COSTA RICAN NATURAL HISTORY

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8 REPTILES AND AMPHIBIANS

Adult *Boa constrictor* killing an adult coati (pisote; *Nasua narica*) in the forest understory, Finca Taboga, Guanacaste Province, Costa Rica (photo, D. H. Janzen).

INTRODUCTION

N. J. Scott and S. Limerick

Costa Rica has been a center of interest to field-oriented biologists for many years. Few places in the world combine such a great diversity of habitats with so rich a tropical fauna and flora. Seacoasts and coral reefs, rain forests and páramo are all represented within a few hours' drive on good roads. The herpetofauna is no exception to the general pattern. Several generations of Costa Rican and foreign scientists have taken advantage of opportunities to study the speciose fauna, and as a result there is a great deal of information available on the reptiles and amphibians.

Much of the voluminous herpetological literature will be reviewed in one way or another in the following accounts of individual species, but it is appropriate here to single out three publications that summarize the ecological and evolutionary backdrop of the Costa Rican herpetofauna. Savage (1966) portrayed the historical faunal elements and geological forces that combined to create the modern herpetofauna, and Duellman (1966*a*) mapped the ecological divisions of Central America and described the associated herpetofaunal patterns. Scott (1976) compared Costa Rican faunas with those studied in other tropical regions.

This paper is designed to serve as an introduction to some aspects of the ecology and evolution of the Costa Rican herpetofauna. The choice of subjects was guided by several criteria: our own interests, broad taxonomic scope, availability of information, group "importance," and ease of study. In each section the information is placed into an ecological-evolutionary framework that is designed to generate hypotheses for future studies. The section on amphibian breeding examines the varied reproductive modes and discusses the selective pressures and opportunities faced by amphibians in a diverse array of habitats. This area of study has a rich literature, but many aspects of amphibian breeding biology remain unknown. The part discussing anuran defenses serves to introduce a rapidly expanding field that has received little attention until recently. We predict that in the future the ecological aspects of how amphibians avoid predation will receive a great deal of attention. Diurnal lizards are often very easy to work with, and many scientists have taken advantage of the opportunity. This is another area

that should yield much information. The final section on turtles and crocodilians was included because their biological traits tend to be similar and they are the most important reptiles from the viewpoints of economics and conservation.

Several general terms need to be defined. In this introduction, lowland refers to elevations below about 800 m, intermediate to elevations from 600 to 1,700 m, and highland to elevations above 1,700 m. "Dry" refers to areas receiving less than about 2,000 mm of annual rainfall (most of lowland Guanacaste Province, northern Puntarenas Province, and the floor of the Meseta Central), and "wet" includes the rest of the country.

Breeding Biology of Amphibians

North American frogs have a generalized life history that is familiar to most people. Male frogs call near a pond, females approach, a pair goes into amplexus, and eggs are fertilized as they are laid. After a few days the tadpoles hatch from the eggs, feed on detritus and algae, and grow. They transform into frogs after a variable period. The metamorphosed froglets grow into adults, usually on land. This scenario, with minor variations, describes the reproductive biology of the great majority of United States frogs. However, in the southwestern United States and in Florida there is a small group of frogs that are the only United States mainland representatives of the tropical American family Leptodactylidae, a group that shows a quite different breeding behavior. The cliff and barking frogs (*Syrrhophyus*, *Halactophryne*) and the introduced greenhouse frog (*Eleutherodactylus*) lay large-yolked eggs on land in moist situations. The tadpole stage develops within the egg, and the egg hatches a froglet. This mode of reproduction is called *direct development*. In the remaining United States genus in this family, *Leptodactylus*, the male whips up a foam nest from mucous secretions of the female and semen. The nest protects the eggs and young tadpoles until they become large enough to move out into the pond.

The generalized pattern described above could fit many United States salamanders too. Quite a few, however, lay terrestrial eggs that hatch either into larvae that complete their development in water or into fully terrestrial young that have the same body form as do the adults. Other differences between salamander and generalized frog reproduction are the courtship patterns (salamanders, unlike most anurans, do not call) and fertilization (all except one species of United States salamander have internal fertilization). Several species and populations of salamanders are aquatic during their entire life.

TABLE 8.1 Reproductive Modes of Costa Rican Amphibians

	Gymnophiona	Caudata	Anura	
Site of Development	Caeciliidae	Plethodontidae	Rhinophrynidae	Microhylidae
I. Eggs and larvae in water				
A. Unconstrained body of water				
1. Temporary pond			1	2
2. Stream				
3. Permanent pond				
B. Arboreal water				
1. Tree cavities				
2. Bromeliads				
C. Constructed basins				
II. Eggs out of water, larvae develop in water				
A. Eggs on vegetation over water				
1. Temporary pond				
2. Stream				
B. Eggs in foam nest				
C. Eggs on land, larvae carried to water				
III. Neither eggs nor larva in water				
A. Direct development		24		
B. Viviparity	3			
IV. Unknown				
Total	3	24		

SOURCES: Data for caecilians from Wake (1977); salamanders from Wake and Lynch (1976); *Rhinophrynus* from Stuart (1961); microhylids from personal observations and Nelson (1972); leptodactylids from Heyer (1969), Starrett (1973), and Breder (1946); bufonids from personal observations, Starrett (1967), Novak and Robinson (1975), and Zug and Zug (1979); hylids from personal

In contrast, Costa Rican amphibians show an incredible diversity of reproductive behavior that is only hinted at in United States amphibians. One of the two leptodactylid breeding adaptations described above occurs in more than forty species, and other forms of reproduction are common. Here we will examine these patterns, suggest adaptive trends, and speculate on the selective forces that produce such a great diversity of breeding types.

The clearest trend in the breeding biology of Costa Rican amphibians is a progression of specializations leading away from dependence on a body of permanent water and toward increased terrestriality. A summary of reproductive modes will define this trend. The changes from completely aquatic to terrestrial breeding are accompanied by several specific adaptive traits, including an increase in parental care, a change from oviparity to viviparity, and changes from an aquatic larval state to direct development on land.

Reproductive Modes

Crump (1974; modified by Duellman 1978) tabulated the reproductive modes found in an Ecuadorian anuran community. Her classification, with minor modifications, can be used for the Costa Rican amphibian fauna (table 8.1). In some cases we have added breeding types not found in Crump's Ecuadorian frogs, such as viviparity and bromeliad breeding; in other instances we have subdivided some of her modes into ecologically meaningful subdivisions, such as permanent versus temporary water and pond versus stream habitats. We have likewise deleted modes found in Ecuadorian frogs but not found in Costa Rican frogs, such as egg transportation by adults. We could not even guess the breeding mode for four species (*Bufo fastidiosus, Hyla colymba, Crepidophryne epioticus,* and *Glossostoma aterrimum*), but where available evidence allowed us to make a reasonable guess we did so. Some species breed in two or more types of aquatic habitat; in those cases they were assigned to the most common developmental site.

Mode IA: Reproduction in Unconstrained Bodies of Water

The most generalized mode of reproduction is similar to that described earlier for most North American anurans. Eggs and larvae are found in ponds or streams. Chorusing males gather at the breeding site and are joined by the females. There is no known extended courtship or parental care in this group.

In Costa Rica most of the mode IA species deposit eggs in temporary ponds, which eliminates some fish and aquatic insect predation, but the eggs and larvae may

	Anura					
Leptodactylidae	Bufonidae	Hylidae	Dendrobatidae	Centrolenidae	Ranidae	Totals
	8	13			1	25
	3	2			1	6
	1				2	3
		2				2
		3				3
		1				1
		7				7
		9		13		22
6						6
			6			6
35						59
						3
	2	1				4
41	14	38	6	13	4	147

observations and Duellman (1970); dendrobatids from personal observations and Savage (1968); centrolenids from personal observations and McDiarmid (1975), and ranids from personal observations and Zweifel (1964*b*).

become desiccated or overcrowded as the pond dries (Heyer, McDiarmid, and Weigmann 1975). The microhylids, rhinophrynid, *Rana palmipes*, most *Bufo* (*coccifer, coniferus, haematiticus, holdridgei, luetkenii, melanochloris, periglenes*, and *valliceps*), some *Hyla* (*rufitela, loquax, microcephala, phlebodes, angustilineata, pseudopuma, boulengeri, eleaeochroa*, and *staufferi*), *Phrynohyas venulosa*, and some *Smilisca* (*baudinii, phaeota*, and *puma*) use temporary ponds. Oviposition is during the wet season, and males call from or near the water. Detailed reproductive information for representatives of this breeding mode can be found in Stuart (1935, 1961), Taylor (1942), and Duellman (1960) for *Rhinophrynus dorsalis;* Novak and Robinson (1975) for *Bufo holdridgei;* Savage and Heyer (1969) and Duellman (1970) for hylids in general; and Zwiefel (1964*a*) and Pyburn (1967) for *Phrynohyas venulosa*.

A few species using this mode of reproduction presumably lay their eggs in streams. They include the three species of *Atelopus* (Bufonidae), *Rana warschewitschii* (Ranidae), *Smilisca sila*, and *S. sordida* (Hylidae). *Atelopus* breeds in the wet season, and the eggs are probably anchored to the undersides of rocks in the stream (Starrett 1967). These two species of *Smilisca* breed in the dry season when the stream volume and rate of flow are lowest (Duellman and Trueb 1966). *Atelopus* may call but do not chorus. They are territorial and pair before moving to the oviposition site (Sexton 1958; McDiarmid 1971), whereas *Smilisca* males form choruses or call in small groups (Duellman 1970; pers. obs.). The breeding habits of *R. warschewitschii* are not known in detail, but they often breed in the quiet backwaters of small stream or other marshy situations (pers. obs.).

