Chapter 10

Foraging Ecology and Diets

Chapter Outline

Amphibians and reptiles are often the most abundant terrestrial vertebrates at any locality in the warmer parts of the world, and like other animals, they must eat other organisms to survive. Given their high species diversity and abundance, their impact on other animal species—and in some instances, plants—is not trivial. Although some particularly interesting exceptions exist, caecilians generally feed on earthworms and other invertebrates, frogs and salamanders feed almost exclusively on insects (at least as adults), crocodylians feed largely on other vertebrates, turtles feed on a combination of plants and animals, and squamates feed largely on invertebrates or vertebrates, although all members of two lizard taxa (Iguanidae and Leiolepidinae) are herbivorous. In addition, a large number of small-bodied liolaemid lizards in southern South America are herbivorous. Many lizard squamates across taxa feed occasionally on fruits and flowers.

In nature, amphibians and reptiles have a huge diversity of food items available, yet no amphibian or reptile eats all available items. More explicitly, none samples available food randomly. Instead, an individual eats a particular subset of available food, and diets of individuals usually reflect diets of a species in a particular habitat. The preferred food can range from a variety of appropriate-sized arthropods or insects to just one prey type, such as termites. Even among species living in the same area, diets differ. Are these differences the result of competition? How much of the variation in diets that we see among species living in the same environment is historical? These issues are examined in Chapter 13. The emphasis here is how amphibians and reptiles detect, pursue, and capture their prey; the relative sizes of prey; the kinds of food they eat; and the evolution of sensory systems relative to prey choice. Diets of amphibians and reptiles are complex and influenced by many abiotic and biotic variables. As a result, methods, analyses, and interpretations of diet studies vary considerably, and no single "best" protocol exists.

FORAGING MODES

Two well-publicized foraging modes are recognized: sit-and-wait foraging (also referred to as ambush foraging) and active foraging (also referred to as wide foraging). These foraging modes were originally defined on the basis of behaviors used to locate and capture prey. Theoretically, sit-and-wait foragers invest little time and energy searching for prey. They typically remain stationary and attack mobile prey that move within their field of vision. Most foraging energy is spent in the capturing and handling of prey. Active foragers move about through the environment in search of prey, expending considerable energy in the search phase but little energy in the capture phase of foraging. Although many species of amphibians and reptiles can easily be placed into one of these two categories, some are herbivorous, and, as a consequence, they do not pursue prey in the classical sense. Whether or not a "continuum" exists between sit-and-wait and wide foraging remains controversial. Early studies indicated that such a continuum should exist based on theoretical grounds. Recent studies showing

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that major dietary shifts (along with associated morphological and behavioral shifts) occurred deep in the evolutionary history of squamates raise questions about the reality of such a continuum. In addition, even though significant data have been collected on relevant behavioral correlates of foraging mode, we have barely begun to scratch the surface in terms of compiling data on most of the world's herpetofauna.

Our theory on foraging is based heavily on the idea that foraging behavior is evolutionarily plastic and responds to differences in prey abundance and behavior. A decade ago, discussions of foraging mode were strictly selection based. Foraging behavior was assumed to be driven in each species by a combination of competition and energetic aspects impinging upon a particular species. This interpretation was made and widely accepted in spite of the observation that specific foraging modes were shared by closely related species and groups of species. One prediction of this hypothesis is that a continuum of foraging modes should exist. The introduction of modern comparative methods that apply evolutionary analyses to behavioral and ecological phenomena provides a different perspective. For example, phrynosomatid lizards are sit-and-wait foragers, whereas teiid lizards are active foragers. Mapping foraging modes on a phylogeny reveals that sit-and-wait foraging is shared between the earliest branching squamate clades (Gekkota) and the other lepidosaurian clade, the sphenodontans or tuataras. This observation argues for the evolution of sit-and-wait foraging in the distant past and the origin of active foraging much later during the evolution of squamates. The observation further suggests that active foraging in lizards likely arose as a single evolutionary event. Evolution of sit-and-wait foraging in iguanians and some smaller clades arose independently even later.

The bimodality of sit-and-wait versus active foraging appears obvious within single assemblages of species (e.g., lizards in the deserts of the southwestern United States or frogs in the Amazonian rainforest). A synthesis of lizard foraging data by Gad Perry shows that bimodality is evident and no continuum of foraging modes is detectable when the confounding effects of phylogeny are removed (Fig. 10.1). Phylogenetic analyses of other behaviors related to foraging also indicate that much of the variation has its origins deep within phylogeny rather than representing repeated adaptive responses to prey types, distribution, or abundance.

Nevertheless, extremes in foraging behavior are apparent regardless of the number of evolutionary events causing them. Foraging behavior does not evolve in a vacuum; consequently, numerous ecological, behavioral, physiological, and life history correlates of foraging mode can be identified. Similar to time spent moving and the number of moves per unit time (behaviors associated with search behavior; Fig. 10.1), the so-called "correlates" of foraging mode likely also have a historical basis. Many correlates are intuitively obvious based on behaviors associated with prey search and capture (Table 10.1). Species that are sit-and-wait foragers typically do not move while waiting for potential prey to pass through their field of vision. They would be expected to be visually oriented or even use thermal cues (as in pit vipers), have cryptic morphology or coloration (so that neither the prey nor predators detect them), and have a physiology that functions optimally under conditions in which little movement, other than prey attack, occurs. Actively foraging species search though a habitat for prey and are expected to use a combination of visual and chemical cues for prey detection. Because they move while foraging and have well-developed chemical senses, they can find nonmoving, clustered, or hidden prey that might not be detected by sit-and-wait foragers. Movement alone offsets crypsis to at least some degree, so active foragers would be expected to be wary because potential predators would have little problem detecting them. Rapid response would be at an advantage for these species,

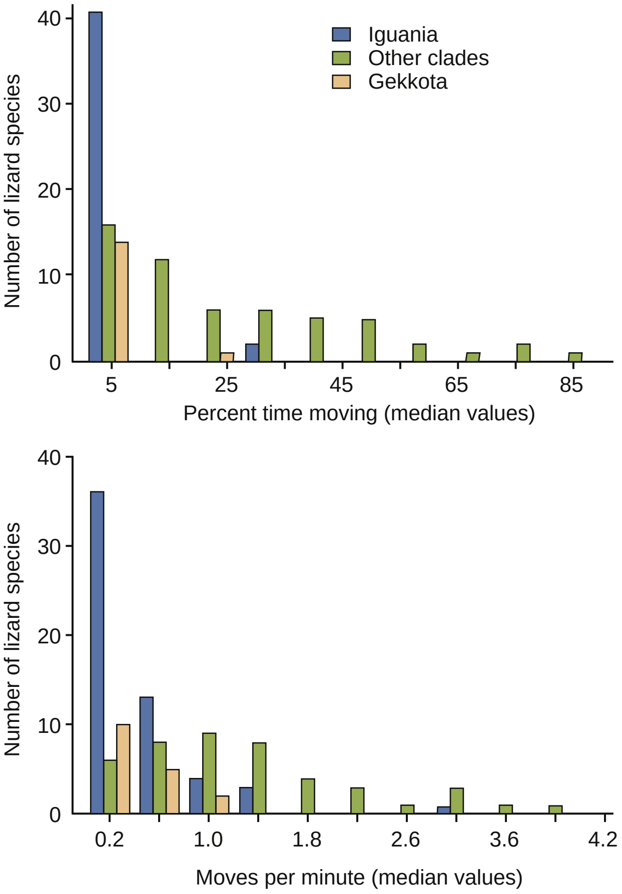

FIGURE 10.1 Two important behavioral attributes of lizard foraging, the number of moves per unit time and the percent of time spent moving, vary considerably across lizard species. Most lizard species in the Iguania, a group typically considered sit-and-wait foragers, make fewer moves and move less distance than lizards in non-gekkotan clades typically considered to be active foragers. Phylogenetic analyses of percent time moving and number of moves per unit time confirm that the apparent bimodality in behavioral attributes of foraging mode have an historical basis (i.e., they reflect phylogenetic patterns rather than easily identifiable ecological patterns). *Adapted from Perry, 2007.*

TABLE 10.1 Correlates of Foraging Mode

Character	Sit-and-wait foraging	Active foraging
Escape behavior	Crypsis, venoms (viperids, one elapid)	Flight, skin or blood toxins (*Phrynosoma* and many frogs), venoms (most elapids, helodermatids)
Foraging behavior		
Movements/time	Few	Many
Movement rate	Low	High
Percent time moving	Low	High
Sensory mode	Vision	Vision and olfactory
Exploratory behavior	Low (social)	High (food)
Prey types	Mobile	Sedentary
Morphology		
Body shape	Associated with microhabitat	Streamlined
Head shape	Short and wide	Long and narrow
Physiological characteristics		
Endurance	Limited	High
Sprint speed	High	Intermediate to low
Aerobic metabolic capacity	Low	High
Anaerobic metabolic capacity	High	Low
Heart mass	Small	Large
Hematocrit	Low	High
Activity body temperatures	Moderate (25–37°C)	High (32–41°C)
Energetics		
Daily energy expenditure	Low	Higher
Daily energy intake	Low	Higher
Social behavior		
Home range size	Variable but smaller	Variable but larger
Territoriality	Common	Rare
Mating system	Resource-defense polygyny	Sequential-mate-defense polygyny
Social signals	Visual	Visual and chemosensory
Reproduction		
Relative clutch mass	If clutch size is variable, relatively high; if clutch size is fixed, low	Relatively low and consistent across species regardless of clutch size

Sources: Bennett and Gleeson, 1979; Brown and Nagy, 2007; Cooper, 1994a, 1995, 1999, 2000, 2002, 2007; Garland and Losos, 1994; Huey and Pianka, 1981; Huey et al., 1984; McBrayer and Corbin, 2007; Miles et al., 2007; Nagy et al., 1984; Perry, 2007; Perry et al., 1990; Perry and Pianka, 1997; Pianka, 1966; Pianka and Vitt, 2003; Pough and Taigen, 1990; Reilly and McBrayer, 2007; Schwenk, 1993, 1995; Secor and Nagy, 1994; Seigel et al., 1986; Vitt and Congdon, 1978; Vitt and Price, 1982; Werner, 1997; Werner et al., 1997; Whiting, 2007.

reducing the probability that predators could capture them. Also, because of their seemingly continual motion while foraging, their physiology should cause them to function optimally while actively searching. Support for this view of the influence of foraging ecology on other aspects of an animal's biology stems mainly from studies comparing two or a few species that differ not only in foraging behavior but also in evolutionary histories. Such analyses cannot distinguish whether the evolution of one foraging mode to the other caused the behavioral, physiological, and ecological differences or is just part of a complex set of coevolved traits. As compelling as foraging behavior appears to be as the driving force behind the traits listed in Table 10.1, an analysis of complete physiological, behavioral, and ecological data testing this hypothesis has not been performed. The analysis by Gad Perry is a bold step toward solving this complex puzzle and should be taken as a challenge to assemble the data set allowing such an analysis. Phylogenetic analyses by others suggest that foraging mode, prey detection systems, and morphology comprise adaptive complexes in amphibians and reptiles.

File snakes (*Acrochordus arafurae*) offer an interesting perspective on the relationship between sensory modes and foraging behavior. Clear differences exist between males and females in foraging behavior. Male file snakes search actively for small fish in shallow water, whereas females ambush large fish in deep water. Males use chemical cues (fish scent) to detect prey, whereas females primarily use prey movement to detect prey. These differences suggest a functional relationship between foraging behavior and types of cues used for prey detection without the confounding effects of phylogeny, geography, or other variables that might account for differences.

Optimal foraging theory is a popular explanation for the evolution of foraging modes. This theory dictates that animals best able to harvest resources should be at a selective advantage when competition among individuals exists. Thus natural selection should favor the fine-tuning of resource acquisition ("optimal foraging"). Because growth, maintenance, and reproduction require energy (Chapter 7), the payoff for foraging "optimally" is presumably increased reproductive success. Although heuristically appealing, optimal foraging theory is overly simplistic, and many empirical studies fail to support most of its predictions. One prediction, however, is supported; when food is scarce, animals tend to eat a greater variety of prey types than they do when food is abundant. In natural environments, foraging is extremely complex. External, internal, and historical factors influence the ability of individual organisms to acquire food, and these factors are difficult if not impossible to model (Fig. 10.2 and Table 10.2).

Although most species of amphibians and reptiles can easily be assigned to one of the two broad foraging categories, cordylid and gerrhosaurid lizards present a remarkable pattern with respect to foraging mode. Cordylids are sit-and-wait foragers; their sister taxon, the gerrhosaurids, are wide foragers; and the cordylids are nested in a clade of wide-foraging lizards (Scinciformata; see Fig. 20.2).

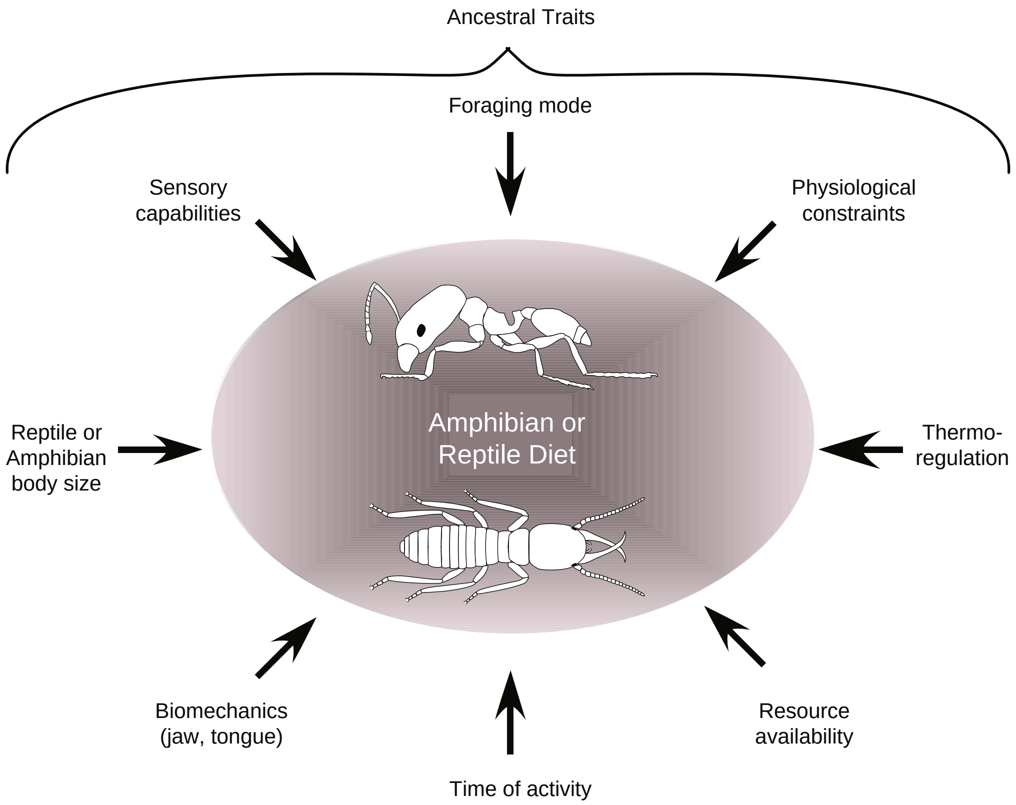

FIGURE 10.2 Diets of amphibians and reptiles are influenced by a variety of abiotic and biotic factors. In addition, the evolutionary history of each species determines a portion of prey preferences. *Adapted from Vitt and Pianka, 2007.*

TABLE 10.2 Factors Influencing Foraging Behavior

External factors
Prey availability
Predation risk
Social interactions (e.g., competition)
Habitat structure (e.g., perch availability)
Opportunities for thermoregulation
Internal factors
Hunger
Learned experiences
Age (e.g., ontogenetic diet shifts)
Sex and reproductive state (e.g., energetic trade-offs)
Epigenetic inheritance (e.g., maternal effects)
Dietary preferences (as influenced by nutrient requirements, toxins, distasteful compounds)
Historical (phylogenetic) factors
Sensory limitations
Morphological characteristics (e.g., mouth shape, head size)
Physiological constraints (e.g., sprint speed)
Behavioral set (e.g., conservative foraging mode)

Source: Adapted from Perry and Pianka, 1997 and Vitt and Pianka, 2007.

