14 Behavioral Energetics

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All animal activities require energy. Foraging for prey and escaping from predators are readily apparent uses of energy, as are the growth of an individual organism and the production of a brood of young. The processes that support these activities, such as movement of blood through the cardiovascular system, elimination of nitrogenous wastes by the kidney, and propagation of action potentials by nerves, also have energetic costs. How does an animal obtain this energy, and, having obtained it, how should it use the energy to best advantage?

These questions define the emerging field of behavioral energetics, and emphasize its close links to topics such as environmental physiology, optimal behavior, and life history theory. The assumption that energy limits ecological processes is a theme in most of these studies, as is the hypothesis that organisms allocate energy among compartments in a web of interactions that ultimately influence their Darwinian fitness. That is, investing energy in foraging reduces the amount of energy immediately available for growth or reproduction, but if foraging is successful, more energy is ultimately available for increasing biomass.

Two papers published during the 1940s were particularly influential in shaping the development of the broad area of physiological ecology and some of the specific topics of behavioral energetics. R. B. Cowles's and C. M. Bogert's (1944) demonstration of thermoregulation by desert lizards and snakes showed that exporting laboratory techniques to the field provided an excellent tool for understanding natural processes. Soon after, F. E. J. Fry's (1947) study of the metabolic capacities of fishes as a function of two or more simultaneously applied variables showed that experiments that attempt to duplicate the complexity of natural situations in the laboratory are another powerful method for asking questions about organisms. These methods underlie much of the current research in behavioral energetics.

Furthermore, both Cowles and Bogert (1944) and Fry (1947) emphasized the responses of individual organisms during short-term activities, such as temperature selection and acclimation, that occur in minutes, hours, or days. That focus on individuals and on discrete activities largely continues to distinguish behavioral energetics from physiology, which emphasizes processes, and from studies of behavior, in which the time frame is often a season or a generation.

Short-term activities carried out by individual organisms lend themselves to measurements of the actual energetic costs of specific behaviors. For example, how much energy is expended in capturing and eating an insect, and how much energy is subsequently realized from digesting the meal? That information can be used to formulate hypotheses about long-term phenomena, for example, about optimal diets and foraging modes or about mating systems and courtship behavior. As a result of this sequence of reasoning, studies of discrete activities—especially foraging behavior, prey selection, digestion, territorial defense, and courtship—dominate the literature of behavioral energetics (Aspey and Lustick 1983; Gittleman and Thompson 1988; Spotila 1989; Townsend and Calow 1981).

Presently a new emphasis has appeared in behavioral energetics. Attention is shifting increasingly from the description of characteristics of species to analysis of the significance of physiological variation among and within species (e.g., Feder et al. 1987). Questions are framed in the contexts of evolutionary biology and sociobiology, and investigations may employ the techniques of quantitative genetics and biophysical modeling. Arnold (1983) has described the interplay of methods needed to elucidate the relationships among behavior, energy, and fitness. The goal remains understanding how organisms work and the ecological and evolutionary consequences of variation in organismal function.

Amphibians and reptiles have been important in many studies of behavioral energetics, and their prominence in several recent reviews attests to the role they have played (Feder and Lauder 1986; Feder et al. 1987; Spotila 1989). Lizards have been the subjects of many investigations because a com-

bination of diurnal activity, conspicuous behavior, and inter- and intraspecific variation makes some species particularly suitable for field and laboratory studies (e.g., Anderson and Karasov 1981; Andrews 1984; Huey and Pianka 1981; Huey et al. 1984; Huey and Bennett 1987).

In contrast to lizards, most amphibians are nocturnal, and many are inconspicuous as well. These characteristics have hampered field studies of behavior, although the present volume attests to the enormous amount of information available concerning the physiology and ecology of amphibians. Despite the logistic difficulties of working with amphibians, two areas of their biology—feeding and reproduction—have been fruitful sources of information about relations among physiology, ecology, and behavior (summarized by Taigen and Pough 1985). These two lines of investigation have had independent origins: many of the assumptions that shaped studies of the foraging behavior of amphibians were derived from work on lizards, whereas students of amphibian mating systems and of the energetics of amphibian reproduction have drawn many of their models from work with birds. But amphibians, of course, are neither lizards nor birds, and an increasing body of evidence suggests that important aspects of their biology are unique.

This chapter reviews progress in studies of the energetic aspects of natural behaviors of amphibians, especially foraging behavior and reproduction. Other activities are no less important, but they have received little attention. As is often the case with studies that integrate laboratory and field components, gathering quantitative information about the ecology and behavior of free-ranging animals has been more difficult than making physiological measurements. The interactions of amphibian behavior, ecology, and morphology are complex, and the difficulties of designing field experiments have not been fully surmounted. Furthermore, nonenergetic factors such as the risk of predation might be important in determining the selective forces that act on individuals, but balancing energy expenditure and risk of predation is not simple because those costs are not expressed in the same units. Assessment of the ecological and evolutionary significance of metabolic characters requires synthesis of diverse aspects of organismal biology. Consequently, our treatment places as much emphasis on the ecological and behavioral context of the studies discussed as on physiological measurements.

MORPHOLOGY, PHYSIOLOGY, AND FORAGING BEHAVIOR
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Interspecific variation in the foraging behaviors of amphibians can be strikingly apparent even on casual observation. At a pond in the evening, toads (Bufonidae) move steadily along the shore, repeatedly flicking out their tongues to capture small prey, while frogs (Ranidae) rest in the aquatic vegetation, lunging at passing insects only at long intervals. These very different foraging behaviors are associated with interspecific variation in diet, morphology, and physiology. Furthermore, examination of independent evolutionary lineages reveals that similar combinations of behavior, morphology, and physiology have evolved repeatedly among anurans. These convergences indicate that at least some of the characters associated with variation in foraging behavior are evolutionarily labile.

Predators have usually been divided into two categories, sit-and-wait or widely foraging, depending on their relative activity during foraging (e.g., Eckhardt 1979; Huey and Bennett 1986; Huey and Pianka 1981; Toft 1981; Webb 1984). Regal (1978, 1983) has proposed a third category, cruising foragers, for species that move frequently but at low speeds. Some authors (e.g., Magnusson et al. 1985; Pietruszka 1986; Pough 1983; Strüssmann et al. 1984; Taigen and Pough 1983) have suggested that foraging mode cannot be divided into discrete classes, but rather varies along several axes. However, Huey and Bennett (1986) defended the use of qualitative categories because in many taxa most species cluster at the ends of a movement spectrum.

Whatever the distribution of foraging modes, the predictability of associations of morphological characters and dietary habits with locomotion and metabolism suggests that interacting cause-and-effect relations may shape these aspects of the ecology and evolution of amphibians. For example, the physiological and morphological requirements of different patterns of locomotion (e.g., the lever arms, contraction velocities, and enzyme activities of limb muscles; see chapter 11) might determine what foraging modes are possible for a particular species. In turn, foraging mode and locomotor patterns might limit the range of structural habitats a species could exploit and the kinds of prey it encountered. Thus, studies of the functional morphology and physiology of amphibians may increase our understanding of the structure and evolution of ecological guilds and communities.

Morphology, Locomotion, and Diet

The ways amphibians move about are clearly associated with the ways they locate prey and the types of prey they find. Morphological specializations of the girdles and limbs are closely associated with locomotor modes, and prey capture often involves specializations of the jaws, tongue, and hyobranchial apparatus (see chapter 11). In fact, some of these anatomical features are so distinctive that they allow inferences about foraging mode when no direct behavioral information about a species is available.

Anurans Studies of anurans by Emerson and her colleagues (Emerson 1976a, 1978, 1979, 1982, 1985, 1988; Emerson and Diehl 1980; Emerson and de Jongh 1980) present the most detailed analyses of the correlations among morphology, locomotion, and foraging mode for amphibians. Pelvic morphology distinguishes anurans that jump (travel ten body lengths or more in one leap) from species that walk, hop, and burrow (Emerson 1979, 1980). The type I pelvic girdle lacks a direct ligamentous connection between the ilium and the sacrum. Instead, the lumbodorsal fascia over the sacrum is thickened and forms a ligament that extends across the pelvis from ilium to ilium. This morphology is found in swimming, walking, hopping, and burrowing frogs including pipids, pelobatids, *Rhinoderma darwinii* (Rhinodermatidae), *Bombina orientalis* (Discoglossidae), and some hylids and microhylids.
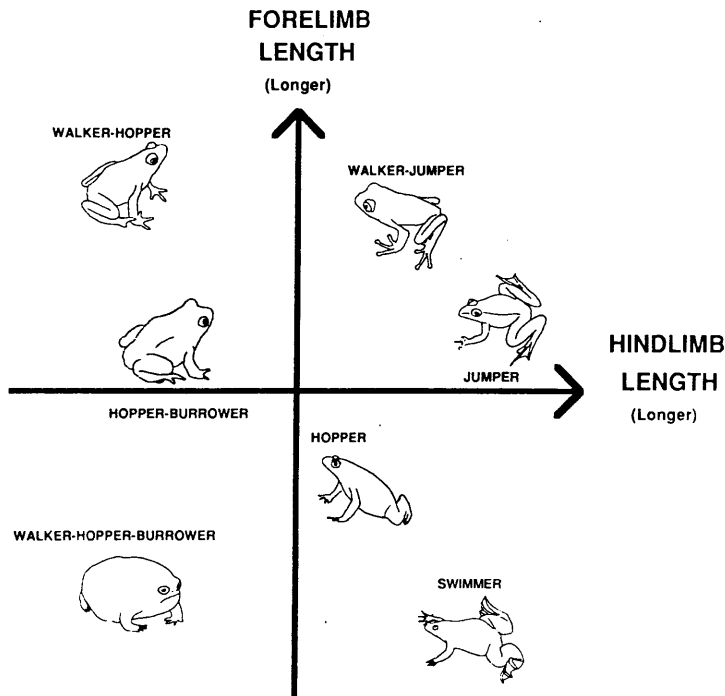
FORELIMB
LENGTH
(Longer)

WALKER-HOPPER

WALKER-JUMPER

HINDLIMB
LENGTH
(Longer)

JUMPER

HOPPER-BURROWER

HOPPER

WALKER-HOPPER-BURROWER

SWIMMER

A second type of pelvic girdle (type IIA) is characteristic of other species of walking, hopping, and burrowing frogs (bufonids, some leptodactylids, some hylids, some microhylids, a few ranids, *Rhinophrynus dorsalis* [Rhinophrynidae], and *Discoglossus pictus* [Discoglossidae]). This pelvic morphology has a direct ligamentous attachment between the pelvic girdle and the vertebral column in addition to the superficial dorsolumbar fascia seen in type I.

A third pelvic morphology (type IIB) has been identified in jumping frogs (most ranids, some leptodactylids, *Ascaphus truei* [Leiopelmatidae], and *Dendrobates tinctorius* [Dendrobatidae]). In these species the pelvic girdle is attached to the vertebral column by a short ligament that runs from the ilium to the sacral diapophysis.

Variation in pelvic morphology appears to be the critical factor leading to differences in the amount and direction of movement at the iliosacral articulation during locomotion, because the sequence of activity of the four paired muscles surrounding the articulation is almost identical in all three types of pelvis. An anteroposterior movement of the pelvis permitted by the type I morphology increases body length by as much as 20%, probably increasing the reach of a frog during walking, climbing, and swimming. Lateral rotation of the pelvis occurs during walking by frogs with pelvic type IIA, moving the femur of the protracting limb to a more anterior position than it would occupy if the pelvis were fixed. Simultaneous lateral flexion of the vertebral column advances the contralateral forelimb. These specializations increase stride length and, provided stride rate is maintained, increase the speed of locomotion. Type IIB pelvises may store elastic energy during jumping as the pelvis flexes in a vertical plane with respect to the vertebral column.

Hindlimb lengths are the most conspicuous morphological features that distinguish among the locomotor modes of frogs

(Emerson 1978, 1988). Species with long hindlimbs are generally jumpers or swimmers, whereas species with short hindlimbs walk, run, or hop (fig. 14.1). Hindlimb muscle mass scales isometrically during ontogenetic growth, and that isometry should result in lower rates of acceleration during a jump for large individuals of a species. However, two of the three species of frogs that Emerson studied maintained constant acceleration over a range of body sizes, and she suggested that changes within the muscles during ontogeny may increase mass-specific energy production. In contrast, interspecific variation in jumping ability appears to be correlated with variation in the mass of hindlimb extensor muscles relative to total body mass. However, variation in limb lengths does not correspond directly to variation in locomotor mode: kinematic analysis of gait distinguished nine locomotor modes, but only two morphological categories (swimmer-jumpers and walker-hopper-burrowers) were distinguished by principal components analysis (Emerson 1988).

Some species of walking/hopping frogs have long forelimbs, but these are not features of all walkers (fig. 14.1), and they may be associated with unusual gaits (e.g., *Atelopus*: Bufonidae) or with the use of the forelimbs during intraspecific combat (e.g., *Dendrobates*). No simple correlation links pectoral girdle morphology and mode of locomotion: firmisternal and arciferal pectoral girdles both occur among jumping frogs and among walking/hopping types (Emerson 1983).

Many of the specializations that facilitate burrowing also enhance walking ability, and the selective pressures for walking and burrowing are difficult to separate (Emerson 1976a). Most terrestrial walking frogs are at least facultative burrowers. However, the morphological specializations that facilitate walking by most frogs permit only backward burrowing. Species that feed underground have morphological

specializations of the cranium, pectoral girdle, and associated musculature that permit the use of the head as a shovel during forward burrowing.

The skull morphology of adult anurans is related to diet (Emerson 1985). Species that eat small, slow prey do not need a large gape, but they make many captures, sometimes in rapid succession at a concentration of prey, and shortening the length of a feeding cycle may be important in maximizing the number of prey that can be captured. These anurans have short jaws and the prey is captured about midway through the feeding cycle. In contrast, anurans that eat large, fast prey require a large gape, rapid tongue extension, and considerable force at closing. These species have long jaws, and prey capture occupies only the first quarter of the feeding cycle.

The genus *Bufo* is an apparent exception to these generalizations. *Bufo* eat slow, small prey, yet their jaws are relatively long (Emerson 1985). However, this anomaly may be an artifact of the presentation of dietary information as percentages of the total diet rather than as absolute values. Most species of *Bufo* are generalists, and the fact that they eat large numbers of ants and termites does not necessarily indicate that they eat small quantities of large prey (e.g., Strüssmann et al. 1984).

Study of both live and dead animals is necessary to understand morphology (e.g., Emerson 1976a, 1978, 1985). Once mechanisms are known, however, the study of preserved specimens yields much supplementary information. Ecologists and physiologists can facilitate this process by identifying and preserving their specimens and depositing them in museums, even if they do not themselves intend to study the morphological correlates of their ecological or physiological data.

Many anuran larvae are nonselective filter feeders, extracting suspended particles from the water (reviewed by Seale 1987; see chapter 16). A buccal pump formed by the paired ceratohyal cartilages in the floor of the mouth creates a flow of water that passes across the branchial food traps and gill filters. Mucus secreted on the ventral velum and on the branchial food traps is driven by cilia medially and caudally into the esophagus. Ingestion rate increases with increasing concentration of suspended particles and asymptotically approaches a maximum. At low particle concentrations larvae decrease filtering rates and perhaps produce less mucus; these mechanisms should reduce the energetic costs of feeding (Seale, Hoff, and Wassersug 1982).

Many anuran larvae employ both aerial and aquatic gas exchange (see chapter 16). Trips to the water surface for air can have direct energy costs (i.e., the cost of locomotion) as well as indirect costs (e.g., resting near the water surface and hence away from food, increased skin capillary density, increased reliance on gills for gas exchange). As predicted by that hypothesis, air-breathing larvae (*Rana pipiens*) kept in moderately hypoxic conditions grew more slowly in deep water than in shallow water (Feder and Moran 1985). Aquatic gas exchange and food capture are potentially competing functions of the buccopharyngeal region, and larval *Xenopus laevis* denied access to the surface increase buccal pumping rates while simultaneously decreasing rates of food ingestion (Feder, Seale, Boraas, Wassersug, and Gibbs 1984). The branchial food traps continue to produce mucus under these conditions, but the food and mucus are expectorated (Wassersug and Murphy 1987).

The larvae of some anurans are obligatory or opportunistic carnivores or oophages (Lannoo, Townsend, and Wassersug 1987; Wassersug 1980). Carnivorous morphs have hypertrophied jaw muscles and short guts compared to omnivorous larvae (Pomeroy 1981; Wassersug 1980). Oophagy has been reported for larvae of *Osteopilus brunneus* (Hylidae) and for larvae of three species of *Dendrobates* (Dendrobatidae; see also chapter 16). The specializations of oophagous larvae include a reduced number of denticle rows. They feed on unfertilized eggs of their own species (Lannoo, Townsend, and Wassersug 1987), and *D. pumilio* also eats conspecific larvae (Brust 1990). Cannibalistic morphs of the salamander *Ambystoma tigrinum* (Ambystomatidae) are larger than noncannibalistic individuals and have broader, flatter heads and more teeth (Collins and Cheek 1983; Lannoo and Bachman 1984a; Pierce, Mitton, and Rose 1981). Cannibalistic larvae of spadefoot toads (*Scaphiopus*: Pelobatidae) grow faster and metamorphose sooner and at larger body sizes than do omnivores (Pomeroy 1981).

Salamanders Aquatic salamanders (and the aquatic larvae of terrestrial species) use the hyobranchial apparatus to expand the buccopharyngeal region, creating a suction that draws prey into the mouth. Most aquatic salamanders have small tongues and robust hyobranchial skeletons (Özeti and Wake 1969). The mechanics of suction feeding by salamanders have been extensively studied by Lauder and his colleagues (Findeis and Bemis 1990; Lauder and Reilly 1988; Reilly and Lauder 1988, 1989a, 1989b; Shaffer and Lauder 1985a, 1985b). Some of this work was reviewed by Lauder (1985a). The ancestral feeding mechanism of terrestrial salamanders is probably illustrated by *Ambystoma* (Ambystomatidae), which combines a limited degree of tongue protrusion when feeding on land with prey capture in the jaws (Regal 1966a; Reilly and Lauder 1989a).

The best-studied morphological specializations of salamanders associated with feeding are the protrusible tongues of plethodontids (Lombard and Wake 1976, 1977, 1986; Roth 1976; Roth and Wake 1985b; Thexton, Wake, and Wake 1977; D. B. Wake 1982; Wake and Larson 1987; Wake, Roth, and Wake 1983; see also chapter 11). Evolutionary modifications of the hyoid apparatus of plethodontids have produced a high-speed projectile tongue. The morphological basis of tongue protrusion by plethodontids is entirely different from that of anurans (Roth et al. 1988a). The tongue is protruded 20 to 25 mm from the mouth in 2 to 4 ms by some species of *Bolitoglossa*, and *Hydromantes italicus* can project its tongue 45 to 50 mm in 6 to 8 ms.

Ecological aspects of these morphological specializations have not been studied. Projectile tongues probably allow specialized plethodontids to capture small or fast-moving prey, but this hypothesis has not been tested with comparative studies, and no information about interspecific variation in foraging modes is available. However, laboratory studies show that plethodontid salamanders are capable of complex feeding behavior that can maximize energy intake (but see chapter 13). Red-backed salamanders (*Plethodon cinereus*) in laboratory experiments captured large fruit flies in preference to

small flies (Jaeger and Barnard 1981). The salamanders were most selective when prey were abundant and maximized net energy intake by eating large flies; they became less selective as prey density decreased. At high prey densities the salamanders used a sit-and-wait foraging mode, but switched to active searching at low prey densities. The sit-and-wait tactic was energetically less costly than active searching (estimated as 1.9×10^{-2} J $\cdot$ min^{-1} $\cdot$ g^{-1} versus 2.4×10^{-2} J $\cdot$ min^{-1} $\cdot$ g^{-1}) and also more successful (0.67 versus 0.42 flies $\cdot$ min^{-1}). When intruding salamanders were introduced to the feeding boxes, the resident salamanders diverted time from feeding to defense and switched from a selective to a generalized diet. As a result of these behavioral changes, the rate of energy intake was reduced by more than 50% (Jaeger, Nishikawa, and Barnard 1983).

