CHAPTER 9

Food and Feeding

The different manners of capturing prey would account for such differences as exist between the diet of adult frogs and urodeles.

G. K. Noble (1931b)

The feeding strategies of amphibians include their choice of prey and the ways in which they locate, capture, and ingest prey. Amphibians generally are considered to be feeding opportunists with their diets reflecting the availability of food of appropriate size. This may be true for some, but results of field and laboratory studies show that some species are selective in their feeding. Many constraints influence the diets and feeding habits of amphibians, including extrinsic factors such as seasonal abundance of food and presence or absence of competitors, and intrinsic factors such as ecological tolerances and morphological constraints that relate to ontogenetic stage, size, and specializations. Ultimately, feeding must be efficient—i.e., more energy must be gained from the food than is expended in obtaining it, thereby maximizing energy gain. These factors, as they pertain to adult amphibians, are discussed in this chapter. The food and feeding of larval amphibians, especially tadpoles, are treated in Chapter 6, and the intraoviducal feeding by viviparous species is discussed in Chapter 5.

PREY SELECTION

Most accounts of amphibian feeding are anecdotal and involve only a few taxa. Consequently, little is known about prey selection and foraging strategies; the latter are discussed in the last section of this chapter: Evolution of Prey-Capturing Mechanisms and Strategies. The limited information on amphibian diets indicates that all adult amphibians are carnivores; most feed principally on insects, although many species eat a wide variety of invertebrates.

Herbivory is characteristic of anuran larvae, but it may occur in other amphibians; for example, the aquatic salamanders of the genus *Siren* have been reported to have large quantities of vegetable matter in their digestive tracts and to eat *Elodea*, as well as aquatic invertebrates (Ultsch, 1973). *Bufo marinus* may eat vegetable scraps and canned dog food (Alexander, 1964; Tyler, 1976).

Some anurans are especially voracious eaters. Large anurans, such as *Ceratophrys ornata*, *Discodeles guppyi*, *Pyxicephalus adspersus*, and *Rana catesbeiana*, commonly feed on large prey items, such as small mammals, birds, turtles, snakes, and other anurans (Fig. 9-1). *Discodeles*, found in the Solomon Islands, eats land crabs (Boulenger, 1884). W. Branch (1976) reported a *Pyxicephalus adspersus* that had eaten 17 newly born cobras (*Hemachatus haemachatus*) and another that had attacked a young chicken. Some large salamanders also capture relatively large vertebrates; *Dicamptodon ensatus* eat plethodontid salamanders, frogs, snakes, mice, and shrews (Bury, 1972). These prodigious gastronomic feats are exceptions, as are the feeding on marine crabs by *Rana cancrivora* (Elliott and Karunakaran, 1974), on ma-

Figure 9-1. A captive South African bullfrog, *Pyxicephalus adspersus*, engulfing a rat. Photo by W. E. Duellman.

rine invertebrates by the leptodactylid *Thoropa miliaria* (Sazima, 1972), and on terrestrial gastropods by hyperoliid frogs of the genus *Tornierella* (Drewes, 1981).

Prey Availability

General availability of prey of the appropriate size and type seems to be a basic constraint on th diets of amphibians. For example, analyses of stomach contents of five species of salamanders in New England (T. M. Burton, 1976), *Acris crepitans* in Indiana (Labanick, 1976), and terrestrial eft stages of *Notophhalmus viridescens* in New York (MacNamara, 1977) revealed that the abundance of food items in the stomachs was correlated with the relative prey abundance in the habitat.

Ontogenetic Changes

As individuals become larger, the kinds of prey that they select may change. Ontogenetic changes in diets of larval salamanders were reported by Brophy (1980); as they grew, larvae of *Ambystoma tigrinum* and *Notophthalmus viridescens* increased their predation on snails and decreased their predation on smaller items (ostracods and cyclopoid copepods). In addition, there was a significant increase in the variety of prey taxa in larger *Ambystoma* larvae. Larval *Triturus vulgaris* feed primarily on small zooplankton (chydorids, daphniids, and cyclopoid copepods); as they grow and develop more teeth, the larvae pursue and capture larger prey (principally chironomid larvae), although larger larvae do not select larger individuals of a given prey species (G. Bell, 1975). During postmetamorphic growth, hylid frogs (*Acris crepitans*, Labanick, 1976; *Pseudacris triseriata*, Christian, 1982) ingest increasingly larger prey items as well as a broader spectrum of prey sizes. Likewise, at least some terrestrial plethodotid salamanders show the same trends in increasing the size, in addition to the diversity, of their prey among larger individuals—e.g., *Plethodon wehrlei* (Hall, 1976) and *Batrachoseps attenuatus* (Maiorana, 1978).

An ontogenetic shift in the size of prey selected by larval salamanders may be a function of developmental changes (e.g., increased number of teeth or increased mobility) as well as increased gape (e.g., in postmetamorphic anurans). Gape is known to be a factor in the size of prey eaten by various species of anurans (Toft, 1980a) and at least one salamander (R. L. White, 1977).

Habitat

Individuals of a particular species may exhibit significant differences in the kinds and amounts of prey eaten in different habitats; this mainly reflects differences in prey availability among habitats. Thus, Inger and Marx (1961) found noticeable differences in stomach contents of several species of anurans at different elevations in the Upemba National Park in Zaire, and Barbault (1974) noted differences in diets of anurans in savanna and forest habitats in the Ivory Coast.

Differences on a more local scale also are evident. For example, in freshwater habitats, the diet of *Rana cancrivora* consists mainly of insects, but in nearby brackish water the frogs eat mostly crustaceans (Elliott and Karunakaran, 1974). Newts (*Taricha granulosa*) in a permanent pond eat a greater diversity of prey than do individuals in a temporary pond (R. L. White, 1977). Different diets of individuals of the Argentine leptodactylid *Pleurodema cinerea* are correlated with terrestrial and aquatic feeding (Hulse, 1979).

Seasonality

Seasonal differences in diets have been reported for various species of amphibians (e.g., *Rana pretiosa*, F. Turner, 1959; *Notophthalmus viridescens*, T. M. Burton, 1977; and *Plethodon glutinosus* and *P. jordani*, Powers and Tietjen, 1974). Surveys of diets of many anurans in a seasonal tropical environment in West Africa revealed noticeable differences throughout the year (Inger and Marx, 1961). Among 13 species of anurans dwelling on the forest floor in Amazonian Peru, the diversity of food eaten by some species was greatest in the dry season (Toft, 1980a). Moreover, a comparison of diets among forest-floor anurans at a drier site and a wetter site in Panama revealed greater differences between sites than between seasons at any one site (Toft, 1980b).