Thus sit-and-wait foraging has likely evolved independently in the ancestor to cordylids. One cordylid, *Platysaurus broadleyi*, can vary its foraging behavior based on age, sex, and food availability. Juveniles spend nearly 10% of their time moving and thus fall on the interface between sit-and-wait and wide foraging. Adults are sit-and-wait foragers, unless figs are available. When figs are available, their foraging behavior is more like that of herbivores; the lizards move considerably, searching for figs.

DETECTING, CAPTURING, AND EATING PREY

Prey Detection

Prey of amphibians and reptiles can be detected by visual (usually moving prey), chemical (usually nonmoving prey), tactile (moving and nonmoving), or thermal (moving and nonmoving) cues. Many species rely on a single type of cue, but others use combinations of cues to detect prey. Caecilians appear to use their tentacles as chemosensory samplers. Salamanders and frogs primarily use visual cues to detect moving prey, and in many species, responses to movement are so stereotypical that inanimate nonfood items can be rolled in front of an individual (e.g., *Rhinella marina*) and will be ingested. In other species (e.g., *Salamandra salamandra*), prey must meet a specific set of criteria to elicit attack. Certain frogs and salamanders, such as *Anaxyrus boreas* and *Plethodon cinereus*, are quite good at locating some prey items on the basis of olfactory clues alone. Prey detection in crocodylians appears to be based on a combination of tactile and visual cues, but chemical cues via olfaction may also play a role. Among turtles, visual, chemical, and tactile cues can be involved in prey detection. Both the olfactory and vomeronasal systems are likely involved. Among squamates, the entire spectrum of cues for prey detection exists. In most iguanian and gekkotan squamates, visual cues associated with prey movement result in prey attack. In most other squamates (including snakes), chemical cues are important in prey detection and discrimination, but visual cues can also be involved, and in some (e.g., viperids and boids), thermal cues are also involved.

Visual Prey Detection

Visual prey detection is used by most amphibians and reptiles that are sit-and-wait predators and to a lesser degree by many active-foraging species. Neurophysiological studies of the anuran eye show that prey recognition derives from four aspects of a visual image: perception of sharp edges, movement of the edges, dimming of images, and curvature of the edges of dark images. Perception is greatest when the object image is smaller than the visual field. Under these conditions, anurans can determine the speed, direction of movement, and relative distance of the prey. Success in capture by visual predators depends on binocular perception in many species; most align their head or entire body axis with the prey before beginning capture behavior. Chameleons are an exception in that they have independently movable eyes, and when one eye detects a prey item, the head turns to allow both eyes to focus on the prey prior to aiming the projectile tongue. These movements give the impression that binocular vision is being used to determine the distance of the prey item (Fig. 10.3). However, accommodation (focus) is most important in coordinating prey detection and prey capture in chameleons. They can accurately orient on and capture a prey item at substantial distances with only one functioning eye.

Frogs are able to respond to prey that appear anywhere in their 360° field of vision at the ground level, although when given choices, they reliably choose prey in some positions over others. Experiments with *Lithobates pipiens* showed that they preferentially choose prey located directly in front of them over prey located to one side, even when the former is further away. They also choose prey at ground level over prey in the superior field. The parts of the brain that mediate these choices are the optic tectum and the midbrain nucleus

FIGURE 10.3 The eyes of chameleons, such as this *Furcifer pardalis*, move independently until a prey item is sighted. *Photograph by Chris Mattison.*

isthmi, although at present the selective advantages, if any, of these choices are unclear. The frogs are equally efficient at capturing prey located to the sides or to the front of their body.

The extensive use of vision in prey capture is also apparent from the number of diurnal and nocturnal species with large, well-developed eyes (Fig. 10.4). Most but not all vertebrates have multifocal lenses that have concentric zones of different focal lengths. Almost all vertebrates, including amphibians and reptiles, that have multifocal lenses have pupils with vertical or horizontal slits, rather than round pupils. Apparently pupils in the shape of slits allow use of the full diameter of the lens whether in low light or bright light (Fig. 10.5). Additional work on snakes has suggested that foraging mode and diel activity times correlate with pupil shape. Most snakes with vertical pupils are nocturnal and are ambush foragers. Snakes with round pupils are generally diurnal, active foragers. Exceptions occur in most clades, and additional work is necessary to understand the combination of traits that select for various optic systems.

Nevertheless, even in species that appear to use visual cues, more than simple detection of movement is involved. For example, most phrynosomatid lizards eat a wide diversity of insects, but lizards in the genus *Phrynosoma* specialize on ants. Arguably, *Phrynosoma* do not specialize on ants because ants are usually the most abundant insects; however, by the same reasoning, other syntopic lizards are selectively not eating ants. Regardless of which species actually are the specialists, amphibians and reptiles relying on visual cues do not randomly capture all available moving prey. Prey selection demonstrates a high level of visual acuity, sufficient to discriminate based on size and shape.

Chemosensory Prey Detection

The use of chemical cues in prey detection of amphibians and reptiles is just beginning to be appreciated. Chemosensory-oriented amphibians and reptiles use one or more of three chemical senses: olfaction, vomerofaction, and taste (gustation) (see Fig. 2.32). The first two are used in prey location and identification; olfaction uses airborne odors and vomerofaction uses airborne or surface odors. The olfactory epithelium in the nasal chamber is sensitive to volatile compounds carried by the air and inspired with respiratory air or “sniffing” by rapid buccal or gular pumping. The vomeronasal (Jacobson’s) organ is especially sensitive to high molecular weight compounds that are transported into the oral or nasal cavity by the snout or tongue. Olfaction acts mainly in long-distance detection, for example the presence of food and its general location, and triggers tongue flicking and the vomeronasal system. Vomerofaction operates as a short-range identifier and appears more important than olfaction or gustation in feeding. The vomeronasal system requires that chemicals be brought in, usually by the tongue, which can pick up volatile chemicals from the air or nonvolatile chemicals by lingual contact with surfaces (Fig. 10.6). Gustation functions during feeding as the final discriminator in those species that have taste buds.

Olfaction and vomerofaction have long been recognized as feeding senses in salamanders and many squamates and are often used in conjunction with vision. Actively foraging predators, such as teiid lizards, use vision while moving across open-surface microhabitats but depend on vomerofaction to locate prey in dark crevices or buried in leaf litter or soil. Likewise, many salamanders probably alternate between visual and vomerofactory searching depending upon the availability of light and crypsis of the prey. Some salamanders, such as *Hydromantes italicus*, locate, orient on, and capture prey in total darkness, based on chemical cues alone. Iguanian lizards (except the Iguanidae and Leiolepidinae) and most anurans are highly visual predators, and most lack well-developed olfactory–vomerofaction systems. However, observations on *Rhinella marina* and a few other anurans that respond to chemical cues in food suggest that the role of chemoreception in prey detection by anurans may be underappreciated. Among iguanid lizards (e.g., *Dipsosaurus dorsalis*) that are herbivorous, species that have been studied are able to discriminate plants on the basis of chemicals. Historically, turtles and crocodylians were considered to be visual–tactile foragers; however, both groups produce pheromones for individual and species recognition and would seem capable of locating prey

FIGURE 10.4 Pupils in the shape of vertical or horizontal slits are common in frogs, lizards, and snakes, and occur in all crocodylians. Pupils in the lizard and snake shown here are closed; those in the frogs are partially open. Clockwise from upper left: *Hemidactylus mabouia*, *Corallus hortulanus*, *Osteocephalus taurinus*, and *Scaphiopus hurterii*. *Photographs by L. J. Vitt and J. P. Caldwell.*

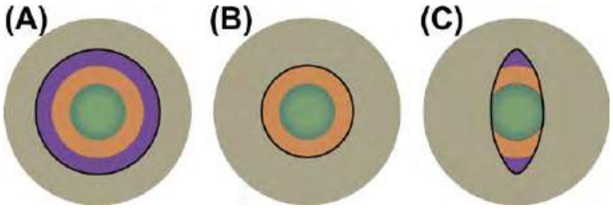

FIGURE 10.5 All zones of the lens in the eye of an amphibian or reptile can be used to focus colors in a fully dilated pupil (A). An iris that constricts concentrically (B) covers the outer area of the lens so that the dark blue spectral range cannot be focused on the retina. An elliptically constricting iris (C) retains all lens zones while cutting down light. *Adapted from Malström, 2006.*

FIGURE 10.6 The long, flexible tongue of *Xenoxybelis boulengeri* picks up particles from the air, surfaces, and potential prey. The odors are transmitted to the vomeronasal organs and allow identification and discrimination. The same sensing system is used in chemosensory-based social communication. *Photograph by L. J. Vitt.*

via odor or vomerodor. Experiments have shown that the American alligator can locate visually hidden food both in the water and on land, suggesting chemoreception in prey identification. Snakes are perhaps best known for their chemosensory abilities because of the often rapid sampling of the air and surfaces with their long, flexible, forked tongues (Fig. 10.6). Not only does the tongue transmit particles to the vomeronasal organs, but because it is forked and thus samples two points, directional information is also conveyed. In some garter snakes (*Thamnophis sirtalis similis*), visual cues alone do not elicit foraging even though they are important for prey capture. Foraging commences when the snakes detect chemical signals with their vomeronasal system. Many squamates that are dietary specialists (e.g., *Heterodon platirhinos* and *Regina septemvittata*) appear to react to specific chemicals contained in prey.

Taste is a chemosensory sense but is used to discriminate rather than locate prey. When combined with the tactile sense organs of the oral epithelium, taste can serve to identify food items once in the mouth and permit rapid acceptance or rejection. Items may be rejected because of taste or because of mechanical stimulation of the tactile sense based on the presence of spines or urticating hairs.

Similar to differences among species in foraging behavior, much of the variation in use of chemical cues has a historical basis in squamates (Fig. 10.7). Chemosensory structures (vomeronasal organs, taste buds) were present in squamate ancestors. Both *Sphenodon* and gekkotans can discriminate prey chemically, so chemical discrimination of prey is likely ancestral in squamates. Chemical discrimination of prey using the vomeronasal system became more prominent in most members of the Scincimorpha, Laterata, and Anguimorpha, with some independent origins of a lack of chemical-based prey discrimination. The exact course of the loss of chemical prey discrimination in most of the Iguania remains unknown, but most likely the ancestor to the Iguania lost the ability to discriminate prey chemically with a shift to visual prey detection, along with a suite of associated behavioral, ecological, physiological, and morphological traits, with at least two clades, Iguanidae and Leiolepidinae, regaining chemical prey discrimination using the vomeronasal system. Many species within the Iguania developed the ability to eat prey such as ants, which contain defensive chemicals (e.g., alkaloids) that might interfere with the lizard's metabolic processes.

Auditory Prey Detection

Use of airborne sound to locate prey may occur widely in amphibians and reptiles, but it remains largely undocumented. The observations are mostly anecdotal, such as *Rhinella marina* orienting and moving toward a calling *Physalaemus pustulosus*, although a recent field experiment showed that the gecko *Hemidactylus turcicus* locates male crickets based on their calls and preys on female crickets coming to the male. The geckos *Hemidactylus frenatus* and *Cosymbotus platyurus* may also use auditory cues in combination with chemical and visual cues.

For some amphibians and reptiles, sensitivity to substrate vibrations or seismic sounds is likely a major prey-detection mechanism. Seismic sensitivity may be particularly important for fossorial (burrowing) species or those with fossorial

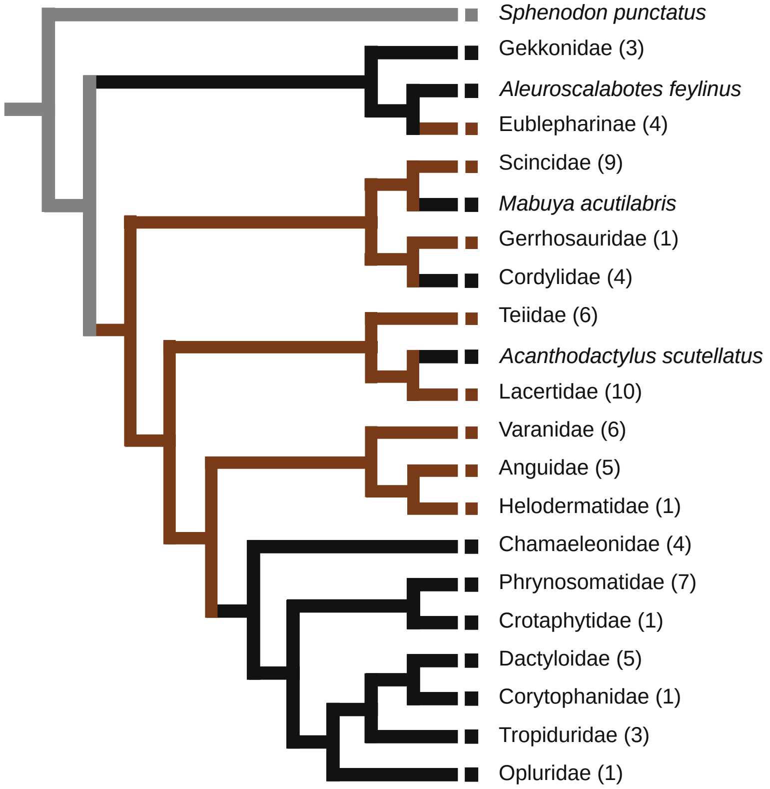

FIGURE 10.7 The evolution of prey chemical discrimination and foraging mode appears linked in squamates. Several evolutionary reversals have occurred within major clades, four of which are shown here (Eublepharinae, *Acanthodactylus scutellatus*, *Mabuya acutilabris*, and Cordylinae). In instances where reversals have occurred, chemical cues are not used for prey discrimination even though the sensing systems are developed. Clade names have been modified to maintain consistency with those in Chapter 20. *Adapted from Cooper, 2007.*

ancestors, both for avoidance of predators and location of prey. Snakes, salamanders, and caecilians have no external ears, so they probably have a high sensitivity to seismic vibration, although actual tests are lacking for most species. Uniquely, both frogs and salamanders have a special pathway (opercularis system) for the transmission of vibrations from the substrate to the inner ear, and the limited data indicate that salamanders are two times more sensitive to these sounds than frogs. The opercularis system links the forelimb to the inner ear through the opercularis muscle that extends from the scapula to the opercular bone lying in the fenestra ovalis of the otic capsule. The muscle acts like a lever arm; vibrations received by the forelimb rock the tensed muscle thereby pushing or pulling the operculum and creating fluid movement in the otic capsule. These seismic vibrations are of low frequency, typically less than 200 Hz, and stimulate the neuroreceptors in the sacculus and lagena rather than those of either the basilar or amphibian papilla, although the latter may be stimulated by frequencies as low as 100 Hz. These low frequencies are made by such activities as the digging of insect prey or mammalian predators. Seismic vibrations appear to be transmitted via the lower jaw through the quadrate to the inner ear in snakes. The desert horned viper *Cerastes cerastes* detects small-amplitude waves in the soil such as that generated by the footfall of prey. The fluid-like motion of the waves causes each jaw bone (quadrate) to vibrate, which transmit vibrations to the inner ear via the stapes. Because both jaws are involved and thus independently detect the signal, stereo precision is achieved and the snakes can easily detect and respond appropriately to passing prey. Snakes also detect seismic vibrations through mechanoreceptors in the skin, although not with the same fine-scaled resolution as with the inner ear. Other fossorial groups (e.g., caecilians, amphisbaenians) likely use mechanoreceptors for detection of seismic vibrations.