Ecological studies of the feeding behavior of salamanders have focused on constraints on food intake imposed by physical factors (principally moisture), predators, or competition within or between species (Davic and Orr 1987; Feder and Londos 1984; Hutchison and Spriestersbach 1986a; Jaeger 1971, 1978; Jaeger, Joseph, and Barnard 1981; Keen 1982, 1984; Keen and Reed 1985; Maiorana 1978; Pauley 1978; Southerland 1986a, 1986b, 1986c; Stauffer, Gates, and Goodfellow 1983; White 1977; Wrobel, Gergits, and Jaeger 1980; Wyman and Hawksley-Lescault 1987). The low metabolic rates of salamanders (see chapter 12) allow them to suspend feeding during unfavorable periods rather than risk injury or death from desiccation, predation, or territorial encounters (Feder 1983b). Parallels between the foraging behaviors of terrestrial species of salamanders and anurans seem plausible. For example, the diurnal activity of red efts (Salamandridae) is associated with toxicity and aposematic color, as is the diurnality of dart-poison frogs (*Dendrobates* and *Phyllobates:* Dendrobatidae). Cryptically colored, palatable salamanders like *Desmognathus* (Plethodontidae) are nocturnal, as are cryptic palatable frogs like *Eleutherodactylus* (Leptodactylidae). Field studies of the foraging behavior of salamanders are lacking, however, and the parallels may not extend beyond very general similarities.

Caecilians Both terrestrial and aquatic species of caecilians are fossorial, digging burrows in the soil or in the sediments of a body of water. They capture prey with a slow approach followed by a quick grab, and a prey item may be sheared into mouth-size pieces against the walls of the burrow as the caecilian rotates about its body axis (Bemis, Schwenk, and Wake 1983; Wake 1986; Wake and Wurst 1979). Most caecilians appear to be opportunistic predators, consuming earthworms, termites, and insect pupae (Taylor 1968). *Afrocaecilia* and *Boulengerula* may specialize on termites, and *Dermophis* on earthworms (Wake 1986). Most caecilians have recurved mono- or bicuspid teeth that penetrate and hold prey (Wake and Wurst 1979). The aquatic caecilian *Typhlonectes obesus* has dilated tooth crowns and may scrape the pupae of aquatic insects from rock surfaces (Wake 1978; Wake and Wurst 1979). Caecilians have a unique form of static pressure jaw system that combines downward rotation of the skull with jaw closure to produce a strong bite while maintaining a small cross-sectional area (Bemis, Schwenk, and Wake 1983).

Foraging, Diet, and Metabolism

Mechanistic interpretations of behavior provide a conceptual basis for studies of the behavioral energetics of foraging by amphibians. This perspective is the product of two decades of investigation of interspecific variation in the exercise physiology of amphibians (see chapter 12). From its beginning in laboratory studies, behavioral energetics has expanded to incorporate ecological and phylogenetic perspectives. Laboratory and field studies are being integrated, and some experiments have measured individual variation in performance capacity and the synergistic effects of environmental parameters. Our changing perspective of amphibian activity metabolism is most clearly illustrated by a chronological summary of the hypotheses that have been tested.

Variation in the Metabolic Capacities of Amphibians Initial attempts to understand interspecific variation in the exercise physiology of amphibians focused on the modes of escape from predators employed by different species of frogs and salamanders, perhaps because escape was the behavior that physiological ecologists most often observed. These studies established that amphibians employ both aerobic and anaerobic metabolic pathways of ATP synthesis during high levels of exercise (see chapter 12 for an extensive discussion of this topic) and that the relative magnitude of the two types of metabolism varied among species (Bennett and Licht 1973, 1974). Oxygen consumption was measured during 2 to 10 min of forced activity that was induced by electrical shock or by prodding animals with a blunt probe, and whole-body lactic acid concentration was used as an index of anaerobic energy output. High rates of aerobic and low rates of anaerobic metabolism were typical of slow-moving amphibians such as toads (*Bufo boreas*) that rely on skin toxins for defense, whereas the opposite balance of metabolic pathways typified treefrogs (*Hyla regilla:* Hylidae) and grass frogs (*Rana pipiens*) that escape predators with a brief series of rapid leaps. The toads sustained their relatively low levels of activity for 10 min of exercise without apparent fatigue, whereas the treefrogs and grass frogs lost coordination or were completely exhausted in less than 5 min.

The salamanders *Batrachoseps attenuatus, Aneides flavipunctatus, A. lugubris* (all Plethodontidae), and *Notophthalmus viridescens* (Salamandridae) conformed to the pattern of anaerobic metabolism exhibited by the frogs. Two of the species (*B. attenuatus* and *A. flavipunctatus*) rely on rapid movement to escape predators: *B. attenuatus* repeatedly springs into the air from a coiled position and *A. flavipunctatus* crawls rapidly away. These species have high anaerobic metabolic capacities and are exhausted quickly during forced exercise. In contrast, *A. lugubris* stands its ground and may attack a predator; it has a low rate of lactate accumulation during exercise as does the aquatic newt *Notophthalmus viridescens,* which has dermal poison glands that secrete a potent toxin.

Reciprocal relations of energy input from aerobic and anaerobic pathways have been reported for several additional species of salamanders and anurans (Hutchison and Turney 1975; Hutchison, Turney, and Gratz 1977; Hutchison and Miller 1979a, 1979b; Miller and Hutchison 1979, 1980; Hillman and Withers 1981; Miller 1983). In general, species that

rely on toxins to deter predators have low rates of lactic acid accumulation and sustain activity for long periods, whereas species that flee rapidly from predators accumulate lactic acid quickly and are soon exhausted. Caecilians and anuran larvae appear to conform to this pattern (Bennett and Wake 1974; Gatten, Caldwell, and Stockard 1984). Measurements of oxygen consumption in some of these studies as well as the initial observations of *Hyla regilla* (Anura: Hylidae), *Bufo boreas*, and *Batrachoseps attenuatus* (Bennett and Licht 1973) are compromised by the use of electrical stimulation to elicit activity (Hillman et al. 1979; see chapter 12 for a discussion of the problems with electrical stimulation), but the general patterns described for those species have been confirmed by subsequent studies using other methods of forcing animals to be active.

The apparent dichotomy in exercise physiology of amphibians based on mode of escape from predators led next to a search for mechanisms at the level of tissues and cells that would account for interspecific differences in metabolic capacity. The activities of the glycolytic enzymes phosphofructokinase and lactic dehydrogenase are higher in limb muscles of *Rana pipiens* than in those of *B. boreas*, whereas activity of the aerobic enzyme citrate synthase is greater in *B. boreas* and in *Xenopus laevis* than in *R. pipiens* (Putnam and Bennett 1983; see also Baldwin, Friedman, and Lillywhite 1977). However, the proportions of three muscle fiber types distinguished by histochemical methods (fast-twitch glycolytic, fast-twitch oxidative glycolytic, and tonic fibers) do not differ among the species (Putnam and Bennett 1983; but see also Sperry 1981). Nonetheless, contractile properties of limb muscles show variation that parallels whole-animal performance: muscles from *B. boreas* contract more slowly and accumulate less lactic acid than do muscles from *R. pipiens* or *X. laevis*.

In addition, heart ventricle mass and blood oxygen capacity are approximately correlated with rates of oxygen consumption during exercise among the anurans *B. cognatus*, *Scaphiopus couchii* (Pelobatidae), *X. laevis*, and *R. pipiens*, and experimentally induced anemia reduces the rate of oxygen consumption of *R. pipiens* during forced activity (Hillman 1976, 1980a; see also chapter 12).

Ecological Correlates of Activity Metabolism The apparently simple dichotomy of metabolic characteristics revealed by physiological studies of amphibian exercise has been challenged by ecologists and morphologists. An initial suggestion of a more complex relation between the ecology and behavior of amphibians and the relative contributions of aerobic and anaerobic metabolic pathways to high levels of activity emerged from a morphological study (Emerson 1976a). Noting the close correspondence among locomotion (walking or hopping versus jumping), fossorial activity, and the importance of ants and termites in the diet, Emerson (1976a) suggested that foraging modes provided another context in which to interpret interspecific variation in the exercise physiology of anurans. She proposed that walking and burrowing frogs have high aerobic scopes and can sustain locomotion for long periods while they search for prey, whereas jumping frogs are sit-and-wait predators. This association between foraging mode and diet presumably reflects the costs and benefits of specialization for active foraging. Emerson suggested that the major advantages of foraging compared to sit-and-wait predation are the increased probabilities of encountering prey and of locating concentrated sources of food such as termite nests. The primary direct cost of active foraging is the energetic expense of locomotion. In addition, an animal is probably more vulnerable to its own predators when it is moving than when it is still. Many widely foraging anurans are toxic and aposematically colored. These characteristics deter predators, but production and sequestration of their toxic compounds probably require energy and could expose the anuran to damage from its own toxins.

Initial field studies of foraging modes of amphibians were based largely on concepts derived from studies of lizards. Huey and Pianka (1981) proposed a network of correlations among the foraging behaviors of lizard species, what and how much they eat, the conditions under which they are exposed to predators and their methods of escape, and their patterns of energy use (table 14.1). Desert lizards figured largely in the development of these hypotheses and their subsequent extension, and the studies drew from and contributed to contemporary ideas in ecology, especially adaptation, optimality, and ecological energetics (Anderson and Karasov 1981; An-

TABLE 14.1 Postulated Correlates of Foraging Mode of Desert Lizards

	Sit and Wait	Widely Foraging
Prey type	Eat mobile prey	Eat sedentary and unpredictable (but clumped or large) prey
Volume prey captured per day	Generally low	Generally high
Daily metabolic expense (Bennett and Gorman 1979	Low	High
Types of predators	Vulnerable primarily to widely foraging predators	Vulnerable to both sit-and-wait and to widely foraging predators
Rate of encounters with predators (Salt 1967)	Probably low	Probably high
Mode of escape from predators (Toft 1980a)	Camouflage, speed, saltation	Camouflage, speed, aposematism (poisonous)
Morphology (Vitt and Congdon 1978)	Stocky (short tails)	Streamlined (generally long tails)
Probable physiological correlates (Bennett and Licht 1973; Ruben 1976a, 1976b)	Limited endurance	High endurance capacity
Relative clutch mass (Vitt and Congdon 1978)	High	Low
Sensory mode (Enders 1975; Regal 1978)	Visual primarily	Visual or chemoreceptory
Learning ability (Regal 1978)	Limited[a]	Enhanced learning and memory, larger brains

Source: Reprinted, by permission, from Huey and Pianka 1981.
[a] Unless use trapline (T. L. Poulson *pers. comm.*).

TABLE 14.2 Postulated Correlates of Foraging Mode of Tropical Leaf-Litter Anurans

	Sit and Wait	Widely Foraging
Prey type	Large, mobile prey, depend on escape as first predator defense	Small, slow-moving prey that sting or are distasteful or chitinous
Number of prey	Lower	Higher
Volume of prey	Might be the same for both modes	
Search cost	Lower[a]	Higher[b]
Handling cost:		
Capture (cost/capture)	Higher	Lower
Digestion (net)	Lower	Higher
Predator defense	Crypticity, escape detection	Skin toxins; may be aposematic
Morphology	Stocky, wide-mouthed	Slim, narrow-mouthed
Physiology (Bennett and Licht 1974)	Anaerobic; capable of large bursts of energy, tire easily	Aerobic; maintain constant but low levels of activity

Source: Reprinted, by permission, from Toft 1981.
[a]Costs may be ameliorated by physiology.

drews 1984; Huey and Bennett 1986; Huey and Pianka 1981; Huey et al. 1984; Pianka 1966, 1973, 1977, 1980; Vitt and Congdon 1978). The questions asked were (1) Do the rate and quality of prey (= energy) acquisition differ among foraging modes? (2) Does the rate of prey acquisition by a given foraging mode depend on the dispersion and quality of the prey? (3) Are foraging mode and morphology correlated? (4) Do the metabolic characteristics of an organism reflect its foraging mode? (5) Does foraging mode influence the intensity of predation or the type of predator to which an organism is exposed? The answers to all of these questions appear to be yes, and the complications derive from identifying interacting components and attempting to define cause-and-effect relations.

Field studies of the foraging behavior of amphibians have dealt exclusively with anurans. Toft (1981) described a continuum of dietary habits among leaf-litter frogs in Panama extending from species that specialize on ants and mites to species that avoid those prey. This variation in diet was associated with a continuum of foraging behaviors. At one extreme, typical sit-and-wait species (e.g., *Eleutherodactylus* [Leptodactylidae]) were characterized as stocky, wide-mouthed anurans that capture small numbers of large, mobile prey and have limited powers of endurance for locomotion, whereas at the opposite end of the spectrum widely foraging species (e.g., *Atelopus* [Bufonidae]) and *Dendrobates* [Dendrobatidae]) were slim and narrow-mouthed, captured large numbers of small sedentary prey, and were able to sustain activity for long periods. The active foragers were mostly toxic, and some were aposematically colored, whereas the sit-and-wait species had cryptic colors and patterns. The ecological correlates of foraging mode that Toft defined among leaf-litter anurans were similar to those of lizards (table 14.2).

The paradox of a relatively simple bipolarity in metabolic capacities, as suggested by studies of exercise physiology, and the more complex picture presented by multivariate ecological hypotheses prompted a broader survey than had previously been attempted of the relative contributions of aerobic and anaerobic metabolism to anuran locomotor physiology (Taigen, Emerson, and Pough 1982). Species were chosen to test the null hypothesis that exercise physiology is a phylogenetically conservative trait in anuran evolution, as

well as to examine possible correlations of aerobic and anaerobic metabolism with locomotion, habitat, and defensive behavior. The seventeen species studied revealed a broad range of combinations of aerobic and anaerobic energy input during forced locomotion (fig. 14.2), and the total energy output during activity varied among species by a factor greater than 2 (see also chapter 12). No dichotomy between predominantly aerobic and predominantly glycolytic species was evident, and Emerson and her colleagues concluded that interspecific variation in exercise physiology forms a continuum like the one Toft (1981) described for variation in behavior and diet.

Phylogenetic conservatism does not appear to explain interspecific variation in the relative importance of aerobic and anaerobic metabolism among the anurans studied, because variation among species within a genus was as large as variation among genera or families. Furthermore, predator avoidance behavior was not a good predictor of the metabolic characteristics of a species: no statistically significant patterns of normalized values of aerobic dependence were detected for active versus static predator avoidance behavior. The structural habitat occupied by a species (terrestrial versus arboreal) also failed to predict metabolic characteristics.

In contrast, aerobic dependence was correlated with mode of locomotion (walkers and hoppers > jumpers) and with foraging behavior (widely foraging > sit-and-wait). That is, species of frogs that walk or hop have high aerobic capacities, and most of these species are also widely foraging predators. These conclusions must be tentative, however, because few quantitative data are available from field observations to characterize the diet or foraging behavior of many of the species tested.

Field Studies of Foraging Behavior

The trend to more ecologically oriented interpretations of the exercise physiology of amphibians has stimulated studies in which observations of free-ranging animals in the field are combined with measurements of metabolism. The information currently available from work with anurans suggests the following generalizations about correlations among foraging behavior, diet, and metabolism: (1) The degree of foraging activity is correlated positively with aerobic metabolic capac-
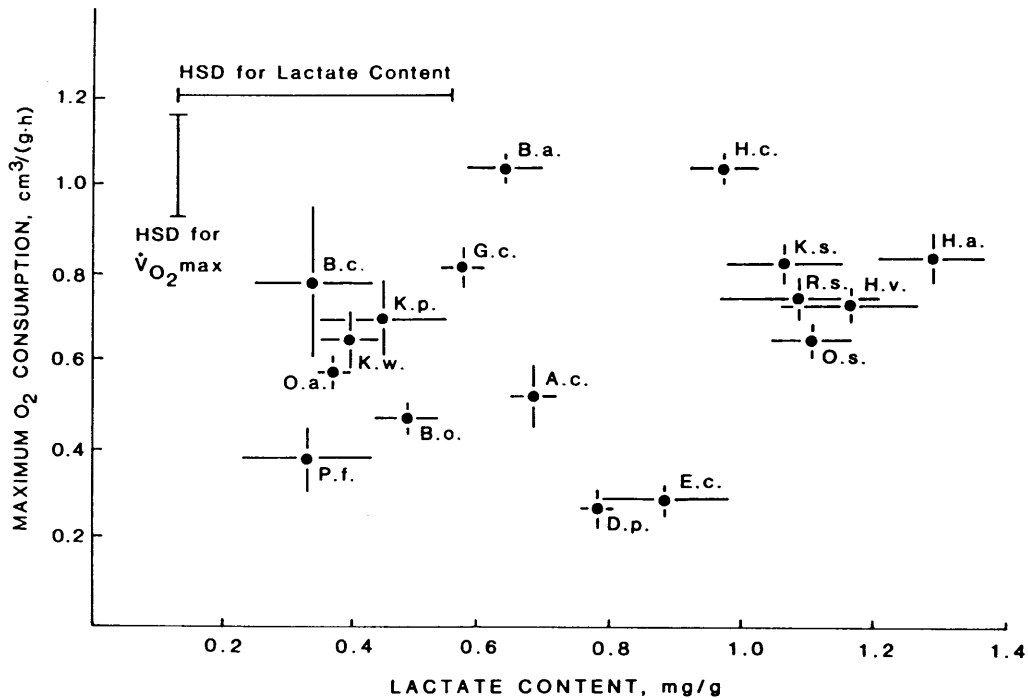
Fig. 14.2 Mass-specific rates of oxygen consumption during activity plotted on logarithmic coordinates as a function of whole-body lactate concentration following forced exercise. Points represent species means and lines show ±1 SE of the mean. The values of Tukey's honestly significant difference (HSD) for oxygen consumption and lacate concentration are shown. *A.c., Agalychnis callidryas; B.a., Bufo americanus; B.c., Bufo calamita; B.o., Bombina orientalis; D.p., Discoglossus pic- tus; E.c., Eleutherodactylus coqui; G.c., Gastrophryne carolinensis; H.a., Hyla arenicolor; H.c., H. crucifer; H.v., Hyperolius viridiflavus; K.p., Kaloula pulchra; K.s., Kassina senegalensis; K.w., Kassina weali; O.a., Odontophrynus americanus; O.s., Osteopilus septentrionalis; P.f., Pternohyla fodiens; R.s., Rana sylvatica.* (Reprinted, by permission, from Taigen, Emerson, and Pough 1982.)

ity and negatively with anaerobic capacity. (2) Widely foraging species capture more individual prey items than do sedentary species. (3) Widely foraging species seek out prey that occur in patches, whereas sedentary species eat prey that are found singly.

Tests of these hypotheses have focused on widely foraging species of anurans, especially dart-poison frogs in the Neotropical family Dendrobatidae. This family is a monophyletic radiation of primarily terrestrial frogs in Central and northern South American (Silverstone 1975; Myers, Daly, and Malkin 1978). Dendrobatids are diurnally active, and the behavior of individual frogs can be observed in the field. An initial analysis combined information about diet from Toft's (1981) study with metabolic measurements of three species of dendrobatid frogs and a leptodactylid (Taigen and Pough 1983). Within those species dietary electivity for ants was correlated positively with rate of oxygen consumption during locomotion and negatively with whole-body lactic acid concentration (fig. 14.3). A stepwise analysis of variance showed that electivity for ants accounted for 77% of the variation in rate of oxygen consumption and for 54% of the variation in lactate concentration.