Seasonal differences in diets reflect availability of prey and, in some cases, seasonal differences in selectivity by amphibians (e.g., certain forest-floor anurans; Toft, 1980a). This selectivity may be "forced" on the amphibians by factors other than food, especially by the necessity of foraging under physiologically tolerable moisture conditions. For example, the plethodontid salamander *Desmognathus fuscus* demonstrates a selection for larger prey with increased precipitation (Sites, 1978). *Plethodon cinereus* forages in moist leaf litter; when the leaf litter is dry, the salamanders are confined to feeding on limited amounts and kinds of prey occurring under rocks or logs (R. Jaeger, 1980). On foggy or rainy nights, *P. cinereus* climbs on vegetation and feeds on kinds of insects not present on the ground, actually ingesting more food than conspecifics on the forest floor (R. Jaeger, 1978).

The seasonal activity of certain species is determined, in part, by the activity of their prey. This is especially evident among prey specialists. The activity of the termite-eating anuran *Breviceps verrucosus* in South Africa is timed to the swarming of termites (Poynton and Pritchard, 1976). The period of feeding activity by the spadefoot, *Scaphiopus couchii*, in southwestern North America also is correlated with the swarming of termites (Dimmitt and Ruibal, 1980).

Diel activity of prey may account for the predator's feeding activity and, therefore, kinds of prey taken. For example, peak surface activity of three species of streamside plethodontid salamanders is highly correlated with the activity of potential prey at dusk or shortly after dark (Holomuzki, 1980). Freed's (1980) analysis of prey behavior and feeding selectivity by the tree frog *Hyla cinerea* suggested that the frogs selected prey in relation to the proportion of time that the prey species was active and the kind of activity displayed by the prey. Thus, increased frequency of prey activity resulted in a perceived increase in the density of that prey species for the predator, thereby resulting in greater predation. When prey selection was limited to prey types having similar activity patterns, size of the prey species became an important factor in prey selection, with the larger prey being selected. Analysis of stomach contents of the Malaysian ranid *Amolops larutensis*, and activity patterns and abundance of prey species throughout the year led Berry (1966) to conclude that diet selection by this frog is associated most closely with activity of the prey.

LOCATION OF PREY

Basically two kinds of foraging strategies are utilized by amphibians. Most anurans have adopted a sit-and-wait strategy, whereas active foraging seems to be more common among some salamanders and apparently is characteristic of caecilians. However, the strategy used by an individual may vary with the abundance of prey. The method of monitoring prey abundance may depend on the sensory mechanism employed by the predator. Predators using olfactory or tactile stimuli to detect prey may not be able to perceive either relative or absolute abundances of different kinds of prey without actually capturing them. Conversely, encounter rates may be used more commonly by species that search for prey visually.

Visual Detection

The vast majority of anurans and salamanders use vision in the final encounter with a prey item, although preliminary location of prey also may involve other cues. Several studies embracing field observations and laboratory experiments indicate that vision is of primary importance in locating prey. This has been demonstrated for such diverse salamanders as *Salamandra* (Luthardt and G. Roth, 1979), *Triturus* (Margolis, 1976), *Notophthalmus* (J. Martin et al., 1974), *Ambystoma* (Lindquist and M. Bachmann, 1982), *Hydromantes* (G. Roth, 1976), and *Plethodon* (R. Jaeger et al., 1982), as well as various anuran species of the genera *Bufo* (Brower et al., 1960; Heatwole and Heatwole, 1968; Ewert, 1976; Borchers et al., 1978) and *Rana* (Maturana et al., 1960; Kramek, 1976).

Visual detection is most common in those species that have adopted a sit-and-wait strategy. Once a prey item is sighted, it may be pursued for a short distance before capture. For example, the tree frog *Hyla cinerea* obtains only 12% of its prey without pursuit; 88% of the prey items are captured after visual detection and a short pursuit (Freed, 1980).

Recent experiments on the elicitation of feeding responses in amphibians that use visual cues (Borchers et al., 1978; G. Roth, 1978) indicate a complex interrelationship among stimulus parameters of velocity, size, and orientation with respect to the direction of movement of the prey. For example, in order to elicit maximal prey-catching behavior by *Salamandra salamandra*, it seems that stimuli of a certain orientation must move at a certain velocity and in a certain manner (Luthardt and G. Roth, 1979). Elongation of the prey image along the axis of movement facilitates prey capture by *Bufo marinus*; the toad strikes mainly at the leading object when stimuli travel orthogonally to the toad's optic axis (Ingle and McKinley, 1978).

Visual cues also can be important in identifying kinds of prey, such as those that may be optimal in energy content or that may be distasteful. Experiments with *Bufo terrestris* (Brower et al., 1960) revealed that the toads learned to reject bumblebees (*Bombus americanorum*) and their robberfly mimics (*Mallophora bomboides*) by sight alone.

Olfactory Detection

Chemosensory cues for the location of prey have been inferred in various aquatic salamanders— *Notophthalmus viridescens* (J. Wood and Goodwin, 1954), *Gyrinophilus porphyriticus* (Culver, 1973), and *Haideotriton wallacei* (Peck, 1973). Heusser (1958) showed that *Bufo calamita* could find prey solely on the basis of olfactory cues. Experiments with *Bufo boreas* (Dole et al., 1981), *B. marinus* (J. Rossi, 1983), *Rana pipiens* (Shinn and Dole, 1978), *Ambystoma tigrinum* (Lindquist and M. Bachmann, 1982), *Plethodon cinereus* (David and R. Jaeger, 1981), and two species of *Triturus* (Margolis, 1976) have demonstrated that these species are capable of locating prey by olfactory cues alone.

The role of olfaction in prey detection probably is much more common among amphibians than indicated by available observations and experiments. The role of olfaction in prey location, particularly in trailing prey, is strongly inferred by specialized chemoreceptors in some amphibians—protrusible tentacles, in which the lumen opens to Jacobson's organ, in caecilians (Badenhorst, 1978, and references cited therein) and nasolabial grooves in plethodontid salamanders (C. Brown, 1968). The location of termitaria by fossorial anurans such as *Rhinophrynus dorsalis* (Trueb and Gans, 1983) and *Myobatrachus gouldii* (Calaby, 1956) may involve olfactory detection.

Experiments on *Ambystoma tigrinum* (Lindquist and M.. Bachmann, 1982) and on *Triturus* (Margolis, 1976) show that the efficiency of detecting, locating, and capturing prey is greatest when both visual and olfactory cues are used. However, the type of prey may dictate which cues are more effective. The location of pill clams (*Musculium rosaceum*) by the newt *Notophthalmus viridescens* apparently is accomplished by olfaction alone (J. Wood and Goodwin, 1954). Although visual cues predominate in the detection of moving insects by many terrestrial salamanders, immobile prey such as insect pupae are located by olfaction in *Plethodon cinereus* (David and R. Jaeger, 1981). Olfaction is strongly implicated in the ability of *Hydromantes* to project its tongue at prey in total darkness (G. Roth, 1983).

