Chapter 2

Amphibian Diversity and Natural History: An Overview

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Introduction

Few vertebrates are as dependent on environmental moisture as amphibians, whose geographic ranges, ecologies, behaviors, and life histories are strongly influenced by the distribution and abundance of water, usually in the form of rain. In fact, the abrupt and often synchronized breeding of many species of frogs with the first rains is a well-known natural phenomenon, especially in areas where rainfall is distinctly seasonal. Likewise, the annual breeding migrations of certain north temperate salamander and frog species to traditionally used vernal ponds are closely linked to melting ice, rising temperatures, and warm spring rains. In contrast, how rainfall, humidity, phases of the moon, and a multitude of other ecological factors interact to affect amphibian activity in tropical wet forests is not well understood. Just when a researcher thinks that he or she knows the "typical" situation, something unusual or unexpected happens. In fact, in some complex assemblages of tropical frogs, the normal pattern may best be described as chaotic or unpredictable. The complex and often poorly understood relation between the behavior and ecology of amphibians and local weather patterns makes designing a sampling protocol for amphibians difficult. This complicated interdependency is something that users of this book need to keep in mind. The three orders of living amphibians—caecilians (Gymnophiona), salamanders (Caudata), and frogs (Anura)—are found in a variety of freshwater aquatic and terrestrial environments throughout the world (Table 1). Whether in shallow seeps on steep slopes or buried in decaying organic material at the bottom of bogs, in deep leaf litter in tropical evergreen rain forest or in bromeliads high in the forest canopy, amphibians occur in nearly every kind of terrestrial and freshwater habitat.

Most species have a biphasic, complex life cycle (Fig. 1). In response to certain environmental cues (e.g., first rain of the season), terrestrial adults typically move to suitable aquatic habitats to breed. Following some form of courtship, adults of oviparous species deposit eggs in or near the water. These eggs hatch into free-swimming larvae that are major consumers in aquatic environments. After a period of growth, larvae undergo metamorphosis and move back into the terrestrial environment where they feed and continue to grow. When mature, they return to the aquatic environment to breed, thereby completing the life cycle.

Other species undergo direct development, that is, they lack an independent larval stage. Their eggs hatch into nonfeeding larvae or small copies of adults. A few forms are ovoviviparous or viviparous.

An understanding of the distributions and life histories of the species under study and knowledge of the habitats in which the organisms occur are essential to project design and to selection of suitable sampling methods. Such information also enhances the effectiveness of sampling and, thereby, the accuracy with which amphibian species richness and abundance can be estimated. In the following pages I briefly discuss pertinent aspects of the life histories of living amphibians and summarize the basic habitats used by different groups. I also provide an overview of the amphibian groups likely to be encountered on each continent and their respective habitats (Table 1). Once the goals of a biodiversity project have been defined (Chapter 3), data in the table should aid in the selection of suitable inventory techniques.

Consider, for example, a study of frog diversity at a lowland rain forest site in South America. Only 3 of approximately 10 families in the region have aquatic adults, and 2 of these families (Pipidae and Pseudidae) include very few species. Thus, aquatic sampling should have low priority if adults are the target stage. However, if an investigator were to inventory both adults and larvae, then aquatic sampling would be appropriate. Nearly all families have aquatic larvae, and sampling for larvae might turn up purely aquatic adults as well. On the other hand, adults of some species in 6 families potentially in the area are arboreal, and several of these families have high species diversity. A check of the literature would show that adults of nearly all species in 1 of the families (Centrolenidae) are arboreal, but only in streamside vegetation, and that adults of many species of 2 other families (Hylidae and Leptodactylidae, especially species in the large genus *Eleutherodactylus*) occur above ground, but only in forest. Thus, the study design should stress techniques for sampling arboreal habitats, but it would also have to specify transects across or along streams and transects in the forest.