A subsequent field study employed focal animal observations lasting from 1 to 12 h (overall average 2.9 h) of each of four species of Panamanian dendrobatid frogs (Pough and Taigen 1990). The average distance that frogs moved per hour of observation was taken as an estimate of how widely a species forages, and the predicted association was found with metabolic characteristics of the species: species that moved
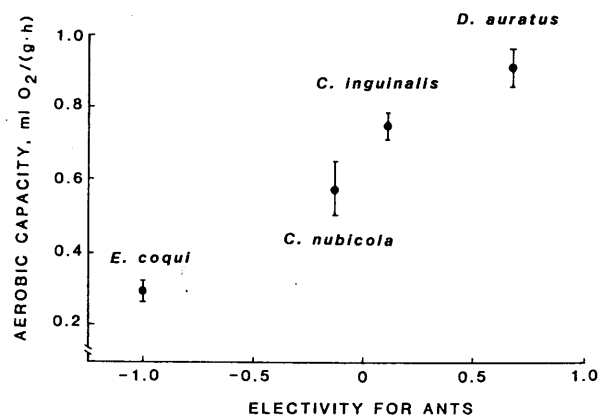

Fig. 14.3 Relation between aerobic capacity for locomotion and dietary preference for ants by *Colostethus inguinalis, C. nubicola, Dendrobates auratus,* and *Eleutherodactylus coqui.* (Reprinted, by permission, from Taigen and Pough 1985.)

long distances had high aerobic and low anaerobic capacities during laboratory measurements of locomotion (fig. 14.4). In addition, the species that moved long distances made more prey capture attempts per hour and made more captures at each feeding location than did the sedentary species.

Field Metabolic Rates Measurements of the daily energy expenditure of free-ranging animals have contributed substantially to understanding the ecological energetics of birds, mammals, lizards, and invertebrates (e.g., Karasov 1981; Nagy 1975, 1987, 1989a; Nagy and Shoemaker 1984). Un-
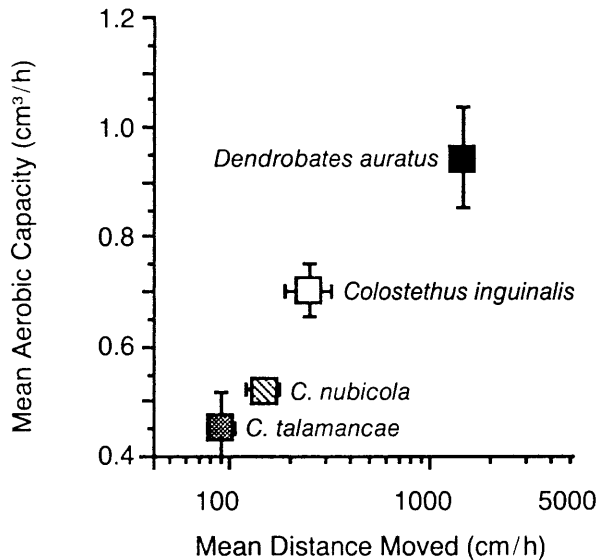
Fig. 14.4 Relation between the mean distance a species of frog moved in 1 h and the mean aerobic capacity for locomotion of the species. Aerobic capacity was calculated for an individual weighing 0.95 g, the grand mean for the sample of four species. Horizontal and vertical lines show ± 1 SE. (Reprinted, by permission, from Pough and Taigen 1990.)

fortunately, the techniques that have been successful with those animals are not well suited to use with amphibians. The most widely used method, doubly labeled water, relies on the differential rates of loss of injected isotopes of oxygen (which is lost as H_2O and as CO_2) and hydrogen (lost as H_2O only). The accuracy of these measurements depends on several assumptions about the routes and rates of movement of hydrogen and oxygen (Nagy 1983a, 1989a). In particular, the rate of water loss must be constant through time, and the animal must not take up unlabeled water from the environment. Thus, the high and variable rates of evaporative water loss and of cutaneous water uptake that are characteristic of amphibians (see chapter 6) make doubly labeled water an unsuitable method for measuring field metabolic rates of these animals.

A method that relies on measuring food intake by determining the rate of turnover of ^{22}Na (Green 1978) may have promise for measuring the field metabolic rates of terrestrial amphibians that do not have large cutaneous sodium fluxes. Knowledge of the sodium content of the diet is required, and species with a narrow range of food items that have stable exchangeable sodium contents are most suitable for this technique (Nagy 1989b). The method has been applied successfully to studies of mammals (Green 1978; Green, Anderson, and Whatley 1984; Green and Eberhard 1984; Green, Griffiths, and Newgrain 1985).

In the absence of direct methods of measuring field metabolic rates, investigators have used extrapolations from laboratory measurements of the energy expenditure during different activities combined with time budgets that estimate the amount of time that animals spend in different activities. This method can give results that correspond well with estimates of energy expenditure obtained with doubly labeled water (Buttemer et al. 1986; Goldstein 1988; Masman and Klaasen 1987; Weathers et al. 1984), but it is fraught with difficulty,

especially for cryptic animals like amphibians that are hard to observe in the field. Consequently, estimates of long-term energy expenditure must be treated cautiously, and the evaluation of specific activities in terms of their magnitude relative to an annual energy budget involves a substantial measure of uncertainty.

Individual Variation

Individual anurans vary in their locomotor and physiological capacities (Preest and Pough 1989; Taigen and Pough 1985; Walton 1988; Wells and Taigen 1984), and part of that variation is probably determined genetically (Travis 1980; Mitton, Carey, and Kocher 1986). Individual variation in metabolic capacities is stable in repeated measurements: 89% of the variation in aerobic capacity of toads (*Bufo americanus*) was attributed to differences among individuals in two measurements separated by a week (Wells and Taigen 1984). Individual variation in aerobic capacity of bullfrogs (*Rana catesbeiana*) was correlated with differences in heart ventricle mass and blood hemoglobin concentration (Walsburg, Lea, and Hillman 1986; see also chapter 12).

Learning and physical conditioning are nongenetic sources of individual variation that could potentially confound experiments. Although amphibians are probably limited to fairly stereotyped behavior (Ewert 1985), they modify their foraging behavior to increase energy gain (Jaeger and Rubin 1982). Physical training improves locomotor endurance of *Rana pipiens* and increases both endurance and sprint speed of *Xenopus laevis* (Cummings 1979; Miller and Camilliere 1981). The roles of learning and physical training in the behavior of anurans in the wild are unexplored.

An adaptationist view regards the character complexes identified by studies of anuran foraging behavior as responses to selection operating on intraspecific variation in physiological and behavioral characters that enhance the fitness of individual frogs (cf. Gans 1988). This hypothesis implies that the correlations of behavior and physiology observed in comparisons among species will also be seen in comparisons of individuals within a species. That is, if widely foraging species A captures more prey, on average, than does sedentary species B, the most widely foraging individuals of species A will capture more prey than more sedentary individuals of the species. Furthermore, for any individual of species A, effort invested in foraging should be repaid by an increase in prey captures compared to spending the same time in sedentary behavior. In turn, individual variation in capacity for active foraging should parallel individual variation in capacity for aerobically sustained locomotion: the individuals of species A with the greatest aerobic capacities to sustain locomotion should be the ones that forage most widely.

These hypotheses can be tested by analyzing individual variation in behavior and physiology. If the hypotheses are correct, that examination should yield positive correlations among distance moved, number of prey-capture attempts, and aerobic capacity for locomotion, and in fact positive correlations between distance traveled by individuals and the number of prey-capture attempts they made were observed for two species (fig. 14.5). Finding statistically significant correlations that support the predictions of the hypothesis in two of
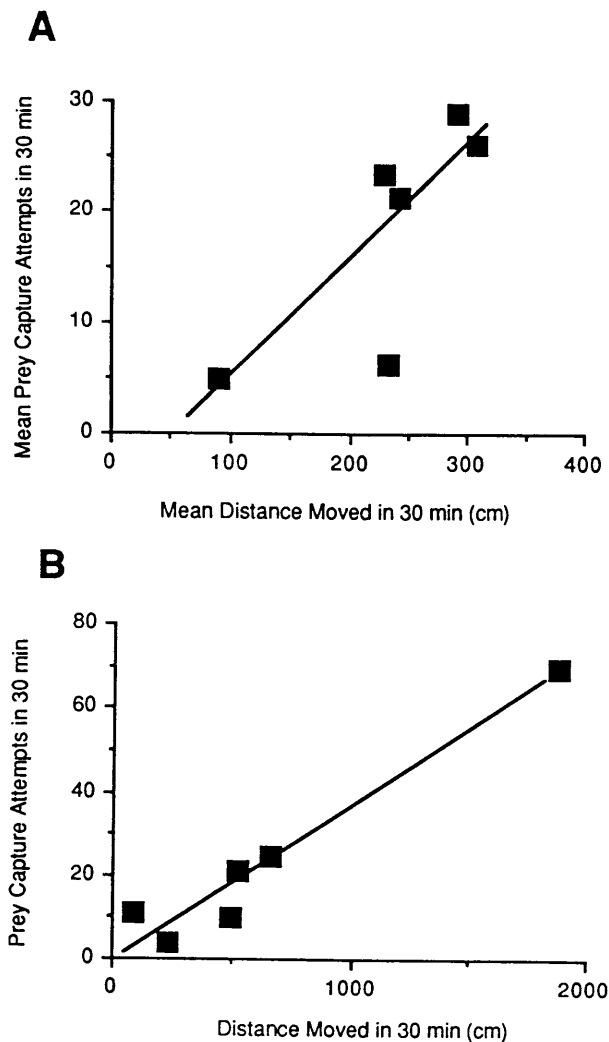
A

B

Fig. 14.5 The relation between distance moved and number of feeding attempts by individual *Dendrobates auratus*. A, overall mean values for six individuals followed for two or more observation periods. (Spearman rank correlation $r_s = 0.771$, $p = .05$). B, values for 30-min observations of *D. auratus* no. 7. (Spearman rank correlation $r_s = 0.899$, $p < .01$. The correlation remains significant when the observation at 1,876 cm is omitted: $r_s = 0.821$, $p < .05$.) (Reprinted, by permission, from Pough and Taigen 1990.)

four species is encouraging and suggests that studies that focus on the role of individual variation could be productive.

The only such study published to date tested the hypotheses that individual variation in foraging behavior of toads (*Bufo woodhousii*) is correlated with variation in prey-capture success and with physiological characteristics (Walton 1988). Toads were followed for periods of 0.25 to 1.97 h (overall average = 0.55 h) as they foraged in a beach habitat at night, and the distance they traveled was recorded. Toads that moved frequently traveled longer distances and encountered and consumed more prey than did individuals that moved less frequently. The animals were returned to the laboratory after the field observations, and aerobic capacity on a treadmill was measured for each individual. No correlation between aerobic capacity and distance moved was detected. Thus, active foraging does appear to pay off with more prey captures, but no evidence yet links individual variation in foraging behavior to individual variation in metabolic characteristics. No

studies have yet attempted to quantify individual variation in the foraging behavior, locomotion, and metabolism of salamanders or caecilians.

Free-ranging amphibians alternate periods of activity and quiescence, and long observation periods are needed to characterize the behavior of individuals. Negative results from short-term studies are probably not informative. At a minimum, records should extend over a day's activity cycle, and repeated observations over a period of days or weeks are desirable. Field enclosures may provide the most satisfactory combination of natural conditions and repeated observations of individuals, and an automated activity monitoring system would be helpful.

Multivariate Analyses of Performance

The study of metabolic capacities and behavioral performance of amphibians originated in the laboratory, and manipulative studies have long retained the traditional form of experimental biology: one parameter (usually temperature or species identity) is varied while other factors that might influence the results (e.g., humidity, feeding status, time of day) are held constant. This approach has the desirable results of isolating the effects of single factors and reducing variation, but it does not attempt to duplicate natural conditions. As the hypotheses proposed by behavioral energetics have become more sophisticated, experimental conditions that more closely approach those that animals encounter in the field have been employed to test them.

The physical environment can strongly influence the behavioral and physiological capacities of ectotherms. Free-ranging animals confront more than one environmental variable at a time, and laboratory studies that manipulate two or more variables simultaneously may provide more realistic estimates of performance under natural conditions than do single-variable studies (e.g., Fry 1947; Truchot 1988; Wheatly 1988). Two-factor interactions that have been studied in detail for amphibians include size × sex (Shine 1979), competition × predation (De Benedictis 1974; Morin 1981, 1983b), size × predation (Cronin and Travis 1986; Formanowicz 1986; Kusano, Kusano, and Miyashita 1985), sex × habitat (Keen, McManus, and Wohltman 1987; T. Lamb 1984), reproduction × daily cycles (Griffiths 1985b), pH × habitat (Freda and Dunson 1986), pH × temperature (Pough and Wilson 1977), pH × density (Cummins 1989), habitat × daily cycles (Gregory 1983), competition × habitat (Maiorana 1978; Keen 1982), temperature × habitat (Stauffer, Gates, and Goodfellow 1983), temperature × dehydration (Preest and Pough 1989), temperature × daily cycles (Smits 1984), social behavior × temperature (Gatten and Hill 1984), habitat × season (Toft 1980b) and parasitism × habitat (Pounds and Crump 1987). Three-factor interactions such as habitat × body size × temperature (Wollmuth et al. 1987), and habitat × body size × daily cycles (fig. 14.9) have also been documented.

Biophysical models predict the consequences of simultaneous variation in several environmental parameters, but translating these predictions into experimental designs is difficult. Temperature and water are probably the environmental parameters that most directly affect the physiological status of an amphibian (Tracy 1976; see also chapters 4, 6, 8, and

9). Recently three studies of metabolism and locomotion by amphibians have applied this multivariate approach with results that emphasize the utility of such investigations. The canyon treefrog of Arizona, *Hyla arenicolor* (Hylidae), rests in sunlit areas on rock outcrops during the day and undergoes

substantial dehydration. Evaporative water loss equivalent to 20% of the fully hydrated body mass had no effect on resting or activity metabolism of frogs at 20°C (fig. 14.6). At 30°C resting metabolism was again unaffected by dehydration, but oxygen consumption during activity was decreased by 36% (Brust and Preest 1988).

Three species of Puerto Rican *Eleutherodactylus* (Leptodactylidae) differed in their response to simultaneous dehydration and thermal stress in ways that appear to correspond to the conditions they may encounter in their habitats (Beuchat, Pough, and Stewart 1984). The jump distance of a lowland species, *E. antillensis,* which is found primarily in grassland habitats that are hot and often dry, was less affected by dehydration at high body temperatures than at low temperatures. In contrast, two forest-dwelling species from higher altitudes, *E. coqui* and *E. portoricensis,* were equally sensitive to dehydration at all temperatures tested.

Body temperature and hydration state had synergistic effects on the locomotor capacity of toads (*B. americanus*) in laboratory trials (Preest and Pough 1989). The distance moved in 10 min of forced locomotion decreased as the animals were dehydrated at body temperatures between 15° and 30°C (fig. 14.7): fully hydrated and slightly dehydrated toads traveled farthest at high test temperatures, whereas more severely dehydrated toads moved farthest at intermediate temperatures. The interaction of body temperature and hydration state was statistically significant, and individual toads varied in their sensitivity to those parameters.

Experiments like these that measure performance as a function of simultaneous variation in two or more environmental parameters provide information that is not available from studies of single variables. For example, the individual variation in sensitivity to the combined effects of temperature and hydration observed for American toads means that the relative performance capacities of individual toads under natural conditions cannot be predicted from laboratory measurements at a single combination of temperature and hydration; the toads that do best under cold wet conditions are not
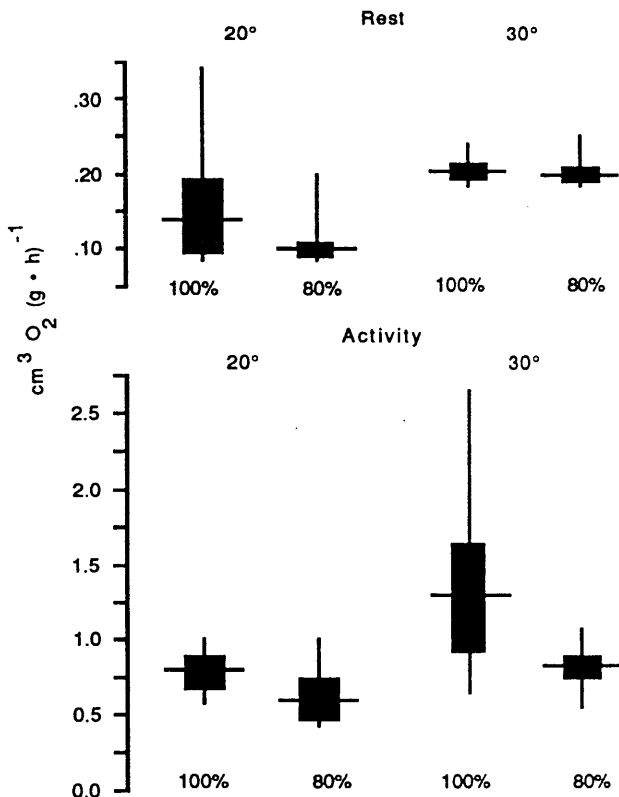
Fig. 14.6 Synergistic effect of body temperature and hydration state on oxygen consumption by *Hyla arenicolor;* only during forced locomotion at 30°C does dehydration to 80% of standard mass significantly reduce the rate of oxygen consumption. *Vertical line,* range; *horizontal line,* mean; *bar,* ±2 SE. (Data from D. G. Brust and M. R. Preest pers. comm.)
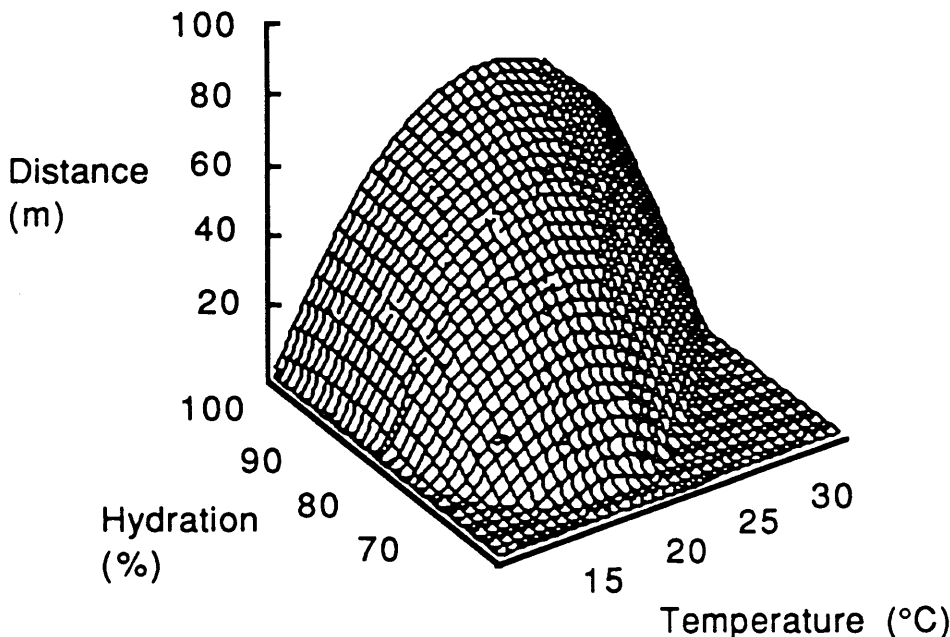

Fig. 14.7 Synergistic effect of body temperature and hydration state on the average distance moved in 10 min of forced locomotion by American toads (*Bufo americanus*). The maximum distance traveled decreased with progressively greater levels of dehydration, and the temperature yielding the maximum distance shifted downward. (Reprinted, by permission, from Preest and Pough 1989.)

necessarily the same individuals that excel when it is hot and dry. This result differs from the observation that the rank order of sprint speeds of lizards was unchanged when only temperature was varied (Huey and Dunham 1987).