Auditory Detection

Few observations are available on auditory stimuli in location of prey by amphibians. Martof (1962) found that *Bufo woodhousii* were alerted to the presence of insects by the sounds they produced. R. Jaeger (1976) observed that *B. marinus* were attracted to calling frogs, *Physalaemus pustulosus*, which they consumed. Large carnivorous anurans that prey on smaller anurans also may utilize auditory cues to locate prey.

CAPTURE OF PREY

In addition to differences in kinds of prey and foraging strategies, amphibians exhibit striking differences in feeding mechanisms. All terrestrial amphibians except caecilians use the tongue in capturing prey; the tongueless pipid frogs and aquatic salamanders have entirely different mechanisms. Even among terrestrial anurans and salamanders there are notably different methods of prey capture. These differences are reflected in the diversity of the the structure of the tongue and its supportive hyobranchial apparatus and associated musculature.

Many caecilians and some large, carnivorous anurans have long, fanglike teeth that may be curved posteriorly; these teeth serve to hold struggling prey. In larval and most neotenic salamanders, the teeth are unicuspid and lack the weak planes of the typically bicuspid pedicellate teeth of adult salamanders and anurans. Teeth are absent from the lower jaws of most anurans, and some anurans (e.g., all bufonids) also lack teeth on the upper jaw. Many frogs have a few vomerine teeth in the palate, whereas salamanders characteristically have patches of vomerine teeth that may extend posteriorly as a parasphenoid series.

The tongues of amphibians possess glands that produce a sticky secretion that serves to adhere the prey to the surface of the tongue. Presumably in all amphibians except caecilians the tongue is used in prey capture. In all groups it is used to hold the prey against the roof of the mouth and to manipulate food in the buccal cavity; this is facilitated by secretions of the intermaxillary glands. In anurans and salamanders, food is pushed posteriorly by the contraction of the m. retractor bulbae, which depresses the eye into the buccal cavity. Once food passes the ciliated pharynx, ingestion is completed by peristaltic action of the esophageal walls. Secretions of mucous glands in the buccal cavity facilitate food transport by lubricating the mouth and pharynx.

Caecilians

Terrestrial caecilians feed primarily on elongate prey, such as earthworms, located on the surface of the ground or, probably more commonly, in burrows. Prey capture involves a slow approach to the prey until contact is almost effected, at which time the prey is seized by a powerful bite. Caecilians tend to bite the prey broadside; they move the head past the prey and bite laterally. If a caecilian has not completely emerged from its burrow when the prey is seized, it retreats into the burrow, spinning in a corkscrew fashion around its body axis. This action creates friction between the prey and the sides of the bur-

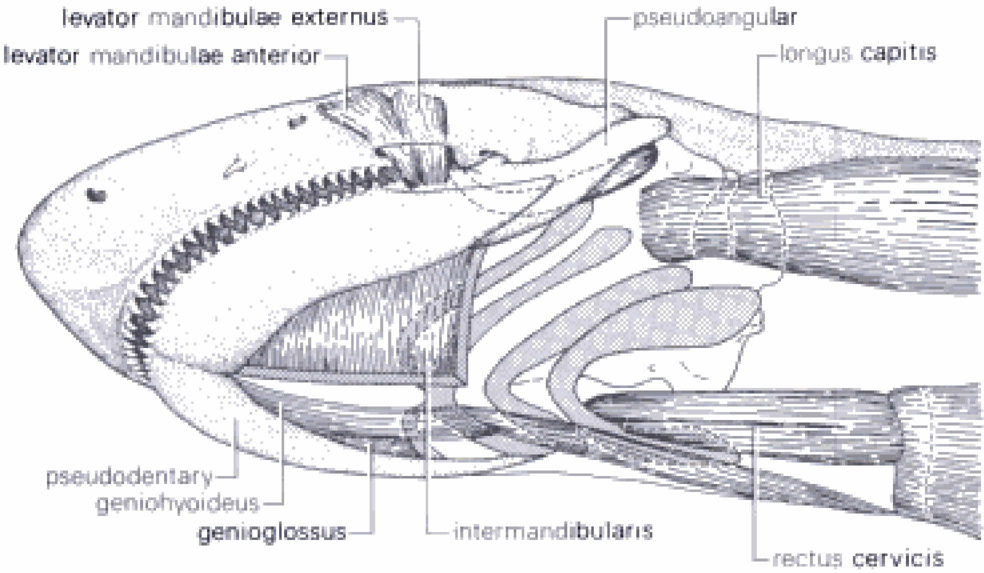

Figure 9-2. Ventrolateral view of cranial, hyoid, and anterior trunk musculature of a caecilian, *Dermophis mexicanus*. Redrawn from Bemis et al. (1983).

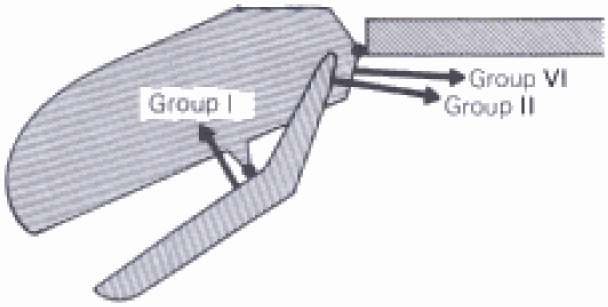

Figure 9-3. Diagram of the jaw-closing mechanism of a caecilian. Three distinct sets of muscles affect this unique mechanism. Dots are fulcra; arrows are direction of muscular contraction.

row, constricting and shearing the prey to approximately the width of the gape of the caecilian.

The tongue is not protrusible, but interspecific variation exists in the amount of free margin of the tongue and the extent of the glandular field on its dorsal surface. The m. genioglossus forms the body of the tongue; it originates at the mandibular symphysis and from the connective tissue overlying the m. geniohyoideus, and inserts on the surface epithelium of the tongue. The muscle fibers in the body of the tongue are dispersed vertically among extensive blood sinuses and the bases of lingual glands. Contraction of these fibers (1) depresses the tongue pad, thereby increasing pressure in the blood sinuses, (2) facilitates extrusion of lingual gland secretions by compressing the bases of these glands, and (3) aids in food transport (Bemis et al., 1983).

Adult caecilians are unique among amphibians in lacking a m. hyoglossus and in having a completely roofed skull, a fixed quadrate, and a lower jaw with a long retroarticular process (Fig. 9-2). Associated with this bony structure are muscles that provide a unique jaw-closing mechanism (Bemis et al., 1983; Nussbaum, 1983). This is a double-lever system with the quadrate functioning as the fulcrum. As in other gnathostomes, contraction of the m. levator mandibulae (m. adductor mandibulae) results in the lower jaw being pulled upward. The novel component in caecilians is that contraction of the m. interhyoideus posterior, which originates on the fascia of the ventral and lateral body wall and inserts on the ventral surface of the retroarticular process, pulls the retroarticular process back and down, thereby causing the anterior jaw ramus to pivot upward around the quadrate. A third muscle that acts synergistically to produce a strong bite is the m. longis capitis, a large ventral trunk muscle that originates on the basapophyses of the anterior vertebrae and inserts on the cranium ventral to the craniovertebral articulation; this muscle is a powerful flexor of the neck and cranium (Fig. 9-3).