Relatively few species of Costa Rican frogs breed in permanent ponds. Fish predation is likely to be intense (Scott and Starrett 1974), and permanent ponds are scarce in the country. Three species might be characterized as breeding more often in permanent than in temporary waters: *Bufo marinus, Rana vibicaria*, and highland *R. pipiens*. *Bufo marinus* has been studied in detail in Panama by Breder (1946) and by Zug and Zug (1979). They breed in many kinds of waters, most of which are permanent. In Costa Rica common breeding sites are the pools left behind by receding rivers (pers. obs.). The highland *Rana vibicaria* has been studied in Panama by Zweifel (1964*b*).

Mode IB: Arboreal Water

A few species of Costa Rican tree frogs live their whole existence in tree canopies, breeding in tree holes and bromeliads. Two species of fringed-limbed *Hyla*, *fimbrimembra* and *miliaria*, are large (>100 mm in length) and very poorly known, and their breeding activity has not been recorded. Taylor (1952) took a specimen from a water-filled tree cavity, and we assume that they breed in similar sites (see Savage 1980). *Anotheca spinosa* is another hylid that has been recorded as breeding in tree holes (Robinson 1961; Duellman 1970) and bromeliads (Taylor 1954). Their tadpoles are carnivorous, eating frog eggs and mosquito larvae (Taylor 1954). *Hyla zeteki* is a bromeliad breeder, and the tadpoles have highly modified mouthparts for eating frog eggs and possibly other tadpoles (Dunn 1937; Starrett 1960). A closely related species, *H. picadoi*, also breeds in bromeliads (Robinson 1977).

Mode IC: Constructed Basins

Males of *Hyla rosenbergi* usually construct mud basins where the females oviposit next to temporary ponds or streams, although in some circumstances eggs are laid in male territories that are in the shallow water at the edge of swamps (Breder 1946; Duellman 1970; pers. obs.). Breder (1946) offers an exceptionally detailed description and photographs of nests, tadpole development, and mating behavior.

Mode IIA: Eggs on Vegetation, Larvae in Water

The trend toward removing part of the amphibian life cycle from aquatic habitats starts with species that lay eggs out of water but whose tadpoles still develop in water. These species lay their eggs on vegetation over temporary ponds or streams, and the tadpoles hatch and drop into the water. Five species of *Agalychnis, Phyllomedusa lemur*, and *Hyla ebraccata* suspend their eggs over temporary ponds (Duellman 1970). Detailed breeding observations have been made on *Agalychnis callidryas* (Pyburn 1963, 1964, 1970; Duellman 1970), *A. annae* (Duellman 1963), and *A. spurrelli* (Boulenger 1913; Scott and Starrett 1974).

Hyla lancasteri and probably eight other species of *Hyla* (*debilis, legleri, pictipes, rivularis, rufioculis, tica, uranochroa*, and *xanthosticta*) and all centrolenids deposit eggs on vegetation over streams, into which the tadpoles fall after hatching. *H. lancasteri* eggs are deposited on the upper leaf surfaces (Trueb 1968). No parental care is known, and breeding is generally in the wet season, depending on the site. The thirteen species of Costa Rican centrolenids (*Centrolenella*) attach their egg clutches to foliage overhanging high-gradient streams. The greatly modified tadpoles fall into the swift current and bury themselves in the detritus and gravel on the stream bottom (pers. obs.). Males are territorial (McDiarmid and Adler 1974; Duellman and Savitsky 1976), and many guard their egg masses (McDiarmid 1975, 1978).

Mode IIB: Eggs in Foam Nest, Larvae in Water

Six species of Costa Rican leptodactylids construct foam nests and deposit their eggs in them, and the tadpoles

develop in temporary ponds. Heyer (1969) detected a definite trend toward terrestriality within the genus *Leptodactylus*, as suggested by the placement of the foam nest. The male uses his hind feet to whip up a mixture of air, water, mucus from the female, and semen (Rivero and Esteves 1969; Heyer and Rand 1977). The most aquatic forms float their nests on water (*Physalaemus pustulosus* [Breder 1946; Sexton and Ortleb 1966]. *Leptodactylus melanonotus* [Heyer 1976; pers. obs.], and *L. bolivianus* [Sexton 1962; pers. observ.]). The next step toward terrestriality is shown by forms that place their nests next to ponds or in burrows, depressions, or potholes that are likely to flood (*Leptodactylus pentadactylus* [Breder 1946; Vinton 1951; Rivero and Esteves 1969; pers. obs.]). A further step is seen in those *Leptodactylus* that place the foam nest in a burrow excavated by the male (*L. fragilis* [Dixon and Heyer 1968; Heyer 1970] and *L. poecilocheilus* [Dixon and Heyer 1968; Heyer 1969]). The latter group breeds before the heavy rains, and the tadpoles living in the nest are more advanced than other anuran tadpoles when the floods finally come (Heyer 1969).

Mode IIC: Eggs on Land, Larvae Carried to Water

The members of an entire family of frogs, the Dendrobatidae, lay their eggs on land and carry the tadpoles to water for development. One Costa Rican species, *Colostethus nubicola*, places its tadpoles in small streams, but the other species generally use tree holes, fallen palm petioles, leaf cups, and the leaf axils of bromeliads and aroids (Savage 1968; Silverstone 1975, 1976; pers. obs.).

Dendrobatids are diurnal and often very common. They have been studied frequently, both in captivity and in the wild. For recent general summaries of social and breeding behavior, see Silverstone (1975, 1976), Salthe and Mecham (1974), and Wells (1977*a*,*b*). In most species of dendrobatids, the males defend calling territories, but *Dendrobates auratus* is an apparent exception (Wells 1978). Dendrobatid mating takes place on land, usually without amplexus, and eggs are deposited in the litter or on low leaves. The eggs are tended, often by the male but sometimes by the female, and the tadpoles are taken onto the back of a parent. The parent carries the tadpoles for a varying number of days or even weeks and then deposits them in water for further development. Field studies of the territorial and breeding behavior of Costa Rican species include those on *Dendrobates auratus*, *D. granuliferus*, and *D. pumilio* (Dunn 1941; Eaton 1941; Breder 1946; Starrett 1960; Duellman 1966*b*; Kitasako 1967; Savage 1968; Goodman 1971*a*; Crump 1972; Bunnell 1973; Silverstone 1975; Wells 1978; Young 1979; Limerick 1980). *Colostethus* and *Phyllobates*, the other two Costa Rican genera, have received much less attention, although Duellman (1967), Savage (1968), and Silverstone (1976) contain some information.

An intriguing question has arisen in dendrobatid studies. There is a possibility that adult frogs regularly monitor tadpoles in water and transfer them from one water source to another. Dunn (1941) discounted the idea, but Eaton's (1941) data show that when a tree hole was cleared of tadpoles, new ones "well past the hatching stage" would appear within a day. Eaton did not measure most of the tadpoles when they were taken from the water, but did so only after they had been in the laboratory for several days or weeks. One of us (Scott) watched a female *D. pumilio* visit sequentially almost all of the water cups in the leaf axils of a tank bromeliad. She was not carrying a tadpole, but she backed down into each cup, stayed a few seconds as if to give tadpoles a chance to climb on, then went on to the next cup. None of the leaf cups contained tadpoles.

Mode IIIA: Direct Development on Land

The direct development of large-yolked eggs in terrestrial nests is displayed by a number of common genera of Costa Rican amphibians. Presumably, all twenty-four species of plethodontid salamanders and the entire frog genus *Eleutherodactylus* (thirty-five species) lay small clutches of eggs on land. The embryos pass through a highly modified larval stage in the egg and hatch as tiny salamanders or froglets (Lynn 1942; Vial 1968; Starrett 1973; Houck 1977). The reproductive behavior of tropical salamanders has been studied in several species, but our knowledge of Costa Rican *Eleutherodactylus* reproduction is fragmentary at best. They do not congregate in breeding choruses like most other frogs, their breeding season is extended rather than concentrated, they are generally quite shy, and many species are nocturnal. It has been discovered that some bats are effective predators on many forest species of *Eleutherodactylus* (M. Tuttle, pers. comm.), which may be a reason for their shyness.

Mode IIIB: Viviparity

This last reproductive mode found in Costa Rican amphibians is viviparity. It occurs only in the caecilians, and all three species are viviparous. Eggs and larvae are retained in the oviduct. The larvae develop a special dentition for scraping and ingesting cells and secretions from the wall of the oviduct (Wake 1977).

The Evolution of Terrestriality

A discussion of the evolution of the terrestrial trend in reproduction of Costa Rican amphibians can best be divided into two parts: one, with some hard data, on the adaptations necessary to accomplish the breeding mode and the second, almost entirely speculative, on the selec-

tive forces operating to produce these adaptations. A parallel discussion, with emphasis on South American frogs, is found in Lutz (1948).

Salthe (1969), Salthe and Duellman (1973), and Salthe and Mecham (1974) have summarized the egg and clutch size adaptations associated with different reproductive modes. A general criticism of these analyses is that "clutch size" is defined in practical terms as the number of eggs found in naturally deposited clusters. For most tropical species we do not know how often egg clusters are produced. Some species divide a single ovarian complement into several clusters (Duellman 1970; Pyburn 1970), some do not breed every year (Vial 1968), and others deposit a few eggs at regular intervals over an extended breeding season (Wells 1978). For these reasons the analyses do not reflect comparable degrees of reproductive effort between different species.

The cited authors formulated several hypotheses that are pertinent to our discussion (Salthe and Duellman 1973):

1. For salamanders and frogs of about the same size, those laying larger clutches lay smaller eggs.
2. Larger eggs produce larger hatchlings.
3. Larger eggs develop more slowly.
4. Larger eggs are associated with species whose larvae develop in streams and terrestrial sites.
5. There has been selection for increased clutch size in large frogs and for larger egg size in small frogs.
6. Because of points 4 and 5, small frogs are better at reproducing in ways novel to anurans.

Recently Crump and Kaplan (1979) tested some of these conclusions with a suite of Ecuadorian hylid frogs. Their results supported the hypothesis that frogs with more terrestrial breeding habits had larger eggs and smaller clutches than equivalent-sized frogs using aquatic breeding habitats.