Do Generalizations about Lizards Apply to Anurans?

Many of the influential ideas in the behavioral energetics of anurans were developed from studies of lizards and snakes and were subsequently applied to frogs. Is this transfer of models justified, or are frogs and other amphibians so different from squamate reptiles that similar ecological pressures produce distinct evolutionary responses? For example, Toft (1980a) noted that ant-specialist frogs are wide foragers but ant-specialist lizards are sit-and-wait foragers. Both Huey and Pianka (1981) and Toft (1981) suggested that prey type should differ among foraging modes. Huey and Pianka (1981) and Huey and Bennett (1986) suggested that widely foraging desert lizards should eat sedentary and unpredictable (but clumped or large) prey such as termites found at a nest or large scorpions. Toft (1981) suggested that widely foraging frogs eat small, slow-moving prey that are distasteful or chitinous; these were mites or ants in her sample. Termites and ants are social insects that share many characteristics of behavior and predator defense, but are they equivalent in food value? Palatability and digestibility vary among termite and ant species as well as among castes within species. Termite alates appear to be higher-quality food for anurans than are worker castes of ants (Dimmitt and Ruibal 1980b). Perhaps the sensory modalities employed by sedentary and searching anurans and lizards contribute to the differences in diet: widely foraging insectivorous lizards like *Cnemidophorus* and *Ameiva* repeatedly extend their tongues and probably locate hidden prey by olfaction, whereas anurans may be sensitive primarily to visual cues. We would expect the lizards to detect termites, which live mainly underground or in covered galleries, whereas anurans would find ants, which forage largely on the surface of the ground. It may be significant in this context that *Bufo marinus*, which is one of the few anurans known to respond readily to olfactory cues when feeding (Rossi 1983), eats large quantities of termites under some conditions (Strüssmann et al. 1984).

The foraging behaviors of frogs and lizards have been difficult to compare because techniques vary among studies and most researchers have not studied the behavior of both frogs and lizards in the field. Figure 14.8 compares the results of two studies of Brazilian anurans and lizards in which the techniques were comparable. At night, on the open sand beaches of Alter do Chao, *Bufo marinus* (Bufonidae) and *Leptodactylus ocellatus* (Leptodactylidae) forage syntopically, and they differ in their frequency of movement and in the proportion (by number) of ants in their diets (Strüssmann et al. 1984). During the daylight hours in the tropical rainforest near Manaus, four species of lizards forage sympatrically. These species also differ in their rates of movement and the proportion of ants in their diets. *Uranoscodon superciliosa* (Iguanidae) sits on tree trunks and captures prey mainly on the ground. *Kentropyx calcaratus* (Teiidae) forages mainly on the ground. *Anolis punctatus* (Iguanidae) is arboreal and forages mainly on foliage and *Plica umbra* (Iguanidae) is arboreal and forages mainly on tree trunks. As Toft (1981)
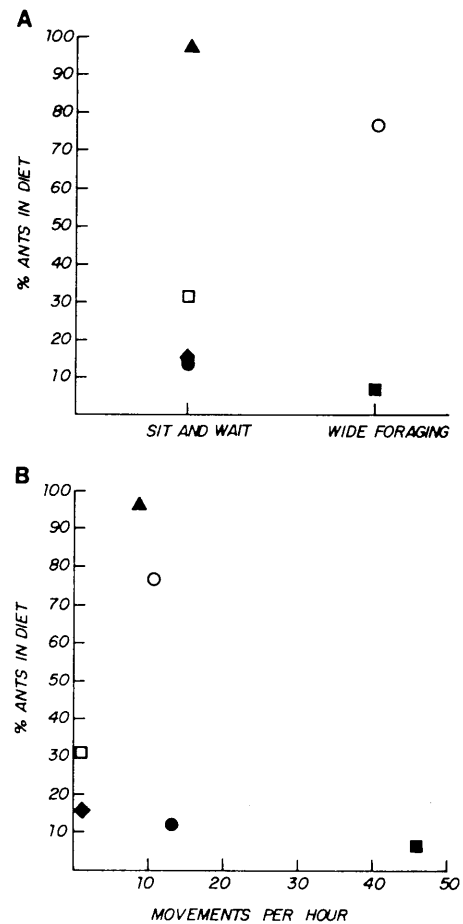

Fig. 14.8 Mean proportion of items in the diet represented by ants for the frogs *Leptodactylus ocellatus* (□), *Bufo marinus* (○), and the lizards *Uranoscodon superciliosa* (◆), *Plica umbra* (▲), *Anolis punctatus* (●), and *Kentropyx calcaratus* (■). A, species classified by subjective indices of foraging mode. B, species ordered by mean number of movements per minute. (Data for frogs are from Strüssmann et al. 1984, and data for lizards are from T. Gasnier, A. Lima and W. Magnusson in preparation.)

noted, lizards and frogs appear to differ when they are lumped into the categories sit-and-wait versus widely foraging (fig. 14.8A). However, a continuous measure such as frequency of movement shows no differences between frogs and lizards (fig. 14.8B).

The velocity of movement by amphibians is substantially lower than that of lizards; the fastest frogs travel only a tenth as far per unit time as widely foraging lizards (table 14.3). In fact, the mean velocities even of large, widely foraging anurans such as *Bufo marinus* fall within the range of velocities of sit-and-wait lizards of similar body lengths. Furthermore, the metabolic correlates of foraging mode are not exactly the same for anurans as for squamate reptiles (Taigen and Pough 1985). Widely foraging species in both groups have high aerobic capacities for locomotion, but the squamates also have high anaerobic capacities whereas widely foraging species of anurans have low anaerobic capacities. Taigen and Pough (1985) proposed two nonexclusive explanations for this divergence, one based on prey-handling behavior and the other on defense. They noted that capturing and subduing prey that is capable of quick evasive movements and prolonged struggle, as squamates often do, is quite a different

TABLE 14.3   Velocities of Movement by Free-Ranging Anurans, Salamanders, and Lizards

	Velocity (m·h^{-1})		
	Mean Velocity[a]	Velocity Moving[b]	Reference
Anurans			
Bufo bufo	20–50		Van Gelder, Aarts, and Staal 1986
Bufo marinus	≤30		Strüssmann et al. 1984
Bufo woodhousii	18		Walton 1988
Colostethus inguinalis	2.5	144	Pough and Taigen 1990
Colostethus nubicola	0.9	57.6	Pough and Taigen 1990
Colostethus talamancae	1.5	230	Pough and Taigen 1990
Dendrobates auratus	13.6	241.2	Pough and Taigen 1990
Eleutherodactylus coqui	0.2		Pough and Taigen unpublished data
Leptodactylus ocellatus	≤20		Strüssmann et al. 1984
Salamanders			
Plethodon jordani	36–60		Madison and Shoop 1970
Lizards			
			Garland 1985
Insectivores and Carnivores **Sit-and-Wait Predators**			
Iguanidae			
Anolis (9 species)	3.1 ± 0.7 ($N = 9$)	234 ($N = 1$)	
Sceloporus (3 species)	5.7 ± 1.0 ($N = 3$)		
Phrynosoma cornutum	8.5		
Uta stansburiana	17.6		
Callisaurus draconoides	25.0		
Lacertidae			
Eremias and *Meroles* (2 species)	67.5 ± 7.0 ($N = 2$)	469 ± 8 ($N = 2$)	
Widely Foraging Predators			
Iguanidae			
Gambelia (2 species)	66.2 ± 3.2 ($N = 2$)		
Lacertidae			
Eremias, Ichnotropis, and *Nucras* (5 species)	341 ± 57 ($N = 5$)	537 ± 72 ($N = 4$)	
Teiidae			
Ameiva, Cnemidophorus, and *Kentropyx* (7 species)	111 ± 30 ($N = 7$)	397 ± 200 ($N = 5$)	
Helodermatidae			
Heloderma suspectum	107		
Varanidae			
Varanus (3 species)	475 ($N = 1$)	812 and 4,800 ($N = 2$)	
Herbivores and Omnivores			
Iguanidae			
Conolophus and *Dipsosaurus* (2 species)	171 ± 129 ($N = 2$)	1,400 ± 111 ($N = 2$)	
Scincidae			
Egernia and *Tiliqua* (2 species)		320 ± 50 ($N = 2$)	
Teiidae			
Cnemidophorus murinus	96	125	

[a]Total distance moved divided by total time observed.
[b]Distance moved divided by time actually moving.

matter from eating prey that is captured and subdued with a flick of the tongue. Lizards and snakes require anaerobic metabolic input during feeding: rates of oxygen consumption of lizards eating insects are as high as 84% of the aerobic scope, and lactic acid accumulates as they chew and swallow prey (Pough and Andrews 1985a, 1985b). Garter snakes also accumulate lactic acid as they subdue and swallow salamanders (Feder and Arnold 1982).

The difference in anaerobic capacities of squamates and anurans might also be related to differences in their defensive behaviors. Widely foraging frogs appear to be toxic and to rely on static defenses, whereas lizards do not have toxins and widely foraging species appear to escape by running, probably using anaerobic metabolism.

Do Studies of Foraging Demonstrate a Direct Relation between Energetics and Fitness?

The early prominence of studies of foraging in our understanding of the behavioral energetics of amphibians resulted

partly from the momentum of similar studies of lizards and partly from the influence of dietary studies in community ecology (see reviews by Hairston 1987; Seale 1987; Toft 1985). However, hindsight suggests that this emphasis on foraging may have been misplaced in two respects. One reason to doubt that studies of foraging will yield evidence of a direct connection between energetics and fitness lies in the apparently low levels of exertion required during most foraging activities. Animals do not appear to be working near their physiological capacities during foraging, and if this is the case, natural selection may not act on exercise physiology via foraging mode.

Furthermore, foraging is a complex behavior that is interwoven with other activities, such as avoidance of predators and territorial defense, that are equally important to the fitness of an individual. The trade-offs that result from the interactions of these activities have provided a fruitful ground for ecological models, but experimentalists have not yet been able to disentangle potentially confounding influences to reveal clear-cut relations among physiology, foraging, and fitness.

Confounding Factors in the Study of Foraging Behavior

Body size is one of the most important variables affecting the life of any organism. The body sizes of amphibian species vary enormously within phylogenetic lineages and within ecological communities. Even among sympatric species of arboreal hylids, body lengths vary by sixfold (fig. 14.9). However, we know little of the effects of this variation in body size on foraging modes and diets of amphibians. Emerson (1985) used deviations from reduced-major-axis regressions to investigate correlates of head morphology in anurans independent of size. However, most studies have simply restricted comparisons to animals of similar size (e.g., Strüssmann et al. 1984) or have apparently assumed that size differences will not confound the results.

Often it is difficult to separate the effects of size, age, and reproduction (see also chapter 15). At the simplest level, the body size of a predator affects the size of the prey it eats because most amphibians (with the exception of some caecilians) do not chew their prey and hence are gape-limited, and qualitative ontogenetic changes have been recorded in diet (e.g., Christian 1982; Luthardt-Laimer 1983; Petranka 1984; Strüssmann et al. 1984). foraging efficiency (Reilly and Lauder 1988), and metabolism (Taigen and Pough 1981; Pough and Kamel 1984). K. L. Jones (1982) suggested that movement rate is proportional to size in a group of sit-and-wait arboreal *Eleutherodactylus*. Changes in foraging behavior may also be mediated by size-related changes in susceptibility to predators (e.g., Brodie and Formanowicz 1983; Cooke 1974; Cronin and Travis 1986; Crump 1984; Formanowicz 1986; Formanowicz et al. 1981; Kusano, Kusano, and Miyashita 1985).

Sexual differences in metabolism of amphibians have been reported (e.g., Fitzpatrick 1971; Taigen, Wells, and Marsh 1985), and gender may also affect habitat selection (e.g., Keen, McManus, and Wohltman 1987) and diet (e.g., T. Lamb 1984). Differences in diet and behavior of lizards have been attributed to the hypothesis that adult males are search-
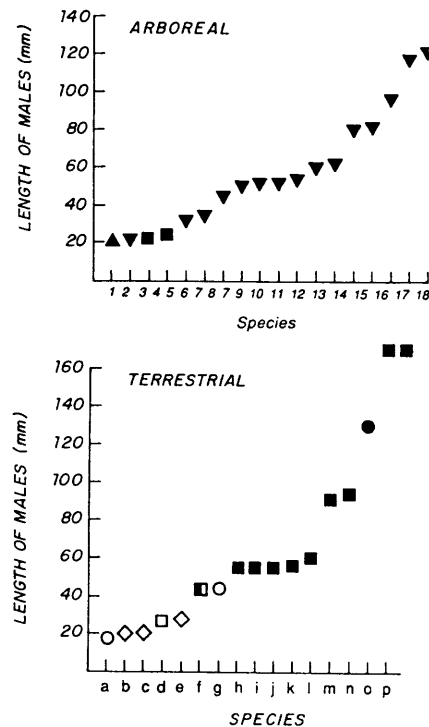

Fig. 14.9 Sizes of anurans that forage above ground (excludes microhylids and pipids) in undisturbed rainforest in Reserva Ducke, central Amazonia. Sizes are based on the largest males in the Instituto Nacional de Pesquisas da Amazônia collections or recorded by Barbara Zimmerman at the World Wildlife Fund, Minimum Critical Size of Ecosystems Project, 90 km north of Reserva Ducke. Mean sizes of males and sizes of females undoubtedly differ from those given, but the general patterns would remain the same for any index of the size of the species. *Open symbols* represent diurnal species, and *filled symbol* represent nocturnal species. The *half-filled symbol* represents a species that has been reported as being diurnally and nocturnally active. ▼, hylids; ▲, centrolenids; *squares*, leptodactylids; *circles*, bufonids; ◇, dendrobatids. Arboreal species are *1, Centrolenella oyampiensis; 2, Hyla minuta; 3, Eleutherodactylus lacrimosus; 4, Eleutherodactylus sp.; 5, H. rubra; 6, H. garbei; 7, Osteocephalus buckleyi; 8, Phyllomedusa tomopterna; 9, Phrynohyas resinifictrix; 10, Osteocephalus sp.; 11, H. granosa; 12, Phyllomedusa vaillanti; 13, H. geographica; 14, H. lanciformis; 15, O. taurinus; 16. Phyllomedusa tarsius; 17, H. boans; 18, Phyllomedusa bicolor.* Terrestrial species are *a, Dendrophryniscus minutus; b, Colostethus marchesianus; c, Colostethus sp.; d, Adenomera andreae; e, Dendrobates femoralis; f, Lithodytes lineatus; g, Bufo cf. typhonius; h, Leptodactylus fuscus; i, Eleutherodactylus fenestratus; j, Leptodactylus mystaceus; k, Leptodactylus wagneri; l, Leptodactylus rhodomystax; m, Leptodactylus stenoderma; n, B. marinus; o, Leptodactylus pentadactylus; p, Leptodactylus knudseni.*

ing primarily for females, whereas adult females search for food (Stamps 1977), and the same phenomenon may occur among amphibians. Studies of anurans are often facilitated by the aggregation of large numbers of males in or around aquatic habitats. Unfortunately, the anurans that are easiest to find are engaged in activities that may exclude or sharply modify foraging behavior (e.g., J. G. M. Robertson 1986b; Woolbright and Stewart 1987). Studies of the correlates of foraging modes of amphibians might be directed more profitably at females and perhaps juveniles.

Parental care by both male and female amphibians is common (see below), and individuals involved in parental care may give low priority to foraging (Forester 1981; Juterbock

1987; Simon 1983; Townsend, Stewart, and Pough 1984; Vaz-Ferreira and Gehrau 1975; Weygoldt 1980; Woodruff 1977; Woolbright and Stewart 1987). An extreme case of conflict between foraging and parental care is the Australian frog *Rheobatrachus silus* (Myobatrachidae), in which the stomach becomes modified as a brood pouch (Tyler and Carter 1981).

Habitat structure can affect both diet and foraging mode of amphibians. The magnitude of variation in diet within species among habitats is sometimes greater than variation among species within habitats (e.g., Strüssmann et al. 1984; Toft 1980b; White 1977). Those differences may reflect only the differences in the availability of prey from habitat to habitat, but differences in habitat structure can induce changes in foraging mode that may in turn lead to differences in diet. For example, habitat structure affects the activity of juvenile *Leptodactylus melanonotus* (Leptodactylidae). Frogs of this species were active during the day and night in a pond-edge habitat with tall vegetation, but were active only at night at an adjacent pond with low vegetation (Gregory 1983). Few species of amphibians forage syntopically, and habitat segregation is characteristic of most amphibian communities (Hairston 1987; Seale 1987; Toft 1985). One of the most difficult tasks confronting a researcher studying the foraging modes of amphibians is to ensure that habitat variability does not confound the behavioral variables being measured. Samples of the prey spectrum potentially available to a predator are an essential part of an analysis of interhabitat or interspecific variation in foraging mode and diet.

Physical characteristics of the habitat such as pH (Freda and Dunson 1986; Wyman and Hawksley-Lescault 1987), water speed (Odendaal and Bull 1980), temperature (Casterlin and Reynolds 1978; Noland and Ultsch 1981; Pauley 1978; Stauffer, Gates, and Goodfellow 1983), moisture (Keen 1984; Duellman and Trueb 1986; van Beurden 1980), salinity (Mullen and Alvarado 1976), and refuge sites (Davic and Orr 1987; Stewart and Pough 1983) may affect the distribution of amphibians and hence their access to prey. The same factors may affect the distribution of the prey species themselves (e.g., Jaeger 1978), and this aspect of the trophic biology of amphibians has been little considered in studies of foraging behavior.

Amphibians have endogenous daily and seasonal rhythms (e.g., Robertson 1976; Weathers and Snyder 1977) that can influence the results of behavioral and physiological studies. In the field, behavior always varies throughout the daily cycle. This variation has been related to predation (Gregory 1983; Holomuzki 1986; Stangel and Semlitsch 1987), thermoregulation (Hutchison and Spriestersbach 1986; Taigen and Pough 1981), or response to light levels (Hailman 1982, 1984; Hailman and Jaeger 1976; Jaeger 1981b; Jaeger and Hailman 1981; Jaeger, Hailman, and Jaeger 1976). Furthermore, characteristics of a habitat are often subject to daily and seasonal changes that may induce predictable changes in prey availability or amphibian behavior (Feder and Londos 1984; Hutchison and Spriestersbach 1986; Jaeger 1978; Keen 1984; Pough et al. 1983; Smits 1984; Smits and Crawford 1984; Toft 1980a). Complex relationships of behavior, ambient light levels, and predator vulnerability may be shown

for amphibian foraging behavior, as they have been for reproductive behavior (e.g., Nunes 1988; Ryan, Tuttle, and Rand 1982).

Predators have undoubtedly influenced the evolution of amphibian morphology and foraging strategies. They may influence the outcome of competitive interactions (e.g., Morin 1981, 1983a, 1983b; Wilbur, Morin, and Harris 1983) and select directly against certain foraging modes (Feder 1983d; Wassersug and Sperry 1977). The presence of fish predators modifies the foraging behavior of fish and salamander larvae (Stangel and Semlitsch 1987; Werner et al. 1983), and similar effects of predators on terrestrial amphibians are likely.

Inter- and intraspecific competition may determine when and where many species of amphibians forage, especially salamanders and larval anurans (Jaeger 1971; Jaeger, Joseph, and Barnard 1981; Keen 1982; Keen and Reed 1985; Odendaal, Bull, and Richards 1984; Richards 1962; Savage 1952; Southerland 1986a, 1986b, 1986c). Such interactions confound simple comparisons of diet. Indeed, Maiorana (1978) suggested that difference in diet of salamanders is an epiphenomenon attributable to habitat differences.