Motion analyses and electromyography of feeding by the caeciliid *Dermophis mexicanus* (Bemis et al., 1983) revealed that during prey capture the lower jaw is pressed against the substrate and the mouth is opened as the cranium is raised as a result of activity of the m. depressor mandibulae and the dorsal trunk musculature. Jaw closing is rapid and involves simultaneous contractions of the m. levator mandibulae and m. interhyoideus posterior and presumably the m. longis capitis. A single bite requires about 0.5 second. Holding onto struggling slippery prey is facilitated by the presence of two rows of long, recurved teeth in the upper jaw.

Salamanders

Although the basic structures are the same in the feeding mechanics of all salamanders, functional and developmental constraints have played an important role in the modification of the hyobranchial apparatus for different kinds of feeding mechanisms. These were summarized by D. Wake (1982) and are grouped into three categories.

Aquatic Salamanders. In larval salamanders, neotenic adults such as proteiids, and terrestrial salamanders (when in water during breeding), the hyobranchial apparatus functions to (1) support and move the gill filaments for respiration (not so in terrestrial adults in the water temporarily), and (2) expand and contract the buccal cavity during feeding. These movements are accomplished by the hyoid musculature in association with the depressor mandibulae. During feeding, most salamanders lunge toward the prey; the buccal cavity is expanded and, almost simultaneously, the rather weak jaws are opened. However, in *Amphiuma tridactylum*, there are two different types of suction feeding (Erdman and Cundall, 1984) depending on the size and activity of the prey. If the prey is small or relatively immobile, the salamander does not thrust its head forward; once the mouth is opened, buccal expansion induces an inward flow of water which sucks the prey into the mouth. The lunge or rapid strike mechanism is used to capture actively moving prey. In this strategy, mouth-opening and buccal expansion are synchronous, and buccal expansion is greater than in stationary feeding. Water and prey are sucked into the mouth by the action of the buccal pump. The rudimentary tongue manipulates the prey against the teeth on the roof of the mouth. The jaws have limited use; their small teeth are used to secure large prey during manipulation (Matthes, 1934).

Generalized Terrestrial Salamanders. In metamorphosed, terrestrial salamanders having lungs (Hynobiidae, Dicamptodontidae, Ambystomatidae, and generalized salamandrids) the tongue is attached anteriorly, is protrusible, and plays an important role in prey capture. The hyobranchial apparatus has a dual role as a buccal pump mechanism in respiration and as the main mechanism of tongue protrusion. Cinematographic investigations coupled with morphological studies (Severtzov, 1971, 1972; Larsen and Guthrie, 1975) provided an interpretation of the feeding mechanisms of these salamanders, but electromyographic evidence is absent.

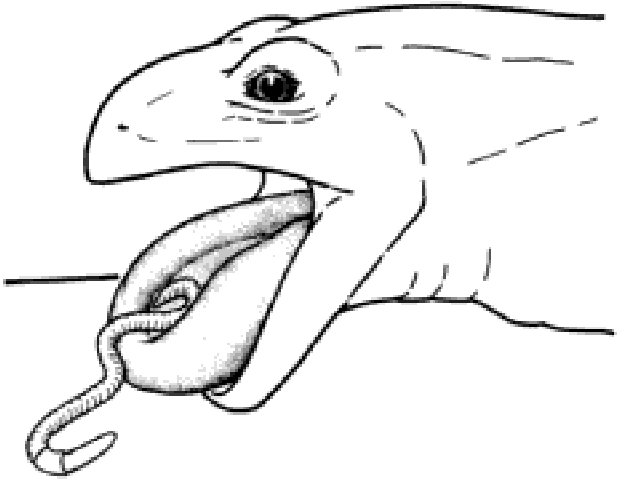

Figure 9-4. Terrestrial prey capture by the salamander *Ambystoma tigrinum*. Note the slight protrusion of the tongue with a noticeable trough and the adpression of the mandibular symphysis to the substrate. Drawn from a photograph in Larsen and Guthrie (1975).

In their analysis of the feeding mechanisms of adult *Ambystoma tigrinum* in the laboratory, Larsen and Guthrie (1975) noted that after an initial lunge the lower jaw is immobilized as it is pressed against the substrate by the contraction of the m. geniohyoideus and m. rectus cervicis superficialis. The cranium is elevated by the contraction of the m. cucullaris major and the m. depressor mandibulae. The gape is increased further as the salamander rocks forward, keeping its lower jaw stationary. The tongue is elevated and protruded up to 8% of the body length beyond the margin of the lower jaw. These complementary actions seem to be accomplished by (1) initial propulsion of the tongue by the medial divisions of the m. genioglossus pulling the copula of the hyoid anteriorly, (2) forward projection of the hyobranchial apparatus by the contraction of the m. subarcualis rectus I acting on the tips of the ceratobranchials (epibranchials of Larsen and Guthrie, 1975), (3) concomitant contraction of the m. geniohyoideus drawing the m. rectus cervicis superficialis and second basibranchial (Copula II) anteriorly, (4) buckling of the anterior radial cartilages providing the form of the outgoing tongue, (5) subsequent shaping of the front and lateral rims of the tongue by the otoglossal cartilage and second radial cartilages, respectively, and (6) turgidity of margins of the tongue increased by fluids forced from the sublingual sinuses posterolaterally into sinus pockets.

When the prey is struck by the posterior half of the tongue, the lingual divisions of the m. genioglossus contract, resulting in the expulsion of a sticky secretion that adheres the prey to the tongue; the m. rectus cervicis profundus then contracts causing the partial collapse of the anterior rim of the tongue, entrapping the prey in a sticky trough (Fig. 9-4). Tongue retraction is accomplished primarily by the m. rectus cervicis profundus and lateral divisions of the m. rectus cervicis superficialis. Small prey is brought within the range of the vomerine teeth, but larger prey commonly escape from the sticky trough during retraction and are held only by the marginal teeth. Once the tongue has retracted completely, the mouth is closed by depressing the cranium sharply through the contraction of the m. levator mandibulae. Immobilization of the lower jaw and opening of the mouth requires 0.05–0.09 second, during which time the tongue protrudes; retraction of the tongue and prey requires 0.03 second and closure requires 0.02–0.03 second. Thus, the entire sequence of prey capture lasts 0.10–0.15 second; subsequent swallowing requires about 0.07 second.