In most instances, researchers will be better prepared to initiate studies if they first read about the general ecology and life history of amphibians likely to be found in the area and consult original literature on specific groups. Excellent summaries of pertinent information can be found in general references (e.g., Duellman and Trueb 1986; Tyler 1989) or in geographically oriented publications (e.g., Africa—Schiøtz 1975; Passmore and Carruthers 1979; Lambiris 1988, 1989; Madagascar—Blommers-Schlösser and Blanc 1991; Europe—Arnold and Burton 1978; Engelmann et al. 1986; Asia—Berry 1975; Inger and Stuebing 1989; Maeda and Matsui 1989; Australia—Cogger 1983; Tyler and Davies 1986; North America—Stebbins 1985; Pfingsten and Downs 1989; Conant and Collins 1991; Middle America—Duellman 1970; Villa

1972; South America—Duellman 1978; Cei 1980; Heyer et al. 1990).

Order Gymnophiona (caecilians)

Caecilians are elongate, limbless amphibians; they lack tails or have short ones. They are pantropical and occur in mesic, forested areas in all parts of the world except Madagascar and the Australopapuan region. Living caecilians are grouped into 6 families and 36 genera; about 165 species are recognized (Frost 1985, updated through 1992 by Frost and McDiarmid, unpubl. data).

Caecilians are difficult to sample because they are aquatic or fossorial and are rarely observed. Because of their secretive habits, we know little about their ecology or life history. Male caecilians have a median, protrusible copulatory organ, and fertilization presumably is internal in all species. Most caecilians are viviparous, although a few are oviparous; some have aquatic larvae, which live in ponds or streams.

There are no widely known techniques for sampling caecilians. However, methods for capturing aquatic frogs, salamanders, and their larvae may be useful (Chapter 6). Aquatic species may be removed with a dipnet from deeper parts of fast-flowing creeks at mid-elevations or found in leaf mats and shallows of meandering lowland streams. Fossorial species may be encountered in soil beneath piles of rotting plant materials, in loose soil and fine gravel along streams, and beneath logs. Individuals occasionally are captured in ditches or on roads, trails, or the forest floor after torrential rains.

Order Caudata (salamanders)

Adult salamanders are terrestrial, aquatic, fossorial, or arboreal amphibians with four legs (no hind limbs in sirenids) and a moderate to long tail. Most groups are prevalent in the Holarctic region, but a major radiation of plethodontid salamanders with direct development has evolved in the New World tropics. Living salamanders are assigned to 10 families, 61 genera, and about 390 species (Frost 1985, updated through 1992 by Frost and McDiarmid, unpubl. data). Salamanders have a variety of courtship patterns and an equally diverse array of reproductive modes. Visual and chemical signals seem to be more important for courtship in salamanders than in frogs. Most salamanders have internal fertilization without copulation, but a few large aquatic species have external fertilization. Eggs of aquatic species are laid singly, in strings, or in clumps in ponds or streams, sometimes beneath stones or attached to vegetation. These species have aquatic larvae that typically metamorphose and move to a terrestrial environment where they feed, grow, and mature. As adults, in response to pertinent environmental cues, they return to aquatic environments, often their natal sites, and reproduce. Some species are permanently aquatic, and larval metamorphosis is incomplete (obligate paedomorphs). Others are facultative paedomorphs and occasionally reproduce while retaining certain larval traits. Many species (most plethodontids) are terrestrial, deposit clumps of eggs in moist sites in burrows, in leaf litter, or beneath rocks and logs, and have direct development; in many of these species the female parent attends the clutch. A few species of salamandrids are ovoviviparous or viviparous, producing live aquatic larvae or fully developed (metamorphosed) young.

Salamanders are primarily nocturnal and have activity patterns that may vary ontogenetically. Individuals may be clumped or dispersed within a habitat, and spatial distributions often vary with sex and reproductive status. Some common temperate species have a synchronous migration from terrestrial habitats to aquatic sites for reproduction. Because of their abundance and position in the food web, in certain habitats salamanders may be the most important vertebrate organism. For ex-

Table 1. Habitat Utilization by Amphibians[a]