Associated with the trend to produce larger eggs in nonpond environments are the changes in developmental rates. As we stated above, larger eggs develop more slowly (up to 3 weeks; pers. obs.), which automatically places more ecological emphasis on the egg stage of development. Slower egg development does not necessarily mean a longer total time between oviposition and metamorphosis; larger eggs produce larger tadpoles, which presumably have shorter larval periods. However, no studies have been made of the consequences of the trade-offs incurred by shifts in developmental rates for different life-history stages.

Shifts in emphasis in developmental rates and egg size and number are not the only ones seen in energy flow pathways between adult frogs and their offspring. Parental investment is measured not only in terms of egg and sperm production but also by the costs of mate attraction, increased exposure to predation, territorial defense, nest production, and parental care. There are few data for the costs involved in the first four categories, but the fifth, parental care, has received a great deal of attention (Salthe and Mecham 1974; McDiarmid 1978).

Parental care is positively associated with terrestrial breeding in amphibians. Salthe and Mecham (1974) detected three major consequences of parental care: protection of eggs and larvae from predation; assurance of an oxygen supply to the eggs by manipulation; and a mechanism to provide a more suitable microhabitat, such as providing moisture to the eggs or moving tadpoles to the most favorable sites for development. All these factors appear to be operating among Costa Rican amphibians. Viewed in this context, parental care is an important acessory to a terrestrial life cycle. All species with documented parental care have smaller clutches than do close relatives lacking parental care (McDiarmid 1978). Whether these are two independent trends that are related through a third (increased terrestriality) or whether one trend causes the other is not clear, although McDiarmid (1978) believes that lowered fecundity is a preadaptation for parental care.

Nest-making is another clear adaptation leading to a more terrestrial breeding habitat. The foam nests of the leptodactylids and the mud basins of *Hyla rosenbergi* protect eggs and tadpoles from desiccation (Heyer 1969). *Leptodactylus fragilis* and *L. poecilocheilus* construct burrows in which they place their nests, with similar advantageous results.

Conspicuous tadpole adaptations are correlated with larval habitats and feeding modes. Starrett (1960, 1967, 1973) described many different types of Costa Rican tadpoles. Major selective forces appear to be associated with water type (stream, pond, bromeliad), position in the water column (interstitial, midwater, surface), substrate (mudbottom, rocky bottom), and diet (filter feeding, carnivory).

The trends toward terrestriality that we have examined are associated with selective pressures upon which we can only speculate. The main selective force appears to be an evolutionary effort to escape predation pressure on eggs and larvae. This pressure comes largely from fish (Heyer, McDiarmid, and Weigmann 1975). Frogs escape by using ephemeral aquatic habitats or terrestrial or arboreal nesting sites. In Costa Rica there are no native fish above about 1,500 m, and a whole radiation of stream-breeding hylids is found above this level (Savage and Heyer 1969). Most of the adaptations we have discussed are conducive to improving egg and larval survival in habitats that are not occupied by fish. The introduction of trout to Costa Rican upland streams is likely to menace their associated frog populations.

A selective regime that is largely unrelated to fish predation pressure is the special requirements imposed by

stream habitats. Without special adaptations, eggs and tadpoles are poorly suited to life in a swift current. Thus, most stream-breeding frogs hang their eggs in trees, and many lay large-yolked eggs that produce large, strong tadpoles. The tadpoles themselves show special stream adaptations (Starrett 1960, 1967).

In summary, the "trend toward terrestriality" that we have discussed is driven not so much by selection for terrestriality per se as by selection for removing eggs and tadpoles from exposure to fish predation. Any water sources unoccupied by fish, or habitats in which tadpoles can hide, such as grass-filled marshes, are usually heavily used by frogs in Costa Rica. Some arboreal trends appear to be alternative adaptations to unfavorable limnological conditions such as strong stream flows.

Anuran Defense Adaptations

Tropical frogs often appear to be among the most defenseless of animals. They are small relative to other terrestrial vertebrates, many are rather slow moving, and they do not usually have teeth or claws suitable for self-defense. In lieu of more obvious structural and behavioral protection, amphibians have evolved an array of more subtle and passive defenses against predators.

TOXINS

One could generalize that all amphibians produce skin toxins. Many are not very potent, and their effects are not obvious, but several produce some of the most potent natural toxins known (Myers, Daly, and Malkin 1978).

The most common effects of skin toxins are the bad taste or other noxious results that serve to discourage or deter predators. Specific kinds of toxins are apparently restricted to certain taxonomic units with anurans. For instance, various species of toads (Bufonidae) have several identified toxins: atelopidtoxin, bufogenin, bufotenidine, and bufotoxin. These can cause hypertension, vasoconstriction, increased power in heartbeat, or hallucination; or they can directly poison the heart muscle. In the leptodactylid *Leptodactylus pentadactylus*, leptodactylin causes a neuromuscular block and a nicotinelike stimulation of the nervous system. South American *Physalaemus* skin toxins cause hypotension and vasocilation. Ranid skin toxins are hypotensive, and certain hylid toxins are hemolytic and hypotensive (Daly and Myers 1967; Habermehl 1974).

Some species of dendrobatids, as their common name "poison dart" frogs suggests, are probably the most toxic Costa Rican frogs. South American Indians used skin secretions from the more poisonous species to tip their arrows (Myers, Daly, and Malkin 1978). Batrachotoxin, found in the Costa Rican species *Phyllobates vittatus* and *P. lugubris*, blocks neuromuscular contraction and transmission (Albuquerque, Daly, and Witkop 1971). It also causes symptoms of muscle poisoning and respiratory paralysis and can cause death. *Dendrobates pumilio* and *D. auratus* secrete pumiliotoxin, which caused convulsions and death with subcutaneous injection in rats (Habermehl 1974). Myers, Daly, and Malkin (1978) reported that a specimen of *P. vittatus* touched on a human tongue caused numbness and a tightening of the throat. A snake (*Leimadophis*) was helpless for several hours after biting this species. These toxins seem to be readily absorbed by the mucosa of the mouth and throat, or by any porous skin, and cause respiratory difficulties. Contact with a cut or entrance into the circulatory system is also harmful and possibly lethal (Myers, Daly, and Malkin 1978). Apparently, in the family Dendrobatidae, the cryptic species in the genus *Colostethus* are relatively nontoxic, whereas members of *Dendrobates* are quite toxic and members of *Phyllobates* are very poisonous.

Several other Costa Rican frogs produce strong toxic symptoms in humans. The hylid *Phrynohyas venulosa* can produce sneezing in susceptible people in the same room, even without physical contact with the frog (pers. obs.). The toxin of this species can produce acute pain and local paralysis when in contact with mucous membranes or breaks in the skin (Janzen 1962). The two largest Costa Rican amphibians, *Bufo marinus* and *Leptodactylus pentadactylus*, both produce copious irritating skin secretions (Daly and Myers 1967; Habermehl 1974). *Bufo marinus* has muscular control over the paratoid gland; the toad can squeeze the gland and squirt the poison in a fine spray more than 30 cm (pers. obs.). This is why *B. marinus* can kill dogs and cats that pick this toad up in their mouths (Krakauer 1968). The small bufonid *Atelopus* is known to have powerful skin toxins, but they are not obvious during normal handling (Fuhrman, Fuhrman, and Mosher 1969).

Villa (1967, 1972) described defensive behavior in captive *Leptodactylus pentadactylus*. Individuals showed defensive behaviors including hissing, inflating the body, and raising of the hind legs with the snout near the ground. During this behavior a toxic skin secretion was produced that irritated open cuts and mucosa and caused sneezing.

Skin glands in tadpoles of some *Bufo* species and some hylids have noxious secretions, making them unpalatable (Wassersug 1973). In experiments in Costa Rica using human subjects, *Bufo marinus* tadpoles were found to have very distasteful skin, while tadpoles of *Smilisca phaeota*, *Hyla rufitela*, and *Colostethus nubicola* had distasteful bodies, perhaps partly because the gut contents were distasteful (Wassersug 1971). Myers, Daly, and Malkin (1978) found no batrachotoxin in tadpoles of a Colombian *Phyllobates* and found only traces in juvenile frogs. This suggests that in this species the toxins are formed in significant amounts only after metamorphosis.

Frog eggs can also be toxic. Licht (1967) recorded the deaths of two Indians who accidentally ate what were probably *Bufo marinus* eggs. Further studies with natural predators confirmed the hypothesis that the eggs of *B. marinus* were unpalatable compared with the eggs of several other anurans (Licht 1968, 1969).

Coloration

Most amphibians are cryptically colored. They bear various shades and patterns of browns, greens, grays, and blacks, thus blending into the environment. Many cryptic species do not have potent skin toxins but depend on their coloration to make them less visible to predators. Some cryptic species, however, also have toxic defenses. *Phrynohyas venulosa*, for example, secretes a substance that can burn skin or mucous membranes (Janzen 1962). Most such species are sit-and-wait predators; being motionless much of the time, they further reduce their visibility. Many cryptic, nontoxic species are crepuscular or nocturnal, while the aposematic (conspicuous), toxic species are usually diurnal.

The species that have conspicuous colors (are aposematic) usually have strong toxins. The warning colors or contrasting patterns serve as a warning to predators, but they may also send an aggressive or courtship message to individuals of the same species. It is believed that birds, known to have color vision, are the main targets of the aposematic color signals. Wild birds react to warning colors in amphibians by avoiding toxic species (Brodie and Brodie 1980), and domestic fowl can learn to avoid dendrobatids (Cott 1904; Daly and Myers 1967; Kitasako 1967; Silverstone 1975).