Lungless Salamanders. Lungs are absent in salamanders of the family Plethodontidae and two genera of salamandrids, *Chioglossa* and *Salamandrina*. In these salamanders, the hyobranchial apparatus no longer functions as a buccal pump to force air into the lungs, and the hyobranchium is modified to project the tongue from the mouth. Not only is the cranium elevated during feeding, but the lower jaw is dropped and is not adpressed against the substrate. Morphological evidence indicates that tongue projection evolved independently in salamandrids and plethodontids, and within the latter group, highly projectile tongues evolved independently in the hemidactylines and the bolitoglossines (D. Wake, 1982). The morphology of the feeding mechanisms and their functions have been described for salamandrids by Özeti and D. Wake (1969) and for plethodontids by Lombard and D. Wake (1976, 1977). Electromyography of the tongue protrusion in one plethodontid, *Bolitoglossa occidentalis*, was accomplished by Thexton et al. (1977).

In those plethodontids with highly projectile tongues, the "projectile" consists of the tongue pad trailed by an elongate bundle of folded cartilages, retractor muscles, nerves, and vessels enclosed in a mucosal sheath (Fig. 9-5). In many plethodontids, the tongue pad either has lost the anterior attachment or has a rather elastic connection to the lower jaw. The hyobranchial apparatus is composed of elongated mobile subunits. A pair of ceratohyals that are attached posteriorly by hyoquadrate ligaments to the suspensoria lie on the floor of the mouth; they are not in contact with one another, nor do they articulate with any other, elements of the hyobranchium. The posterior part of each ceratohyal is cylindrical and hooked, and the anterior part is flattened and expanded. The cartilages that move out of the mouth with the tongue are articulated to form a single complex unit. The principal element of this unit is the unpaired, median basibranchial or copula. The anterior end of the basibranchial has a projection that is either continuous with the basibranchial proper or united with it by connective tissue. If detached, the element is called the lingual cartilage. A pair of radial cartilages also is attached anteriorly to the basibranchial, and two pairs of hypobranchials articulate with the posterior part of the basibranchial. The first pair of hypobranchials are the longest elements; they articulate with the basibranchial just posterior to its midpoint. The second pair of hypobranchials articulate with the basibranchial at its posterior end. The first and second hypobranchials on each side approximate each other posteriorly, and both articulate with the ceratobranchial, a tapered element of varying length. The median second basibranchial (Copula II) lies at the juncture of the m. rectus cervicis superficialis and m. geniohyoideus; it has no connections with other elements and is lost in bolitoglossine plethodontids.

Figure 9-5. Highly projectile tongue of the plethodontid salamander *Hydromantes italicus* in the capture of an insect. Drawn from a photograph in Lombard and D. Wake (1976).

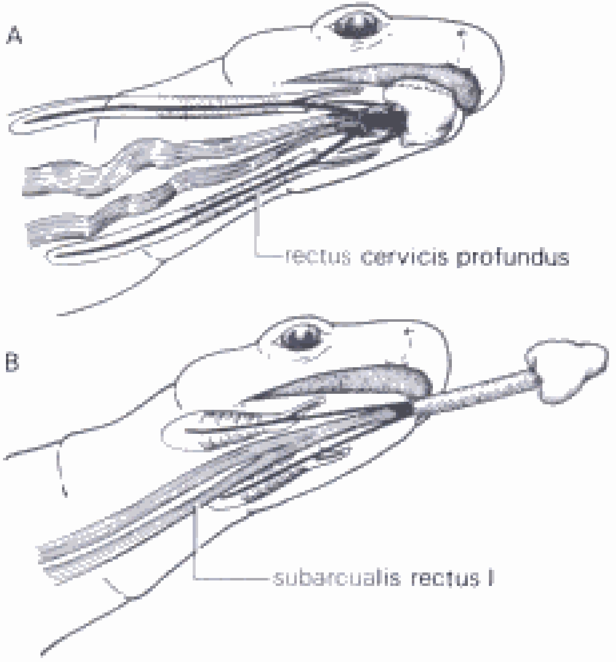

Figure 9-6. Diagrammatic representation in ventrolateral view of the tongue projection mechanism in the plethodontid salamander *Bolitoglossa occidentalis*. **A.** Tongue retracted. **B.** Tongue projected. Modified from Thexton et al. (1977).

The tongue pad is large, and its base is supported by the anterior end of the basibranchial. The radial and lingual cartilages extend into the pad. The principal muscles associated with the hyobranchium are the m. rectus cervicis profundus and the m. subarcualis rectus I. The former is an anterior continuation of a muscle that arises on the ischium and inserts principally into the muscular body of the tongue. The m. subarcualis rectus I originates on the ventral surface of the ceratohyal and wraps around the epibranchial (sensu D. Wake) in a complex spiral, forming a muscular bulb.

Analysis of muscle action in *Bolitoglossa occidentalis* (Thexton et al., 1977) showed that the tongue and hyoid apparatus are projected by contraction of the m. subarcualis rectus I. Upon contraction of these protractors, the epibranchials are forced out of the cavity within the subarcualis muscles (Fig. 9-6). Simultaneously the entire muscle shortens, and the posterior end moves toward the gular region. The forward-moving ceratobranchials conduct force via the first and second ceratobranchials to the median basibranchial and thence to the tongue

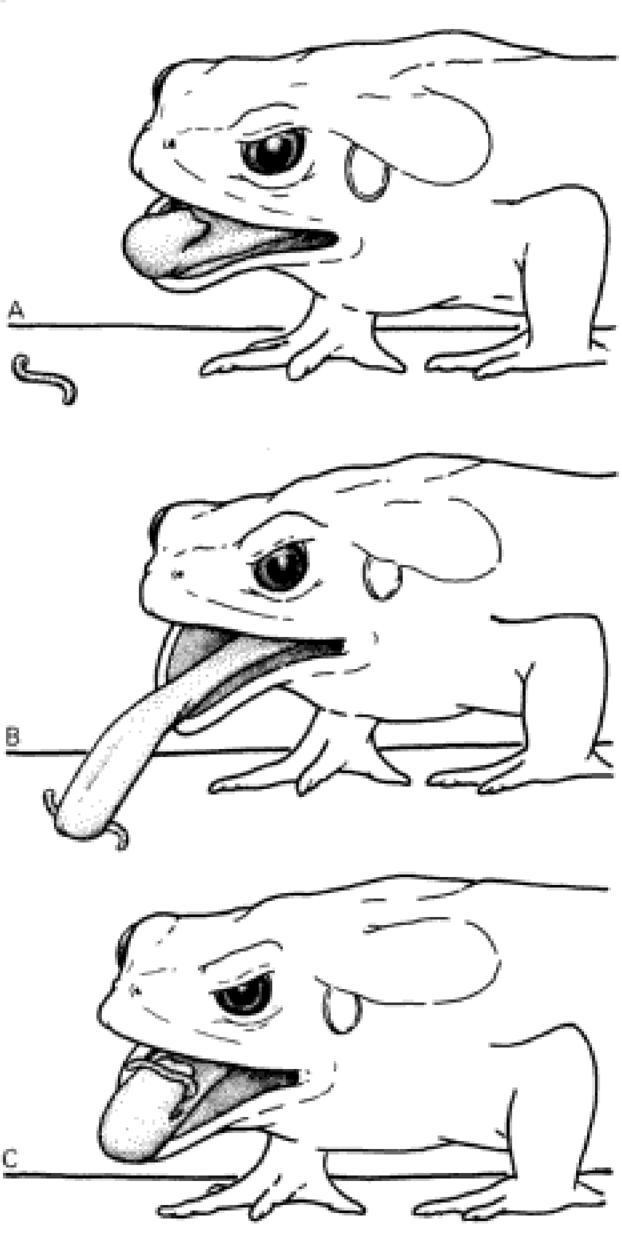

Figure 9-7. Lingual flipping feeding mechanism in the toad *Bufo marinus*. **A.** Initiation of the lingual flip. **B.** Fully extended tongue contacts prey. **C.** Partially retracted tongue with prey. Note depressed anterior part of jaw. Adapted from Gans and Gorniak, 1982a, *Science* 216:1335. Copyright 1982 by the AAAS.