The effects of diseases and parasites on wild populations of vertebrates have largely been overlooked despite their probable importance (May 1983). Amphibians are susceptible to debilitation by a variety of microorganisms and parasites (reviewed by Duellman and Trueb 1986). However, studies such as those of Schall (1983), which relate infection by pathogens to reduced physiological, whole-animal, and reproductive performance, are unavailable for amphibians. Infection by pathogens might change an animal's principal motivation from foraging to thermoregulation (Hutchison and Erskine 1981; Kluger 1979), so knowledge of the health of the study animals would undoubtedly be of use in the interpretation of behavioral studies.

Is Foraging Hard Work? The prediction that the aerobic capacity of species or individuals will be correlated with behavioral characters such as mode of foraging or velocity of movement is based on the assumption that normal activity requires rates of oxygen consumption approaching the maximum aerobic scope. That assumption was a natural outgrowth of the observation that many species of frogs and salamanders are exhausted by a few minutes of forced locomotion (see chapter 12). However, natural velocities of movement by free-ranging animals appear to be substantially lower than those imposed on animals in laboratory experiments. Velocities of spontaneous movement by amphibians in the field (table 14.3) are within the range they sustain on treadmills with little increase in rate of oxygen consumption and little or no accumulation of lactic acid (Taigen and Beuchat 1984). Rates of oxygen consumption during most other natural activities are well below those elicited by forced activity in the laboratory (table 14.4).

Foraging lizards in the field also rarely reach the maximum speeds they can sustain with aerobic metabolism (Hertz, Huey, and Garland 1988). These observations suggest that the energy requirements of foraging would not be an important selective force in the evolution of the physiological characteristics of either amphibians or lizards, but if that is the

TABLE 14.4   Mass-specific Metabolic Rates and Net Cost of Activity for Selected Amphibians Engaged in Natural Behaviors and at Rest

	Activity	Temp. (°C)	Mass (g)	$\dot{V}O_{2rest}$ (ml $O_2 \cdot g^{-1} \cdot h^{-1}$)	$\dot{V}O_{2act}$ (ml $O_2 \cdot g^{-1} \cdot h^{-1}$)	Net Cost $(J \cdot h^{-1})$
Scaphiopus hammondii[a]	Burrowing	30	11.8	0.11	0.51	95
Bufo woodhousii fowleri[b]	Foraging	21	25.8	0.13	0.30[c]	85
Physalaemus pustulosus[d]	Nest building	25	1.7	0.16	0.77	20
Desmognathus ochrophaeus[e]	Aggression	15	2.0	0.07	0.11	1.6
	Courtship	15	2.0	0.07	0.10	1.2

Note: Net cost = $(\dot{V}O_{2act} - \dot{V}O_{2rest}) \times$ mass $\times$ 20.1 $J \cdot ml^{-1} O_2$. (See also table 14.10.)
[a]Seymour 1973c.
[b]Walton 1988; Walton and Anderson 1988.
[c]$\dot{V}O_2$ during foraging calculated from regression of $\dot{V}O_2$ versus speed of locomotion (Walton and Anderson 1988) and average speed of foraging toads of 0.018 $km \cdot h^{-1}$ (Walton 1988).
[d]Ryan, Bartholomew, and Rand 1983.
[e]Bennett and Houck 1983.

case, what accounts for the correlations that do exist for both groups among aerobic capacity, diet, and foraging mode?

Possibly the metabolic demands of free-ranging animals are not well duplicated by laboratory studies, and the activities of free-ranging animals may require higher rates of energy input than we realize. That hypothesis is supported by two studies showing that, despite the apparently low levels of exertion by lizards under natural conditions, free-ranging lizards accumulate elevated concentrations of lactic acid. This indicates that routine locomotion, feeding, and territorial defense require rates of energy input higher than those that can be sustained aerobically (Bennett, Gleeson, and Gorman 1981; Pough and Andrews 1985b).

The use of glycolysis by amphibians in the field or in the laboratory while engaged in activities other than locomotion has received little attention. Plethodontid salamanders (*Plethodon jordani*) accumulated high concentrations of lactic acid during staged encounters with predatory snakes, and lactate concentration was correlated with the duration of an encounter (Feder and Arnold 1982). Male *Hyla crucifer* (Hylidae) captured in a breeding chorus (not necessarily individuals that had been vocalizing) had an average whole-body lactate concentration of 0.062 mg $\cdot$ g^{-1}. This was nearly twice that of control frogs resting in a laboratory at the same temperature and time of day (0.037 $\cdot$ g^{-1}; Pough and Gatten 1984). Two samples of vocalizing *H. versicolor* had whole-body lactate concentrations higher than resting levels (Taigen and Wells 1985). Lactate concentrations were higher early in the evening than later (0.225 mg $\cdot$ g^{-1} versus 0.103 mg $\cdot$ g^{-1}), suggesting that the effort of moving to the breeding pond from daytime retreat sites may have been responsible for the accumulation of lactic acid. This hypothesis is consistent with the observation that vocalization by anurans is sustained aerobically (see below).

Alternatively, the metabolic capacities of species may not reflect the demands of day-to-day life. Instead they could be examples of excess construction (in the sense of Gans [1979] as proposed by Walton [1988]). That is, the selective forces that are important in determining metabolic capacity might be found not among the routine activities of organisms but in rare events such as defending a territory or sprinting to escape a predator. Unfortunately, phenomena of this sort are not likely to be observed often enough to provide a useful basis for testing hypotheses about the significance of interspecific

or individual variation in metabolic capacities (e.g., van Berkum, Huey, and Adams 1986).

DISCRETE ACTIVITIES AS MEASURES OF PERFORMANCE AND FITNESS

Attempts to understand the relations of physiological, behavioral, and ecological aspects of foraging mode may be frustrated by the lack of a clear link between physiological and behavioral capacities and by the complexity of the day-to-day life of an amphibian. Foraging is not a simple behavior: at a minimum an amphibian must simultaneously confront the costs and benefits of searching versus ambushing and the risks of predation during activity or concealment. Individual fitness will be related to an individual's performance in diverse and sometimes conflicting activities, and one-to-one correspondences are less likely than multivariate relationships that may shift spatially, daily, seasonally, and during the lifetime of an individual.

Correlations of physiological variation with variation in performance and fitness might be seen more clearly if we chose an energetically costly behavior that occupies an animal to the near exclusion of other activities (Pough 1989b). Sociobiologists have found it productive to concentrate on limited aspects of the biology of organisms, choosing activities in which a link between behavior and some aspects of fitness can be demonstrated (e.g., Clutton-Brock 1988). Some of the activities associated with reproduction by amphibians require high rates of energy input and exclude for a time most or all confounding behaviors. Thus, studies of the energetics of reproduction may illuminate constraints and selective forces that are associated with natural activities.

THE ENERGETICS OF REPRODUCTIVE BEHAVIOR
Kentwood D. Wells and Theodore L. Taigen

In many species of animals, sexual selection appears to favor males that maximize the repetition rate, intensity, duration, or complexity of their displays, because such signals enhance a male's ability to attract mates or retain possession of groups of females (e.g., insects: Forrest 1983; Hedrick 1986; fishes: Farr 1980; Schmale 1981; frogs: Arak 1983a; Ryan 1985b; Pallett and Passmore 1988; Wells 1988; birds: Gibson and Bradbury 1985; Höglund and Lundberg 1987; Radesäter et al. 1987; mammals: Clutton-Brock and Albon 1979; Lund-

berg and Gerell 1986; McComb 1987). In addition, energetically costly displays could provide females with information about variation in overall male quality that may be genetically based (Andersson 1982b; Kodric-Brown and Brown 1984; Lambrechts and Dhondt 1986; Klump and Gerhardt 1987; Reid 1987). However, physiological constraints may limit the ability of males to perform these displays (Parker 1982, 1983; Halliday 1987). Hence, the energetic costs of display behavior are of interest not only to physiologists, but to behavioral ecologists as well.

Measurements of the metabolic costs of displays are difficult to obtain, especially for large vertebrates, but indirect evidence suggests that physiological constraints limit display rates. For example, singing rates of some birds decrease at cold temperatures, possibly because thermoregulatory requirements reduce the energy available for singing (Garson and Hunter 1979; Higgins 1979; Gottlander 1987; Reid 1987). On the other hand, singing rates increase when food resources increase (Searcy 1979; Wilhelm, Comtesse, and Phlumm 1980; Davies and Lundberg 1984; Gottlander 1987; Radesäter et al. 1987; Reid 1987).

Relatively small animals such as amphibians are ideal subjects for studies of behavioral energetics because they often will perform natural activities inside metabolic chambers. Studies of anuran vocalization are particularly interesting because vocalization is a natural activity that may require rates of energy input that approach an animal's physiological limits (see above and chapter 12). Other activities, such as foraging, are supported by metabolic rates well below maximum sustainable levels (table 14.4). Laboratory measurements of physiological performance, such as maximum rate of oxygen consumption during forced exercise, can reveal significant correlations between physiology and behavior at the interspecific level (e.g., Taigen, Emerson, and Pough 1982; Taigen and Pough 1983, 1985; chapter 12), but attempts to relate individual variation in metabolic performance to behavioral performance in the field have not been very successful (Wells and Taigen 1984; Sullivan and Walsberg 1985; Walton 1988).

This section reviews the energetic costs of reproductive behavior of both urodeles and anurans, although relatively little information is available for urodeles. The focus of the discussion will be on males, because only males of most species engage in costly display behavior during the breeding season. Differences between males and females in patterns of energy use are discussed elsewhere in this chapter. After reviewing the metabolic costs of vocalization in some detail, we consider the relationship between whole-animal behavior and physiology and the morphological and biochemical features of the muscles involved in call production. Because anurans can be studied in the laboratory and the field, they provide a unique opportunity to integrate behavioral, morphological, physiological, and biochemical studies into an interdisciplinary approach to behavioral energetics, as recently advocated (Feder et al. 1987).

Costs of Reproductive Behavior of Salamanders

Terrestrial plethodontid salamanders are good examples of amphibians as low-energy systems (Pough 1983). They have
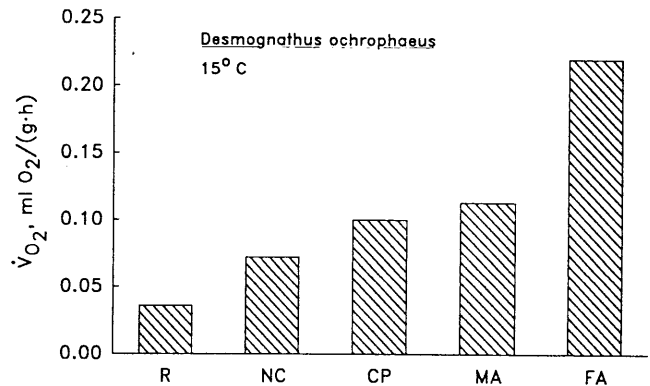

Fig. 14.10 Mean metabolic rates of *Desmognathus ochrophaeus* during natural activities. *R*, rest; *NC*, noncourting pairs; *CP*, courting pairs; *MA*, male-male aggression; *FA*, forced activity. (Resting metabolism from Fitzpatrick 1973a; forced activity from Feder 1986; all others from Bennett and Houck 1983.)

low resting metabolic rates compared to other terrestrial ectotherms (Feder 1983b; Pough 1983) and generally have very low capacities for sustained locomotor activity (Hillman et al. 1979; Withers 1980; Feder 1986, 1987b; see also chapter 12). The lives of most terrestrial plethodontids are characterized by long periods of inactivity punctuated by bouts of foraging, courtship, or aggressive behavior (Feder 1983b).

The only attempt to determine the energetic costs of reproductive behavior for a salamander is Bennett and Houck's (1983) study of the plethodontid *Desmognathus ochrophaeus*. They measured oxygen consumption of noncourting pairs of males and females, courting pairs, and pairs of males engaged in aggressive interactions. Courtship bouts lasted more than an hour on average, but metabolic rates of courting pairs were only 38% higher than those of noncourting pairs (fig. 14.10) and less than three times the resting rates of males and females measured by Fitzpatrick (1973). This is a small increase when one considers that metabolic rates of inactive salamanders may increase by as much as 77% simply as a result of feeding (Feder, Gibbs, Griffith, and Tsuji 1984). Metabolic rates of males engaged in aggressive behavior were only slightly higher. Courting and fighting pairs of *Desmognathus* did not approach levels of oxygen consumption achieved by individuals during forced exercise, which averaged six to ten times resting rates (Feder 1986; see also chapter 12).

Bennett and Houck (1983) also reported significant increases in whole-body lactate following courtship and aggressive behavior. However, lactate levels were only 10 to 30% of those found in males after forced activity. Anaerobic metabolism accounted for about 10% of ATP production during courtship or aggressive behavior. The estimated cost of an average courtship bout (1.23 h) was 2.70 J for the male and female combined, or about 1 to 2% of a salamander's daily energy intake. For comparison, a 1.2-g male *Hyla crucifer* (Anura: Hylidae) calling for an hour at 15°C would use about twenty-five times as much energy as a 2.0-g male *Desmognathus ochrophaeus* engaged in an hour of courtship at the same temperature (Taigen, Wells, and Marsh 1985). These figures do not include all possible costs of reproductive be-

havior for a male salamander; searching for mates, production of pheromones, and production of spermatophores also require energy. In fact, the cost of spermatophore production in this species can exceed the cost of courtship behavior (Marks and Houck 1989), but both costs are small, and it seems unlikely that males of most species of terrestrial salamanders are energy-limited in their reproductive behavior.

The urodeles most likely to have energetically costly courtship are aquatic salamandrids (*Triturus, Notophthalmus,* and *Paramesotriton*), and physiological constraints may limit their courtship activities. Newts have prolonged breeding seasons lasting from several weeks to several months (Verrell and Halliday 1985; Verrell, Halliday, and Griffiths 1986; Verrell and McCabe 1988). Breeding males of most species develop elaborate secondary sexual characters, such as bright colors and enlarged tail fins, and engage in vigorous courtship that may last up to several hours (Halliday 1974, 1975, 1976, 1977a; Verrell 1982; Sparreboom 1983, 1984a; Giacoma and Sparreboom 1987). Males of some species also engage in aggressive interactions that can lead to prolonged struggles for possession of females (Verrell 1983, 1986; Sparreboom 1984a, 1984b; Zuiderwijk and Sparreboom 1986). Although metabolic rates of courting and fighting newts have not been measured, the length and vigor of courtship and aggressive interactions suggest that such behavior is supported mainly by aerobic metabolism.

The ability of male newts to sustain courtship directly affects their success in fertilizing eggs. Males that engage in more than one courtship bout with a female and deposit more than one spermatophore are more likely to achieve fertilization than those that go through a single courtship sequence (Halliday 1976, 1977a). Displays by male *Triturus vulgaris* have a cumulative affect on female receptivity (Teyssedre and Halliday 1986). Males that deposited spermatophores for females had significantly longer courtship bouts than did unsuccessful males. The number of individual courtship acts by male *Notophthalmus viridescens* can reach several thousand per courtship bout and is positively correlated with success in transferring spermatophores (Verrell 1982). A similarly strong correlation exists for *T. cristatus* between total time spent in courtship and mating success.

Several lines of evidence suggest that physiological constraints limit these courtship activities by newts (Halliday 1987). The frequency with which male *T. vulgaris* go to the surface to breathe is directly related to their level of activity (Halliday and Worsnop 1977). Breathing frequency increases during sexual activity, and the need to breathe can significantly limit the duration of courtship bouts (Halliday and Sweatman 1976). Breathing rates increase if oxygen dissolved in the water or in the gas phase decreases, whereas breathing rates decrease when the water is aerated (Spurway and Haldane 1953; Halliday 1977b). These results do not demonstrate that newts are energy-limited during courtship, but they do suggest that metabolic rates during vigorous activity exceed levels that can be supported solely by cutaneous respiration.

Changes in body mass are not very useful for estimating depletion of energy substrates by male newts during the breeding season because adult newts typically absorb a substantial amount of water when they first enter the breeding

ponds (Verrell and Halliday 1985). Most species of newts feed during the breeding season (Verrell 1985) and may increase in mass if they remain in ponds for long periods (Verrell and Halliday 1985). On the other hand, the mass of the liver and abdominal fat bodies of male *T. vulgaris* decreased during the summer breeding season and increased during the fall (Verrell, Halliday, and Griffiths 1986). The proportion of energy reserves used for production of sperm and spermatophores versus reproductive behavior has yet to be determined, but breeding males do appear to be under some energy stress. Fat body mass and carcass lipids of males of another aquatic salamander, *Amphiuma means* (Amphiumidae), decrease during the breeding season (Rose 1967), but the courtship behavior of this species is completely unknown.

Costs of Reproductive Behavior of Anurans

No urodele has a display equivalent to the loud and sustained calling of frogs and toads. That calling can be a very metabolically expensive activity has forced a revision of earlier views of amphibians as animals poorly adapted for sustained activity and heavily dependent on anaerobic metabolism (Bennett 1978; Pough 1980, 1983; Taigen and Pough 1985; see also chapter 12). The energetic costs of vocalization may stress male anurans during the breeding season. Growth rate, total body mass, and the masses of energy-storing organs may decrease during the breeding season and increase when reproductive activities cease (Jenssen 1972; Wells 1978; MacNally 1981b; Morton 1981; Woolbright 1983, 1985a; J. G. M. Robertson 1986b; Long 1987a, 1987b; Given 1988; McKay 1989). While this cycle may be due in part to reduced opportunities for foraging during the breeding season (Martof 1956; Jenssen and Klimstra 1966; Woolbright and Stewart 1987), it also may reflect the energetic cost of calling. For example, individual male *Rana virgatipes* show a negative relationship between calling rates and growth rates during the breeding season (Given 1988; see also below).

Intensity of Anuran Vocalizations The energetic cost of calling is related to both the sound power of a male's calls and the amount of time invested in calling. Therefore, a brief review of anuran call intensities and calling persistence will provide a useful background for a more detailed discussion of calling energetics. Sound pressure levels (SPL) of selected anuran species are shown in table 14.5; data for additional North American and African species were given by Gerhardt (1975) and Passmore (1981). For most species, only peak SPL measurements are available, but whenever possible, root-mean-square (RMS) values have been included as well. The latter are the measurements most appropriate for calculating total sound power (MacNally and Young 1981; Kavanagh 1987; Prestwich, Brugger, and Topping 1989), and they are also useful for comparison with other animals. Most anurans measured to date have peak SPLs exceeding 100 dB at 50 cm in front of the frog, and some are as high as 115 dB (table 14.5; Gerhardt 1975; Passmore 1981). RMS SPLs average about 10 dB lower, but the precise relationship depends on the structure of the call (Gerhardt 1975).