Many frogs have "flash" colors that are assumed to serve a defensive function. Flash colors are bright colors, usually red, yellow, orange, or blue, sometimes with dark barring or mottling, on the surfaces of the hind legs and groin that are concealed when the frog is at rest. The resting frog is cryptic, but movement exposes a flash of bright color for a moment until the frog folds its legs again. This sudden change from procrypsis to a flash of color to procrypsis again is believed to confuse, startle, or misdirect a predator (Cott 1940). Like aposematic coloring, flash colors probably function against bird predators. Flash colors are seen in a wide variety of Costa Rican frogs, including four species of *Eleutheordactylus*, *Leptodactylus pentadactylus*, all five species of *Agalychnis*, three species of *Hyla*, and one species of *Rana*.

Jumping Ability

Many authors have suggested that the unique saltatorial locomotion of frogs evolved as an escape mechanism (review in Inger 1962). Jumping has several advantages over the primitive salamanderlike walk. In dense grasslands or in low-shrub habitats, it is almost impossible to move very rapidly at or near ground level. Jumping is a much faster and more efficient mode of locomotion. The same applies to many riparian habitats. To this frog collector, the most elusive frogs are those that leap into a grass or vine tangle or jump from the shore into deep water.

Another likely advantage of saltatorial locomotion is that it leaves a discontinuous odor trail, which probably confounds the many snakes that are excellent scent followers.

Jumping is also a key frog adaptation in the exploitation of arboreal habitats. Flying, gliding, or leaping are the only methods of rapidly moving about in a tree canopy. The leaping ability of frogs enable them to use the discontinuous leaf and small twig substrate more effectively than any other vertebrate except birds. Some frogs are even able to glide (review in Scott and Starrett 1974). An important component of arboreal survival is rapid escape from predators, especially snakes.

Voice

A few frogs emit a loud scream or squall when grabbed by a predator, especially a snake. Two Costa Rican species known to do this are *Leptodactylus pentadactylus* and *Rana pipiens* (Villa 1967; pers. obs.). Two escape opportunities may stem from this behavior. A mammalian predator could be startled enough to drop the frog. Another possibility is suggested by the observation that caimans are attracted to squalling *L. pentadactylus* (pers. obs.). If the caiman attacked the frog's captor, the frog might escape.

How to Overcome Anuran Defenses

Even the most effective anuran defense mechanisms can be circumvented by some predators. *Bufo marinus*, which has been known to lethally poison naive dogs and cats (Krakauer 1968), is eaten by opossums (*Didelphis* spp.), which open the toad's belly, where poison glands are scarce or absent, and eat the internal organs. Raccoons (*Procyon* spp.) do the same thing (pers. obs.).

Some toad-eating snakes are relatively immune to specific frog toxins compared with other species that do not ordinarily eat toads. Small doses of *Bufo marinus* venom killed snakes of the genera *Salvadora* and *Coluber*, but garter snakes (*Thamnophis sirtalis*) were not killed until the dose was tripled (Licht and Low 1968). Myers, Daly, and Malkin (1978) found that a common tropical frog-eating snake, *Leimadophis epinephalus*, was able to digest a juvenile *Phyllobates terribilis*, whose adults are the most toxic frogs known, but a presumably larger dose of toxin immobilized another snake of the same species for several hours. The mechanism by which snakes tolerate frog toxins is unknown, but an enlarged

adrenal gland has been implicated in some species (Smith and White 1955).

Since amphibian toxins are generally concentrated in skin secretions, predators that avoid the skin can successfully feed on toxic frogs and tadpoles. Many invertebrate predators feed by puncturing their prey and sucking the body fluids (Wassersug 1973), and spiders and water bugs appear to be regular predators on Costa Rican frogs and tadpoles (pers. obs.).

Some tadpoles, including those of *Bufo marinus* and *Leptodactylus melanonotus*, are jet black and aggregate into dense clusters containing hundreds of individuals. The adaptative significance of this behavior is obscure. The aggregations are very conspicuous, and the tadpoles would be very vulnerable to predation except that, at least for *B. marinus*, they are unpalatable (Wassersug 1971, 1973).

The leaping ability of frogs is matched by a large radiation of dirunal sight-feeding snakes that eat mostly frogs. In Costa Rica, the majority (about thirty-five species) are forest-floor forms, but several (nine species) are arboreal.

Lizard Food and Feeding Habits

Feeding Habits

As a group, lizards are a highly successful line of reptilian evolution. Along with frogs, birds, and bats they share the distinction of being able to populate many diverse habitats with large numbers and many species of insectivorous forms. Lizards are often the commonest vertebrates in an area. Part of their success is almost certainly due to the fact that they are, in many habitats, the most effective terrestrial-arboreal predators on arthropods, a very abundant food resource.

Although most lizards feed primarily on arthropods, many species and even families have diverged into other feeding niches. A fair number of lizards are vegetarian, at least as adults. The related families Helodermatidae and Varanidae (with the exception of one species) are adapted to general carnivory; small species feed largely on insects, but large species take amphibians, other lizards, mammals, birds, and fish. Other lizard species are specialized for certain diets; for instance, one species of South American teiid feeds on aquatic snails.

The great majority of Costa Rican lizards eat arthropods, without specialization on any one taxon; there are no really carnivorous species like the tegus (*Tupinambis*) of South America or the varanid lizards (*Varanus*) of the Old World. Their diets differ between sites and seasons of the year because the types of arthropods available to them vary with habitat and season (Janzen and Schoener 1968; Hillman 1969; Sexton, Bauman, and Ortleb 1972; Fleming and Hooker 1975). Most lizards seem to feed opportunistically, attempting to catch most of the apparently potential prey they encounter. Generally, the sizes of prey items are positively correlated with the sizes (snout-vent length [SVL] or biomass) of the lizards. Individuals are limited by the maximum size they can capture and swallow, but larger individuals can also take smaller prey.

In Costa Rica the families taking arthropods exclusively are Teiidae, Gekkonidae, Anguidae, and probably Scincidae and Xantusiidae (Hillman 1969; Pough 1973; Duellman 1978). Although most species are opportunistic feeders on insects, spiders, and mites, one anguid, *Diploglossus monotropis*, is thought to specialize on land crabs (D. C. Robinson, pers. comm.). Members of the family Iguanidae are usually insectivorous, but the largest species, *Ctenosaura similis*, *Iguana iguana*, and the three species of *Basiliscus*, also eat vegetation (Taylor 1956; Montanucci 1968; Pough 1973; VanDevender 1978). *Ctenosaura* and *Basiliscus* are insectivorous as juveniles and more herbivorous as adults, while juvenile *Iguana* are generally herbivorous (pers. obs.). Plant parts eaten are fruits, buds, seeds, and leaves (Taylor 1956; Montanucci 1968). Adult *Basiliscus* may eat 25% to 50% vegetation, and large individuals also eat vertebrates and crustaceans (Montanucci 1968; VanDevender 1978).

Pough (1973) pointed out that iguanid and scincid lizards that weigh over 100 g are mainly herbivorous and those weighing less than 100 g are mainly insectivorous. The large lizards have a greater total energy requirement for body maintenance, but smaller lizards have a higher energy need per unit of body weight. Anthropod food is more abundant in small packages (insects) than in large ones, and there is more energy per unit of prey in animals than in plants. Plants also take longer to be digested and the percentage of assimilation is lower (Bennett and Dawson 1976). Small lizards are more adept at catching small, fast-moving prey. Compared with large lizards, they have a smaller body mass to move when pursuing prey and use less energy in doing so. Most lizards are not physiologically adapted to long pursuit times, since respiration quickly changes to the anaerobic pathway (Bennett and Licht 1972). Pursuit of small, fast-moving prey by large lizards is thus doubly inefficient. For large lizards it is often more efficient to eat plants, which require no energy for pursuit and are usually present in large quantities. Large lizards are also less vulnerable to predation and therefore they can spend more time basking in the sun. By doing so they can raise their body temperature and increase the otherwise slow rate of digestion of plant material.

Foraging Behavior

For those lizards with insectivorous and carnivorous food habits, there are two main types of foraging strategies—sit-and-wait and active searching (Pianka 1966). Of the

sit-and-wait predators, there are two patterns in Costa Rica, that shown by *Corytophanes cristatus* and that used by the species of *Anolis* and *Norops* (Iguanidae).

Corytophanes is a generally lethargic, cryptic species that eats large, slow-moving prey, mostly leipdopteran larvae, beetle larvae, and orthopterans, but not vegetation (Ream 1965; Andrews 1979). Individuals feed infrequently and eat few but relatively large items. Such large prey are not abundant in the habitat. This feeding strategy may have evolved as a means of predator avoidance. A cryptic species that spends little time foraging will reduce the risk of a predator's seeing individuals while they are moving (Andrews 1979).

Many anoles, *Anolis* and *Norops*, perch head downward on tree trunks and visually search for prey, usually in the leaf litter. When they see the movements of a prey item, they run from their perch and attempt to catch it. Furthermore, most of their hunting time is spent in searching and little in pursuit (Andrews 1971; Goodman 1971*b*; Scott et al. 1976). Goodman (1971*b*) found that forest anoles (e.g., *N. polylepis*) seem to rely on prey movements to locate prey, while the stream-dwelling *N. aquaticus* may not need such cues. Goodman believed that, perhaps since the latter species lives in a habitat with much moving water, it had to use some cue other than movement to locate food.

The anoles are generalized and opportunistic arthropod eaters (Rand 1967; Schoener 1968; Fleming and Hooker 1975), although Scott et al. (1976) found that males ate more ants and small insects because they spent more time on their perches than females. Subadults and females with oviducal eggs contain larger volumes of prey than males of the same size (Rand 1967; Schoener 1968; Scott et al. 1976; Stamps 1977). Taylor (1956) reported an 88 mm SVL *Norops capito* that was taken with a half-swallowed 50 mm SVL *Norops lemurinus* in its mouth.

Fleming and Hooker (1975) found that the food of *N. cupreus* in Guanacaste Province varied seasonally and with sex of the lizard. In the dry season, the mean prey size for males was greater than that for females, as was the range of prey sizes. The number of prey items eaten by the two sexes was similar. The mean prey size of females was greater in the wet season than in the dry season. In the dry season, both males and females ate more prey items than in the wet season.