pad. The retractors (m. rectus cervicis profundus and m. rectus abdominis profundus) are lax and lie in loops when the tongue is in the mouth. When the tongue is projected, the retractor muscles become taut; as their tension becomes greater than that of the protractors, the tongue is retracted into the mouth.

When the sticky tongue pad is projected and contacts a prey item, adhesion permits retraction of the prey into the mouth. As the mouth closes, the tongue presses the prey against the teeth in the roof of the mouth and permits it to be manipulated and swallowed. This feeding mechanism is most effective for the capture of relatively small prey and is accomplished rapidly (<50 milliseconds). Salamanders with highly projectile tongues can capture prey at distances equal to 44–80% of their body length.

Anurans

The feeding mechanism of most advanced anurans involves a lingual flip during which the posterodorsal surface of the retracted tongue becomes the anteroventral surface of the fully extended tongue (Regal and Gans, 1976). In such anurans the hyobranchium provides the mechanical base for the forceful flipping of the tongue; as such, it has a limited amount of anteroposterior movement and is not projected as in salamanders. The hyobranchium also functions as part of the buccal pump mechanism, as it does in generalized terrestrial salamanders.

The adductor musculature is similar to that of salamanders, except that the m. adductor mandibulae posterior is a single slip in anurans instead of two as in salamanders (Salomatina, 1982). A unique feature among most anurans is the ability to depress the mandibular symphysis during the lingual flip. This is possible because of the flexibility afforded to the jaw by the presence of mentomeckelian cartilages and bones at the mandibular symphysis (Fig. 9-7). Contraction of the m. submentalis, a median muscle extending transversely just posterior to the symphysis, rotates the anterior parts of the dentaries downward and brings them closer together, thereby depressing the anterior margin of the lower jaw (Gans and Gorniak, 1982a).

Cinematographic and electromyographic studies on the toad *Bufo marinus* (Gans and Gorniak, 1982b) show the sequential steps in what is assumed to be the generalized feeding mechanism of most anurans. During the tongue-flipping movement, the tongue is supported by the m. genioglossus medialis, which stiffens the tongue when contracted. Simultaneous contraction of the m. genioglossus basalis provides a wedge under the anterior tip of the rodlike m. genioglossus medialis. In addition to depressing the mandibular symphysis, the m. submentalis acts on the wedge of the m. genioglossus basalis to raise and rotate the rod of the m. genioglossus medialis over the symphysis. The tip of this lingual rod carries along the pad and soft tissues of the tongue. Contraction of the long, parallel fibers of the m. hyoglossus retracts the medial sulcus of the tongue pad and holds the prey by a cuplike effect, which is enhanced by the sticky secretion of the glands in the lingual pad. The extensibility of the buccal membranes allows the pad to be retracted first; the pad reaches the posterior part of the buccal cavity before the still-rigid, backward-rotating m. genioglossus medialis reaches the level of the symphysis. During this process, protraction of the hyoid facilitates the extension of the m. hyoglossus; the m. sternohyoideus retracts and stabilizes the hyoid when the tongue starts to retract; it does not function in tongue protrusion.

There is considerable diversity in tongue structure among anurans (Magimel-Pelonnier, 1924; Horton, 1982b), principally involving modifications of the m. genioglossus. In the archaic families, Leiopelmatidae and Discoglossidae, there is little free margin to the tongue. In *Bombina* the tongue can be protruded slightly, as in *Ambystoma*, but presumably it cannot be flipped as in most other anurans (Regal and Gans, 1976). The m. genioglossus is rather poorly developed in some myobatrachids, and in the aquatic *Rheobatrachus* the tongue is firmly attached to the floor of the mouth (Horton, 1982b). Some of the carnivorous frogs (e.g., *Ceratophrys* and *Hemiphractus*) that feed on large prey have exceedingly strong mandibular symphyses with dorsally directed odontoids that hold prey. Most likely, these anurans do not depress their mandibular symphyses during feeding. Some megophrine pelobatids, myobatrachids, and microhylids have variously modified tongues, but no functional studies have been performed. However, feeding mechanisms have been studied in two groups of anurans that differ significantly from the tongue-flipping mechanism.

Pipids. The completely aquatic pipids are unique among anurans in lacking tongues. The hyobranchial apparatus and associated musculature are quite different from that in anurans which have tongues (Chaine, 1901; Trewavas, 1933). The aquatic feeding mode of pipids (*Hymenochirus*, *Pipa*, and *Xenopus*) is accomplished by transportation of the food into the mouth with water currents produced by hyobranchial pumping movements (Sokol, 1969); essentially these are the same movements characteristic of anuran larvae. Compression of the buccopharyngeal cavity results from the protraction of the hyobranchial apparatus by the m. geniohyoideus and by the flattening of the buccal floor by the m. interhyoideus and m. intermandibularis posterior.

Essentially, these aquatic frogs suck in food and water; the water is expelled before the mouth is closed completely. This is an effective mechanism for feeding on zooplankton. *Pipa* and *Xenopus* sometimes take larger prey, using their long fingers to push the food into the mouth.

Fossorial Anurans. Many kinds of fossorial anurans are known, or presumed, to feed underground; most of these frogs feed on ants, termites, and worms. Obviously, tongue-flipping is not a useful mechanism underground unless the frog is in an open burrow. *Rhinophrynus dorsalis*, a fossorial anuran that feeds on ants and termites, not only differs structurally from other frogs but has a unique method of tongue protrusion (Trueb and Gans, 1983). The contraction of one intrinsic tongue muscle, m. hyoglossus, results in reshaping the tongue from a flat, triangular structure to a rodlike tube by stiffening the tongue and exerting hydrostatic pressure on the fluids in the lingual sinus. Actual protrusion of the tongue is accomplished by a forward shift of the hyoid plate and cornua, from which the m. hyoglossus originates. This forward movement is accomplished by contraction of the m. geniohyoideus and apparently is facilitated by contraction of the m. mandibulomentalis, which elevates the buccal floor. Retraction of the tongue is accomplished by contraction of the m. sternohyoideus, which retracts the hyoid, and the subsequent relaxation of the m. hyoglossus.