Thermal Prey Detection

Some snakes use thermal cues to locate and orient on prey. Infrared light (long wavelength light) is sensed by trigeminal-innervated blind nerve endings in the skin of the head. Many boas and pythons (e.g., *Corallus*, *Morelia*, *Chondropython*) and all viperid snakes in the Crotalinae (e.g., *Crotalus*, *Agkistrodon*, *Lachesis*, *Bothrops*) have infrared sensitive pits either along the jawline in the labial scales (boids) or in the loreal scales (crotalines) at the front of the jaw (Fig. 10.8). The pits open (face) anteriorly and provide a binocular perception field. These receptors are capable of detecting thermal objects moving within the snake's sensory thermal landscape. Temperature changes lower than 0.05°C elicit a response from some snakes. Experiments have demonstrated that snakes can accurately orient on and strike objects based on thermal cues alone. Infrared cues are putatively most effective for nocturnal snakes that feed on mammals and birds because of the large temperature differential between the background thermal landscape and the moving prey, but these cues are likely to be equally effective for a pit viper hidden in a crevice, for example when a lizard with an elevated body temperature enters the crevice. Vipers (Viperinae), *Azemiops feae* (Azemiopinae), and colubrids that have been tested cannot detect thermal cues.

Tactile Prey Detection

Tactile prey detection is poorly understood in amphibians and reptiles, but some rather obvious examples exist. Popular films of large crocodiles appearing to come from nowhere in rivers and ponds to capture large mammals when they break the water surface likely result from tactile cues transmitted through water. The mechanism involves use of mechanoreceptors in the skin. Aquatic amphibians use the lateral line, a string of mechanoreceptors, to sense changes in water pressure reflecting from stationary or motile objects in the near vicinity to identify and locate prey. Such recognition would certainly be enhanced by a weak electric field (see lateral line

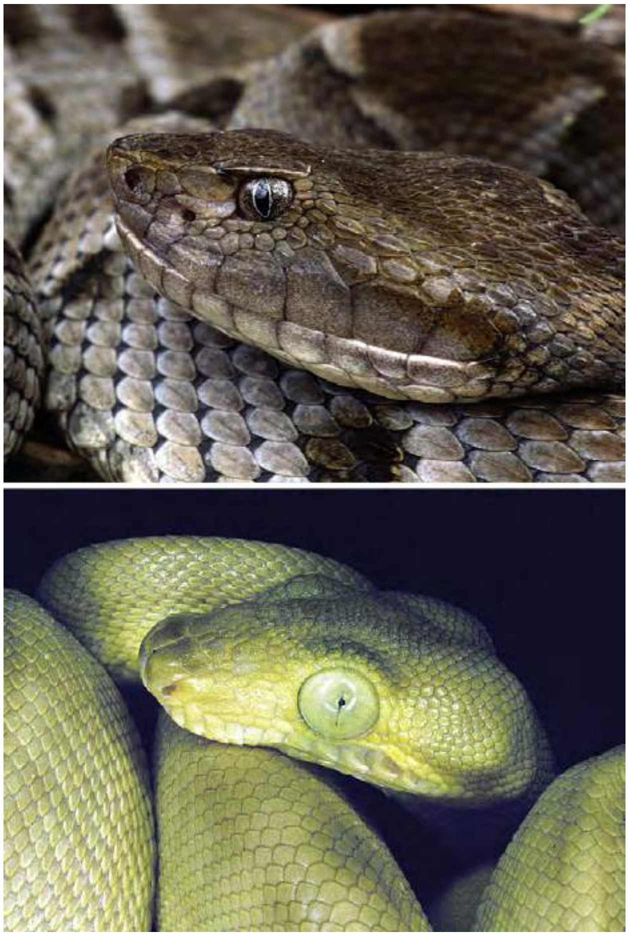

FIGURE 10.8 Facial heat-sensing pits between the nares and the eye on *Bothrops moojeni* and along the jaw of *Corallus hortulanus* allow these snakes to detect moving prey on the basis of their thermal image. *Photographs by L. J. Vitt.*

in "Sense Organs," Chapter 2). Preliminary evidence from aquatic salamanders indicates that prey identification and size determination occur solely by the lateral-line system.

Alligator snapping turtles (*Macrochelys temminckii*) certainly use tactile cues when making the decision to close their mouths on an unsuspecting fish that tries to sample their wormlike tongue (Fig. 10.9). Tactile cues may also be important for turtles, such as *Chelus fimbriatus*, that expand their throats rapidly to vacuum in fish or tadpoles moving in front of them. Flaps of skin are highly innervated and undoubtedly are involved in detection of tactile cues. Many other turtles have barbels about the jaw that are sensitive to water displacement and likely aid in feeding. The tentacled snake *Erpeton tentaculatum* uses a sit-and-wait strategy to attack fish underwater (Fig. 10.10). Appendages on the head (tentacles) may provide tactile cues allowing the snake to accurately strike and capture the fish.

FIGURE 10.9 The alligator snapping turtle *Macrochelys temminckii* lures fish into its mouth by waving its fleshy tongue. The cryptic morphology of the nonmoving turtle combined with the resemblance of the tongue to a small earthworm facilitates prey capture. *Photograph by R. W. Barbour.*

FIGURE 10.10 The aquatic snake *Erpeton tentaculatum* uses appendages on the front of the head to detect tactile stimuli from fish when they approach the snake. *Photograph by R. D. Bartlett.*

Prey Capture and Ingestion

Once detected, prey must be subdued and ingested in order for an amphibian or reptile to appreciate a net gain in energy from the pursuit of prey. A vast majority of amphibians and reptiles swallow their prey whole, and in most species prey are very small relative to the size of the predator. Toads (*Rhinella* and *Anaxyrus*, for example) flick the tongue in and out at such a rapid rate that the entire event cannot be detected easily by the human eye (Fig. 10.11). At the opposite extreme are crocodylians such as *Crocodylus moreletii* in Veracruz, Mexico, which drown large prey and hold them in their mouths for as long as 3 days until they begin to decompose and then dismember and eat them. Komodo dragon lizards fatally wound moderate-sized mammals by slicing through the musculature of their body or legs with

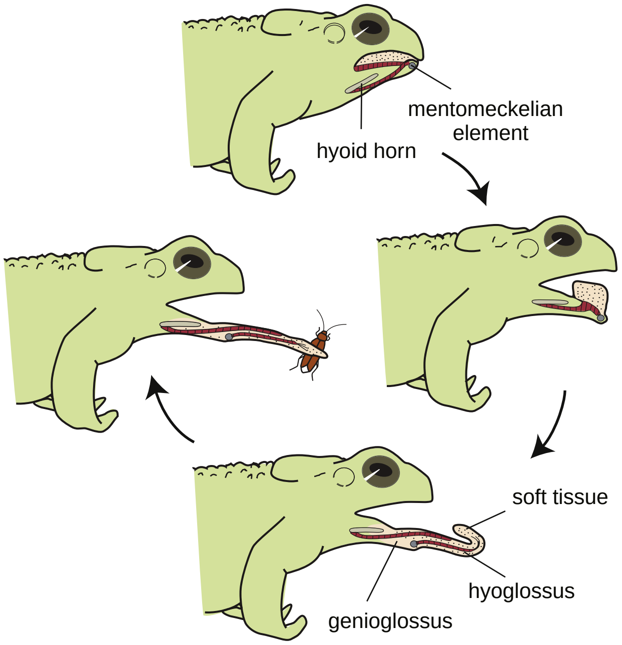

FIGURE 10.11 The anatomical mechanics of an anuran projectile tongue (*Rhinella marina*). The four schematic stages show the projection sequence from tongue at rest on the floor of the oral cavity (top) to its full extension and capture of an insect (left). Five anatomical features are highlighted: the soft tissue of the tongue (stippled); two muscles (black), the genioglossus from the hyoid to the base of the tongue and the hyoglossus from the mentomeckelian element (mm) to the base of the tongue; and two skeletal elements (white), the hyoid horn lying below the tongue and mm at the tip of the jaw. Projection begins (right) with the mouth opening; the mm snaps downward by the contraction of a transverse mandibular muscle (not shown), and the genioglossus contracts to stiffen the tongue. The tongue flips forward (bottom) from the momentum generated by the downward snap of the mentomeckelian element and the genioglossus contraction; the two tongue muscles then relax and are stretched. The tongue is fully extended and turned upside down (left), and the dorsal surface of the tongue tip encircles the prey. The genioglossus and hyoglossus muscles contract, drawing the tongue with the adhering insect back through the mouth as it closes. *Adapted from Gans and Gorniak, 1982.*

their serrated teeth. The mammals die, and monitors are attracted to the putrefying corpse, which the lizards are able to dismember, swallowing large pieces. Alethinophidian snakes swallow prey that are much larger in circumference than they are, and some frogs, such as *Ceratophrys cornuta*, often eat verebrates that are nearly as large as they are. Herbivorous lizards feed on clumped, stationary plant parts, so prey "capture" is a trivial problem. Many species of snakes kill their prey by constriction or envenomation, but some simply swallow their prey alive.

Numerous behavioral and morphological adaptations are associated with capturing and subduing prey. In catching mobile prey, motor and sensory units are finely coordinated to intercept the moving prey, and usually the strike–capture mechanism aims at the center of the mass or gravity of the prey. The center of gravity is the most stable part of the target and has the least amount of movement.

Some reptiles and amphibians use lures to attract their prey. Juvenile viperids use caudal luring enhanced by bright coloration on the tail and cryptic coloration of the body (Fig. 10.12), and lingual-appendage luring occurs in alligator snapping turtles (*Macrochelys*; Fig. 10.9). Pedal luring using the back feet occurs in some species of *Ceratophrys* frogs, and juveniles of *Ceratophrys cornuta* have white toes and webbing, possibly to enhance the outline of the foot against their leaf-litter habitat (Fig. 10.13). *Phyllomedusa burmeiseri* also use pedal luring and appear to discriminate when they use it. When offered crickets, they slowly undulate the fourth and fifth toes, which have white dorsal tips, alternating between feet. When offered cockroaches or mealworms, they do not use this behavior.

FIGURE 10.13 Some frogs, such as *Ceratophrys cornuta*, use pedal luring to attract prey. The light color of the toes on the back feet disappears as the frogs increase in size. *Photograph by J. P. Caldwell.*

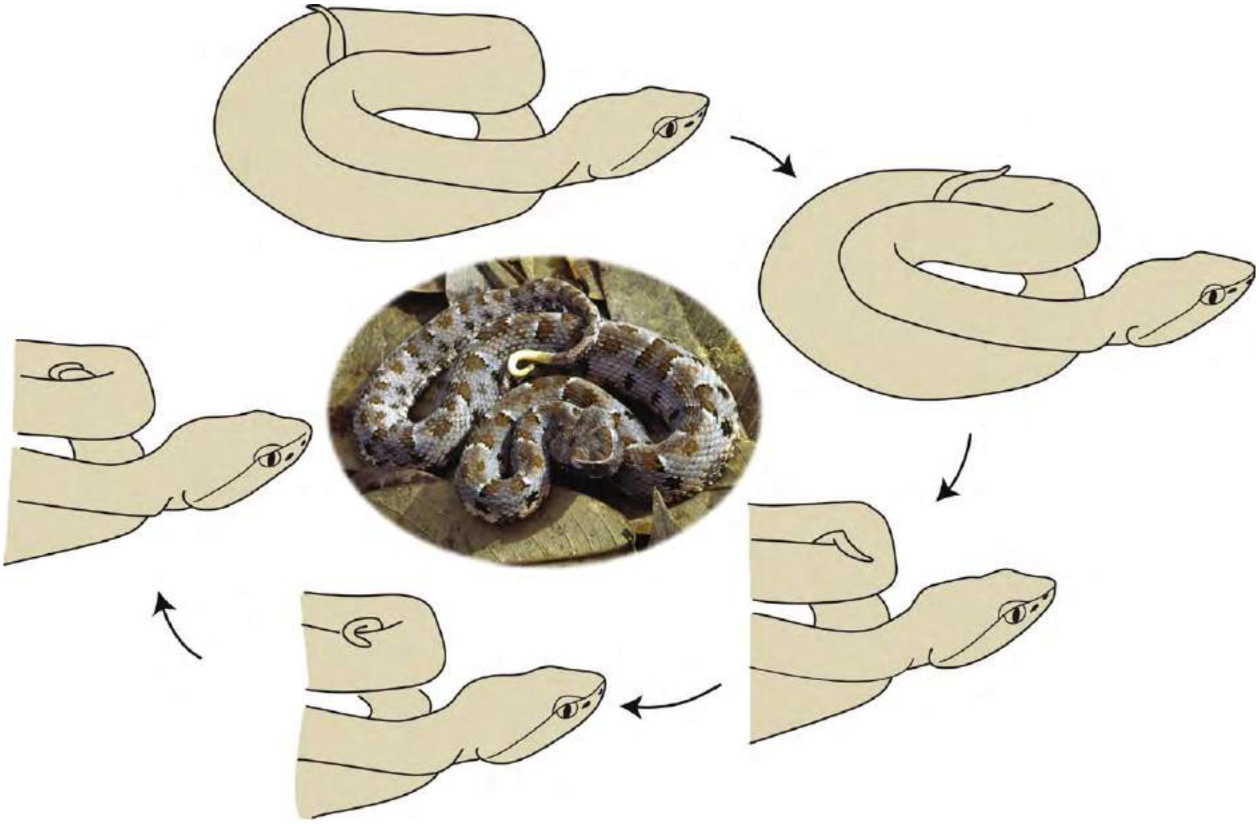

FIGURE 10.12 By waving its brightly colored tail, juvenile *Bothrops* attract frogs and other small insectivorous animals within strike range. The insert shows the contrast between the tail color (yellow in life) and the cryptic coloration of the snake. *Adapted from Sazima, 1991. Photograph by L. J. Vitt.*

Biting and Grasping

Prey capture by most amphibians and reptiles involves biting and grasping. Prey are attacked, either as the result of a rapid sprint by the predator followed by biting the prey, or by a rapid movement (e.g., strike) of the head and neck from a stationary position. Reptiles or amphibians with long, flexible necks (turtles, varanid lizards) and limbless ones (amphiumas, pygopodids, snakes) can and regularly use the strike mechanism, often from ambush but also following a slow stalk of the prey. In both strikes and bites, the mouth commonly does not open until the head moves toward contact with the prey, and the bite–strike is an integrated behavior of motor and sensory units. When the open mouth contacts the prey, the tactile pressure on teeth and oral epithelium triggers rapid closure of the mouth.