Andrews and Asato (1977) studied the physiology and energy budget of Panamanian *Norops limifrons*, a sit-and-wait species. They found that, in the field, adult males had the lowest energy intake (63 cal/g/day), with immatures and adult females consuming considerably more food (90 and 124 cal/g/day, respectively). They attribute these differences to the increased energy demands of growth in immatures and egg production (one per 7 days) in females. A similar study has been done for one actively searching lizard species in Europe, although energy devoted to reproduction is not included (Avery 1971).

The active search strategy is found in species of such lizards as *Ameiva* and *Cnemidophorus* (Teiidae). They are opportunistic arthropod feeders, scrambling about in the litter, pushing their heads into the leaves and looking for food (Hillman 1969; pers. obs.). Hillman (1969) found that *A. festiva* and *A. quadrilineata* from the Osa Peninsula ate a few amphibians in addition to arthropods. These two species were broadly sympatric in his study area, and there was a great deal of overlap in prey taxa, but there were some differences owing to their feeding in different microhabitats. *Ameiva quadrilineata*, the smallest species, took significantly smaller prey than *A. festiva* and a third sympatric species, *A. leptophrys*.

Feeding strategies also place constraints on other aspects of the lizard's biology. For instance, lizards using the sit-and-wait strategy cannot thermoregulate as easily as lizards that are almost constantly on the move. They also use less energy, so they require less food. Because they cannot tolerate continuous exposure to the sun, they usually perch in the shade. As a result, sit-and-wait species tend to be thermal conformers, while active searchers usually thermoregulate to rather high temperatures. *Norops limifrons* in Panama, a sit-and-wait strategist, maintains a "normally active" temperature between 24° and 31° C, which is 1° to 2° C above ambient air temperature (Ballinger, Marion, and Sexton 1970), while foraging individuals of the three species of *Ameiva* (active searchers) studied by Hillman (1969) had relatively constant body temperatures between 37° and 38° C, which were 4° to 10° C higher than ambient temperatures.

Turtles and Crocodilians

The turtles of Costa Rica include both freshwater and marine forms. There are six species of marine turtles in two families, Cheloniidae and Dermochelyidae. There is a great deal of information on the Costa Rican population of the green turtle (*Chelonia mydas*), but very little is known about the hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), olive ridley, (*Lepidochelys olivacea*), leatherback (*Dermochelys coriacea*) and Pacific green (*Chelonia agazzisii*) turtles.

The freshwater and terrestrial turtles of Costa Rica belong to three families: the snapping turtle, *Chelydra serpentina* (Chelydridae), the aquatic and terrestrial Emydidae, and the semiaquatic mud turtles, Kinosternidae. Little is known about the aquatic tropical snapper so it will not be discussed further, but the other groups will be discussed below.

The biology of the two species of crocodilians in Costa Rica is poorly known. The caiman (*Caiman crocodilus*) is

a small (to 2.5 m) species that inhabits many interior lowland swamps and slow rivers. The crocodile (*Crocodylus acutus*) is a coastal species that was formerly common in mangrove swamps and coastal rivers. It is a large animal, with reliable records from Mexico of more than 4 m (Alvarez del Toro 1974).

Sea Turtles

The green sea turtle that nests on the Caribbean (especially at Tortugero, Limón Province, Costa Rica), is there only for the nesting period between June and October. The rest of the year the adults are at their feeding grounds, which include other parts of Costa Rica, the Gulf of Mexico, and parts of the western Caribbean. The population is characterized by the long migrations of 200 to 2,000 km between feeding grounds and nesting beaches (Carr and Giovannoli 1957; Carr and Ogren 1960; Carr and Hirth 1962; Carr, Ross, and Carr 1974; Carr, Carr, and Meglan 1978).

Mating occurs at the breeding area in the first half of the breeding season. The eggs that are fertilized in one season are laid 2 to 3 years later. From studies of tagged turtles it has been found that females return to a nest site near previous nest areas, and possibly near their hatching site. Individuals seem to be able to recognize a specific area of beach, but the method of discrimination is not well understood. Recognition may be visual, using distinct land features, whether recognizable by the turtle from far offshore or closer in.

Eggs are laid every 2 to 4 years, and females lay more than one clutch per season, perhaps up to five (Carr and Giovannoli 1957; Carr and Ogren 1960; Carr and Hirth 1962). Successive clutches are laid about 2 weeks apart. If a female nesting on Tortugero is disturbed by a light, person, or noise, she will return to the ocean and attempt to nest later. Between clutches, the females remain in the general area, resting and sleeping in crevices or caves in cliff bases or under rock ledges (Carr, Ross, and Carr 1974). It is thought that they feed little or not at all between successive nestings, since there is little marine vegetation near the nest site. Adults are mainly herbivorous, while the young are mainly carnivorous (Carr and Ogren 1960).

Clutch size at Tortugero is from 18 to 193 eggs ($\bar{x}$ = 100, 406 clutches), and the incubation period is about 2 months. Reports of hatching success are from 50% to 83%. About 50% of those emerging from nests reach the water. In 1977, about 50% of nests at Tortugero were destroyed by predators, mainly dogs, but also some coatis. Most young emerge at night when temperatures are most favorable, and those emerging during the day were eaten by vultures. Predation was greatest on nests farthest from the ocean, and beach erosion destroyed some nests nearer the water. The habit of long migration and nesting in remote areas may have evolved to lessen egg predation. Predation by dogs is a recent development but is potentially very harmful if allowed to continue (Carr and Giovannoli 1957; Carr and Ogren 1960; Carr and Hirth 1962; Carr, Ross, and Carr 1974; Fowler 1979).

The loggerhead turtle is very similar to the green turtle in its reproductive habits. Eggs are laid every 2 to 3 years, and up to four clutches are laid every 12 to 19 days within a season. Females return to the same beach to nest within and between seasons. Individuals lay 48 to 159 eggs per clutch ($\bar{x}$ = 100). If a female is interrupted during nesting, she will return on the same night or later to renest (Caldwell 1962; Kaufman 1971; Davis and Whiting 1977).

The hawksbill sea turtle is a circumtropical species that is associated with coral reefs and rocky shores. Carr, Hirth, and Ogren (1966) described nesting in Costa Rica. Hawksbills appear to nest earlier in the year than the green turtles. Also, in contrast to green turtles, which nest in concentrated colonies, hawksbill turtles, along with loggerhead and leatherback sea turtles, are usually solitary nesters. Nearly any tropical deep-sand beach free of human activity will be visited by nesting hawksbills (Carr, Hirth, and Ogren 1966). Formerly hawksbills were taken in larger numbers for the tortoise shell (*carey*), but the major threats now are meat and leather hunters and egg collectors.

Olive ridley sea turtles may nest singly, in small colonies, or in massive diurnal nestings, called *arribadas*, containing up to one hundred thousand females (Pritchard 1979). This behavior is restricted to a few beaches throughout the tropics, one of which is Santa Rosa National Park in Guanacaste Province, Costa Rica (Hughes and Richard 1974).

The leatherback turtle was studied at Tortuguero by Carr and Ogren (1959). They found that nesting females clustered in a small portion of the beach. Like the hawksbill, they nested before the green turtles that nested on the same beach. The general nesting pattern is similar to that of the green turtle. Four nests had between forty-five and eighty eggs with yolks.

Freshwater and Terrestrial Turtles

The aquatic tropical slider, *Chrysemys ornata*, has a wide distribution in a broad range of habitats in tropical America. In Central America they occupy lowland waters, usually in permanent freshwater, especially larger, slow-moving rivers or tributaries with much submerged vegetation. Other important features of this species' habitat are basking sites and scattered open areas in adjacent forest where eggs are laid. Moll and Legler (1971) have carried out on this species the most intensive investigation yet done on a tropical freshwater turtle. Their

Panamanian studies should be directly applicable to Costa Rica, and the following paragraphs summarize their findings.

Adult *C. ornata* remain in sections of the river with much floating vegetation such as *Elodea*. Juveniles and hatchlings are found in backwaters and quieter areas. The turtles sleep in the daytime in a customary place on the edges of the floating vegetation mats. The food of adults is mostly aquatic and semiaquatic plants, with some animal material (about 17% by volume). Juveniles take about 19% animal matter by volume. Feeding is underwater and appears to be opportunistic.

Eggs are laid from January to May, in the dry season when rivers are lower and less likely to flood nests. Females may lay up to five clutches per season, with the number of clutches proportional to the size of the female. Nesting occurs at night in open areas that are exposed to sunlight for part of each day. The home ranges of females are different areas than the nesting sites. Migration to the sites occurs early in the dry season. It is not known how females select an area in which to nest, since sites are as far as 400 m from water. Clutch size is from nine to twenty-five eggs ($\bar{x}$ = 17.4, from nineteen nests and nineteen dissections). The eggs hatch in May and June during the early rainy season, a pattern similar to that in other tropical reptiles. When the hatchlings are ready to emerge from the nest, the rain softens the nest plug, facilitating their exit. Food and cover are also more available at this time.

Predation on this species occurs mainly on eggs. A large proportion of nests are destroyed, principally by armadillos and the Panamanian teiid lizard *Ameiva ameiva*, but also by black rats, opossums, coatis, birds, dogs, swine, and humans. Fire ants prey on some hatchlings, and man is the greatest predator on adults. The female urinates on the completed nest, so the smell of the nest may be a means by which predators locate nests up to 2 to 3 days after oviposition.

The other emydid genus, *Rhinoclemys*, has three Costa Rican species. *Rhinoclemys funerea* is a larger (to 320 mm carapace length), flat, slider type of turtle found in wet Atlantic lowland rivers. Iverson (1975) describes the aquatic courtship of captives in Costa Rica, and Moll and Legler (1971) and Medem (1962) provide details of their life history. They leave the water to bask in the daytime and to feed at night. For this reason they are able to live in rivers without vegetation, unlike *C. ornata*. Their eggs are relatively large, with hard, brittle shells, and they are placed singly under leaf litter. No nest is dug, and they may breed at any time during the year (Medem 1962; Moll and Legler 1971; pers. obs.).