Presumably *Rhinophrynus* positions itself with its highly glandular, elongate snout just penetrating the wall of a termitarium or termite tunnel (Fig. 9-8). As termites are

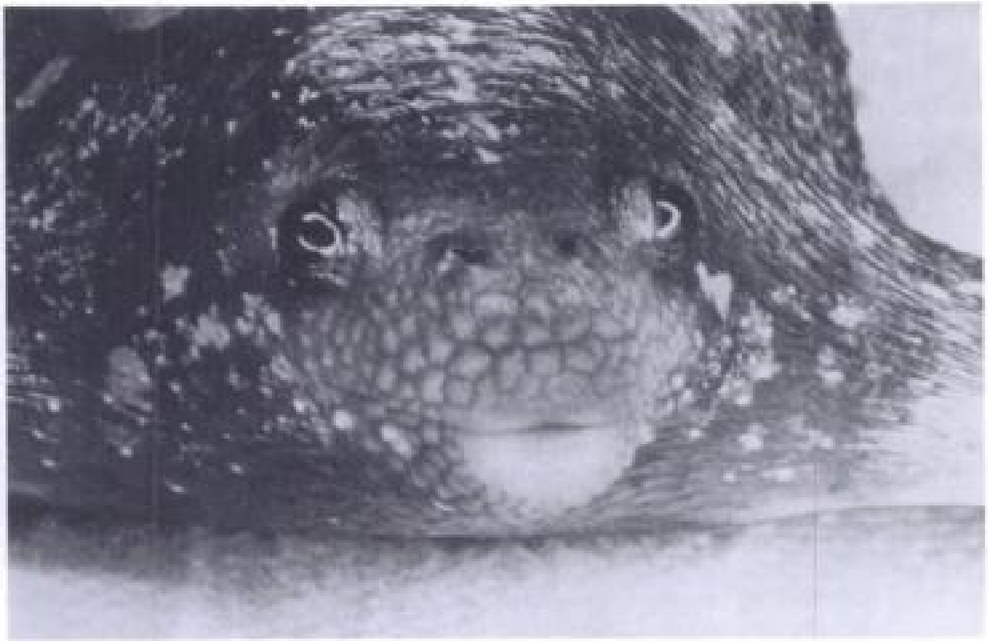

Figure 9-8. Burrowing toad, *Rhinophrynus dorsalis*, showing the calloused tip of the snout and the opening of the buccal groove through which the tongue protrudes. Photo by L. Trueb.

detected, the tongue is protruded through a groovelike vault in the buccal ceiling. Prey are enfolded by the cup-shaped, villous lingual tip and withdrawn into the mouth.

EVOLUTION OF PREY-CAPTURING MECHANISMS AND STRATEGIES

The feeding mechanisms of living amphibians have evolved in response to natural selection and phylogenetic constraints, and are limited somewhat by the involvement of the hyobranchial apparatus in both feeding and ventilation. Moreover, striking differences exist in the metabolism and energy budgets among amphibians. The dual function of the hyobranchial apparatus leads to interrelationships that affect the foraging strategies of amphibians, but these aspects of amphibian biology are poorly understood.

Morphological Constraints on Foraging Tactics

Various evolutionary lineages of amphibians have evolved specialized feeding mechanisms that are effective in obtaining prey of certain sizes and/or shapes under given environmental conditions. How do these functional specializations correspond with (1) the kind of prey that are eaten and (2) the tactics used to obtain the prey?

The size of the gape is an important factor; obviously, smaller amphibians are limited to smaller prey than species that are much larger, but within size classes, some species have much smaller gapes than others. This is especially evident in comparing ant-eating specialists, such as many microhylid and dendrobatid frogs, with terrestrial leptodactylids and ranids that feed on other kinds of prey. The former have relatively small gapes and are limited to small prey, of which ants are the most abundant. The larger gapes of other anurans allow ingestion of larger prey; these frogs have a more diversified diet including large as well as small prey.

The generalized feeding mechanisms of some terrestrial salamanders (hynobiids, ambystomatids, most salamandrids, and desmognathine and plethodontine plethodontids) and archaic frogs (leiopelmatids and discoglossids) involve only slight protrusion of the tongue, subsequent manipulation of the prey by the tongue against the vomerine teeth, and use of the jaws. The size of the prey seems to be limited solely by the gape. In caecilians, gape is a major factor when feeding on the surface, but positioning and shearing the prey also are important when feeding underground. Most anurans that capture prey by a lingual flip and salamanders that have a projectile tongue have a further constraint—the load-bearing capacity of the extended tongue. Thus, amphibians that extend the tongue may be limited in the size of the prey that they can hold and retract. Carnivorous frogs that ingest large prey lunge at their prey while extending the tongue and use their jaws to secure the prey; thus, they do not rely solely on the tongue as the prey-capturing mechanism. The opposite is true in *Rhinophrynus dorsalis*, in which the tongue and its protrusion mechanism are highly specialized for the ingestion of small prey.

With some notable exceptions, amphibians that have generalized feeding mechanisms are active foragers with highly diverse diets, whereas those that have specialized feeding mechanisms tend to use a sit-and-wait strategy. The latter include many kinds of semiaquatic, terrestrial, and arboreal anurans and hemidactyline and bolitoglossine salamanders. Most of these amphibians are cryptic and nocturnal. Because of their ability to extend the tongue for moderate to great distances, these amphibians can afford to sit and wait until suitable prey come within striking distance of the tongue, or sufficiently close that the amphibian needs to move only a short distance before capturing its prey and returning to its feeding site. Selection of a suitable feeding site is a critical aspect of success as a sit-and-wait predator. Observations on *Rana pipiens* by Dole (1965) and on *R. septentrionalis* by Kramek (1976) showed that these frogs would move farther from the feeding site for a large prey item than they would for a small one. Moreover, if feeding success was low, the frogs moved to a different site. Capture success in *R. septentrionalis* was higher (84%) for slow-moving aphids and chrysomelids than for aerial insects (16% for dragonflies and damselflies).

Among the notable exceptions are various groups of anurans that are ant specialists (Toft, 1980a). These include many dendrobatids and bufonids, all of which have noxious or toxic skin secretions (see Chapter 10). These active foragers with their effective antipredator mechanism are "released" from the constraints of the cryptic, innoxious anurans that use the sit-and-wait strategy to obtain food. However, other ant specialists, notably some microhylids, are cryptic and seem to search for ant trails; presumably these trails are located by olfaction. Once an ant trail is found, these anurans tend to sit and wait and pick up ants as they pass by. A similar strategy presumably is used by fossorial ant and termite specialists such as *Rhinophrynus* and *Hemisus*. Most large predatory frogs also have adopted a sit-and-wait strategy. At least in *Ceratophrys* this behavior may be enhanced by pedal luring, the habit of vibrating and undulating the fourth and fifth toes of the elevated hindfoot, thus attracting smaller amphibians toward the *Ceratophrys* (Murphy, 1976).