Only minimal food processing occurs in the mouth of amphibians and reptiles. Teeth may crush or perforate food items, which are commonly swallowed whole. Some evidence suggests that most lizards, for example, do not swallow arthropod prey items until they have crunched the exoskeleton. If hard-bodied prey fail to crush when bitten, the broad-headed skink *Plestiodon laticeps* repositions the prey repeatedly and attempts to crush it. If the hard-bodied prey happens to be a female mutilid wasp (velvet "ant"), repeated biting allows the insect to use all its defense mechanisms. The powerful sting, injected deep into the tongue, causes the lizard to release the wasp. When approached by a snake, some species of *Rhinella* inflate their body by filling their lungs and tilt their back toward the snake. In response, some snakes, such as the South American snake *Waglerophis merriami*, puncture the inflated lungs of *Rhinella* with their razor-sharp and enlarged maxillary teeth. In these species, the maxillary is reduced in length and rotates forward during biting. Once deflated, the toads can be swallowed by the snake.

Fragmentation of food is limited to herbivores that bite off pieces of foliage, and large lizards, turtles, and crocodylians that use a combination of sharp jaw sheaths or teeth and limb–body movements to break up large items. Turtles have continuously growing keratinous sheaths on upper and lower jaws; each sheath provides a uniform bladelike labial surface that is effective in cutting food (Fig. 10.14). Tooth structure in other reptiles and amphibians is highly variable, ranging from simple cone-like teeth to molar-like teeth or blade-like teeth with serrated edges. Specialized diets usually are associated with specialized teeth: broad and sturdy teeth for crushing mollusks are found in *Dracaena*; blade-like teeth for cutting vegetation or fragmenting large prey are found in *Iguana* and *Varanus*, respectively; long recurved teeth for feathered prey occur in *Corallus hortulanus*; and hinged teeth for capturing skinks occur in *Scaphiodontophis*.

Once captured, prey must be moved through the oral cavity into the esophagus. Three main "swallowing" mechanisms are recognized in amphibians and reptiles. Inertial feeding is mechanically the simplest and most widespread in reptiles. In its simplest form, inertial feeding involves moving the head–body over the food based on inertia alone. The food is held stationary in the mouth. Each time the mouth is slightly opened, the head is thrust forward, thereby shifting the head forward over the food (Fig. 10.14). Snakes swallow large prey in this manner by alternately advancing the left and right sides of the head over the prey using the movement of the palatoquadrate–mandibular skeletal complex. Prey are held secure by this complex on one side of the head, while the bite–grip on the opposite side of the head is relaxed with the jaws on that side of the head shifting forward and then contracting to gain a grip. The alternate forward movement of the left and right sides moves the head and body over the prey. Inertial feeding works well for soft-bodied prey such as slugs (Fig. 10.15) and teeth on the lower jaws can be used to pull snails from their shells.

FIGURE 10.14 Juvenile Aldabran tortoises (*Dipsochelys dussumieri*) eating a leaf from their shade tree. *Photograph by G. R. Zug.*

Manipulation of the tongue and hyoid appears to be the principal swallowing mechanism in amphibians. Some salamanders use hyoid–tongue retraction to swallow prey. After capturing a prey item and with the mouth closed, the tongue presses the prey tightly against the roof of the mouth and the vomerine and palatine teeth. The mouth opens quickly and, with the tongue still firmly holding the prey, retracts and draws the prey inward as the mouth slowly closes. This cycle is repeated until the prey move through the buccopharyngeal cavity. Swallowing in frogs also involves tongue–hyoid movement. Frogs have voluminous oral cavities, and captured prey are usually completely engulfed. Leopard frogs, *Lithobates pipiens*, use different strategies to capture prey, depending on prey size. For small prey, tongue prehension is used to contact the prey and deliver it directly to the esophagus. The head does not move during this motion. With larger prey, jaw prehension is used. In this case, the tongue initially contacts the prey, but the forelimbs are used to help transfer the prey to the mouth. The head moves down as the jaws close on the prey. The ability to use either tongue prehension or jaw prehension occurs in other frogs and in many lizards.

FIGURE 10.15 The mollusk-eating snake *Dipsas indica* uses inertial feeding behavior to swallow a large slug (left) and extended teeth on the lower jaw to extract a snail from its shell (right). *Photographs by I. Sazima.*

Constriction

Constriction is a specialized bite-and-grasp technique used by numerous snakes to hold or kill prey. A constricting snake strikes its prey, and if its bite–grip is secure, a loop of the body is thrown on and around the prey. Additional loops (coils) of the body encircle the prey with continual adjustment to reduce overlapping loops. As the prey struggles and then relaxes parts of its body, the snake tightens its grip. The tightening continues, and ultimately circulatory failure causes death. Increasing compression of the thorax stops the flow of blood to the heart. In species that have been well studied (gopher snakes and king snakes), constriction is much more controlled than generally believed. The snakes can detect muscular, ventilatory, and circulatory movements in the rodent being constricted and respond by tightening and loosening coils accordingly. The snakes maintain a constriction posture several minutes after the rodent stops moving, but if the snake detects circulatory, ventilatory, or muscular movement by the rodent, it reapplies pressure. When struggling ceases and the prey is dead or unconscious, the snake relaxes its coils, locates the head of the prey, and begins to swallow it. Constriction is best known in boas and pythons (Fig. 10.16), and boa constrictors can modify the pressure and duration of constriction based on the heartbeat in their prey. Early snakes (Macrostomata) are flexible in prey restraint behaviors and they can quickly integrate complex prey restraint behaviors such as constriction resulting in greater overall improvement in their feeding behavior.

Some highly venomous snakes constrict their prey after biting and injecting venom. It is easy to visualize constriction in boids, where the prey typically are birds or mammals. However, snakes that constrict fish best exemplify the effectiveness of constriction as a means of subduing and killing prey. The file snake (*Acrochordus*) can attach its tail to underwater roots of mangroves as an anchor, strike a large fish, and rapidly subdue it by constriction. The rough scales on the file snake facilitate holding the fish, and the elastic body apparently serves to buffer the thrashing movements of the struggling fish. Some limbless amphibians (e.g., *Amphiuma*) may use constriction to subdue prey as well. Even snakes such as *Anilius* us constriction when feeding on certain types of prey such as amphisbaenians, which comprise most of their diet.

FIGURE 10.16 Following prey detection and strike and grasp, many snakes, like this Burmese python, coil around their vertebrate prey. Not only does constriction subdue the prey, but it also causes cardiac failure, which kills the prey. *Photograph by S. C. Secor.*

Injected Venoms

Venom delivery systems have evolved independently at least twice within the Squamata. Nevertheless, considerable variation in morphology, development, and effectiveness of venom-delivery systems exists. All members of the Helodermatidae, Elapidae, and Viperidae are venomous, as are several groups of colubrids. Venom subdues prey by either anesthetizing or killing it. A nonstruggling prey is much safer and less energetically demanding to capture and swallow than a struggling one. Also, a predator can eat larger prey if they do not resist capture and consumption. Many of the viperids add a third benefit to the injection of venom by injecting proteolytic enzymes that aid in digestion.

A venom-delivery system contains four elements: glands to produce the venom, muscles to force venom from the glands, ducts to transport venom from the gland to the injection system, and fangs (modified teeth with open or closed canals) to inject the venom into the prey (Fig. 10.17). The fangs of helodermatids and most venomous colubrids bear a single groove on one side of each enlarged tooth, whereas the fangs of elapids and viperids have closed canals. The venom is produced continuously in the venom glands and stored in venom-gland chambers. When elapids or viperids bite a prey animal, muscles over (adductor superficialis in elapids) or around (compressor glandulas in viperids) the glands contract and squeeze a portion of the venom through the venom ducts and into the fang canals. The snake can regulate the venom dose depending on the size of the prey and possibly how much venom is available. Viperids and some elapids strike, bite, inject venom, and release the prey, whereas most elapids, colubrids, and *Heloderma* maintain their bite–grip and chew the wound to ensure deep penetration of venom. Elapids and most rear-fanged colubrids have relatively small fangs. With few exceptions, these fangs are fixed in an erect position. The greatest deviation from fixed fangs in elapids occurs in the death adder (*Acanthophis antarcticus*) of Australia, which has morphology and foraging behavior strikingly convergent with that of terrestrial viperids. The front fangs are fixed on a highly movable quadrate bone.

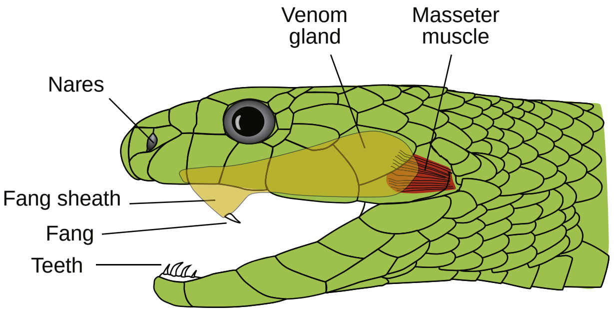

FIGURE 10.17 Venomous snakes have movable (Viperidae) or fixed (Elapidae, some Colubridae) fangs to inject venom. Venom is delivered to the fangs from venom glands via venom ducts. *Modeled after a drawing of a taipan, Oxyuranus scutellatus, in Shine, 1991.*

Recent evidence from developmental biology indicates that fangs in snakes likely arose only once, contrary to prior

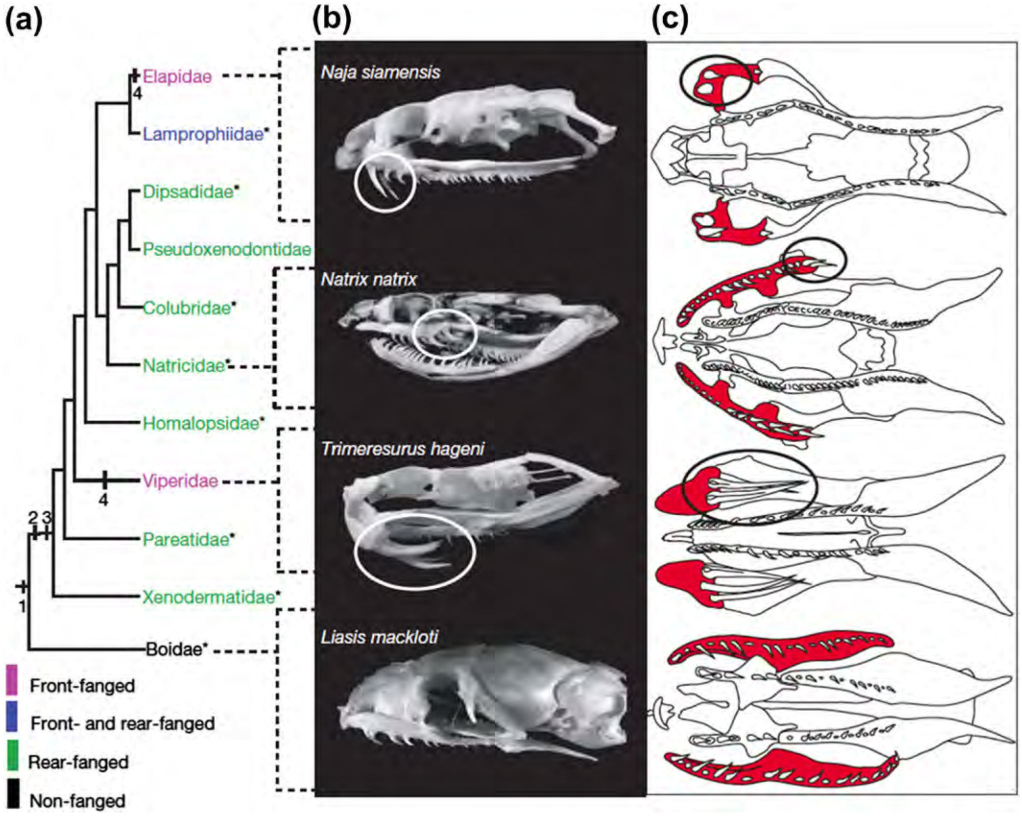

FIGURE 10.18 Molecular snake phylogeny showing adult maxillary dentition and relative positions of the various fang types in snakes. a. Phylogeny of snakes; b. lateral views of adult snake skulls with fangs circled in white; c. drawings of corresponding snake palates (ventral views) with maxilla colored red and fangs circled in black. Species studied with electron microscopy are indicated by asterisks. Evolutionary changes leading from an unmodified maxillary dentition (bottom) to the different fang types in advanced snakes are indicated at nodes on the phylogeny: (1) continuous maxillary dental lamina, no specialized subregions—ancestral condition for advanced snakes; (2) evolution of posterior maxillary dental lamina—developmental uncoupling of posterior from anterior teeth; (3) differentiation of the posterior teeth and the venom gland; (4) loss of anterior dental lamina and development of front fangs. *Adapted from Vonk et al., 2008.*

belief, and thus are homologous. Erectable front fangs (viperids) and fixed rear (colubrids) and front (elapids) fangs lie on modified maxillary bones, which hold the outer rows of teeth in fangless ancestors, such as boids (Fig. 10.18). During development, a specialized maxillary dental lamina not present in boids appears in viperids and ultimately bears fangs. The maxillary dental lamina dilates into a bifurcated epithelial sac, the lateral part of which gives rise to the venom gland and duct by growing out from the dental lamina and turning back into the jaw reaching the post-orbital region. Even though adult morphology of the maxillary bones differs considerably among colubrids, viperids, and elapids, the developmental sequences producing those differences are similar early in development, suggesting homology.

Venom of each snake species is a composite of several compounds that work synergistically to subdue prey (Table 10.3). Typically, venom causes either tissue destruction or neurological collapse. Tissue-destruction venoms subdue prey because the prey goes into shock, and neurological-collapse venoms prevent nerve impulse transmission and interrupt all motor activity, including respiration. The immobile prey can then be eaten safely.

Projectile Tongues

Tongues are small and usually have limited or no mobility in aquatic amphibians and reptiles. Tongues became important in terrestrial animals when water was no longer present to carry food through the oral cavity into the esophagus. A protrusible tongue for sampling the environment and gathering food probably evolved early in terrestrial tetrapods, because protrusion is widespread in amphibians and reptiles. Many bite-and-grasp feeders (herbivores and carnivores) use their tongues to retrieve small items. The tongue is extended through the mouth and the item is touched by the tip or dorsal surface of the tongue. The item is held by sticky saliva and the tongue is retracted. The most dramatic tongue protrusions are the projectile tongues, which have evolved independently several times in amphibians and reptiles.

