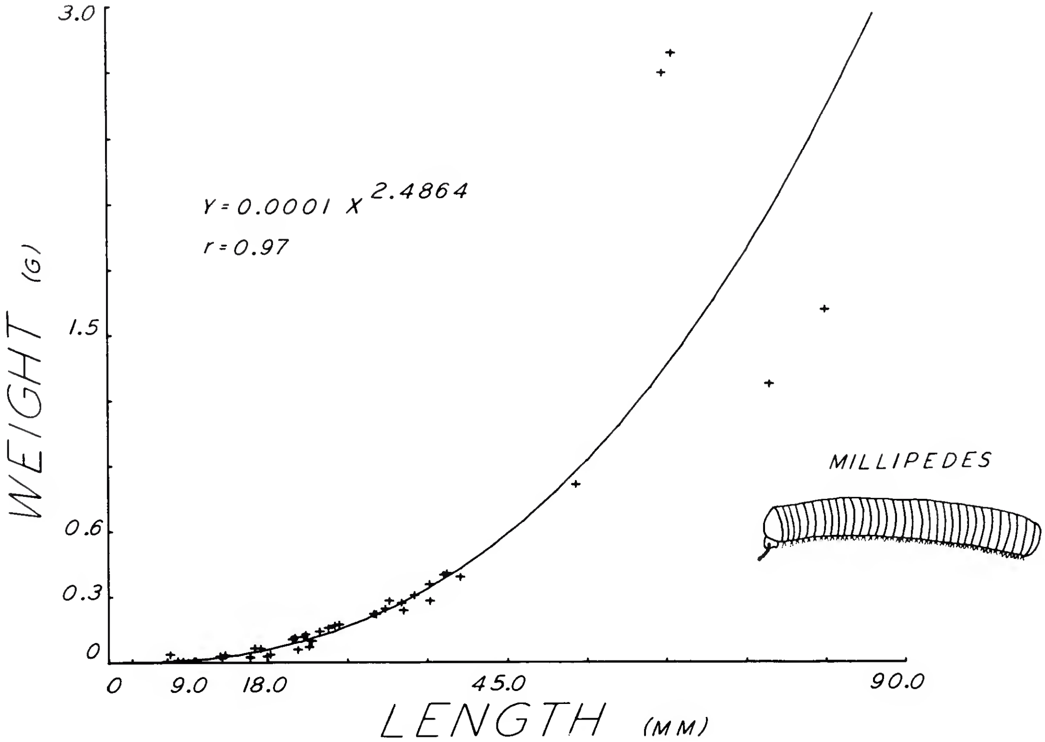
$r = 0.97$
ANTS
0
2.5
5.0
12.5
25.0
0.25
0.125
0.05
0.025
0
$Y = 0.0001 X^{2.8198}$
$r = 0.94$
WINGED
HYMENOPTERANS
0
3.5
7.0
17.5
35.0
WEIGHT (G)
LENGTH (MM)


3.0
1.5
0.6
0.3
0
WEIGHT (G)
0
9.0
18.0
45.0
90.0
LENGTH (MM)
Y = 0.0001 X 2.4864
r = 0.97
MILLIPEDES

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