Physiological Constraints on Foraging Tactics

Two aspects of physiology are important in feeding—energy metabolism and energy budgets. In some amphibians, such as *Bufo*, lactate production is low (see Chapter 8), so these animals are capable of long periods of sustained activity. Other amphibians, such as *Hyla* and *Rana*, produce large amounts of lactic acid and are capable of bursts of activity over short periods of time. As first pointed out by Toft (1980a), these metabolic attributes may be correlated with foraging strategies. Thus, active foragers are species that are capable of sustained, low levels of activity, whereas sit-and-wait strategists are capable of bursts of activity. The few species that have been studied metabolically conform to this dichotomy, but a wide range of taxa need to be examined before any generalizations can be made.

Little is known about energy budgets of amphibians. G. Smith (1976) assumed an assimilation efficiency of 74% for *Bufo terrestris* with approximately half of the energy going into metabolic costs. In the salamander *Plethodon cinereus*, digestive efficiency does not change with size or sex, but caloric intake increases with size (Crump, 1979). Also, digestive assimilation is negatively correlated with temperature in this species and in *P. shenandoah* (Bobka et al., 1981). However, assimilation efficiency also varies with the kind of food. Assimilation efficiency by *Scaphiopus couchii* is 90% when fed on *Tenebrio* larvae but only 69% when fed on *Tenebrio* beetles, which contain proportionately more indigestible chitin (Dimmitt and Ruibal, 1980).

Rates of food consumption are highly variable. The semiaquatic hylid frog *Acris crepitans* is active for about 7 months and feeds by night and day (B. Johnson and Christiansen, 1976). These frogs contain an average of 6.74 prey items in the stomach, and the rate of food passage through the digestive system is about 8 hours. Thus, it was calculated that each frog consumes about 20 prey items per day. Food consumption was greater in larger individuals, females, breeding individuals, and frogs with small fat bodies. It seems that this small frog must feed nearly continuously throughout its activity season in order to maintain a positive energy budget. This is in striking contrast to some desert anurans that are active for only short periods of time during the year. On the basis of diet, stomach capacity, and energy budgets, Dimmitt and Ruibal (1980) concluded that *Scaphiopus couchii* (which may consume termites equal to 55% of its body weight at one feeding) is capable of consuming enough food at a single feeding to provide it with energy reserves for 1 year. Other desert-dwelling anurans are not so efficient; *S. multiplicatus* requires 7 feedings, and various species of *Bufo* require 11–22 feedings in order to accumulate sufficient fat reserves and other necessities (e.g., trace elements and electrolytes) for 1 year. Because of fluctuating availability of prey or environmental limitations (e.g., dry weather), amphibians may not be able to feed effectively throughout their season of activity. Thus, R. Jaeger (1980) found that some individuals of *Plethodon cinereus* were existing on negative energy budgets during hot, dry weather.

Interrelationships of Foraging Strategies and Constraints

An animal must maintain a positive energy budget in order to grow, reproduce, and survive periods of inactivity. Optimal foraging behavior of predators varies when they have a choice of prey differing in quality and/or varying in abundance, either temporally or spatially (Pyke et al., 1977; Krebs, 1978). Optimal diet includes the kinds of prey which, if eaten whenever encountered, will maximize the intake of caloric value per unit time. Optimal prey choice depends on the predator's ability to distinguish among prey of varying profitability and to choose the more profitable kinds. Ideally, the predator needs information about six more or less constant values in order to evaluate the caloric profitability of a kind of prey (R. Jaeger and Barnard, 1981): (1) gross calories per prey; (2) predator's assimilation efficiency; (3) rate of digestion of prey; (4) calories expended in pursuit of the prey once encountered; (5) probability of capturing the prey once pursued; and (6) calories expended in handling the prey once captured. The most profitable kind of prey gives maximum values for 1, 2, 3, and 5, and minimum values for 4 and 6. When the most profitable kind of prey is abundant and easy to capture, the energy expended per search time is low, so theoretically the predator can maximize net energy gain by specializing on that kind of prey. As the abundance of that prey decreases and energy per search time increases, the predator can maximize net energy gain by expanding its diet to include the next most profitable kind of prey. When all kinds of prey are scarce, the predator must be indiscriminate in its choice of diet in order to maintain a positive energy budget.

The only empirical tests of these ideas using an amphibian are included in R. Jaeger and Barnard's (1981) study on *Plethodon cinereus*. They found that the salamanders had an indiscriminate diet at low prey densities and specialized on larger prey at high densities, but at such times the salamanders did not exclude small prey. Also, salamanders switched from pursuit to sit-and-wait tactics with increasing prey density. R. Jaeger and Barnard (1981) concluded that the salamanders compromise between maximizing net energy while foraging and minimizing the time for passage of prey through the digestive tract; small prey (in this case, flies) take longer to digest than larger flies because of their proportionately larger exoskeletons. Experiments on feeding of *Bufo marinus* by Heatwole and Heatwole (1968) revealed that hungry toads selected larger prey, but as the toads became satiated they selected smaller prey.

Therefore, digestive time, as well as assimilation efficiency, is important in regulating the net energy gain from a given amount of food in a given amount of time. The energy gained from any feeding sequence determines the amount of energy available for a subsequent (although not necessarily sequential) feeding without drawing on fat reserves. In this context, a sit-and-wait strategist capable of ingesting large prey uses very little energy in obtaining food and obtains large quantities of energy from a given prey. Therefore, amphibians such as *Ceratophrys* and *Pyxicephalus* need to eat infrequently. Feder (1983) suggested that low metabolic rates, relatively large energy reserves, and thus profound resistance to starvation enable plethodontid salamanders to survive indefinite periods between feedings. On the contrary, amphibians that actively search for prey and consume small prey items (e.g., *Dendrobates*) must maintain a continuous feeding schedule in order to maximize fitness. Those amphibians that have evolved highly specialized feeding mechanisms specialize on small prey, of which ants are the most abundant; many feeding specialists have diets composed entirely of ants. In at least three species of dendrobatids, predation on ants is correlated with high aerobic activity, low anaerobic capacity, and high resting metabolism, as contrasted with the sit-and-wait strategist, *Eleutherodactylus coqui* (Taigen and Pough, 1983).

The different feeding mechanisms that evolved in diverse lineages of amphibians, whether these be the highly projectile tongues of bolitoglossine plethodontid salamanders or the paedomorphic conditions of pipid frogs, simultaneously increase the effectiveness of capturing particular prey and impose morphological constraints. The more complex a morphological mechanism, the more rigid its associated physiological attributes and behavioral traits. The foraging strategies of species may be affected by proximal temporal variation in both prey abundance and the physical environment. Ultimately, the feeding tactics employed by any organism are constrained by the morphological mechanisms available to the species.