Most frogs capture prey by projecting the tongue (Fig. 10.11), but the mechanism is different from that found in salamanders (Fig. 10.19) and even differs among frogs. The frog's tongue is attached at the front of mouth and has a direct attachment to the cartilaginous symphysis joining the right and left sides of the mandible. When a prey item is identified, the frog orients its body perpendicular to the prey. The mouth opens and the lower jaw drops downward. The genioglossus muscle, which lies within the tongue, contracts, stiffening the tongue. The submentalis muscle (linking left and right mandibles beneath the middle of the tongue) contracts to form a pivot point that yanks the symphyseal cartilage downward. This movement pulls the anterior end of the tongue downward, and the momentum imparted to the tongue flicks the posterior end outward in much the same fashion as a catapult. The weight of the tongue's posterior half stretches the tongue to twice its length, and as the upper surface of the tongue hits the prey, the posterior tip wraps over the prey. The tongue is

TABLE 10.3 Major Types of Reptilian Venoms and Some Examples of the Function of Each Type

Enzymes	
All venoms contain several different enzymes; more than 25 enzymes occur in reptilian venoms.	
Proteolytic enzymes	digest tissue protein and peptides causing hemorrhagic necrosis and muscle lysis; also known as endopeptidases. Common in crotalines, less in viperines, absent in elapids.
Thrombin-like enzymes	interfere with normal blood clotting, either by acting as an anticoagulant or procoagulant. Common in viperids, rare in elapids.
Hyaluronidase	breaks down mucopolysaccharide links in connective tissue and enhances diffusion of venom. In all venomous snakes.
Phospholipase	modifies muscle contractibility and makes structural changes in central nervous system; also interferes with the prey's motor functions. Common in colubrids, elapids, viperids.
Acetylcholinase	interrupts ganglionic and neuromuscular transmission and eventually affects cardiac function and respiration. Common in elapids, absent in viperids.
Polypetides	
The polypetides are toxic nonenzymatic proteins of venoms. These toxins commonly act at or near the synaptic junctions and retard, modify, or stop nerve-impulse transmission.	
Crotactin	produces paralysis and respiratory distress. In rattlesnakes, crotalines.
Cobrotoxin	acts directly on heart muscle to cause paralysis. In cobras, *Naja*.
Viperatoxin	acts on medullary center in brain, resulting in vasodilation and cardiac failure. In *Vipera*.
Miscellanea	
Various ions and compounds that are found in venoms but as yet have no recognizable prey-type or taxonomic-group association.	
Inorganic ions	sodium, calcium, potassium, iron, zinc, and others; some enhance the activity of specific enzymes.
Glycoproteins	anticomplementary reactions that suppress normal immunological tissue response.
Amino acids and biogenic amines	

Note: Reptilian venoms are an admixture, consisting mainly of enzymatic and nonenzymatic proteins.

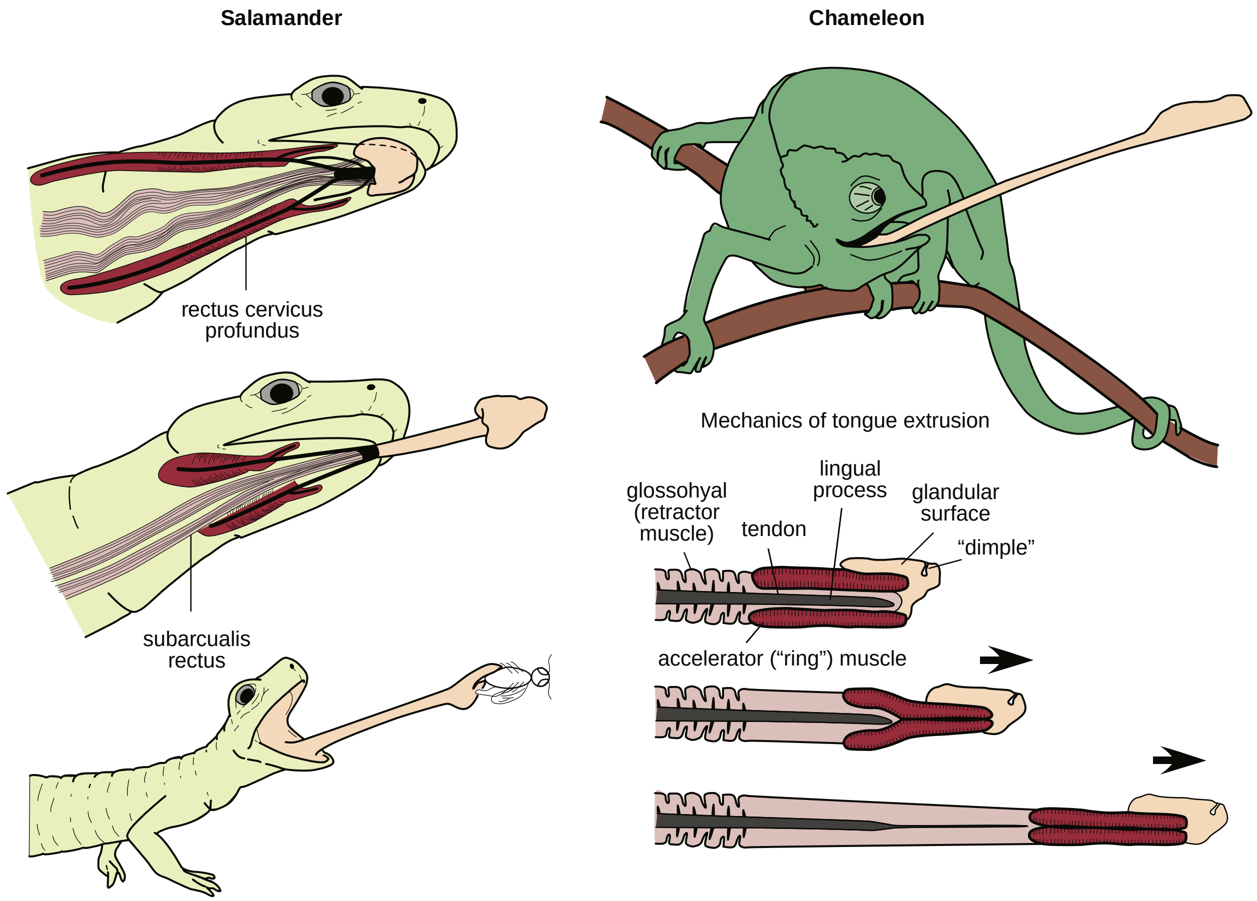

FIGURE 10.19 Anatomical mechanics of a salamander and a chameleon tongue. *Salamanders redrawn from Duellman and Trueb, 1986; chameleon redrawn from Kardong, 1998.*

retracted by a quick contraction of the hyoglossus muscle in the posterior region of the mouth, with the prey stuck to the tip of the tongue. For most frogs, direct orientation on the prey is necessary because the tongue flips out in direct line with the frog's head. However, the microhylid *Phrynomantis bifasciatus* is able to send its tongue out in nearly every possible direction (Fig. 10.20). Rather than using muscles to pull the tongue and flip it out as in other frogs, *Phrynomantis* has a hydrostatic muscle that pushes the tongue out. The hydrostatic mechanism allows the frog to send out its tongue within a range of about 105° to either side of center. A tongue that functions in this manner should be particularly useful for frogs that feed on tiny prey, such as termites.

The Indian frog *Nasikabatrachus sahyadrensis* uses an entirely different mechanism for feeding. This fossorial frog lives entirely underground except when it migrates to pools for breeding at the beginning of the monsoon season. Whereas most frogs have a wide gape and flip their tongues out to catch prey, *N. sahyadrensis* has a narrow, pointed head with a small ventral mouth. The head has a hard callus on the tip of the snout to facilitate burrowing (Fig. 17.35). The upper jaw is rigid and overlaps the lower jaw, which is flexible and can be formed into a small tube-like oral groove. The frog feeds almost exclusively on underground termites by breaking into underground runs and consuming the insects by protrusion of its fluted tongue through the groove formed by the lower jaw. Many species of termites commonly live underground in rainforest. In addition to being the frogs' preferred prey, termites create tunnels that allow penetration of water into the subsoil, providing an aerated, moist habitat for the frog. Two other unrelated fossorial frogs, *Rhinophrynus dorsalis* and *Hemisus guttatus*, have similar morphology for living underground and consuming termites.

Terrestrial salamanders orient on prey and rapidly extrude the tongue, which, in many species, has a large pad on the tip (Fig. 10.19). Mucous on the tongue tip adheres to the prey item, and longitudinal muscles retract the tongue and prey. The mechanics of tongue extrusion vary among salamander taxa. The large fleshy tongue of most ambystomatids is flopped out on a prey item, whereas highly derived elongate tongues with fleshy tips are projected for considerably longer distance in various plethodontids. Projectile tongues appear to have evolved independently several times in salamanders, including in lungless hynobiids (*Onychodactylus*), lungless salamandrids (*Chioglossa* and *Salamandrina*), and all plethodontids. Lung respiration and gill waving (a function of the tongue in larvae) likely constrain the evolution of projectile tongues in salamanders because they depend on very different biomechanical mechanisms involving the tongue. The projectile mechanisms in salamanders derive from modifications of the hyoid apparatus, a structure that usually functions to move the floor of the buccal cavity during respiration. The general mechanism of tongue extension includes the projection from the mouth of the pedestal-like tongue tip by the hyoid apparatus. The posterior, bilaterally paired hyoid arms lie in the floor of the mouth like a partially opened fan with the hinge-tip pointed anteriorly. When the hyoid muscles contract, the fan closes and drives the tip outward. The movement is rapid and the momentum, as in frogs, assists in stretching the tongue as much as 40–80% of the salamander's body length. The structure of the hyoid apparatus varies considerably among salamander species. Tongue movement in *Bolitoglossa* is so rapid that a sensory feedback system is not involved. The extensor and retractor muscles fire simultaneously, but the retractor muscle contains enough slack that it does not begin to retract the tongue until the tongue is fully extended.

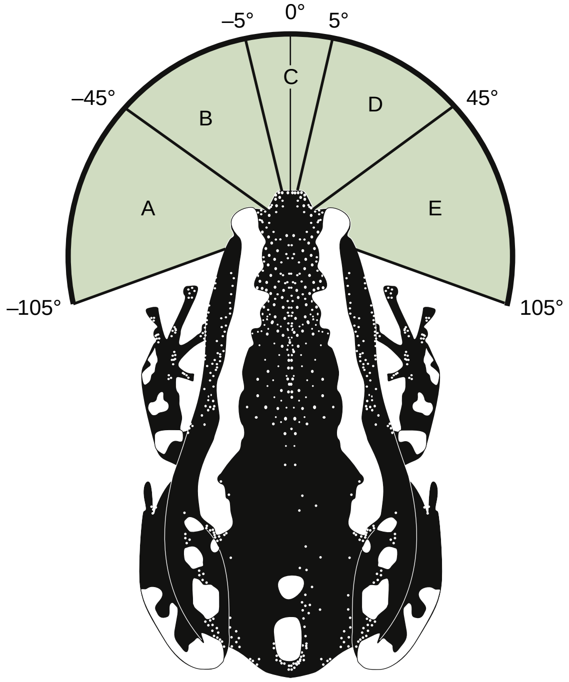

FIGURE 10.20 Unlike most frogs, the microhylid frog *Phrynomantis bifasciatus* can extend its tongue in an arc of 105° to either side of center to capture prey. It does so using hydrostatic force to push the tongue directly out of the mouth. *Adapted from Meyers et al., 2004.*

Chameleons have one of the most spectacular tongue-projection systems known in vertebrates (Fig. 10.19). They can project their tongues at high speed for as much as 200% of their snout–vent length and accurately hit and capture an insect. Precise integration between the ocular system and the tongue-projection system is critical. The projectile tongue of chameleons shoots forward by a hyoid mechanism. Once a chameleon has oriented on an insect after detecting it visually, the head is extended toward the prey, the lower jaw opens, and the tongue slowly extends a short distance out of the mouth. The zygodactylus toes and prehensile tail hold the chameleon firmly to branches from which they forage. The tongue then shoots out toward the prey, the sticky tip captures the insect, and the tongue is drawn back into the mouth with the insect (Fig. 10.21). The mechanism includes a precision system of depth perception based on accommodation, a highly modified hyoid apparatus including a powerful accelerator muscle, and exceptionally contractile hyoid muscles. A nearly constant tongue retraction force over variable tongue extension lengths is attributed to a supercontracting muscle, which, among vertebrates, occurs only in chameleons. Smaller chameleons have relatively larger tongues than larger ones, likely a mechanism allowing ingestion of relatively larger prey when lizards are small.

Filter Feeding

No reptiles and no adult amphibians filter-feed. However, tadpoles of most frogs filter-feed. The diets of

FIGURE 10.21 Ballistic tongues of some chameleons, such as this *Furcifer pardalis*, can extend out more than two times the length of the lizard's body. The short section of the tongue nearest the head that is directed slightly upward contains the process entoglossus, which is part of the hyglossal skeleton that is situated inside the tongue and gives it support. *Photograph by M. Vences and F. Rauschenbach.*

most tadpoles consist mainly of algae and protists, and hence tadpoles are microphagous ("small eating"). Comb-like labial teeth that occur in rows on the oral disc scrape detritus from surfaces. Tadpoles use the movement of water in through the mouth, buccal, and pharyngeal cavity, and out through the gills (branchial arches) for both respiration and food entrapment. Microphagy requires a filter or straining mechanism to capture tiny items and direct them into the gut. A system that includes branchial food traps and gill filters in the pharynx captures smaller particles (Fig. 10.22). Buccal papillae extract large particles and funnel them directly into the esophagus.

The buccopharyngeal cavity of tadpoles is large, more than half the volume of the head of most tadpoles. The upward and downward movement of the buccal floor in association with the opening and closing of the mouth and gill filter valves (vela) moves water through this large cavity. As the mouth opens, the floor drops and draws water into the cavity. The vela prevent a major backflow through the gill openings. The mouth then closes and the floor rises, forcing the water outward through the gill slits. The flow of water brings the food particles to the rear of the cavity and in contact with the gill filter surface. Large particles cannot pass through the filter and are picked up by the papillae, which move them into the esophagus. Strings of mucus snare smaller particles touching the surface. A combination of water movement and ciliary activity moves the strings and trapped food rearward. The strings aggregate into larger clumps before passing into the esophagus with the larger food particles. The volume of food entering the mouth cavity regulates this filtering mechanism. When particle suspension density is high, the buccal pump works more slowly to prevent the gill filters and mucus traps from clogging, and, conversely, if particles are sparse, the system works more rapidly.