The other two species of *Rhinoclemys* are more terrestrial. A colorful red-striped form (*R. pulcherrima*) is found in the dry lowlands of Guanacaste Province in Costa Rica. During the wet season individuals can be found moving about in temporary marshes, fields, and woodlands. They disappear during the dry season (pers. obs.). Little else is known about their biology. The third Costa Rican species, *R. annulata*, is a terrestrial box-turtle-like species of the Atlantic lowlands. Mittermeir (1971) studied this species briefly in Panama. These turtles eat a wide variety of plant foods and apparently mate on land.

The family of mud turtles, Kinosternidae, is represented in Costa Rica by three species in the genus *Kinostetnon*. Some biological information is available for *K. leucostomum*, but we can assume that the other two species are similar. According to Moll and Legler (1971) and Medem (1962), this species is generally found in swamps, slow streams, and temporary ponds, although individuals may also travel overland. These turtles are omnivorous and, though aquatic snails often make up a large part of their diet, may feed on land (pers. obs.). One or two brittle eggs make up a clutch, which may be laid at any time. Eggs are placed under leaf litter or in shallow nests. *Kinosternon angustipons* differs in that it lays about four eggs per clutch (Legler 1966).

The life histories above demonstrate two reproductive patterns (Moll and Legler 1971). *Chrysemys ornata* exemplifies a generalized or north-temperate mode. This species has generally similar reproduction in temperate and tropical sites, with large clutches, relatively small egg size, seasonal egg production, several clutches per season, and a nest that is constructed in a particular habitat. This mode is successful in many habitats and is similar for most of the species in the family Emydidae. *Rhinoclemys* and *Kinosternon* have a more specialized or tropical mode of reproduction. The eggs are laid singly or in small clutches, are relatively large, and are produced continuously or nearly so, and there is no special nest construction or site. These features are adapted to a tropical climate, since reproduction is not limited to a few months of the year.

These two patterns can be viewed as different responses to selective pressure, perhaps predation. The small and scattered clutches laid by *Rhinoclemys* and *Kinosternon* may reduce the number of eggs destroyed by predators; the discovery of one egg would not mean the destruction of most of the offspring laid by a female. *Chrysemys* may avoid total loss of offspring by saturating an area with many nests containing large numbers of eggs (Moll and Legler 1971).

There are some differences between the tropical and temperate subspecies of *C. ornata*. Panamanian sliders produce larger eggs and larger and more clutches per season than does the temperate species *C. scripta*. This is a reversal of a trend common in many tropical vertebrates, including some birds, mammals, lizards, frogs, and other

turtles. The reproductive season is two months longer in Panama than in temperate areas. Females of this species are larger in the tropics than outside, and fecundity is probably greater (Moll and Legler 1971).

Crocodilians

The spectacled caiman continues to be common in parts of wet lowland Costa Rica. Its biology has not been studied in Costa Rica, but Staton and Dixon (1975, 1977) provide information about the Venezuelan llanos and Alvarez del Toro (1974) describes Mexican populations. Caiman biology does not differ markedly from the crocodilian norm. The female scrapes vegetation into a pile to make a nest in which she buries twenty to thirty eggs. She (and sometimes a male) usually tends the nest for the incubation period of about 73 days. One or both parents may help the hatching young get out of the nest and may guard them for an indefinite period. Of thirty-two nests observed by Staton and Dixon (1977), 9% hatched; the others were destroyed by humans, cows, flooding, and large tegu lizards (*Tupinambis teguixin*). All but the last factor may be important in Costa Rica.

Almost nothing is known about Costa Rican crocodiles except their distribution. Natural history observations by Alvarez del Toro (1974) in Mexico are probably applicable. *Crocodylus* makes a nest that differs from that of caimans. Usually the crocodile digs a hole in sandy soil and deposits the eggs. Then the nest is covered and the sand packed down much like a marine turtle's nest. The female parent often tends the nest and helps the young emerge.

The social behavior of crocodilians is often mediated by acoustical signals, a mode of communication that is lacking in most other reptiles. The significance of most signals is not well established. The most common and strongest response is that of adults to calls given by young (Campbell 1973; Alvarez del Toro 1974; Garrick and Lang 1977; Garrick, Lang, and Herzog 1978; Staton 1978).

The Conservation of Marine Turtles and Crocodilians

The marine turtles and crocodilians of Costa Rica are not the only reptiles that are exploited by man, but human impacts are greatest on their populations. It is probably safe to say that their numbers are continually declining owing to harvest of eggs and adults for food, shells or skins. The major green turtle nesting beaches and one of the olive ridley beaches are well protected by the national park system, but egg poaching remains the rule in other areas, and all species of marine turtles except leatherbacks are taken in the ocean. Up until about 15 years ago, the crocodile was the only object of hide exploitation, but recent developments in processing the skins of caimans and sea turtles have led to their harvest also. Crocodiles are scarce along both coasts, except for a healthy protected population in Corcovado National Park on the Osa Peninsula. Caiman are more common, but numbers have recently decreased markedly in areas near human habitation.

Many authors have written of the plight of the esteemed green turtle, but perhaps none so eloquently as Archie Carr (1967). His efforts, and those of his colleagues have stimulated international support for marine turtle conservation, and nowhere has the response been more effective than in Costa Rica. The famous nesting aggregations in Tortugero and Playa Nancite are protected, and public sentiment is turning against turtle exploitation in other parts of the country. Unfortunately, crocodiles are not as easy to love as sea turtles (even though both shed real tears), and the future of *Crocodylus* is much less secure. We may never again see the huge 4 m animals that used to terrify the *campesinos* and eat their dogs. However, a dim light may be on the horizon, as represented by newborn juveniles in the estuarine waters of Corcovado National Park and Santa Rosa National Park (D. H. Janzen, pers. comm.).

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Albuquerque, E. X.; Daly, J. W.; and Witkop, B. 1971. Batrachotoxin: Chemistry and pharmacology. *Science* 172:995–1002.

Alvarez del Toro, M. 1974. *Los crocodylia de México (estudio comparativo)*. México, D. F.: Instituto Mexicano Recursos Naturales Renovables, A.C.

Andrews, R. M. 1971. Structural habitat and time budget of a tropical *Anolis* lizard. *Ecology* 52:262–70.

———. 1979. The lizard *Corytophanes cristatus:* An extreme "sit-and-wait" predator. *Biotropica* 11:136–39.

Andrews, R. M., and Asato, T. 1977. Energy utilization of a tropical lizard. *Comp. Biochem. Physiol.* 58A: 57–62.

Avery, R. A. 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *J. Anim. Ecol.* 40: 351–65.

Ballinger, R. E.; Marion, K. R.; and Sexton, O. J. 1970. Thermal ecology of the lizard, *Anolis limifrons* with comparative notes on three additional Panamanian anoles. *Ecology* 51:246–54.

Bennett, A. F., and Dawson, W. R. 1976. Metabolism. In *Biology of the Reptilia*, vol. 5, ed. C. Gans. London: Academic Press.

Bennett, A. F., and Licht, P. 1972. Anaerobic metabolism during activity in lizards. *J. Comp. Physiol.* 81: 277–88.

Boulenger, G. A. 1913. On a collection of batrachians and reptiles made by Dr. H. G. F. Spurrell, F. Z. S., in the Choco, Colombia. *Proc. Zool. Soc. London* 1913: 1019–38.

Breder, C. M., Jr. 1946. Amphibians and reptiles of the Río Chucunaque drainage, Darien, Panamá, with notes on their life histories and habits. *Bull. Am. Mus. Nat. Hist.* 86:375–436.

Brodie, E. D., Jr. and Brodie E. D., III. 1980. Differential avoidance of mimetic salamanders by free-ranging birds. *Science* 208:181–82.

Bunnell, P. 1973. Vocalizations in the territorial behavior of the frog *Dendrobates pumilis*. *Copeia* 1973:277–84.

Caldwell, D. K. 1962. Comments on the nesting behavior of Atlantic loggerhead sea turtles, based primarily on tagging returns. *Quart. J. Florida Acad. Sci.* 25: 287–302.

Campbell, H. W. 1973. Observations on the acoustic behavior of crocodilians. *Zoologica* 58:1–11.

Carr, A. F. 1967. *So excellente a fishe*. New York: Natural History Press.

Carr, A.; Carr, M. H.; and Meglan, A. B. 1978. The ecology and migration of sea turtles. 7. The west Caribbean green turtle colony. *Bull. Am. Mus. Nat. Hist.* 162:1–46.

Carr, A. F., and Giovannoli, L. 1957. The ecology and migrations of sea turtles. 2. Results of field work in Costa Rica. *Am. Mus. Nov.* 1835:1–32.

Carr, A. F., and Hirth, H. 1962. The ecology and migrations of sea turtles. 5. Comparative features of isolated green turtle colonies. *Am. Mus. Nov.* 2091:1–42.

Carr, A. F.; Hirth, H.; and Ogren, L. 1966. The ecology and migrations of sea turtles. 6. The hawksbill turtle in the Caribbean Sea. *Am. Mus. Nov.* 2248:1–29.

Carr, A. F., and Ogren, L. 1959. The ecology and migrations of sea turtles. 3. *Dermochelys* in Costa Rica. *Am. Mus. Nov.* 1958:1–29.

———. 1960. The ecology and migrations of sea turtles. 4. The green turtle in the Caribbean Sea. *Bull. Am. Mus. Nat. Hist.* 121:1–48.

Carr, A. F.; Ross, P.; and Carr, S. 1974. Internesting behavior of the green turtle, *Chelonia mydas*, at a mid-ocean island breeding ground. *Copeia* 1974: 703–6.