The acoustic energy output of these frogs is impressive compared to the songs of small birds. Mean RMS SPLs of twenty species of frogs were 84 to 100 dB ($\bar{x} = 91$ dB) at 50

TABLE 14.5 Mean Sound Pressure Levels of the Calls of Selected Anuran Species at 50 cm in Front of the Frog

| | Peak SPL (dB) | | RMS SPL (dB) | | |
	Mean	Range	Mean	Range	Reference
Bufonidae					
Bufo americanus	106	102–109	96	91–100	Gerhardt 1975
Centrolenidae					
Centrolenella fleischmanni	100	92–104			Wells and Schwartz 1982
Hylidae					
Hyla chrysoscelis	105	101–108		88–97	Gerhardt 1975
Hyla cinerea	103	97–107	89	84–94	Gerhardt 1975
Hyla crucifer	103	100–106	94	92–97	Gerhardt 1975
Hyla ebraccata	100	96–105			Schwartz and Wells 1984
Hyla gratiosa	108	106–109	90	86–93	Gerhardt 1975
Hyla microcephala	106	101–109			Schwartz and Wells 1984
Hyla squirella	103		88	86–89	Gerhardt 1975
Hyla versicolor	109	108–113	100	99–103	Wells and Taigen 1986
Litoria ewingi	105	103–106			Harrison 1987
Litoria verreauxi	100	96–101			Harrison 1987
Hyperoliidae					
Hyperolius argus	108	105–111			Passmore 1981
Hyperolius marmoratus	104	102–105			Passmore 1981
Kassina maculata	114	112–116			Passmore 1981
Leptodactylidae					
Eleutherodactylus coqui[a]	100	96–105			Narins and Hurley 1982
Physalaemus pustulosus	90				Ryan 1985b
Myobatrachidae					
Geocrinia victoriana	94	90–97			Littlejohn and Harrison 1985
Ranidella signifera	100	98–101			Littlejohn, Harrison, and MacNally 1985
Ranidella parinsignifera	96	93–98			Littlejohn, Harrison, and MacNally 1985
Uperoleia laevigata[b]	85				Robertson 1984
Ranidae					
Rana lessonae	105				Brzoska 1982
Rana ridibunda	116				Brzoska 1982
Rana virgatipes	109	102–112			Given 1987

Note: Data for some species were calculated from measurements made at 15 or 25 cm.
[a] High-altitude population.
[b] The population referred to *U. rugosa* by Robertson (1984) was placed in *U. laevigata* by Davies and Littlejohn (1986).

cm (Gerhardt 1975). Values for seventeen species of European songbirds were 80 to 106 dB ($\bar{x} = 89$ dB; Brackenbury 1979). Subsequent measurements of European blackbirds (90 dB) and red-winged blackbirds (97 dB) fall in the same range (Dabelsteen 1981; Brenowitz 1982). However, the birds measured by Brackenbury (1979) averaged 23 g in mass, whereas most of the frogs have masses of less than 10 g, and many species are only 1 to 2 g. No strong interspecific relationship between body size and sound intensity was apparent for frogs or birds. A tiny (1.2 g) *Hyla crucifer* (Hylidae) has an SPL of 94 dB RMS, which is similar to that of a 10-g wren (96 dB), a 20-g warbler (94 dB), or a 96-g blackbird (93 dB; Brackenbury 1979).

The frogs shown in table 14.5 also appear to be considerably louder than most insects. Some of the loudest species of insects are shown in table 14.6. The songs of some tettigoniid bush crickets and katydids reach RMS SPLs of 90 dB at 50 cm, which is about average sound intensity of North American frogs. The bladder cicada (*Cystosoma saundersii*), which is a loud insect, has an SPL of about 82 dB, lower than any of the frogs measured by Gerhardt (1975). Many insects, including the common house cricket (*Acheta domesticus*) and a

number of acridid grasshoppers, have SPLs of only 25 to 50 dB at 50 cm (Dumortier 1963). These data are not strictly comparable to measurements for frogs because they represent instantaneous sound pressure levels. Many insects have continuous trills that may last for minutes at a time. Hence, total sound power output per hour could be higher than that of many frogs, even if SPLs are equal or lower. Nevertheless, anurans do appear to have some of the loudest acoustic signals of any small terrestrial animals, and they have very high sound power outputs for their body sizes.

The data in table 14.5 do not give a complete picture of intraspecific variation in sound power of anuran vocalizations. The calls of different individuals in a population often vary in sound pressure level by 6 to 10 dB (Gerhardt 1975; Passmore 1981). An increase of 10 dB represents a tenfold increase in sound power (measured in watts), and a 6 dB increase translates to about a fourfold increase in power output. Therefore, relatively small differences in SPL could translate into substantial differences in the energetic cost of calling. Few workers have investigated sources of intraspecific variation in sound pressure levels of anuran calls. However, in some species, including *Bufo americanus* (Gerhardt

TABLE 14.6 Root-Mean-Square Sound Pressure Levels of Selected Insect Species at 50 cm Directly above the Insect

	Family	SPL at 50 cm (dB)	Reference
Ephippiger terrestris	Ephippigeridae	89	Dumortier 1963
Acheta domesticus	Gryllidae	49	Dumortier 1963
Teleogryllus commodus	Gryllidae	64	Kavanagh 1987
Gryllotalpa australis	Gryllotalpidae	79	Kavanagh 1987
Conocephalus brevipennis	Tettigoniidae	69	Bailey and Morris 1986
Neoconocephalus affinis	Tettigoniidae	87	Brush, Gain, and Greenfield 1985
Psorodontus illyricus	Tettigoniidae	69	Keuper et al. 1988
Tettigonia cantans	Tettigoniidae	81	Keuper et al. 1988
Tettigonia viridissima	Tettigoniidae	90	Keuper et al. 1988
Cystosoma saundersii	Cicadidae	82	MacNally and Young 1981

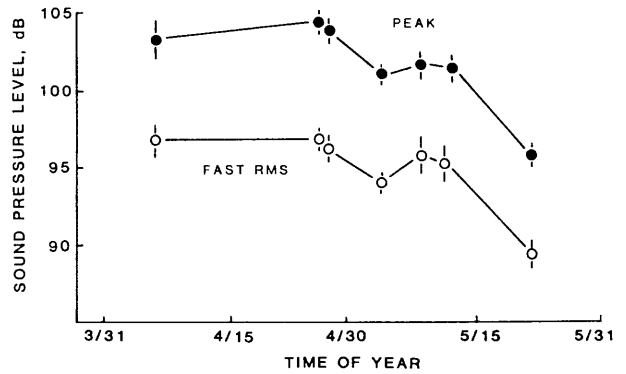*Note:* All the insects are orthopterans except the cicada.

Fig. 14.11 Seasonal changes in sound pressure levels of *Hyla crucifer* calls measured at 50 cm directly in front of the frog. Data are shown as means ± 1 SE. (Unpublished data collected by K. D. Wells and T. L. Taigen in 1988.)

1975), *B. calamita* (Arak 1983a, 1983b), and *Rana virgatipes* (Given 1987), SPL is positively correlated with body size. Call SPLs also may vary seasonally as the physical condition of calling males changes. Wells and Taigen (unpublished) measured SPLs of *Hyla crucifer* throughout the breeding season and found a substantial decline toward the end of the season (Fig. 14.11). This change could have resulted from recruitment of smaller males into the population late in the season, as documented by McKay (1989), as well as the deterioration of calling muscles of males that had been in the chorus for several weeks (see discussion of muscle physiology below). In either case, the sound power of calls produced by males late in the season is much lower than that of males calling earlier in the year.

Duration of Anuran Vocalization Frogs can be remarkably persistent in their vocalization, often calling almost continuously for several hours each night. Precise data on calling effort are difficult to obtain because most workers have been content to describe features of individual calls without recording hourly calling rates, call durations. or the number of hours of calling per night. Several measures of calling effort for both tropical and temperate zone species are shown in table 14.7. Some species have calls consisting of simple single-note calls, whereas others produce complex multinote calls that may have more than one type of note. For comparison, calling rates of most species in table 14.7 are reported as the number of individual notes per hour. The number of seconds of calling per hour was estimated from average note durations and does not include intervals between call notes. Most figures for number of hours of calling per night and total number of notes given per night are estimates based on average calling times for the chorus as a whole. Only a few investigators have monitored individual males throughout the

night to obtain precise estimates of total calling times (e.g., Ryan, Bartholomew, and Rand 1983; Wells and Taigen 1986; Grafe 1988).

Frogs vary considerably in hourly calling efforts. Some species, such as *Hyla rosenbergi* and *Ranidella signifera* (Myobatrachidae), may produce more than 7,000 call notes per hour and more than 25,000 notes per night. Others, such as *Rana virgatipes,* produce fewer than 200 notes per hour. The data in table 14.7 probably are biased toward active callers and may not be representative of frogs as a whole. All of these species call in relatively dense choruses where complex vocal interactions among males and high calling rates are common (Wells 1988). In contrast, many tropical frogs call from isolated positions in the forest, and their low calling rates suggest that energetic costs of calling are lower than costs for actively chorusing species.

Energetic Costs of Calling Because sustained vocalization by frogs is supported almost entirely by aerobic metabolism (see discussion of anaerobic metabolism below), energetic costs can be estimated directly by measuring the metabolic rates of males calling in small chambers. This was first done with a tropical leptodactylid frog, *Physalaemus pustulosus* (Bucher, Ryan, and Bartholomew 1982), and subsequently with several other tropical and temperate zone frogs (table 14.8). In most of these studies, frogs are placed in closed metabolic chambers from which an initial air sample is drawn before the animal begins calling. After a period of vocalization by the frog, a second air sample is withdrawn, and the fractional oxygen content of the two samples is measured with an oxygen analyzer (Bucher, Ryan, and Bartholomew 1982; Taigen and Wells 1985; Taigen, Wells, and Marsh 1985; Prestwich, Brugger, and Topping 1989; Wells and Taigen 1989). Flow-through respirometry, such as that used by Lighton (1987) to measure the cost of substrate tapping in beetles, has not been attempted for frogs. However, Grafe (1988) used an open-flow system to measure carbon dioxide production by calling *Hyperolius viridiflavus* (Hyperoliidae) with an infrared gas analyzer; these data were then converted to oxygen consumption using a respiratory quotient measured in the laboratory for frogs that were not vocalizing. This procedure could introduce a substantial error if

TABLE 14.7 Estimates of Calling Effort for Selected Anuran Species

	Temp (°C)	Measure of Calling Effort				Reference
		Notes·h⁻¹	s·h⁻¹	h·night⁻¹	Notes·night⁻¹	
Bufonidae						
Bufo woodhousii	20	240	360			3, 5
Centrolenidae						
Centrolenella fleischmanni	18	580	120	4	2,320	9
Hylidae						
Hyla cinerea	27	3,100	430	2–4		20
Hyla crucifer	16	4,500	500	2–4	13,500	12
Hyla ebraccata	26	2,700	270	2–4	8,100	7
Hyla gratiosa	29	3,600	650			20
Hyla microcephala	26	3,800	355	2–4	11,500	21
Hyla rosenbergi	26	7,200	430	4	28,800	1
Hyla squirella	27	6,600	1,320			20
Hyla versicolor	19	1,000	700	2–4	3,000	16
Litoria ewingi	10	2,200	450			18
Hyperoliidae						
Hyperolius marmoratus	24	3,300	330	4	13,200	8
Hyperolius viridiflavus	25	5,400[a]	330	2–4	10,000[a]	19
Leptodactylidae						
Eleutherodactylus coqui	23	1,450[b]	350	3	4,350[b]	13, 14
Physalaemus pustulosus	25	1,000[b]	400	5–7	6,000[b]	2, 4
Myobatrachidae						
Geocrinia victoriana	13	3,840	350			10
Ranidella signifera	12	7,800	940			6, 11
Uperoleia laevigata	14	1,200	580	4–5	5,400	15
Ranidae						
Rana virgatipes	26	180	20	7	1,260	17

Sources: (1) Kluge 1981; (2) Bucher, Ryan, and Bartholomew 1982; (3) Sullivan 1982b; (4) Ryan, Bartholomew, and Rand 1983; (5) Sullivan 1983; (6) MacNally 1984; (7) Wells and Schwartz 1984; (8) Dyson 1985; (9) Jacobson 1985; (10) Littlejohn and Harrison 1985; (11) Littlejohn, Harrison, and MacNally 1985; (12) Taigen, Wells, and Marsh 1985; (13) Woolbright 1985c; (14) Zelick and Narins 1985; (15) J. G. M. Robertson 1986a; (16) Wells and Taigen 1986; (17) Given 1987; (18) Harrison 1987; (19) Grafe 1988; (20) Prestwich, Brugger, and Topping 1989; (21) Wells and Taigen 1989.

[a]Measurements for frogs in the laboratory.

[b]Number of calls·h⁻¹; calls are composed of two distinct types of notes.

TABLE 14.8 Oxygen Consumption of Male Frogs during Rest, Forced Exercise, and Calling

	Temp. (°C)	$\dot{V}O_2$ (ml $O_2 \cdot g^{-1} \cdot h^{-1}$)				Reference
		Rest	Exercise	Call (avg)[a]	Call (max)[b]	
Hyla cinerea	27	0.14	1.02	0.92	1.20	7
Hyla crucifer	19	0.11	1.10	1.51	1.70	4
Hyla gratiosa	29	0.10	1.25	1.22[c]	1.21[c]	7
Hyla microcephala	26	0.15		1.70	2.80	8
Hyla squirella	27	0.17	1.79	2.27[c]	2.10[c]	7
Hyla versicolor	19	0.08	1.09	1.70[c]	1.67[c]	3, 5
Hyperolius viridiflavus	25	0.13[d]	1.10[d]	1.37	1.40	6
Physalaemus pustulosus	26	0.15	1.82	0.91	1.18	1, 2
	25	0.16[e]		0.98	1.83	9

Sources: (1) Bucher, Ryan, and Bartholomew 1982; (2) Ryan, Bartholomew, and Rand 1983; (3) Taigen and Wells 1985; (4) Taigen, Wells, and Marsh 1985; (5) Wells and Taigen 1986; (6) Grafe 1988; (7) Prestwich, Brugger, and Topping 1989; (8) Wells and Taigen 1989; (9) T. L. Taigen and K. D. Wells unpublished data.

[a]Estimated metabolic rate at the average calling rate measured in the field.

[b]Highest rate for a frog calling in a metabolic chamber.

[c]Average calling rates in field exceeded those of most males calling in metabolism chambers.

[d]Data from Taigen, Emerson, and Pough 1982 adjusted to 25°C, assuming a Q_{10} of 2.0.

[e]Resting rates measured at 26°–28°C and adjusted to 25°C assuming a Q_{10} of 2.0.
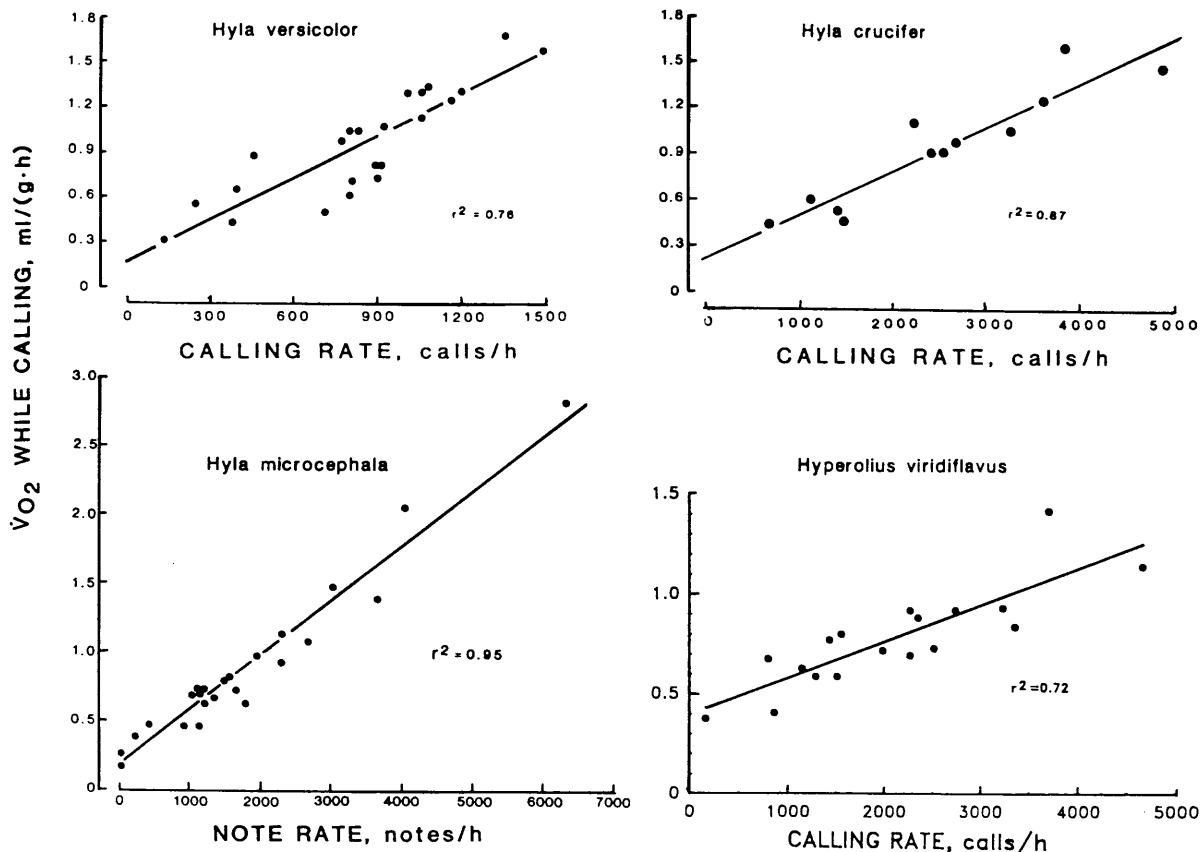
Fig. 14.12 Rate of oxygen consumption during calling in relation to calling effort for selected anurans. (*Hyla crucifer* data from Taigen, Wells, and Marsh 1985; *Hyla versicolor* from Taigen and Wells 1985; *Hyla microcephala* from Wells and Taigen 1989; *Hyperolius viridiflavus* from Grafe 1988, pers. comm.)

the metabolic substrates differ when frogs are at rest and vocalizing.

Average metabolic rates for several species of frogs at rest, while calling, and during forced exercise are given in table 14.8. Both the metabolic rate of males calling at average rates in the field and maximum rates of oxygen consumption measured for any individual calling in a metabolic chamber are included. Metabolic rates of calling frogs are very high compared to other measurements of activity metabolism in amphibians (see chapter 12). In fact, the maximum values for *Hyla microcephala* and *H. squirella* (Hylidae) at 26° to 27°C are the highest yet measured for any ectothermal vertebrate. In all of the species, the maximum rate of oxygen consumption while calling is more than ten times resting metabolism, and average levels for males in the field are six to twenty times resting rates. Maximum oxygen consumption while calling equals or exceeds maximum metabolic rates during exercise for almost all of the species. The maximum values shown in table 14.8 may be underestimates for some species, because frogs often call at higher rates in the field than in metabolic chambers. For example, male *H. versicolor* in a chorus call at rates equivalent to an oxygen consumption of 2.2 to 2.4 ml · g^{-1} · h^{-1}), or nearly thirty times resting metabolism (Wells and Taigen 1986). Clearly, oxygen consumption during forced exercise is not the maximum aerobic capacity of many anurans (Taigen and Wells 1985; see also chapter 12).

For most of the species in table 14.8, the rate of oxygen consumption while calling is a simple linear function of calling effort measured as number of notes or as number of seconds of calling per hour (fig. 14.12). For species such as *Hyla crucifer*, *Hyla microcephala*, and *Hyperolius viridiflavus*, call note duration varies little, and call rate alone explains most of the variation in oxygen consumption (Taigen, Wells, and Marsh 1985; Grafe 1988; Wells and Taigen 1989). On the other hand, *Hyla versicolor* gives relatively long trills that vary in duration, and the best predictor of oxygen consumption is the product of note rate and duration (Taigen and Wells 1985). *Physalaemus pustulosus* (Leptodactylidae) is unusual in that oxygen consumption appears to increase at an accelerating rate as calling rate increases, a pattern found in both the original data reported by Bucher, Ryan, and Bartholomew (1982) and in more recent data collected over a wider range of calling rates (fig. 14.13; Taigen and Wells unpublished). In the combined data, maximum calling rates and maximum rates of oxygen consumption are higher than those reported by Bucher, Ryan, and Bartholomew, but estimated oxygen consumption for an average calling rate in the field is similar (table 14.8; oxygen consumption based on an average calling rate of 1,200 calls · h^{-1}).