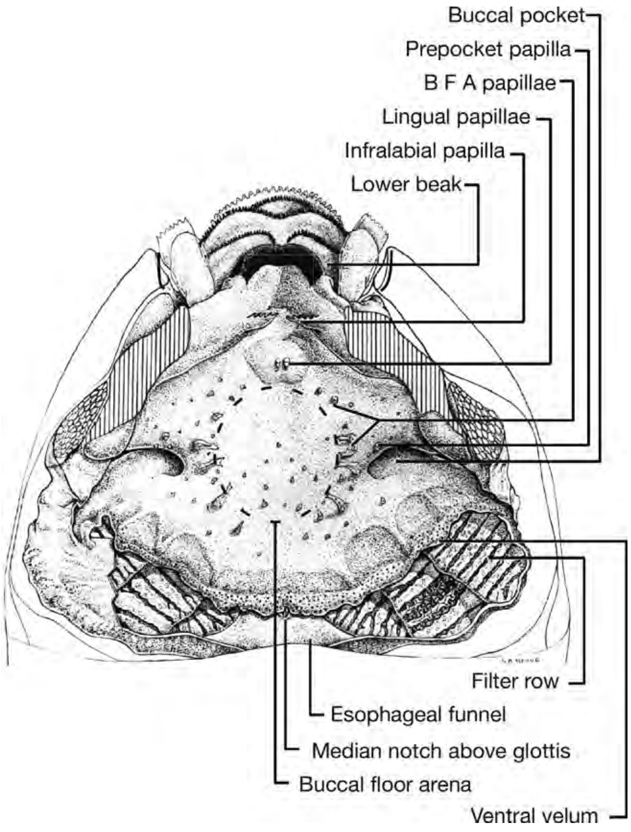

FIGURE 10.22 Floor of the mouth of the tadpole of *Pseudacris regilla*. Tadpoles have several mechanisms for filtering food particles from the water taken into their mouths. Large food particles are channeled into the esophagus by rows of papillae on the floor and roof of the mouth. Smaller particles are strained out of the water as it passes through elaborately folded filters located on the gill bars. Even smaller particles are trapped in mucous strands secreted from glands located in the mouth. *Adapted from Wassersug, 1976.*

Inertial Suction Feeding

Inertial suction feeding is the ancestral mode of feeding in aquatic vertebrates and remains the primary mode of feeding in most aquatic vertebrates. Most teleost fishes, aquatic salamanders and frogs, and aquatic turtles use this mode of feeding. Inertial suction feeding involves capturing prey by quickly opening the mouth while at the same time enlarging the buccopharyngeal cavity. This action generates a negative pressure gradient, carrying nearby prey into the mouth with the rush of flowing water. The hellbender, *Cryptobranchus alleganiensis*, can capture prey alongside its head in addition to prey situated in front of it. This primitive salamander is capable of asymmetrical movements of its lower jaw and hyoid apparatus, which allow it to open its mouth on only one side. The key feature is the ligamentous attachment of the left and right dentaries at the front of the mouth. The flexible attachment permits one side of the jaw to remain in place while the opposite side swings downward, accompanied by a unilateral depression of the hyoid apparatus; this series of movements results in asymmetrical suction.

Pipid frogs are entirely aquatic when active, feeding and breeding in water. They have numerous adaptations for aquatic life, including retention of the lateral line system in adults, which aids in detecting prey. Whereas other frogs rely almost exclusively on their tongues to capture prey, pipids exhibit a complete loss of the tongue, requiring them to rely on other prey acquisition modes. Carrie Carreño and Kiisa Nishikawa studied prey acquisition behavior of four species of pipids in different genera using high-speed imaging of feeding behavior combined with measurements of buccopharyngeal pressure during feeding. Previous observations of *Xenopus laevis* using their forelimbs to push food into their mouths led to speculation about whether inertial suction feeding occurred in pipids. The high-speed recordings and pressure measurements revealed that the four species of pipids studied, and likely all pipids indeed use inertial suction for feeding. Feeding in the four species begins with a lunge toward a prey while opening the mouth at the same time. The major difference among the four species is use of the forelimbs. The two smallest species, *Hymenochirus boettgeri* and *Pseudhymenochirus merlini*, do not use their forelimbs during feeding. However, the two largest species, *Xenopus laevis* and *Pipa pipa*, use their forelimbs to aid in propelling themselves toward the prey, and both species sometimes grab the prey and push it into the mouth. Even in cases in which the forelimbs are used, however, pressure in the mouth drops, indicating that inertial suction is used to obtain the prey, whether or not forelimbs are used. Additionally, both *X. laevis* and *P. pipa* show a high level of dexterity in their ability to manipulate their digits to grasp prey; previously, grasping was thought only to occur in arboreal anurans during climbing. Further, the study revealed that, like some salamanders, *Pipa pipa*, but none of the other pipids, is able to move each of its mandibles independently to manipulate prey once in its mouth.

The Matamata turtle *Chelus fimbriatus* offers the most vivid demonstration of inertial suction feeding. A combination of features results in an enormous suction force when the mouth and throat are opened; a flattened skull, cheeklike lateral surfaces, ability to rapidly depress the mandible, a large ossified hyoid apparatus, and a highly distensible esophagus. Well-developed hyoid musculature aids in producing a high velocity depression of the lower jaw. Either from ambush or by slowly stalking or even herding prey, the Matamata moves its head so that it is aligned with the prey, usually a fish or a tadpole. The head shoots forward while the hyoid musculature simultaneously contracts, dropping the floor of the buccal cavity. With the valvular nostrils closed, the suction vacuum results. The buccal cavity may increase by three to four times its normal size. Just prior to reaching the prey, the mouth opens and prey and water surge into the buccal cavity. The mouth is shut, but not tightly. The floor of the buccal cavity rises, expelling the excess water without losing the prey. The success of this prey-capture technique depends upon accurate alignment of the head to the prey, good timing, and rapid enlargement of the buccal cavity. Matamatas respond to increased prey density by moving less in search of prey.

Prey Types and Sizes

The kinds of prey eaten by amphibians and reptiles have already been introduced in a very general way. A multitude of factors determines the kinds of prey a particular species will eat (Fig. 10.2). The spectrum of prey available in a particular habitat is certainly a major limiting factor. For example, sea turtles would not be expected to eat insects simply because there are no truly pelagic insects. Species that ingest a random sample of prey available in a particular habitat are considered generalists, whereas species that select specific portions of the prey availability spectrum are specialists. Measuring prey availability independent of predators, however, has proven difficult. Different sampling regimes produce different results, and often the sample does not contain all prey captured by the amphibians and reptiles living in the sampled habitat.

Eating Other Animals

A statement by Kirk Winemiller and Eric Pianka (1990) exemplifies the problem. “Considerable effort has been expended in grappling with the difficult problem of resource availability. Resource availabilities are not easily measured in the field. For example, when insects are sampled with sweep nets, D-vac, Tanglefoot sticky traps, and/or pitfall traps, results differ dramatically. In a study of the herpetofaunas of several sites in the high Andes, Jaime Pefaur and William Duellman fenced study plots and conducted exhaustive collections of all herps and insects encountered within the plots with the intention of using the insects as intact whole specimens for comparison standards with the stomach contents of the herps. Yet fewer than 10% of the insect species actually eaten by the herps were collected by diligent humans….”

Winemiller and Pianka recommended using all prey from the pooled set of consumers as a measure of resource availability. Even though the sample is not independent from the consumers, it contains only the prey eaten by the consumers and, thus, may better represent the actual prey-availability spectrum.

Most species of amphibians and reptiles eat a variety of prey types and sizes. In leaf litter habitats of the Brazilian Amazon, the frog *Leptodactylus mystaceus* relies heavily on beetles, termites, and grasshoppers. In the same microhabitat, the lizard *Anolis planiceps* feeds primarily on insect larvae, roaches, and spiders (Fig. 10.23). In both species, many other prey items are eaten but to a lesser extent. Prey data based on volumetric data differ somewhat from prey data based on numeric data, largely because taxonomic groups of invertebrates vary greatly in size. Ants, for example, rank second numerically for *L. mystaceus* and third numerically for *A. planiceps*, yet volumetrically, they are relatively unimportant. From an energetic standpoint, a single large prey item is worth much more than many small ants, not just because the single large prey contains more total energy in its digestible tissues, but also because many small ants contain relatively more un-digestible exoskeleton simply as a result of greater surface to volume ratios. Because the diets of these two species are strikingly different even though they live in the same microhabitat (leaf litter), it is clear that frogs and lizards do not randomly sample available prey.

Sea turtles, sea snakes, and the marine iguana provide a different perspective on feeding in reptiles because all of their foraging occurs in sea water. Green sea turtles feed on

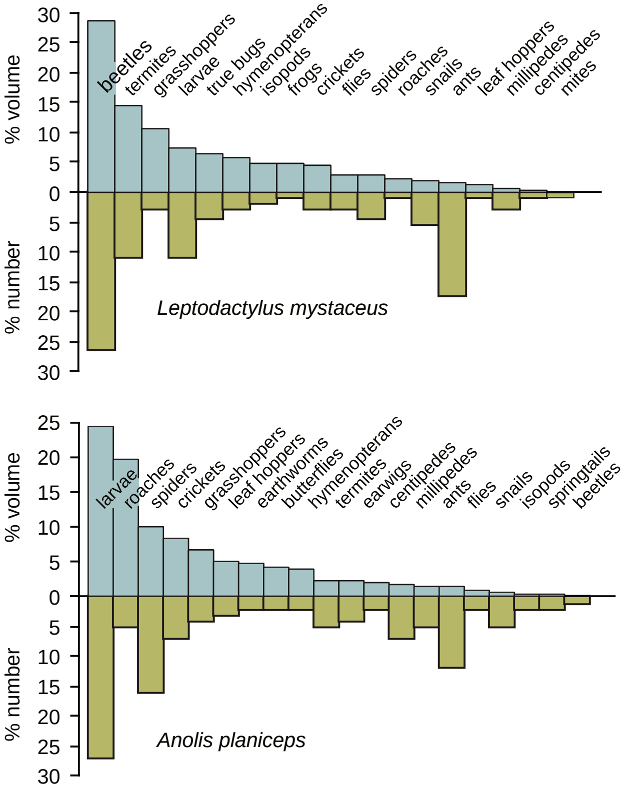

FIGURE 10.23 Representative diets of a frog, *Leptodactylus mystaceus*, and a lizard, *Anolis planiceps*, that occur in the same microhabitat (leaf litter) in an Amazonian rainforest. Both species feed on a variety of arthropods and other invertebrates, but the diets are considerably different. In both species, a few prey categories dominate the diet. Volumetric data, which indicate energy gain, are not always reflected in numerical data, which indicate the cost of acquiring prey. *Unpublished data from Vitt and Caldwell.*

a wide variety of red, green, and brown algae, sea grasses, jellyfish, mollusk eggs, and sponges. At some localities, such as near the coast of Peru, invertebrates are much more common in green sea turtle diets, and some fish are taken. Loggerhead sea turtles feed mostly on marine invertebrates, including horseshoe crabs. Hawksbills appear to feed largely on sponges but also take other invertebrates. The diets of other species include combinations of algae and invertebrates. The leatherback sea turtle, however, feeds mostly on gelatinous organisms, usually scyphozoans, pelagic coelenterates, and their parasites and commensals.

Sea snakes feed on a diversity of fishes and marine invertebrates, but they mostly eat fish that are sedentary, bottom-dwelling species with fine scales or no scales at all (Fig. 10.24). Different feeding modes translate into different prey types. Marine iguanas feed exclusively on algae that they scrape off submerged rock surfaces. Marine iguanas do not forage in the terrestrial environment, but high temperatures associated with the rocks make it possible for these lizards to bask and raise their body temperatures, which aids in processing their plant diet.

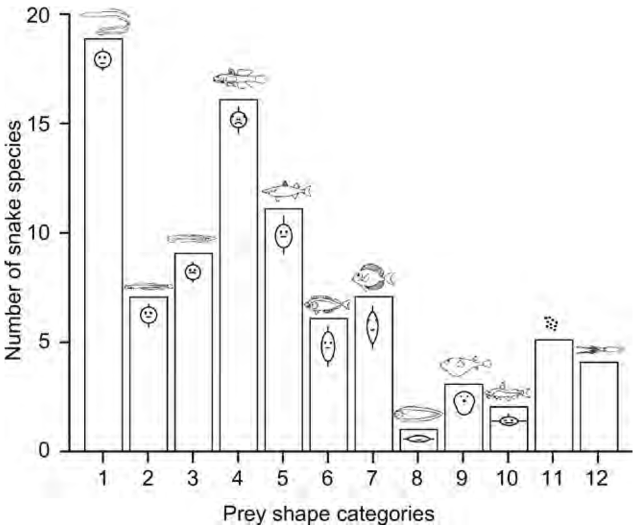

FIGURE 10.24 An examination of the shapes of prey fed on by species of sea snakes reveals that the majority of species feed primarily on fish that are elongate and nearly circular in cross-section. The last two columns represent fish eggs and squids. *Adapted from Voris and Voris, 1983.*

Taken together, sea turtles, sea snakes, and the marine iguana sample a broad taxonomic diversity of food items available in the oceans. The overall lack of amphibians in sea water does not seem surprising because water and electrolyte balance in salt water present major challenges to animals with permeable skin. Nevertheless, it seems surprising that such a vast and resource-rich habitat has not been exploited by more reptiles, given their ability to regulate water loss in hyperosmotic environments (Chapter 6). Of course, reptile diversity has been high in oceans in the past, and reasons for extinctions of marine clades remain unclear.

Body size of amphibians and reptiles also plays an important role in prey selection. Small species simply cannot eat prey as large as large species can. A summary of data for eight frog and seven lizard species from the northern Amazon rainforest, all living in leaf litter, shows that body size and prey size are related (Fig. 10.25). Careful examination of the data shows also that the relationship between prey size and frog or lizard body size differs among species. Frogs that are ant specialists tend to eat relatively smaller prey than species that are not ant specialists and the same is true for lizards. Not only do ant specialists eat relatively smaller prey than similar-sized non-ant specialists, but they also eat more prey items. Similar data for many lizard species not only confirm the relationship of prey size to body size, but also shows that as lizard body size increases, smaller prey disappear from the diet and consequently dietary niche breadth goes down. Gabriel Costa and his collaborators argue that this results from optimal foraging because larger species are targeting more profitable prey.

Small species of reptiles and amphibians often feed on some of the smallest arthropods available. Mites, collembola, and tiny ants are among the smallest arthropods available in

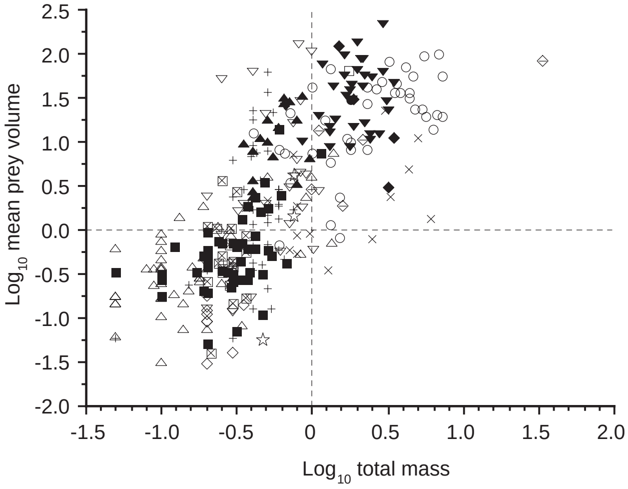

FIGURE 10.25 Both the mean size of prey eaten and the maximum prey size (not shown here) are correlated with body size of frogs and lizards. Even though a strong correlation exists with all species included, species differences in the relationship also exist. In general, species that feed on the smallest prey, mites and ants, tend to eat smaller prey and more of them than species eating other prey types. Frog species are *Elachistocleis ovalis* = x, *Leptodactylus andreae* = upright triangle, *Leptodactylus bolivianus* = parallelogram with cross, *L. fuscus* = closed parallelogram, *L. mystaceus* = closed upside-down triangle, *Leptodactylus lineatus* = open star, *Physalaemus ephippifer* = closed square, and *Pseudopaludicola boliviana* = open square with cross. Lizard species are *Anolis planiceps* = open circle, *Chatogekko amazonicus* = open parallelogram, *Coleodactylus septentrionalis* = cross, *Arthrosaura reticulata* = open square, *Gymnophthalmus underwoodi* = closed triangle, *Leposoma percarinatum* = upside-down open triangle, and *Tretioscincus oriximinensis* = closed circle. *Adapted from Caldwell and Vitt, 1999.*

TABLE 10.4 The Four Distinct Feeding Types of Snakes

Type I	Extremely small prey (e.g., termites, ant larvae) that require no immobilization
Type II	Heavy, elongate prey (e.g., caecilians, other snakes) that because of their shape do not require large gapes, but because of their size require constriction or envenomation for subduction
Type III	Heavy, bulky prey (e.g., mammals, lizards) that require specializations for both subduction and swallowing
Type IV	Prey that are lightweight relative to diameter (e.g., fishes, birds) and that require gape specializations but not subduction specializations (venom or constriction)

Note: The categories are based on two measures of prey size: relative mass and relative girth.
Source: Adapted from Greene, 1997.

tropical rainforest leaf litter. Although many frog species eat some mites, most larger frogs eat very few. However, several small species of frogs, such as dendrobatids and brachycephalids, consume significant numbers of mites.