Cott, H. B. 1940. *Adaptive coloration in animals*. London: Methuen.

Crump, M. L. 1972. Territoriality and mating behavior in *Dendrobates granuliferus* (Anura: Dendrobatidae). *Herpetologica* 28:195–98.

———. 1974. Reproductive strategies in a tropical anuran community. *Misc. Pub. Mus. Nat. Hist. Univ. Kansas* 61:1–68.

Crump, M. L., and Kaplan, R. H. 1979. Clutch energy partitioning of tropical tree frogs (Hylidae). *Copeia* 1979:626–35.

Daly, J. W., and Myers, C. W. 1967. Toxicity of Panamanian poison frogs (*Dendrobates*): Some biological and chemical aspects. *Science* 156:970–73.

Davis, G. E., and Whiting, M. C. 1977. Loggerhead sea turtle nesting in Everglades National Park, Florida, USA. *Herpetologica* 33:18–28.

Dixon, J. R., and Heyer, W. R. 1968. Anuran succession in a temporary pond in Colima, México. Bull. *Southern California Acad. Sci.* 67:129–37.

Duellman, W. E. 1960. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. *Pub. Mus. Nat. Hist. Univ. Kansas* 13:19–72.

———. 1963. A new species of tree frog, genus *Phyllomedusa*, from Costa Rica. *Rev. Biol. Trop.* 11:1–23.

———. 1966*a*. The Central American herpetofauna: An ecological perspective. *Copeia* 1966:700–719.

———. 1966*b*. Aggressive behavior in dendrobatid frogs. *Herpetologica* 22:217–21.

———. 1967. Social organization in the mating calls of some Neotropical anurans. *Am. Midl. Nat.* 77:156–63.

———. 1970. The hylid frogs of middle America. *Monogr. Mus. Nat. Hist. Univ. Kansas* 1:1–753.

———. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Misc. Pub. Mus. Nat. Hist. Univ. Kansas* 65:1–352.

Duellman, W. E., and Savitsky, A. H. 1976. Aggressive behavior in a centrolenid frog, with comments on territoriality in anurans. *Herpetologica* 32:401–4.

Duellman, W. E., and Trueb, L. 1966. Neotropical hylid frogs, genus *Smilisca*. *Pub. Mus. Nat. Hist. Univ. Kans.* 17:281–375.

Dunn, E. R. 1937. The amphibian and reptilian fauna of bromeliads in Costa Rica and Panamá. *Copeia* 1937: 163–67.

———. 1941. Notes on *Dendrobates auratus*. *Copeia* 1941:88–93.

Eaton, T. 1941. Notes on the life history of *Dendrobates auratus*. *Copeia* 1941:93–95.

Fleming, T. H., and Hooker, R. S. 1975. *Anolis cupreus:* The response of a lizard to tropical seasonality. *Ecology* 56:1243–61.

Fowler, L. E. 1979. Hatching success and nest predation in the green sea turtle, *Chelonia mydas*, at Tortugero, Costa Rica. *Ecology* 60:946–55.

Fuhrman, F. A.; Fuhrman, G. J.; and Mosher, H. S. 1969. Toxin from skin of frogs of the genus *Atelopus:* Differentiation from dendrobatid toxins. *Science* 165: 1376–77.

Garrick, L. D., and Lang, J. W. 1977. Social signals and behaviors of adult alligators and crocodiles. *Am. Zool.* 17:225–39.

Garrick, L. D.; Lang, J. W.; and Herzog, H. A., Jr. 1978. Social signals of adult American alligators. *Bull. Am. Mus. Nat. Hist.* 160:153–92.

Goodman, D. E. 1971*a*. Territorial behavior in a Neotropical frog, *Dendrobates granuliferus*. *Copeia* 1971: 365–70.

———. 1971*b*. Differential selection among immobile prey among terrestrial and riparian lizards. *Am. Midl. Nat.* 86:217–19.

Habermehl, G. G. 1974. Venoms of amphibia. In *Chemical zoology*, vol. 9, *Amphibia and reptilia*, ed. M. Florkin and B. T. Scheer. New York: Academic Press.

Heyer, W. R. 1969. The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution* 23:421–28.

———. 1970. Studies on the genus *Leptodactylus* (Amphibia: Leptodactylidae). II. Diagnosis and distribution of the *Leptodactylus* of Costa Rica. *Rev. Biol. Trop.* 16:171–205.

———. 1976. Studies in larval amphibian habitat partitioning. *Smithsonian Contrib. Zool.* 242:1–27.

Heyer, W. R.; McDiarmid, R. W.; and Weigmann, D. L. 1975. Tadpoles, predation, and pond habitats in the tropics. *Biotropica* 7:100–111.

Heyer, W. R., and Rand, A. S. 1977. Foam nest construction in the leptodactylid frogs *Leptodactylus pentadactylus* and *Physalaemus pustulosus* (Amphibia, Anura, Leptodactylidae). *J. Herp.* 11:222–25.

Hillman, P. E. 1969. Habitat specificity in three sympatric species of *Ameiva* (Reptilia: Teiidae). *Ecology* 50:476–81.

Houck, L. D. 1977. Life history patterns and reproductive biology of Neotropical salamanders. In *The reproductive biology of amphibians*, ed. D. H. Taylor and S. I. Guttman. New York: Plenum Press.

Hughes, D. A., and Richard, J. D. 1974. The nesting of the Pacific ridley *Lepidochelys olivacea* on Playa Nancite, Costa Rica. *Marine Biol.* 24:97–107.

Inger, R. F. 1962. On the terrestrial origin of frogs. *Copeia* 1962:835–36.

Iverson, J. B. 1975. Notes on courtship in *Rhinoclemys funerea*. *J. Herp.* 9:249–50.

Janzen, D. H. 1962. Injury caused by toxic secretions of *Phrynohyas spilomma* Cope. *Copeia* 1962:651.

Janzen, D. H., and Schoener, T. W. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49: 96–110.

Kaufman, R. 1971. Studies on the loggerhead sea turtle, *Caretta caretta caretta* (Linné) in Colombia, South America. *Herpetologica* 31:323–26.

Kitasako, J. T. 1967. Observations on the biology of *Dendrobates pumilio* Schmidt and *Dendrobates auratus* Girard. M.S. thesis, University of Southern California, Los Angeles.

Krakauer, T. 1968. The ecology of the Neotropical toad, *Bufo marinus*, in south Florida. *Herpetologica* 24: 214–21.

Legler, J. M. 1966. Notes on the natural history of a rare Central American turtle, *Kinosternon angustipons* Legler. *Herpetologica* 22:118–22.

Licht, L. E. 1967. Death following possible ingestion of toad eggs. *Toxicon* 5:141–42.

———. 1968. Unpalatability and toxicity of toad eggs. *Herpetologica* 24:93–98.

———. 1969. Palatability of Rana and Hyla eggs. Am. *Midl. Nat.* 82:296–98.

Licht, L. E., and Low, B. 1968. Cardiac response of snakes after ingestion of toad parotoid venom. *Copeia* 1968:547–51.

Limerick, S. 1980. Courtship and oviposition in the poison-arrow frog, *Dendrobates pumilio*. *Herpetologica* 35:69–71.

Lutz, B. 1948. Ontogenetic evolution in frogs. *Evolution* 2:29–39.

Lynn, W. C. 1942. The embryology of *Eleutherodactylus nubicola*, an anuran which has no tadpole stage. *Pub. Carnegie Inst. Washington* 541:27–62.

McDiarmid, R. W. 1971. Comparative morphology and evolution of frogs of the Neotropical genera *Atelopus*, *Dendrophryniseus*, *Melanophryniscus*, and *Oreophrynella*. *Sci. Bull Los Angeles County Mus. Nat. Hist.* 12:1–66.

———. 1975. Glass frog romance along a tropical stream. *Terra, Los Angeles County Mus.* 13:14–18.

———. 1978. Evolution of parental care in frogs. In *The development of behavior: Comparative and evolutionary aspects*, ed. G. M. Burghardt and M. Bekoff. New York: Garland STPM Press.

McDiarmid, R. W., and Adler, K. 1974. Notes on territorial and vocal behavior of Neotropical frogs of the genus *Centrolenella*. *Herpetologica* 30:75–78.

Medem, F. 1962. La distribución geográfica y ecología de los Crocodylia y Testudinata en el Departamento del Chocó. *Rev. Acad. Colombia Cienc. Exactas Fis. Nat.* 11:279–303.

Mittermeir, R. A. 1971. Notes on the behavior and ecology of *Rhinoclemys annulata* Gray. *Herpetologica* 27: 485–88.

Moll, E. O., and Legler, J. M. 1971. The life history of a Neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. *Sci. Bull. Los Angeles County Mus. Nat. Hist.* 11:1–102.

Montanucci, R. R. 1968. Comparative dentition in four iguanid lizards. *Herpetologica* 24:305–15.

Myers, C. W.; Daly, J. W.; and Malkin, B. 1978. A dangerously toxic new frog (*Phyllobates*) used by Emberá Indians of western Colombia, with discussion of blowgun fabrication and dart poisoning. *Bull. Am. Mus. Nat. Hist.* 161:307–66.

Nelson, C. E. 1972. Systematic studies of the North American microhylid genus *Gastrophryne J. Herp.* 6:111–37.

Novak, R. M., and Robinson, D. C. 1975. Observations on the reproduction and ecology of the tropical montane toad, *Bufo holdridgei* Taylor in Costa Rica. *Rev. Biol. Trop.* 23:213–37.

Pianka, E. R. 1966. Convesity, desert lizards, and spatial heterogeneity. *Ecology* 47:1055–59.

Pough, F. H. 1973. Lizard energetics and diet. *Ecology* 54:836–44.

Pritchard, P. C. H. 1979. Taxonomy, evolution and zoogeography. In *Turtles: Perspectives and research*, ed. M. Harless and H. Morlock. New York: Wiley.