	North America[c]					Middle America[d]					South America[e]				
Taxon[b]	*Aq*	*Se*	*Te*	*Fo*	*Ar*[j]	*Aq*	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*
CAECILIANS (Gymnophiona)															
Caeciliidae			—						A[k]					A	
(24 genera, 89 sp.)									V					V	
Epicriidae			—					—					—		
(2 genera, 36 sp.)															
Rhinatremidae			—					—			A			A	
(2 genera, 9 sp.)											L	E			
Scolecomorphidae			—					—					—		
(2 genera, 5 sp.)															
Typhlonectidae			—					—			A				
(5 genera, 22 sp.)											V				
Uraeotyphlidae			—					—					—		
(1 genera, 4 sp.)															
SALAMANDERS (Caudata)															
Ambystomatidae	A		A			A		A					—		
(2 genera, 33 sp.)	L					L									
Amphiumidae	A							—					—		
(1 genus, 3 sp.)	L	E													
Cryptobranchidae	A							—					—		
(2 genera, 3 sp.)	L														
Dicamptodontidae	A		A					—					—		
(1 gen, 4 sp.)	L														
Hynobiidae			—					—					—		
(10 genera, 35 sp.)															
Plethodontidae	A	A	A	A				A	A	A			A	A	A
(27 genera, 244 sp.)	L	E	D	D				D	D	D			D		
Proteidae	A							—					—		
(2 genera, 6 sp.)	L														
Rhyacotritonidae		A						—					—		
(1 genus, 4 sp.)	L														
Salamandridae	A	A	A				A						—		
(13 genera, 55 sp.)	L					L									
Sirenidae	A							—					—		
(2 genera, 3 sp.)	L														
FROGS (Anura)															
Allophrynidae			—					—							A
(1 genus, 1 sp.)											L?				
Arthroleptidae			—					—					—		
(7 genera, 73 sp.)															
Ascaphidae		A						—					—		
(1 genus, 1 sp.)	L														

Europe[f]					Africa[g]					Asia[h]					Australia[i]				
Aq	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*
		—					A	A					A D				—		
		—					—			 L	A E		A				—		
		—					—					—					—		
		—						A D				—					—		
		—					—					—					—		
		—					—						A D?				—		
		—					—					—					—		
		—					—					—					—		
		—					—			A L							—		
		—					—					—					—		
		—					—			A L	A	A					—		
		A D					—					—					—		
A L							—					—					—		
		—					—					—					—		
A L	A	A V			A L		A V			A L	A	A V					—		
		—					—					—					—		
		—					—					—					—		
		—			A L	A	A D					—					—		
		—					—					—					—		

(*Continued*)

Table 1. (*Continued*)

	North America[c]					Middle America[d]					South America[e]				
Taxon[b]	*Aq*	*Se*	*Te*	*Fo*	*Ar*[j]	*Aq*	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*
Brachycephalidae			—					—					A		
(2 genera, 3 sp.)													D?		
Bufonidae			A					A	A				A	A	A
(31 genera, 356 sp.)	L					L		D?			L		D		L
Centrolenidae			—							A					A
(3 genera, 88 sp.)						L				E	L				E
Dendrobatidae			—					A		A		A	A		A
(6 genera, 148 sp.)						L		E		L	L		ED		L
Discoglossidae			—					—					—		
(4 genera, 15 sp.)															
Heleophrynidae			—					—					—		
(1 genus, 5 sp.)															
Hemisotidae			—					—					—		
(1 genus, 8 sp.)															
Hylidae		A	A	A	A		A	A	A	A		A	A		A
(39 genera, 686 sp.)	L					L		B		BL	L		B		BL
Hyperoliidae			—					—					—		
(19 genera, 227 sp.)															
Leiopelmatidae			—					—					—		
(1 genus, 3 sp.)															
Leptodactylidae			A				A	A	A	A	A	A	A	A	A
(50 genera, 813 sp.)	L	E	D			L	E	D	D	DV	L	L	DLN	LN	DL
Microhylidae			A	A				A	A				A	A	
(66 genera, 308 sp.)	L					L					L	E	DN	N	
Myobatrachidae			—					—					—		
(20 genera, 114 sp.)															
Pelobatidae				A					A				—		
(11 genera, 89 sp.)	L					L									
Pelodytidae			—					—					—		
(1 genus, 2 sp.)															
Pipidae			—			A					A				
(5 genera, 27 sp.)						L					BL				
Pseudidae			—					—			A				
(2 genera, 4 sp.)											L				
Ranidae		A	A			A	A	A				A			
(48 genera, 669 sp.)	L					L					L				
Rhacophoridae			—					—					—		
(10 genera, 197 sp.)															
Rhinodermatidae			—					—					A		
(1 genus, 2 sp.)											L		NB		
Rhinophrynidae				A					A				—		
(1 genus, 1 sp.)	L					L									