Bucher, Ryan, and Bartholomew (1982) reported that noncalling male frogs exposed to a chorus had metabolic rates elevated above resting levels. They suggested that this stimulated rate of oxygen consumption should be considered an

additional cost of reproduction. In subsequent studies, zero-intercepts for regressions of oxygen consumption versus calling rate have been only slightly above resting levels (fig. 14.13) and within the 95% confidence intervals for resting metabolism (Taigen and Wells 1985; Taigen, Wells, and Marsh 1985; Prestwich, Brugger, and Topping 1989; Wells and Taigen 1989). Hence, stimulation by a chorus probably does not cause a significant increase in metabolic rate for most frogs. Slight elevations above daytime resting metabolism are to be expected, because inactive frogs measured at night are never as quiescent as frogs measured during the day. Furthermore, frogs that give relatively few calls are more likely to move than those calling at high rates, leading to slightly inflated values of metabolic rate at low calling rates. For example, reliable measurements of *Physalaemus pustulosus* in the field were difficult at low calling rates because most males moved during measurements (Taigen and Wells unpublished). Even if metabolic rates of noncalling frogs are slightly elevated above resting rates, the increase in oxygen consumption is trivial compared to levels achieved during sustained calling (compare figs. 14.12 and 14.13).

Social Interactions and Calling Energetics   The strong correlation between metabolic rate and calling effort in all of the species of frogs studied to date suggests that social interactions that increase calling should have a strong influence on its total cost. Males of many anuran species respond to the calls of other individuals in a chorus by increasing their calling rate, call duration, or the number of notes per call (reviewed by Wells 1988). Often this behavior leads to substantial variation in calling effort among males in the same population. For example, calling efforts (seconds of calling per hour) of *Hyla microcephala* can vary by more than 300% (Wells and Taigen 1989). In dense choruses, males increase calling efforts by increasing the number of secondary click notes in their calls (Schwartz and Wells 1985; Schwartz 1986). This makes the calls more attractive to females (Schwartz 1986) but also increases the cost of calling. Males appear to conserve energy by maintaining a low calling effort when only a few males are present, but increase calling effort and energetic expenditures when competition among males is intense (Wells and Taigen 1989). Consequently, average metabolic rates of males in a chorus are only about 60% of the maximum level measured in a metabolic chamber (table 14.8).

Other anuran species do not show such a simple relationship between chorus density and energy expenditure. Male *Hyla versicolor* respond to the calls of other males by adding pulses to their calls, thereby increasing call duration (fig. 14.14; Wells and Taigen 1986; Klump and Gerhardt 1987). However, males exhibit a simultaneous decrease in calling
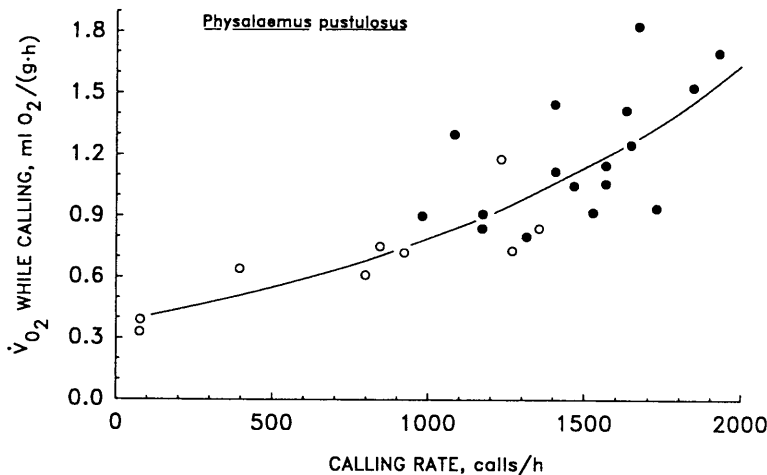

Fig. 14.13   Rate of oxygen consumption during calling in relation to calling rate for *Physalaemus pustulosus*. O, data from Bucher, Ryan, and Bartholomew 1982. ●, unpublished data collected by T. L. Taigen and K. D. Wells in 1986. The equation is for a linear regression with a log-transformed value of rate of oxygen consumption.
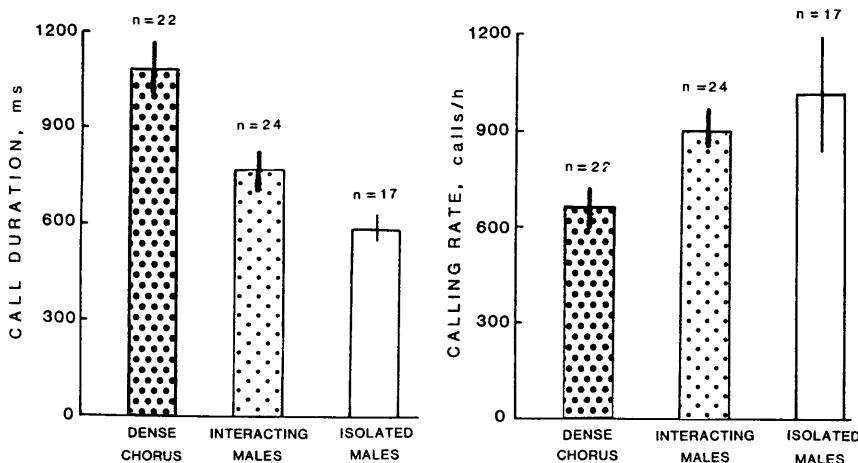

Fig. 14.14   Relation of call duration and calling rate to chorus density for *Hyla versicolor*. (Reprinted, by permission, from Wells and Taigen 1986.)
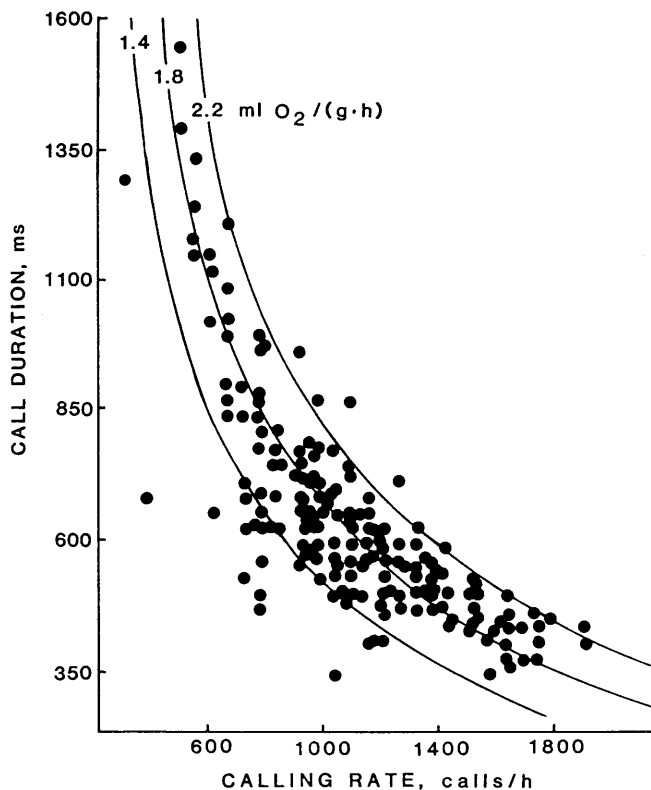
Fig. 14.15 Relation between call duration and calling rate for *Hyla versicolor*. *Lines* show approximate rates of oxygen consumption at different combinations of rate and duration. (Reprinted, by permission, from Wells and Taigen 1986.)

rate (fig. 14.15), resulting in a relatively constant level of calling effort regardless of chorus density. Playback experiments have shown that females prefer long calls to short calls, and high calling rates to low rates (Klump and Gerhardt 1987). More importantly, as predicted by Wells and Taigen (1986), females prefer long calls delivered at slow rates to short calls delivered at fast rates, even when total calling effort is equal (Klump and Gerhardt 1987). Therefore, males in dense choruses alter their calls in ways that enhance their attractiveness to females. However, most individuals appear to be calling near maximum sustainable levels, even when calling in isolation, and males may be unable to increase calling rate and call duration simultaneously because of energetic constraints (fig. 14.15).

The effects of social interactions on calling energetics also has been examined in *Physalaemus pustulosus*. This species has an unusual call consisting of a frequency-modulated whine note that may be combined with one or more secondary chuck notes. The latter are given simultaneously with the whine note and are not added onto the end of the call as in other species with complex multinote calls (Ryan 1985b). Males calling in low-density choruses generally give calls with relatively few chucks. In dense choruses, males call at faster rates and add more chuck notes to their calls. Females prefer high calling rates to low rates and calls with chuck notes to whines alone (Rand and Ryan 1981). Although energetic expenditures increase with increasing calling rate (fig. 14.13), there is no evidence from the data of Bucher, Ryan, and Bartholomew (1982) or the data collected by Taigen and

Wells (unpublished) that number of chucks is related to the energetic cost of calling. Probably this is because the chuck is produced by passive vibration of a fibrous mass in the airstream of the larynx, not by additional contractions of the trunk muscles (Drewry, Heyer, and Rand 1982; Ryan 1985b). Variation in the number of chuck notes appears to be mediated by risks of predation, rather than by energetic constraints (see below).

Temperature Effects Most of the frogs studied to date are tropical species or summer-breeding temperate zone species that call at body temperatures within a relatively narrow range. Consequently, variation in temperature explains little of the variation in rate of oxygen consumption while calling (Bucher, Ryan, and Bartholomew 1982; Wells and Taigen 1985; Grafe 1988; Wells and Taigen 1989). However, *Hyla crucifer* calls at a wide range of temperatures during a breeding season that can last from late March through late May. Early in the season males call at temperatures as low as 3° to 4°C, whereas late in the season temperatures can be as high as 25°C. Previous work has shown that calling rate is closely correlated with ambient temperature (Lemon and Struger 1980). However, seasonal variation complicates this relationship. Early in the breeding season, calling rates are tightly coupled with ambient temperature, and become decoupled late in the season (McKay 1989). Late-season males have lower calling rates than males calling at the same temperature earlier in the year, probably because energy reserves are depleted and the aerobic capacity of their muscles is decreased (see discussion of enzyme activities below).

Although intercepts of regressions relating oxygen consumption to calling rate change at different temperatures because of changes in resting metabolism, the relation between calling rate and metabolic rate for *H. crucifer* was essentially the same for temperatures from 5° to 23°C (fig. 14.16; T. L. Taigen and K. D. Wells unpublished). When data for all temperatures were combined into a single regression equation, calling rate explained 91% of the variation in rate of oxygen consumption. In a multiple regression analysis of oxygen consumption, calling rate explained 82% of the variance, mass explained an additional 7%, and temperature explained only 3%. Hence, temperature has relatively little effect on the energetic cost of calling independent of its effect on calling rate.

Contributions of Anaerobic Metabolism Because calling is a vigorous activity that is sustained for many hours, anaerobic pathways are unlikely to make a substantial contribution to calling metabolism. Measurements of lactate accumulation by calling frogs support this prediction. Pough and Gatten (1984) reported levels of whole-body lactate in male *Hyla crucifer* from a chorus that were double those of animals resting in the laboratory and slightly above those of noncalling males in the field. They concluded that calling animals may exceed maximum aerobic capacity and obtain some of their energy for calling through anaerobic pathways. However, whole-body lactate levels in calling frogs were less than 10% of those found in animals exercised to exhaustion and would make a trivial contribution to total ATP production. In *Hyla regilla* and *Physalaemus pustulosus*, whole-body lactate levels of calling males were not significantly different from those
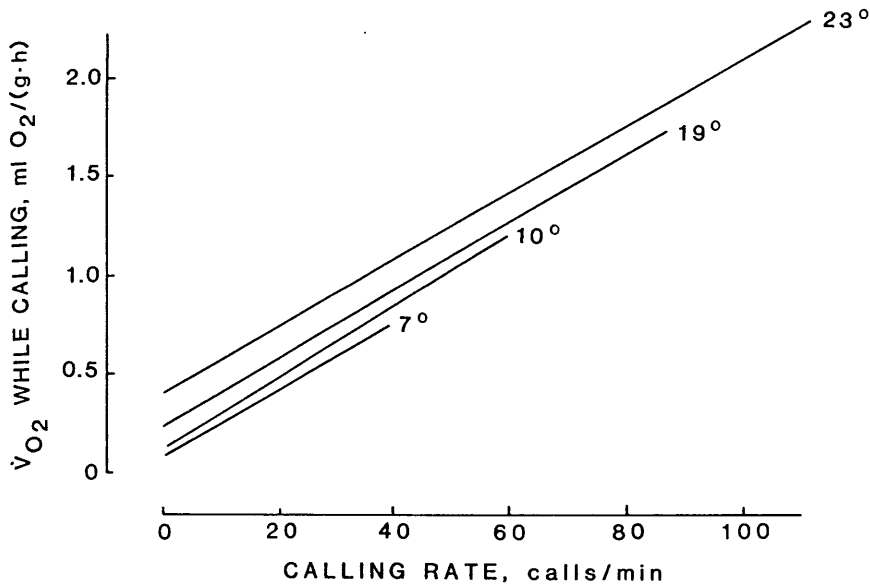
Fig. 14.16 Relation of rate of oxygen consumption to calling rate for *Hyla crucifer* at different temperatures. (T. L. Taigen and K. D. Wells unpublished data.)

TABLE 14.9 Net Cost of Calling for Eight Species of Frogs

	Temp. (°C)	Mass (g)	Net Cost of Calling[a]			Reference
			$J \cdot h^{-1}$[b]	$J \cdot g^{-1} \cdot h^{-1}$	$J \cdot min^{-1}$ calling[c]	
Hyla gratiosa	29	12.5	280	22	25.9	7
Hyla versicolor	19	8.6	280	33	24.0	3, 5
Hyla cinerea	27	5.1	80	16	11.2	7
Hyla squirella	27	2.2	93	42	4.2	7
Hyperolius viridiflavus	25	2.0	50	25	9.1	6
Physalaemus pustulosus	25	1.8	29	16	3.6	9
	26	1.7	25	15	3.8	1, 2
Hyla crucifer	19	1.2	25	21	3.0	4
Hyla microcephala	26	0.6	20	33	3.4	8, 9

Source: (1) Bucher, Ryan, and Bartholomew 1982; (2) Ryan, Bartholomew, and Rand 1983; (3) Taigen and Wells 1985; (4) Taigen, Wells, and Marsh 1985; (5) Wells and Taigen 1986; (6) Grafe 1988; (7) Prestwich, Brugger, and Topping 1989; (8) Wells and Taigen 1989; (9) T. L. Taigen and K. D. Wells unpublished data.

[a] From table 14.7.
[b] Calculated from $\dot{V}O_{2call}$ (avg) and $\dot{V}O_{2rest}$ in table 14.8. Hourly cost $= (\dot{V}O_{2call} - \dot{V}O_{2rest}) \cdot mass \cdot 20.1 \, J \cdot ml^{-1}O_2$.
[c] Cost/min of calling = hourly cost/calling effort · 60.

of resting animals (Whitney and Krebs 1975; Ryan, Bartholomew, and Rand 1983), and in *Hyla versicolor,* lactate levels decreased after several hours of calling (Taigen and Wells 1985). T. U. Grafe, R. Schmuck, and K. E. Linsenmair (in preparation) found high whole-body lactate levels in calling male *Hyperolius viridiflavus* (Hyperoliidae) compared to resting animals, but this was due entirely to elevation of lactate in the leg muscles. Lactate levels in the rest of the body, including the trunk muscles, was virtually identical in calling and resting frogs. Similar results were obtained by Prestwich, Brugger, and Topping (1989) with *Hyla squirella.* In summary, evidence that anaerobic metabolism makes a significant contribution to ATP production to support routine calling behavior is lacking, and anaerobic contributions generally can be ignored in calculating total energetic costs.

Total Energetic Costs of Calling

Estimates of total energetic costs of calling for eight species of frogs are given in table 14.9. These estimates are based on metabolic rates of average-size males calling at average rates in the field and do not indicate the range of variation within species. In some cases, such variation can be considerable. For example, a large *Hyla microcephala* with the highest metabolic rate measured for a calling frog would have a net cost of calling of about 38 J · h⁻¹, nearly double the average figure (Wells and Taigen 1989). In *H. versicolor,* the largest males in a chorus (12 g) can be 2.5 times the mass of the smallest males (5 g). If the largest and smallest males had the same calling effort, the larger individual still would have a net cost of calling 2.5 times that of the smaller male, presumably reflected in the louder calls and greater sound power output of large males.

Interspecific differences in net cost are due in part to greater sound power of larger species. For example, *Hyla versicolor* has an RMS SPL at least 15 dB higher than that of *Physalaemus pustulosus,* representing more than a thirtyfold difference in instantaneous sound power output, but the net cost of calling is only ten times higher, suggesting that *H. versicolor* is probably a more efficient caller than *P. pustulosus* (see Ryan 1985a). The exact relationship depends on the relative duration of their calls as well as instantaneous power

output. Some small species, such as *H. microcephala,* have remarkably loud calls relative to their body size (table 14.5), again suggesting substantial differences among species in calling efficiency (see also Prestwich, Brugger, and Topping 1989).

Table 14.9 also shows the cost per minute of actual sound production. With the exception of *Hyperolius viridiflavus,* all of the small species (body mass = 1 to 2 g) have similar costs per minute of calling, despite major differences in the structure of their calls. *Hyla crucifer* has a simple tonelike call, while *Physalaemus pustulosus* has a much longer and more complex frequency-modulated call. *Hyla microcephala* and *H. squirella* both have rather "noisy" calls, but the former has distinct pulses in the calls, while the latter does not. Most of the differences in call structure reflect differences in the structure and action of the larynx and laryngeal muscles (Ryan 1985b; Schneider 1988), which probably contribute relatively little to total energetic costs. The power for sound production is provided by the trunk muscles, and the similarity in cost per minute of sound production may reflect similarities in trunk muscle structure and function. Nevertheless, interspecific differences in trunk muscle physiology are related to differences in calling effort (see further details below).

Vocalization Compared to Other Activities of Amphibians

Information on the energetic cost of natural activities in amphibians is very limited, but the available data indicate that calling is by far the most expensive behavior performed by these animals (tables 14.4 and 14.8). The only activity that entails rates of oxygen consumption approaching that of calling males is construction of foam nests by *Physalaemus* (table 14.10). In this species, the male uses his hind legs to kick the mucous coating around the eggs into a froth as the eggs are laid (Ryan 1985b). Metabolic rates of nest-building pairs of males and females are about five times resting rates (Ryan, Bartholomew, and Rand 1983), and the net cost of nest building is about 70 to 80% of the cost of calling (tables 14.9 and 14.10). Ryan, Bartholomew, and Rand (1983) estimated that frogs actually kick their legs only about 20% of the time, so the net cost per minute of activity would be about 1.7 J, or about 45% of the cost of a minute of sound production.

Burrowing is another vigorous activity that many species of anurans perform. Metabolic rates of burrowing spadefoot toads, *Scaphiopus hammondii* (Pelobatidae), are up to 4.5 times resting rates, and the net cost of an hour of burrowing for a 12-g toad is about 95 J (Seymour 1973c). The cost of calling for spadefoot toads is unknown, but in two hylids of about the same size, *Hyla gratiosa* and *H. versicolor,* the cost of calling is about three times the cost of burrowing in *Scaphiopus.* Seymour (1973c) estimated that the toads were actually burrowing only about 22% of the time, or about 13 min · h⁻¹, so the cost per minute of burrowing is approximately 7.3 J at 30°C. By comparison, a minute of sound production by *H. gratiosa* at a similar temperature costs about 25.9 J.

Other routine activities by amphibians probably are much less expensive. For example, Walton (1988) reported that foraging toads (*Bufo woodhousii fowleri*) typically move at a very slow rate ($\bar{x}$ = 0.018 km · h⁻¹). From a regression of metabolic rate versus movement speed (Walton and Anderson 1988), the estimated rate of oxygen consumption during foraging is about 2.3 times resting metabolism, yielding a net cost of 85 J · h⁻¹ for a 26-g toad (table 14.4). This is a downward extrapolation from the metabolic data, because natural foraging velocities were only 20% of the lowest speed at which oxygen consumption was measured. This figure is well below maximum rates of oxygen consumption during forced exercise, indicating that toads probably do not approach their physiological limits during routine foraging (Walton 1988). The same is true of courting and fighting salamanders, which have been discussed already. Net costs of reproductive activities in *Desmognathus* (Caudata: Plethodontidae) are only about 5% of the cost of calling in a frog of similar size, and routine locomotion appears to be equally inexpensive.