Pyburn, W. F. 1963. Observations on the life history of the treefrog, *Phyllomedusa callidryas* (Cope). *Texas J. Sci.* 15:155–70.

———. 1964. Breeding behavior of the leaf frog, *Phyllomedusa callidryas*, in southern Veracruz. *Year. Am. Phil. Soc.* 1964:291–94.

———. 1967. Breeding and larval development of the hylid frog *Phrynohyas spilomma* in southern Veracruz, México. *Herpetologica* 23:184–94.

———. 1970. Breeding behavior of the leaf-frogs *Phyllomedusa callidryas* and *Phyllomedusa dacnicolor* in México. *Copeia* 1970:209–18.

Rand, A. S. 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. *Proc. U.S. Nat. Mus.* 122:1–77.

Ream, C. 1965. Notes on the behavior and egg laying of *Corythopanes cristatus*. *Herpetologica* 20:239–42.

Rivero, J. A., and Esteves, A. E., 1969. Observations of the agonistic and breeding behavior of *Leptodactylus pentadactylus* and other amphibian species in Venezuela. *Breviora* 321:1–14.

Robinson, D. C. 1961. The identity of the tadpole of *Anotheca coronata* (Stejneger). *Copeia* 1961:495.

———. 1977. Herpetofauna bromelicola Costarricense y renacuajos de *Hyla picadoi* Dunn. In *Historia natural de Costa Rica*, ed. L. D. Gomez, San José: Museo Nacional de Costa Rica.

Salthe, S. N. 1969. Reproductive modes and the numbers and sizes of ova in the urodeles. *Am. Midl. Nat.* 81:467–90.

Salthe, S. N., and Duellman, W. E. 1973. Quantitative constraints associated with reproductive mode in anurans. In *Evolutionary biology of the anurans*, ed. J. L. Vial. Saint Louis: University of Missouri Press.

Salthe, S. N., and Mecham, J. S. 1974. Reproductive and courtship patterns. In *Physiology of the amphibia*, ed. B. Lofts, vol. 2. New York: Academic Press.

Savage, J. M. 1966. The origins and history of the Central American herpetofauna. *Copeia* 1966:719–60.

———. 1968. The dendrobatid frogs of Central America. *Copeia* 1968:745–76.

———. 1980. The tadpole of the Costa Rican fringe-limbed tree-frog, *Hyla fimbrimembra*. *Proc. Biol. Soc. Wash.* 93:1177–83.

Savage, J. M., and Heyer, W. R. 1969. The tree-frogs (family Hylidae) of Costa Rica: Diagnosis and distribution. *Rev. Biol. Trop.* 16:1–127.

Schoener, T. W. 1968. The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology* 49:704–26.

Scott, N. J. 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* 8: 41–58.

Scott, N. J., Jr., and Starrett, A. 1974. An unusual breeding aggregation of frogs, with notes on the ecology of *Agalychnis spurrelli* (Anura: Hylidae). *Bull. Southern California Acad. Sci.* 73:86–94.

Scott, N. J., Jr.; Wilson, D. E.; Jones, C.; and Andrews, R. M. 1976. The choice of perch dimensions by lizards of the genus *Anolis* (Reptilia, Lacertilia, Iguanidae). *J. Herp.* 10:75–84.

Sexton, O. 1958. Observations on the life history of a Venezuelan frog, *Atelopus cruciger*. *Acta Biol. Venezuela* 2:235–42.

———. 1962. Apparent territorialism in *Leptodactylus insularum* Barbour. *Herpetologica* 18:212–14.

Sexton, O. J.; Bauman, J.; and Ortleb, E. 1972. Seasonal food habits of *Anolis limifrons*. *Ecology* 53: 182–86.

Sexton, O. J., and Ortleb, E. P. 1966. Some cues used by the leptodactylid frog, *Engystomops pustulosus*, in selection of the oviposition site. *Copeia* 1966:225–30.

Silverstone, P. A. 1975. A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. *Sci. Bull. Los Angeles County Mus. Nat. Hist.* 21:1–55.

———. 1976. A revision of the poison-arrow frogs of the genus *Phyllobates* Bibron in Sagra (family Dendrobatidae). *Sci. Bull. Los Angeles County Mus. Nat. Hist.* 27:1–53.

Smith, H. M., and White, F. N. 1955. Adrenal enlargement and its significance in the hognose snakes (*Heterodon*). *Herpetologica* 11:137–44.

Stamps, J. A. 1977. The relationship between resource partitioning, risk, and aggression in a tropical territorial lizard. *Ecology* 53:349–58.

Starrett, P. 1960. Descriptions of tadpoles of middle American frogs. *Misc. Pub. Mus. Zool. Univ. Michigan* 110:1–37.

———. 1967. Observations on the life history of frogs of the family Atelopodidae. *Herpetologica* 23: 195–204.

———. 1973. Evolutionary patterns in larval morphology. In *Evolutionary biology of the anurans: Contemporary research on major problems*, ed. J. L. Vial. Saint Louis: University of Missouri Press.

Staton, M. A. 1978. "Distress calls" of crocodilians—whom do they benefit? *Am. Nat.* 112:327–32.

Staton, M. A., and Dixon, J. R. 1975. Studies on the dry season biology of *Caiman crocodilus* from the Venezuelan llanos. *Mem. Soc. Cienc. Nat. La Salle* 35:237–65.

———. 1977. Breeding biology of the spectacled caiman, *Caiman crocodilus crocodilus*, in the Venezuelan llanos. *U.S. Fish Wildl. Serv. Wildl. Res. Rep.* 5:1–21.

Stuart, L. C. 1935. A contribution to a knowledge of the herpetology of a portion of the savannah region of central Petén, Guatemala. *Misc. Pub. Mus. Zool. Univ. Michigan* 29:1–56.

———. 1961. Some observations on the natural history of tadpoles of *Rhinophrynus dorsalis* Dumeril and Bibron. *Herpetologica* 17:73–79.

Taylor, E. H. 1942. Tadpoles of Mexican anura. *Univ. Kansas Sci. Bull.* 28:37–55.

———. 1952. A review of the frogs and toads of Costa Rica. *Univ. Kansas Sci. Bull.* 35:577–942.

———. 1954. Frog-egg-eating tadpoles of *Anotheca coronata* (Stejneger) (Satientia, Hylidae). *Univ. Kansas Sci. Bull.* 36:589–95.

———. 1956. A review of the lizards of Costa Rica. *Univ. Kansas Sci. Bull.* 38:3–322.

Trueb, L. 1968. Variation in the tree frog *Hyla lancasteri*. *Copeia* 1968:285–99.

VanDevender, R. W. 1978. Growth ecology of a tropical lizard, *Basiliscus basiliscus*. *Ecology* 59:1031–38.

Vial, J. L. 1968. The ecology of the tropical salamander. *Bolitoglossa subpalmata*, in Costa Rica. Rev. Biol. Trop. 15:13–115.

Villa, J. 1967. Comportamiento defensivo de la "rana tenero," *Leptodactylus pentadactylus*. *Rev. Biol. Trop.* 15:323–29.

———. 1972. *Anfibios de Nicaragua*. Managna: Instituto Geográfico Nacional, Banco Central de Nicaragua.

Vinton, K. W. 1951. Observations on the life history of *Leptodactylus pentadactylus*. *Herpetologica* 7:73–75.

Wake, D. B., and Lynch, J. F. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. *Sci. Bull. Los Angeles County Nat. Hist. Mus.* 25:1–65.

Wake, M. H. 1977. The reproductive biology of caecilians: An evolutionary perspective. In *The reproductive biology of amphibians*, ed. D. H. Taylor and S. I. Guttman. New York: Plenum Press.

Wassersug, R. 1971. On the comparative palatability of some dry season tadpoles from Costa Rica. *Am. Midl. Nat.* 86:101–9.

———. 1973. Aspects of social behavior in anuran larvae. In *Evolutionary biology of the anurans: Contemporary research on major problems*, ed. J. L. Vial. Saint Louis: University of Missouri Press.

Wells, K. D. 1977*a*. The courtship of frogs. In *The reproductive biology of amphibians*, ed. D. H. Taylor and S. I. Guttman. New York: Plenum Press.

———. 1977*b*. The social behavior of anuran amphibians. *Anim. Behav.* 25:666–93.

———. 1978. Courtship and parental behavior in a Panamanian poison-arrow frog (*Dendrobates auratus*). *Herpetologica* 34:148–55.

Young, A. M. 1979. Arboreal movement and tadpole-carrying behavior of *Dendrobates pumilio* Schmidt (Dendrobatidae) in northeastern Costa Rica. *Biotropica* 11:238–39.

Zug, G. R., and Zug, P. B. 1979. The marine toad, *Bufo marinus:* A natural history resumé of native populations. *Smithsonian Contrib. Zool.* 284:1–58.

Zweifel, R. G. 1964*a*. Life history of *Phrynohyas venulosa* (Salientia: Hylidae) in Panamá. *Copeia* 1964: 201–8.

———. 1964*b*. Distribution and life history of a Central American frog, *Rana vibicaria*. *Copeia* 1964: 300–308.

CHECKLIST OF REPTILES AND AMPHIBIANS

N. J. Scott, J. M. Savage, and D. C. Robinson

Taxon	La Selva	Osa	Cañas, Taboga	San José	Las Cruces	Cerro
Amphibia						
Gymnophiona						
Caecilidae						
Dermophis mexicanus				X		
D. parviceps		X		X	X	X
Gymnopis multiplicata	X		X			
Caudata						
Plethodontidae						
Bolitoglossa alvaradoi						
B. arborescandens						
B. cerroensis						X
B. colonnea	X	X		X		
B. epimela						
B. lignicolor		X				
B. robusta						
B. sooyorum						X
B. striatula						
B. subpalmata						X
B. sp. 1						
B. sp. 2						
Chiropterotriton diminuta						
C. picadoi				X		