Europe[f]					Africa[g]					Asia[h]					Australia[i]				
Aq	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*
		—					—					—					—		
		A					A		A		A	A		A			—		
L					L	L	NV			L				N					
		—					—					—					—		
		—					—					—					—		
	A	A	A			A	A			A	A						—		
L		B	B		L		B			L?									
		—				A						—					—		
					L														
		—						A				—					—		
					L			E											
				A					A					A		A	A	A	A
L					L					L					L				
		—					A	A	A			—					—		
					L		E	E	E										
		—					—					—				A	A		
																N	N		
		—					—					—					—		
		—					A	A	A		A	A	A	A		A	A	A	A
					L			D	L	L	N?					D?	D	D	D
		—					—					—			A	A	A	A	
															BL		BLD	D	
			A					A			A	A					—		
L					L					L									
		A					—					—					—		
L																			
		—			A							—					—		
					L														
		—					—					—					—		
	A	A				A	A	A	A		A	A	A	A		A	A		A
L					L		DN		DE	L		DL		DL	L		D		
		—					A		A		A			A			—		
					L				E	L	E	E		DEL					
		—					—					—					—		
		—					—					—					—		

(*Continued*)

Table 1. (*Continued*)

	North America[c]					Middle America[d]					South America[e]				
Taxon[b]	*Aq*	*Se*	*Te*	*Fo*	*Ar*[f]	*Aq*	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*
Sooglossidae (2 genera, 3 sp.)			—					—					—		

[a] Only naturally occurring species are scored. Generally a species is scored only once and is assigned to the habitat that most typifies the life history stage; exceptions are salamanders that have populations that are facultatively neotenic and populations that regularly undergo metamorphosis. A dash signifies that the taxon does not occur on the continent indicated.

[b] Family designations and the numbers of genera and species follow Frost (1985) as updated to 1992 (Frost and McDiarmid, unpubl. data).

[c] Includes the United States and Canada.

[d] Includes Mexico, Central America, and the Caribbean.

[e] Includes Trinidad.

[f] Includes the area west of 36° E (see Arnold and Burton 1978).

ample, in a northern hardwood forest in New Hampshire the eastern red-backed salamander (*Plethodon cinereus*) exists in densities approaching 2,500 per hectare and converts energy into new tissue at about 5,000/kcal/ha/yr. Its standing crop biomass of about 1,650 g/ha is about 2.6 times the biomass of birds in the area at the peak of their breeding season, and about equal to that of the shrews and mice (Burton and Likens 1975). In contrast, certain tropical arboreal salamanders are encountered only rarely, when bromeliads are removed from trees and systematically searched. Unfortunately, this sampling method also destroys their habitats.

The diversity of salamander life histories, behaviors, and habitat preferences necessitates a diversity of methods for sampling populations and estimating their sizes. Fortunately, salamanders are reasonably well known and, except for some tropical species, easily sampled.

Order Anura (frogs)

Frogs are jumping amphibians with elongate hind limbs and no tails (all larval anurans and male *Ascaphus truei* have tails). They are the most diverse and abundant group of living amphibians, are cosmopolitan in distribution, and occur in essentially all terrestrial and freshwater habitats. Their species diversity is highest in tropical wet forests. Taxonomically, living frogs are distributed among 25 families; currently about 333 genera and 3,843 species are recognized (Frost 1985, updated through 1992 by Frost and McDiarmid, unpubl. data). Frogs may be aquatic, terrestrial, fossorial, arboreal, or some combination thereof. Some are diurnal, but most are nocturnal. Adults of most species are widely dispersed in the environment except at specific times of the year when they congregate at aquatic sites to breed.

Vocalization is an important component of the reproductive behavior of most frogs. Among terrestrial vertebrates (perhaps all vertebrates), frogs have the highest diversity of reproductive behaviors and parental care known. Breeding may be explosive (synchronous over one or a few days at aquatic sites) or prolonged (spread over a few weeks or months at aquatic or terrestrial sites) [Wells 1977]. Most species breed only once each year, but certain tropical forms

Europe[f]					Africa[g]					Asia[h]					Australia[i]				
Aq	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*	*Aq*	*Se*	*Te*	*Fo*	*Ar*
		—					A					—					—		
							BD												

[g] Includes Madagascar and the Seychelles.