All blindsnakes (Leptotyphlopidae, Typhlopidae, and Anomolepididae) eat small prey, usually social insects in their nests. Even though most of these snakes are small themselves, they are large compared with their prey. Consequently skull kinesis is not necessary to successfully prey on social insect castes. A majority of snakes eat very large prey and are capable of doing so because of their feeding apparatus. The upper and lower jaws are highly kinetic, and the right and left sides of each move independently. Moreover, unlike in other reptiles and amphibians, in snakes the lower jaws are not fused, which allows even more freedom of movement. Taken together, these characteristics allow a large expansion of the feeding apparatus, leading to the accommodation of large prey. Based on variation in relative size and shape of prey, four distinct feeding types are recognized in snakes (Table 10.4).

Most dietary studies of amphibians and reptiles rely on stomach-content data, either taken from necropsied animals or by flushing stomachs. Obtaining reliable diet data on secretive or uncommon species has always been a challenge. Recently, David Brown and his collaborators analyzed fecal deposits of slow worms (*Anguis fragilis*), which were known to eat earthworms, using pyrosequencing techniques with earthworm-specific PCR primers. They determined that *Anguis* consumed numerous earthworm species whose occurrence varied among habitats sampled. With respect to earthworms, *Anguis* appears to be a generalist, eating the most common earthworms in each respective habitat.

Herbivory

Among amphibians, herbivory is almost entirely limited to anuran tadpoles. Ingestion of plant materials has been reported in a few frogs. This limitation is due to the difficulties of digesting fiber. Tadpoles avoid the herbivory conundrum by consuming mainly the algal and bacterial scum (aufwuchs) in the water. Herbivory in tadpoles appears widespread but is poorly verified owing to few studies on tadpoles that examine which cells in the gut contents are digested and which are voided whole. Tadpoles gather their food from all levels of the water column: grazing on bottom sediments, filtering midwater phytoplankton, and skimming the surface scum. Most species specialize on a particular section of the water column and use a certain style of harvesting.

Obligate herbivory is absent in adult amphibians and uncommon in adults of reptiles even though many typically insectivorous reptiles occasionally feed on at least some plant material (Table 10.5). For example, *Tropidurus* lizards on two isolated rock outcrops in the western Amazon rainforest of Brazil eat as much as 17.6% plant materials (flowers). A population on the Rio Xingu in the eastern Amazon eats 26.5% plant materials, mostly fruits. Insects, spiders, and other

TABLE 10.5 Examples of Reptilian Herbivores, Whose Diets as Adults are Predominantly Plant Matter

Taxon	Food items
Turtles	
Batagur baska	Foliage, fruit, animal
Chelonia mydas	Seagrasses, algae
Melanochelys trijuga	Foliage, animal
Pseudemys nelsoni	Foliage, animal
most Testudinidae	Foliage, fruit, flowers
Chelonoides carbonaria	Fruit, flowers, foliage, animal
Dipsochelys dusumieri	Foliage
Gopherus polyphemus	Foliage, fruit
Lizards	
Gerrhosaurus skoogii	Foliage, animal
Aporosaurus anchietae	Seeds, animal
Corucia zebrata	Foliage, fruit, flowers
Dicrodon guttulatum	Fruits
Hoplodactylus pacificus	Nectar, fruit, animal
Lepidophyma smithii	Fruit, animal
all Iguanidae	Foliage, fruit, flowers
Amblyrhynchus cristatus	Marine algae (mainly *Ulva lobata*)
Cyclura carinata	Foliage, fruit, flowers, animal
Dipsosaurus dorsalis	Flowers, foliage, animal
Iguana iguana	Foliage, fruit, flowers
Sauromalus hispidus	Foliage, flowers, fruit
All *Phymaturus*	Foliage, flowers, fruit

Note: Some have a cellulolytic microflora in the digestive tract and/or colic modifications of the hindgut. The list does not include all well-documented cases of herbivory nor does it include the many examples of omnivory. Plant matter is arranged in order of decreasing volume in the taxon's diet.
Sources: Turtles—*Bb*, Moll, 1980; *Cm*, Bjorndal, 1980; *Mt*, Wirot, 1979; *Pn*, mT, Ernst and Barbour, 1989a; *Cc*, Moskovits and Bjorndal, 1990; *Dd*, Hamilton and Coe, 1982; *Gp*, MacDonald and Mushinsky, 1988; Lizards—*Gs*, Steyne, 1963; *Aa*, Robinson and Cunningham, 1978; *Cz*, Parker in Greer, 1976; *Dg*, Holmberg, 1957; *Hp*, Whitaker, 1968; *Ls*, Mautz and Lopez-Forment, 1978; aI, Iverson, 1982; *Ac*, Nagy and Shoemaker, 1984; *Cc*, Auffenberg, 1982; *Dd*, Mautz and Nagy, 1987; *Ii*, Rand et al., 1990; *Sh*, Sylber, 1988; *Phymaturus*, Espinoza et al., 2004.

invertebrates make up the remainder of the diet. Populations of *Tropidurus torquatus* along the Atlantic coast of Brazil vary geographically in the proportions of plants in their diets, possibly as a result of availability of appropriate plant parts.

Herbivory poses a digestive problem for vertebrates. Vascular plants contain cellulose in the support structure of their cells. No vertebrates produce cellulase to break down cellulose. Thus, vertebrate herbivores must depend upon the presence of a gut microflora of cellulolytic bacteria to digest plant food. Without such a microflora, it is doubtful that an amphibian or reptile could eat and process enough plant matter to survive on a strictly herbivorous diet. To maintain an efficient gut microflora, a constant and elevated body temperature appears necessary. Other requirements are a constant food supply, slow passage of food items to permit adequate time for bacterial degradation, anaerobic gut environment, regulation of gut pH, and removal of fermentation waste by-products. Lowland tropical reptiles feed year-round and maintain fairly high and constant body temperatures. Once a cellulolytic microflora is obtained, it is improbable that the microflora would need to be renewed. Such microflora stability is less certain for temperate-zone reptiles because of low body-core temperatures and possible absence of a food bolus during dormancy. Low temperature and/or the purging of the digestive tract prior to hibernation or aestivation might well eliminate a specialized microflora. The gopher tortoise (*Gopherus polyphemus*) efficiently digests a high-fiber diet and effectively absorbs the nutrients generated by bacterial fermentation in the hindgut. It either retains a microflora bolus or restores its microflora each spring.

The how and when of gut microflora acquisition remains unknown for many herbivorous reptiles. For *Iguana iguana*, a complex behavioral mechanism has evolved to ensure the acquisition of plant-digesting microbes. The hatchlings eat soil before emerging from the nest cavity and continue to do so after emergence as they begin to feed regularly on plants. After a few days, the young iguanas move from low shrubbery around the nesting area upward into the canopy and join older juveniles and/or adults; here they consume the feces of older individuals, and this inoculate ensures the presence of the correct microflora in their guts. Inoculation of gut microflora in hatchlings from ingestion of adult feces likely occurs in other reptilian herbivores, but direct observations have not been made. *Gopherus polyphemus* defecates within its burrows and presumably eats some of its feces prior to emerging in the spring. But where do juvenile gopher tortoises and, for that matter, the young of all other reptilian herbivores obtain their fiber-digesting microfauna? In mammalian herbivores, gut microflora acquisition poses no problem, because the young and their parents are closely associated from birth through weaning. The mammalian mother regularly licks the young, and the young feed from the mother's mammary glands, so young mammals acquire the microflora early from the ingestion of the mother's saliva or fecal material. This close association of mother and offspring does not exist for any reptilian herbivore. In herbivorous Aldabra tortoises, the absence of a gut microflora leads to a low digestive efficiency (30%), in contrast to digestive efficiencies of about 65% for red-footed tortoises and 85% for green iguanas, both of which have gut microfloras.

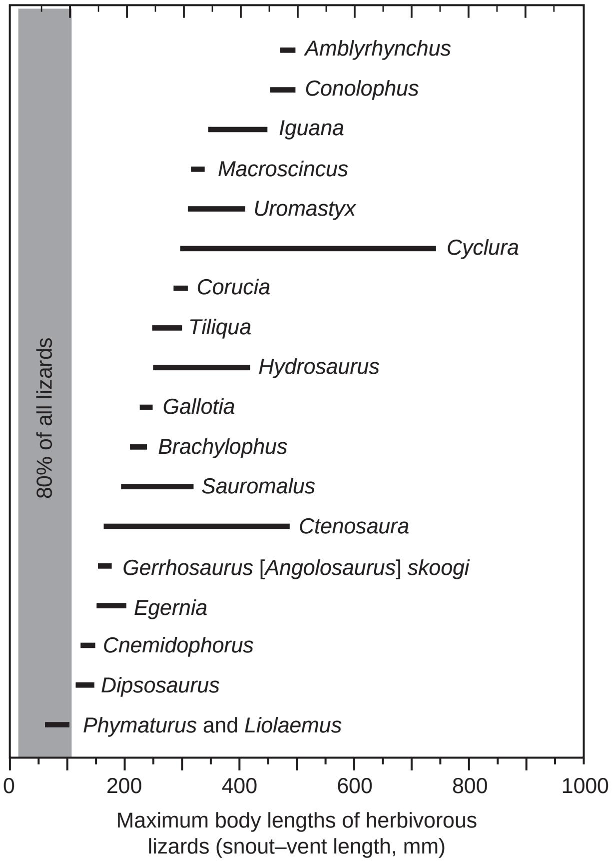

FIGURE 10.26 Body sizes of herbivorous lizards showing that herbivorous *Phymaturus* and *Liolaemus* are smaller than all other herbivorous lizards, with body sizes falling well into the size distribution for insectivorous lizards. *Adapted from Espinoza et al., 2004.*

It has long been argued that large body size is necessary for reptiles to maintain energy balance on a strictly herbivorous diet, and until recently, most known herbivorous lizards were large. This idea has been challenged by an impressive data set compiled by Robert Espinoza and his collaborators. Phylogenetic analysis of diets of a monophyletic clade of liolaemid lizards in the genera *Ctenoblepharys*, *Phymaturus*, and *Liolaemis* revealed an estimated 18.5 independent origins of herbivory. All 10 species of *Phymaturus* are herbivorous (one origin), and the other herbivorous liolaemids are in the genus *Liolaemis*. Not only has herbivory evolved more times within these lizards than in all other lizards combined, but the rate at which the evolution of herbivory occurred is 65 times greater than that for all other lizards. Moreover, these lizards are smaller in general than all other herbivorous lizards but are well within the size range of most lizards that are not herbivorous (Fig. 10.26). After removing the effect of phylogeny, a negative correlation exists between plant consumption and environmental temperature. Thus, the evolution of herbivory is associated with low rather than high temperatures. Isolation of lizards in montane habitats that are not interconnected accounts for repeated independent origins of herbivory. Small body size appears necessary for herbivorous lizards in these habitats because they can gain heat rapidly, given an unpredictable thermal environment. While active, they maintain body temperatures typical of other herbivorous lizards.

In an interesting analysis of traditional large-bodied herbivorous lizards, Anthony Herrel points out that herbivorous lizards are wide foragers only because they move from plant to plant (plants are stationary). These herbivorous lizards, all in the Iguania, also discriminate chemical cues, a trait that is associated with wide-foraging lizards in other taxa. A large number of lizard species eat some plant material and can be considered omnivorous, and the most logical way to evolve herbivory is from omnivorous lizards, which already have some of the morphological adaptations necessary to feed on plants. A translocation experiment with the lacertid *Podarcis sicula* suggests that the shift to herbivory initially involves morphological and physiological changes that are not necessarily genetic. When individuals from an island (Pod Kopište) on which the lizards ate less than 7% plants were translocated to an island (Pod Mrčaru) with few insects, not only did their diets shift to plants (34% in spring, 60% in summer), but morphological and physiological changes occurred in the lizards. The shifts occurred over a period of about 40 years and included changes in dentition, gut morphology, digestive efficiency, gut passage time, and endosymbiont density, all in the direction expected based on a shift to herbivory. The study suggests that morphological and physiological responses to dietary shifts in *P. sicula*, may be relatively plastic. Nevertheless, many questions remain about the evolution of herbivory and how herbivorous lizards fit in the classical foraging-mode dichotomy.

Ontogeny of Diets

Ontogenetic dietary shifts are probably common in amphibians and reptiles but are not well studied. Adult amphibians and reptiles do not necessarily eat the same prey as larvae or juveniles. The most dramatic example of a dietary shift is in amphibians with aquatic larvae and terrestrial adults. Most anurans are detritivores as larvae and insectivores as adults. Among dendrobatid frogs with predaceous tadpoles (e.g., *Adelphobates castaneoticus*), the dietary shift is from eating aquatic insect larvae and other tadpoles during the larval stage to eating ants during the adult stage. A dramatic example of a dietary shift occurs in semiterrestrial tadpoles of the dicroglossid frog *Nannophrys ceylonensis* of Sri Lanka. These strange tadpoles have a number of morphological adaptations that allow them to live and feed on damp rocks where they forcefully scrape the surface film off rocks using strong, serrated jaw sheaths. No filter feeding occurs because tadpoles are usually covered by only a thin film of water. Although the diet consisted of a variety of plants and animals, including algae, mosses, protozoans, rotifers, arthropods, nematodes, and occasionally conspecific eggs and tadpoles, a dietary shift from a greater proportion of plant material to a greater proportion of animal material occurred during tadpole development. Older tadpoles consumed more rotifers, arthropods, and nematodes that younger tadpoles. The dietary shift was correlated with changes in the gut. Shortening of the gut in tadpoles of most frog species occurs during metamorphosis, but in *N. ceylonensis*, the timing of shortening of the gut occurred earlier and was more protracted. Consequently, a developmental shift in gut development allows these tadpoles to take advantage of animal food matter in densely shaded forests with low primary productivity. Tadpoles at Stage 34 coiled around patches of food, apparently excluding smaller tadpoles, possibly because animal food is patchier in occurrence and therefore a limited resource. Ontogenetic dietary shifts likely occur in many tadpoles, but few species have been studied. In some frogs, such as the Chilean giant frog (*Calyptocephalella gayi* [formerly *Caudiverbera caudiverbera*], family Calyptocephalellidae), phenotypic plasticity in gut morphology and physiology suggests that adjustments necessary for dietary shifts are not uncommon in tadpoles. Interestingly, phenotypic plasticity in gut morphology and intestinal enzymes in the Chilean giant frog resulted from different temperature treatments rather than different diet treatments. The ecological significance of this result remains unstudied, but it would be interesting to examine whether changes in types of food available to these tadpoles vary with temperature, and, if so, then the connection between phenotypic plasticity and diet could be made. Temperature may cause the phenotypic change, and the underlying adaptive significance may be associated with correlated changes in food supply.