[h] Includes the area east of Europe to Wallace's line.

[i] Includes all areas east of Wallace's line, including New Guinea, New Zealand, and certain Pacific Island groups.

[j] Habitats: *Aq* = aquatic; *Se* = semiaquatic; *Te* = terrestrial; *Fo* = fossorial; *Ar* = arboreal.

[k] Life history stages and developmental modes: A = adults; E = eggs; L = larvae; D = direct development; N = nidicolous larvae (nidicolous endotrophs of Altig and Johnston 1989); V = live birth, ovoviviparous or viviparous species; B = "brooded" eggs and/or larvae (attached to or in some modified structure [e.g., pouch] of adult), equal to paraviviparous and exoviviparous endotrophs of Altig and Johnston (1989). L in one habitat with no E in another habitat indicates a species that places eggs in the same habitat in which the larvae occur; an E in the arboreal habitat and L in the aquatic habitat, for example, indicate a species whose eggs are placed on leaves and whose tadpoles, on hatching, drop into water to feed. D? or L? indicates the habitat in which eggs with direct development or eggs and larvae presumably are placed, but data are lacking.

are reported to breed throughout the year whenever conditions are favorable. Most frogs have external fertilization, aquatic eggs, and feeding larvae called tadpoles; a major reorganization of the tadpole during metamorphosis distinguishes frogs from most other amphibians.

Females of a few species deposit eggs in leaf litter or wet moss; the eggs hatch into nonfeeding larvae that undergo metamorphosis at the nest site. Adults of other species carry strings of eggs wrapped around their hind legs or transport tadpoles from terrestrial sites to aquatic sites on their backs. In a few species, females place tadpoles in water held in bromeliads and then return to feed the larvae with nonfertile eggs that they deposit. Many species, especially in the Neotropics, have direct development (no free-swimming larval stage). These species deposit eggs in moist terrestrial or arboreal sites; after an appropriate period, the eggs hatch into small copies of the adult. Some frogs brood eggs on their backs; others brood eggs or tadpoles in pouches on their backs or sides, in vocal pouches, or even in their stomachs. Some of these brooding species have typical aquatic larvae, but most exhibit direct development. Almost every reproductive mode, including nonplacental viviparity and ovoviviparity, occurs in frogs.

The high species diversity of frogs, their variety of life history modes, and the wide assortment of habitats they use pose a substantial challenge to the researcher interested in sampling these organisms. Fortunately, the aquatic breeding behavior of most species, the pervasiveness of the aquatic larval stage, and the species specificity of reproductive vocalizations allow for effective sampling methods.

Amphibian larvae

Most amphibian larvae occur in aquatic habitats, including moving water (streams and rivers), still water (ponds and lakes), and phytotelmata (tree holes, plant axils and stems, bromeliads, and so forth). Terrestrial larvae develop in moist microhabitats such as moss, under and within

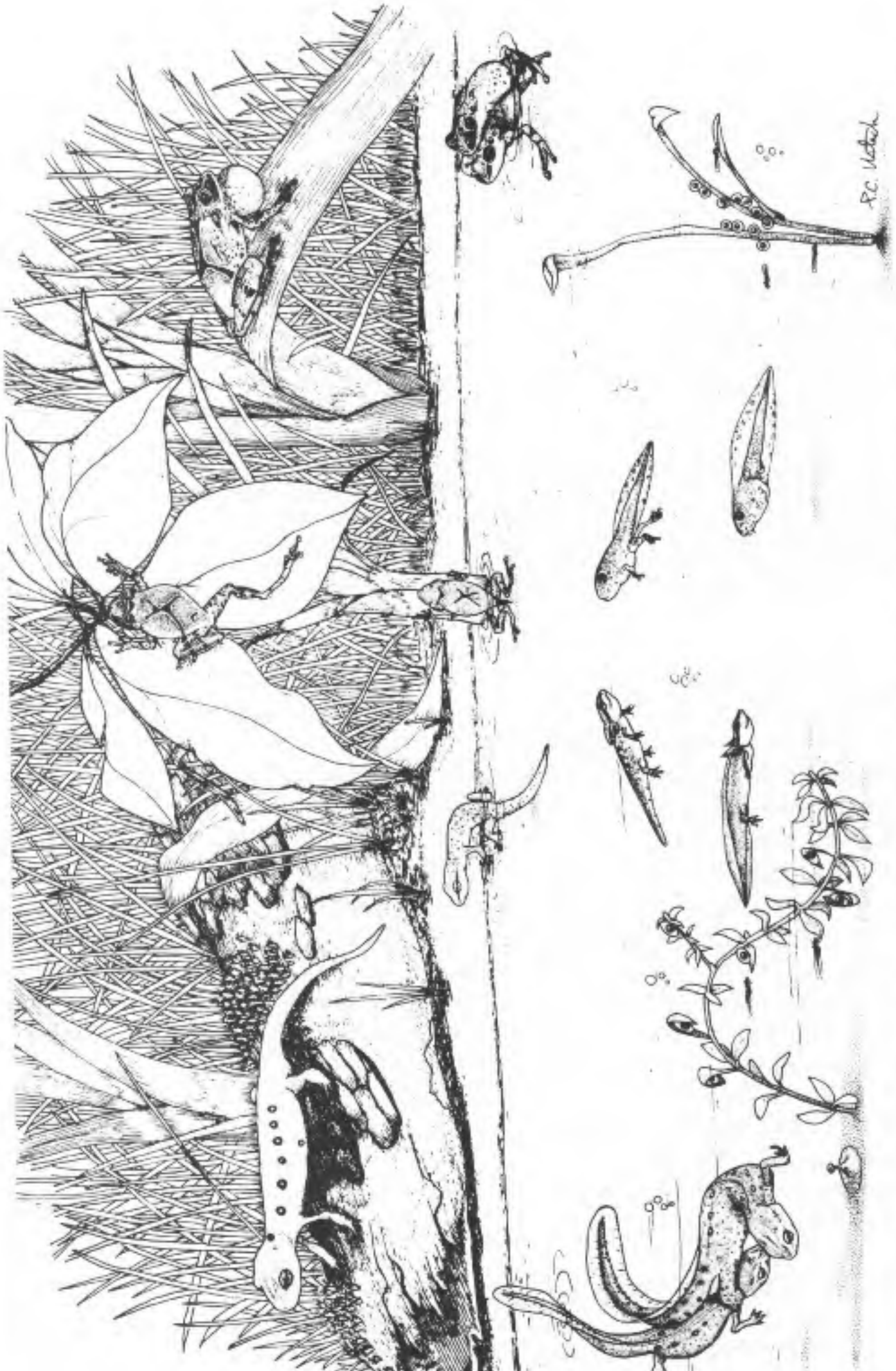

Figure 1. Representative life cycles of a salamander and of a frog. Adults move from the terrestrial to the aquatic environment to breed. In salamanders, mating follows a brief period of courtship; in frogs, a period of calling by the male is followed by amplexus. In both groups, eggs are laid in or near water and hatch into feeding, swimming larvae. Following a period of growth, the aquatic larvae undergo metamorphosis and move onto land, where they feed and mature, eventually repeating the cycle. Printed by permission of Paul C. Ustach.

decaying logs, and in hollows in stems of plants (e.g., bamboo). The relationships among developmental mode, larval morphology, and habitat of anuran tadpoles are summarized in Altig and Johnston (1989). No comparable publication exists for salamander larvae, although references to differences in gill structure, body form, and fin shape among stream, pond, and direct-developing forms are scattered through the literature. Little is known about caecilian larvae.

Amphibian larvae often are found in large concentrations at breeding sites over long periods. As a result, sampling larvae may be a more efficient and quicker method for inventorying species at a site than sampling adults (Gascon 1991), even though eggs and larvae of many species are poorly known. In fact, for many species these stages are reasonably well documented, and more are being described every year. In addition, collecting vouchers of amphibian larvae often is easier and probably has less impact on the population than collecting adults. Even though larval sampling may be somewhat destructive of certain aquatic habitats (e.g., ponds with dense, submerged aquatic vegetation, or bromeliads), it should form an integral part of any sampling program.