Among amphibians and reptiles in which juveniles have the same morphology as adults, a large component of the dietary shift is associated with body size and thus age. Water snakes in Florida provide an example. *Nerodia erythrogaster* and *N. fasciata* feed primarily on fish as juveniles but switch to mostly frogs when they reach about 50 cm in snout–vent length (Fig. 10.27). Even though *N. rhombifera* and *N. cyclopion* feed on fish throughout their lives, the kinds of fish they eat change with snake age and size. Several factors contribute to ontogenic diet shifts in these snakes, including the effect of snake body size on the size of prey that can be taken, differences in microhabitat use between juveniles and adults, and sexual differences (size-based) in prey types taken. Even though the evolution of prey detection closely tracks the evolution of odors produced by prey, ontogenetic shifts in prey choice based on chemicals do occur (e.g., juvenile versus adult *Crotalus viridis*).

Potential ontogenetic shifts in diet can be offset by morphological variation among age groups. Juveniles and adults of the salamander *Plethodon cinereus* feed on the same prey types; small mites are among the most common prey. Prey size does not vary with head size in adults, but size of the largest prey items does vary with head size in juveniles. Consequently, size constrains the diet of juveniles in that they cannot eat the larger items that adults eat. Nevertheless, juveniles have relatively broader heads than adults,

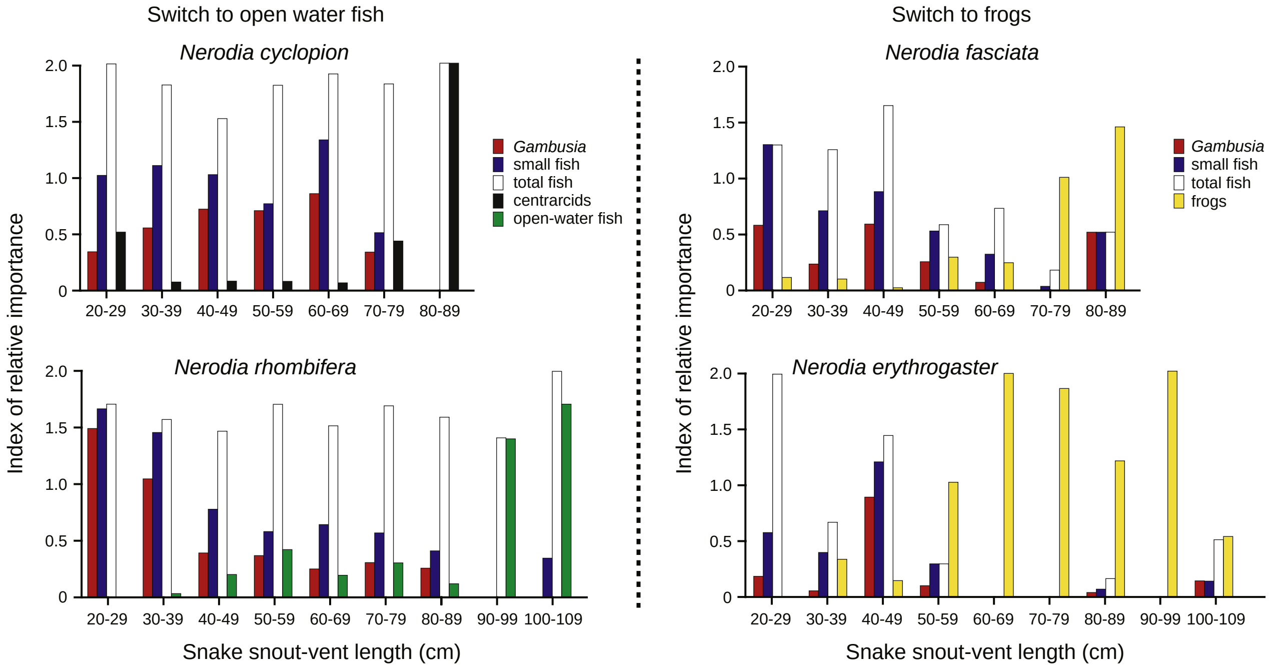

FIGURE 10.27 The diets of four species of watersnakes change with age and size. *Adapted from Mushinsky et al., 1982.*

which allows them to eat all but the largest prey taken by adults (Fig. 10.28).

Evolution of Diets

Recognition that diets of amphibians and reptiles might evolve just as morphological or physiological traits is just gaining acceptance. It has long been known, for example, that within some clades, all species share a diet preference unlike that of species in closely related clades. For example, horned lizards (*Phrynosoma*) as a group eat primarily ants; all Iguanidae are herbivorous, at least as adults; dendrobatid frogs in the genera *Dendrobates*, *Oophaga*, *Ranitomeya*, and *Adelphobates* primarily eat ants; and snakes in the closely related families Typhlopidae, Leptotyphlopidae, and Anomalepidae eat eggs, larvae, and pupae of ants and termites. Indeed, insectivory in these snakes (the Scolecophidia) is one piece of evidence suggesting that they are the most primitive snake clade. Snakes in the genus *Tantilla* feed on centipedes, and *Atractus* feeds on earthworms. A recent comparison of diets in major snake clades has identified major shifts in snake diets historically as well. These and many other examples suggest that similarity in diets within particular clades reflects dietary shifts early in the evolutionary history of the clade, which, among other things, has changed the way we think about species assemblages and communities (discussed in more detail in Chapter 12).

Specialization on ants provides a particularly instructive example of the evolution of diets and exemplifies the complexity of trade-offs between foraging and predator escape strategies. Ant specialization has evolved independently in a number of families of lizards and frogs. Within the Phrynosomatinae, species in the genus *Phrynosoma* feed primarily on ants. These tank-like lizards are cryptic in morphology and coloration, move very little, and eat literally hundreds of ants each day. Most other genera of phrynosomatine lizards eat a diversity of insects, including some ants. From a strictly energetic perspective, eating ants seems to be inefficient because ants are generally small and contain a large amount of exoskeleton compared with larger insects such as caterpillars. If a lizard had to move to find each ant, the energy gain would be less than the energy required to capture the ant. Ants also often contain noxious chemicals. Consequently, eating ants incurs energetic costs as well as potential metabolic-processing costs to handle ingested chemicals. Several benefits of ant eating offset the potential costs. First, ants often occur in clusters, and, as a consequence, the energy involved to find a thousand ants may be the same or less than the energy to find a single large grasshopper. More importantly, the same chemicals that ants use for defense are metabolized by *Phrynosoma* and contribute to the bad taste of their blood, which appears to repel canid predators (see Chapter 11). Likewise, in dendrobatoid frogs, ants comprise most of the prey eaten by many species. Other species feed on relatively fewer ants. Most interesting is the observation that ant specialization in these small tropical frogs appears to be related to a behavioral defense complex involving toxic or bad-tasting skin secretions and aposematic coloration (Fig. 10.29). Among other things, bright coloration of numerous species warns predators that the frogs have bad-tasting or toxic skin, resulting from the ingestion of ant chemicals as well as ingestion of chemicals from other tiny leaf litter arthropods. Brightly colored species move frequently while foraging and thus are conspicuous, whereas cryptic (non-ant specialists and nontoxic) species do not move much while foraging. Specialization on ants and the associated predator escape mechanisms have evolved repeatedly within these frogs, and in two instances (Dendrobatinae and one clade in the Colostethinae), entire clades of frogs with these coevolved traits have been generated (bottom two shaded boxes in Fig. 10.29). Additional details on predator escape in these frogs appear in Chapter 11. A similar radiation of frogs with the same set of traits (ant specialization associated with aposematic coloration and skin toxins) has evolved independently in the frog family Mantellidae in Madagascar. In addition to acquiring alkaloids from ants, some mantellids also acquire nicotine from ants that get nicotine from plants. Thus a nicotine food chain exists from plant to ant to frog! The preceding examples, from both frogs and lizards that eat ants, which are in general small and low-energy prey, exemplify the complexity of the evolution of diets in ectothermic vertebrates. Based on energy gain alone (i.e., optimal foraging), ant specialization should be a poor strategy and selectively disadvantageous. However, because it can have added benefits in terms of sequestering chemicals for defense, energetic disadvantages are compensated for by advantages in offsetting predation.

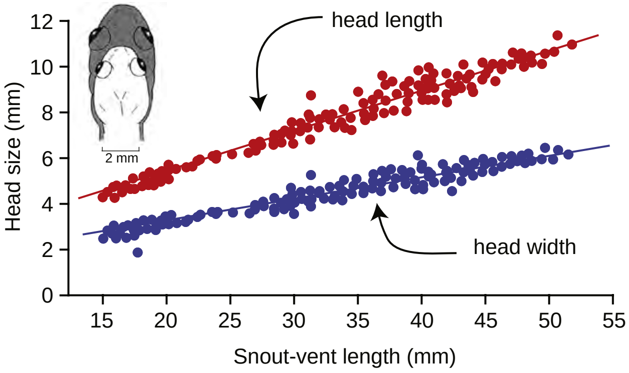

FIGURE 10.28 Although both head width and length increase with body size (snout–vent length) in *Plethodon cinereus*, head width of juveniles is proportionately greater in juveniles, which allows them to feed on relatively large prey. *Adapted from Maglia, 1996.*

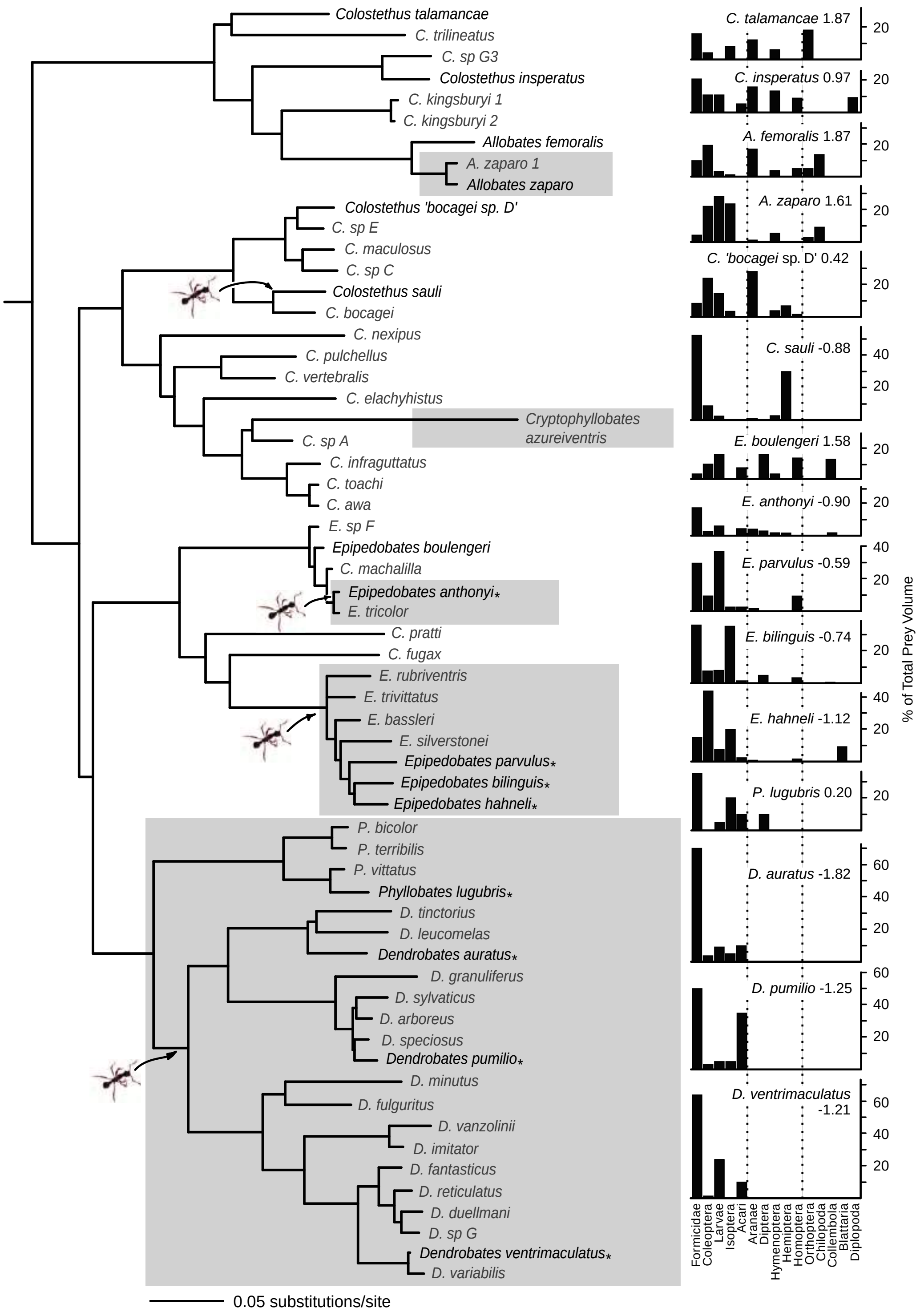

FIGURE 10.29 In dendrobatoid frogs, the evolution of specialization on ants is linked with aposematic coloration and production of skin toxins. Ants (myrmicine ants in particular) produce the alkaloids for chemical defense against predators; frogs eat the ants and are able to either move the alkaloids to the skin or combine them with other chemicals and move them to the skin and use them for predator defense. Bright coloration of these frogs usually, but not always, signals to a predator that the frog is distasteful or toxic. Ant icons indicate a dietary shift to ant specialization based on an *a priori* categorization of generalists versus specialists. Shaded boxes indicate conspicuously colored frog species, and asterisks indicate that the species are known to contain alkaloids in the skin. Frequency histograms on the right indicate relative volume contributed by the 15 most common prey types to the diet of each frog species for which dietary data were available, and these are indicated in the phylogeny by boldfaced type. Numbers to the right of frog species names in the diet panel refer to the principal components scores of dietary niche breadths, essentially ranking frogs across prey types. Note that we have retained genera and species names as in the original graphic, and thus they are inconsistent with the taxonomy that appears in Chapter 17. Nevertheless, phylogenetic relationships are the same, and, as a result, interpretations regarding evolution of diets, coloration, and defensive chemicals remain unchanged. For the interested reader, we suggest tracking species names on the website http://research.amnh.org/herpetology/amphibia/. *Adapted from Darst et al., 2005.*

QUESTIONS

1. Describe in detail similarities and differences in how tongues work for prey capture in toads, plethodontid salamanders, and chameleons.
2. Some lizards and many snakes can and do eat large prey. Describe how this is possible and compare how lizards that eat large prey differ from snakes that eat large prey.
3. Reptiles and amphibians are often categorized in two broad foraging modes based on foraging behavior. What are these foraging modes and what are the behavioral and energetic bases for these different modes? List as many ecological, morphological, and physiological correlates of each foraging mode that you can think of.
4. Although the argument has been made that herbivory in lizards is associated with large body size, recent data on small-bodied South American lizards suggests that large body size is not a necessary condition of herbivory. Moreover, phylogenetic analyses show that the evolution of herbivory has occurred much more frequently in small-bodied lizards. Explain the physiological arguments for associating herbivory with body size and the phylogenetic arguments that associate herbivory with small body size.
5. Why might you expect ontogenetic dietary shifts to be more common in snakes than in lizards?

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