Comparisons with Acoustic Insects

The only measurements of the costs of signaling behavior comparable to those for frogs are for acoustic behavior of insects (table 14.11). These include a cicada and several species of orthopterans that produce sound by stridulation, as well as the tok-tok beetle, *Psammodes striatus,* which produces sound by tapping its hard abdomen on the substrate (Lighton 1987). For the stridulating insects, the rate of oxygen consumption during calling is generally four to twenty times resting metabolism, a range similar to that found in frogs, whereas oxygen consumption during substrate tapping in the tok-tok beetle is only about 2.5 times resting rates. The figure for a cricket, *Neoconocephalus robustus,* is much lower than that frequently cited by other authors (Bucher, Ryan, and Bartholomew 1982; Kavanagh 1987) because it represents the average rate of oxygen consumption of males that called sporadically during a 4-h period in a metabolic chamber. Peak rates during actual calling are much higher (15.8 ml O₂ · g⁻¹ · h⁻¹), or about twenty times resting rate (Stevens and Josephson 1977). However, these peak levels cannot be translated directly into hourly costs because the insects do not call continuously. Comparing the costs of calling by frogs and insects is difficult because information about calling efforts in the field is not generally available for insects.

In insects with a body mass similar to the small frogs in table 14.9, the range of variation in net cost of calling also is similar to that of the frog (10 to 90 J · h⁻¹). Differences among species reflect mainly differences in the structure and intensity of their calls. For example, the crickets *Gryllotalpa*

TABLE 14.10 The Average Rate of Oxygen Consumption for Various Activities of the Frog *Physalaemus pustulosus*

Activity	$\dot{V}_{O_2}$ (mg·g⁻¹·h⁻¹)
Daytime resting	0.15
Nighttime resting	0.32
Sound of chorus audible	0.40
Calling	0.58
Nesting	0.77
35-min forced activity	1.16
3-min continuous activity	1.82

Source: Data from Ryan 1985a.

TABLE 14.11 Mass-specific Metabolic Rates of Selected Insects during Rest and Signaling and the Net Cost of Signaling

	Temp. (°C)	Mass (g)	$\dot{V}O_{2rest}$ (ml $O_2 \cdot$ g^{-1}h^{-1})	$\dot{V}O_{2act}$ (ml $O_2 \cdot$ g^{-1}h^{-1})	Net Cost[a] (J·h^{-1})	Reference
Cystosoma saundersii	23	1.20	0.30	6.28	150	MacNally and Young 1981
Gryllotalpa australis	23	0.87	0.42	5.30	90	Kavanagh 1987
Neoconocephalus robustus	23	0.87	0.80	4.40	65	Stevens and Josephson 1977
Anurogryllus arboreus	24	0.39	0.32	3.89	30	Prestwich and Walker 1981
Psammodes striatus	23	3.01	0.22	0.55[b]	20	Lighton 1987
Teleogryllus commodus	23	0.60	0.31	1.21	10	Kavanagh 1987
Oecanthus celerinictus	23	0.06	0.44	3.37	4	Prestwich and Walker 1981
Oecanthus quadripunctatus	23	0.06	0.48	3.82	4	Prestwich and Walker 1981

Sources: Modified from table 9 of Kavanagh 1987.

[a]Net cost = ($\dot{V}O_{2call} - \dot{V}O_{2rest}$) · mass · 20.8 J·ml$^{-1}O_2$. Values for net cost are rounded off. Prestwich and Walker (1981) used a conversion factor of 21.97 J·ml$^{-1}O_2$, while MacNally and Young (1981) and Kavanagh (1987) used 19.796 J·ml$^{-1}O_2$; the average of the two values is used here.

[b]Substrate tapping at 12,000 taps·h^{-1}.

and *Neoconocephalus* have continuously trilled calls that are relatively loud (table 14.6), whereas the cricket *Teleogryllus* is a chirping species with a much softer call. Prestwich and Walker (1981) found that interspecific differences in the cost of calling were best predicted by differences in wing-stroke rate. The cicada *Cystosoma saundersii* has a much higher net cost of calling (150 J · h^{-1}) than frogs of similar body size, such as *Hyla crucifer* (25 J · h^{-1}), even though instantaneous SPL is much lower (table 14.6). The difference is due in part to the nature of its call, which is a trill given without interruption for up to 35 min per night (MacNally and Doolan 1982). Therefore, an hour of calling by this species represents a full hour of sound production, whereas an hour of calling by *H. crucifer* entails less than one-seventh of an hour of sound production (table 14.7). Hence, the sixfold difference in cost of calling is not surprising.

Physiological and Biochemical Basis of Vocalization

High metabolic rates in vertebrates usually are associated with high levels of muscular activity, and anuran vocalization is no exception. Each call a frog produces requires a forceful muscle contraction to drive air over the vocal cords and into the vocal sac. A male *H. crucifer* calling on a warm night in the midst of a dense chorus may contract the trunk muscles twice per second for several hours each night. Some individuals may produce as many as 30,000 full contractions of the sound-producing muscles in a single evening, although a rate of 13,000 to 15,000 per night probably is more typical (table 14.7). This performance becomes even more impressive when one considers that the frogs maintain these levels of vocal activity night after night during a breeding season that may last for several weeks. Few other natural activities of ectothermal vertebrates entail such high levels of sustained muscle contraction.

These levels of activity are possible only if the muscles are endowed with the structural and biochemical features necessary for sustained rates of contraction. The next four sections will discuss how the muscles used for calling work to produce sound, the structural and biochemical characteristics associated with their function, the metabolic events that occur in these muscles during vocalization, and the ways in which

these features and processes combine to constrain the behavior of individuals in a chorus.

Muscle Activity during Vocalization Anuran vocalization varies greatly among species in sound power output, calling effort, fundamental frequency, and pulse repetition rate. In addition, most species produce more than one type of call: advertisement calls that signal to females, aggressive calls that convey information to males, and release calls produced when two males come into direct contact (Littlejohn 1977; Wells 1977, 1988). In virtually all cases, however, sound is produced when air is moved from the thoracic cavity, across the vocal cords, and into the vocal sac. The pipids (*Pipa* and *Xenopus*) are an exception; they do not produce sound by means of a moving airstream, although sound production does involve rapid contraction of laryngeal muscles (Rabb 1960; Yager 1982; Tobias and Kelley 1987). Nothing is known about the energetics of acoustic communication in these animals.

At least two features of the mechanics of call production in anuran amphibians are clear from previous studies. First, the fundamental frequency of a call is determined mainly by the rate at which the vocal cords vibrate (Martin 1971, 1972). Second, the pressure to drive the movement of air is created by active contraction of muscles surrounding the thorax and abdomen. These consist of two broad sheets of muscle, the external oblique and the internal oblique (also known as the transverse muscle), along with the smaller rectus abdominis (Martin 1972; Martin and Gans 1972; Schneider 1988). In species with simple single-note calls, such as *Hyla crucifer*, or those that give a series of short notes (e.g., *H. microcephala*), the trunk muscles contract to produce each call note. In some species with long, amplitude-modulated (pulsed) calls, periodic contractions of the trunk muscles may be involved in producing the amplitude modulations. This has been best documented in studies of release calls in bufonids, but Martin (1972) suggested that the trunk muscles may be involved in amplitude modulation of advertisement calls in species such as *Bufo americanus*. The low rates of amplitude modulation that are characteristic of the aggressive calls of several European hylid frogs also appear to be produced by contractions of the trunk muscles (Schneider 1977, 1988). In

H. savignyi these pulses are produced even when laryngeal muscles have been removed, indicating that trunk muscles are involved (Weber 1976).

In some anurans, the laryngeal muscles are involved in active amplitude modulation of the call. For example, Schmidt (1965, 1972) demonstrated that the laryngeal dilators and constrictors are activated alternately and coincidentally with the pulses of advertisement calls of *Hyla chrysoscelis* and the release calls of *Rana pipiens*. The same mechanism appears to be responsible for amplitude modulation of the advertisement calls of several species of European hylids (Schneider 1977, 1988). In bufonids, the larynx apparently is opened passively by pulmonary gas pressure, rather than by contraction of laryngeal muscles. However, the muscles are involved in positioning the edges of the arytenoid cartilages (the major cartilage of the larynx) in the moving gas stream (Martin 1971, 1972). Vibration of these cartilages at a characteristic resonant frequency produces passive amplitude modulation that resembles the active modulation of other frogs but does not require active muscle contraction for each pulse. Species with passive amplitude modulation typically have calls consisting of a series of very short pulses, each with a very rapid onset time.

This sort of passive amplitude modulation may account for the very high pulse repetition rates of some anuran calls that appear to exceed the sustainable contraction rates of most vertebrate muscles. For example, *Hyla microcephala* produces advertisement calls with a pulse repetition rate of more than 200 pulses $\cdot$ s^{-1} and aggressive calls with rates of up to 320 pulses $\cdot$ s^{-1} (Schwartz and Wells 1985; Schwartz 1987). If these pulses were produced by active mechanisms, the muscles would be contracting at a rate approaching or perhaps exceeding the capacity of the fastest vertebrate muscles known. Most mammalian skeletal muscles are locked in completely fused tetanus by stimulation frequencies of 50 Hz or less. Even the pectoral muscles of hummingbirds during hovering flight are contracting at a rate well below the pulse repetition rate of several tropical hylids.

Structural and contractile properties indicate that the laryngeal muscles of some species of anurans are also very fast. The muscles of two species of hylids are composed almost entirely of fast oxidative fibers and have well-developed sarcoplasmic reticulum, high mitochondrial densities, and high

fusion frequencies (Eichelberg and Schneider 1973, 1974; Schneider 1977, 1988; Marsh and Taigen 1987). In fact, fusion frequencies, the lowest stimulation frequency that results in full tetanic contraction, correlate with the rate of amplitude modulation in the call. The laryngeal muscles of male *Hyla arborea* have a fusion frequency of 180 to 195 Hz at 20°C (Manz 1975), which appears adequate to accommodate a pulse rate of more than 130 $\cdot$ s^{-1} at that temperature (Schneider 1977). This would be true especially if the muscles are operating in a partially fused tetanus, as occurs during stridulation in some tettigoniid grasshoppers (Josephson 1973). The laryngeal muscles of female *H. arborea* have lower fusion frequencies and would not be capable of sustaining such high rates of contraction. The fusion frequency in muscles of male *H. versicolor* is about 100 Hz (R. L. Marsh, pers. comm.), which is fast enough to accommodate the observed pulse rate of 20 $\cdot$ s^{-1}.

Although data are not available to evaluate directly the role of active muscle contraction in producing the very high pulse repetition rates of some hylid frogs, the possibility that this occurs cannot be dismissed without additional experiments, because there are vertebrate muscles with even higher fusion frequencies. Many fish produce sounds by contracting specialized muscles surrounding air-filled spaces such as the swim bladder (Schneider 1964; Cohen and Winn 1967; Daugherty and Marshall 1976; Fine 1979). Electromyographic studies of sound production have documented active contraction of the sonic muscles at frequencies up to 230 Hz at a temperature of approximately 23°C (Gainer, Kusano, and Mathewson 1965; Cohen and Winn 1967). These muscles also have extraordinarily short contraction times and high fusion frequencies (Skoglund 1961; Gainer, Kusano, and Mathewson 1965).

Structural Characteristics of Trunk Muscles The most obvious structural characteristic of the trunk muscles of male anurans is their size (table 14.12). The combined mass of the internal and external oblique muscles accounts for 7 to 15% of total body mass. Variance in the mass of the trunk muscles appears to arise from two sources: (1) variation in calling effort and (2) variation in the amount of lipid present in the muscle. *Rana virgatipes*, the species with the smallest relative muscle mass, also has the lowest calling effort. This pat-

TABLE 14.12 Comparison of Body Mass and Trunk Muscle Mass for Selected Tropical and Temperate Zone Anurans

	Distribution	Sex	Body Mass (g)	Trunk Muscle Mass		Reference
				Grams	% Body Mass	
Hyla crucifer	Temperate	M	1.25	0.19	14.8	1
		F	1.05	0.04	3.3	
Hyla versicolor	Temperate	M	9.90	1.24	12.5	2
		F	6.60	0.16	2.5	
Hyla microcephala	Tropical	M	0.60	0.06	10.1	5
Hyla rubra	Tropical	M	3.35	0.32	9.7	5
Hyla ebraccata	Tropical	M	0.87	0.05	5.7	5
Physalaemus pustulosus	Tropical	M	1.64	0.12	7.3	5
Rana virgatipes	Temperate	M	8.00	0.55	6.7	3
		F	10.80	0.23	2.1	
Rana sylvatica	Temperate	M	12.17	0.39	3.2	4
Bufo americanus	Temperate	M	22.73	0.77	3.4	4

Sources: (1) Taigen, Wells, and Marsh 1985; (2) Marsh and Taigen 1987; (3) Given and McKay 1990; (4) M. T. Lawrence and T. L. Taigen unpublished data; (5) T. L. Taigen and K. D. Wells unpublished data.

tern is consistent with generalizations concerning the extent of muscle hypertrophy and muscle use. Additional data are needed to test the hypothesis that species that call at low rates have lower relative trunk muscle mass than those that call at high rates.

The presence of lipid in the muscles also contributes to the overall muscle size. Among the hylids studied to date, the species with the most northerly distribution (*Hyla crucifer*) has the largest muscles (15% of body mass). The large size of these muscles may be due in part to the presence of stored lipids that fuel calling early in the spring when few prey are available. Lipids account for 45% of the trunk muscle mass of some males at the start of the breeding season (McKay 1989) and are fully depleted after 6 weeks of calling. In contrast, male gray treefrogs (*H. versicolor*) have a lower lipid content in the trunk muscles (14% of muscle mass; Marsh and Taigen 1987), and muscle lipid content does not appear to decrease as the breeding season progresses (Walker 1989). This pattern is consistent with the seasonal timing of reproduction of gray treefrogs; males call primarily during the

months of June and July when prey are readily available. Tropical species probably rely on stored fats to fuel calling activity even less than *H. versicolor*, and the somewhat lower mass of their trunk muscles reflects this.

Biochemical Features of Trunk Muscles The biochemical characteristics of muscles involved in vocalization vary interspecifically with vocal behavior. The muscle biochemistry of species with high calling efforts and long breeding seasons is distinctive, perhaps unique, among ectothermal vertebrates. For example, the trunk muscles of male *Hyla crucifer* exhibit activities of citrate synthase (CS), a rate-limiting enzyme in the citric acid cycle, that rival those of the most oxidative endothermic muscles, including cardiac muscle of small mammals and flight muscles of passerine birds (table 14.13). Female spring peepers do not call, and their trunk muscles are not impressive in either size (3% of body mass, table 14.12) or oxidative capacity (table 14.13). In fact, the CS activity of trunk muscle of males is twenty to thirty times that of females.

TABLE 14.13   Citrate Synthase (CS) Activity in Selected Muscles of Anurans and Other Vertebrates (per Gram of Fresh Muscle)

	Sex	Muscle Type	Assay Temp. (°C)	CS Activity (μmoles· min^{-1}·g^{-1})	Reference
Anurans					
Hyla crucifer					5, 8
Early season	M	Trunk	25	166	
Midseason	M	Trunk	20	86	
Late season	M	Trunk	25	96	
Midseason	M	Leg	20	14	
Midseason	F	Trunk	20	5	
Hyla versicolor	M	Trunk	20	79	6
	M	Larynx	20	65	
	M	Leg	20	17	
	F	Trunk	20	6	
Hyla microcephala	M	Trunk	25	119	10
	M	Leg	25	11	
Hyla ebraccata	M	Trunk	25	63	10
	M	Leg	25	24	
Rana virgatipes	M	Trunk	20	13	9
	M	Leg	20	6	
Rana sylvatica	M	Trunk	20	23	11
	M	Leg	20	12	
Rana pipiens		Leg	25	7	1, 4
Bufo boreas		Leg	25	40	4
Xenopus laevis		Leg	25	26	4
Mammals					
Laboratory mouse		Heart	25	146	1
Laboratory rat		Heart	25	96	1
Rabbit		Heart	25	69	1
Bat		Flight	25	200	3
Birds					
Pigeon		Pectoral	25	115	1
Sparrow		Pectoral	25	112	1
		Heart	25	120	
Catbird		Pectoral	25	200	2
Tufted duck		Pectoral	25	87	7
		Heart	25	108	

Sources: (1) Alp, Newsholme, and Zammit 1976; (2) Marsh 1981; (3) Yacoe et al. 1982; (4) Putnam and Bennett 1983; (5) Taigen, Wells, and Marsh 1985; (6) Marsh and Taigen 1987; (7) Turner and Butler 1988; (8) McKay 1989; (9) Given and McKay 1990; (10) T. L. Taigen and K. D. Wells unpublished data; (11) M. T. Lawrence and T. L. Taigen unpublished data.

The CS activity of the trunk musculature of the six anuran species for which data are available exceeds that of leg muscles. In some cases the differences are striking and appear to underlie differences in metabolic performance during calling and during exhaustive locomotor exercise (table 14.8). For example, the rate of oxygen consumption by *Hyla versicolor* during sustained calling is 60% greater than that achieved during forced locomotor exercise. CS activity in the trunk muscles of these animals is five times greater than that found in the muscles of the leg. Similar patterns are evident in other species, with trunk muscle exhibiting from two to ten times the oxidative capacity of leg muscle. These biochemical data help explain why calling frogs can achieve higher metabolic rates than frogs engaged in locomotor exercise, but they also generate new and more subtle questions concerning the nature of the interrelationships among muscle biochemistry, metabolic performance, and vocal behavior.

Not all anuran species possess vocalization muscles with extreme oxidative capacities. Trunk muscle CS activities of *Rana virgatipes* and *R. sylvatica* are not distinctive (table 14.13). Interspecific variation in muscle biochemistry appears to correlate with metabolic rates achieved during sustained vocalization (fig. 14.17). Species with high calling efforts and rates of metabolism during vocalization have high CS activities, whereas those with less active vocal behavior and lower vocalization costs have lower CS activities. Similar relationships between enzyme activities and patterns of behavior have been observed in fish (Johnston 1987). Mitochondrial density in slow muscle fibers of several species of fish correlates with swimming velocities; species with high sustained speeds have higher densities of mitochondria than species that are sedentary or only moderately active. Activities of individual enzymes also varied with interspecific differences in activity patterns.

Tissue aerobic capacity of ectothermal vertebrates can be altered by environmental temperature (Sidell 1983), and some of the extreme biochemical profiles of the vocalization muscles can be attributed to the demands imposed by high calling efforts at low ambient temperatures. This explanation is not generally acceptable because tropical anurans and temperate zone species exhibit similar CS activities for a given rate of metabolism during sustained vocalization (fig. 14.17). An important exception to this generalization may be male *Hyla crucifer* that call very early in the breeding season when air temperatures are low. Only a small subset of males call under these conditions, despite the fact that female availability is very high (McKay 1989). The ratio of females to males early in the year is approximately 1 to 2; by the end of the breeding season, it is less than 1 to 20. The trunk muscle biochemistry of male spring peepers collected early in the breeding season is strikingly different from that of males collected later in the spring. Citrate synthase activity is nearly twice as high in these males (table 14.13), suggesting that individual variation in tissue aerobic capacity may be closely correlated with differences in behavior and reproductive success. Calling activity at very low temperatures may include only those males that possess the biochemical characteristics necessary to meet the rigorous demands of sustained muscle activity under these conditions. Additional data are needed to determine the extent to which muscle biochemistry constrains the vocal behavior of individuals within a chorus and contributes to their reproductive success.

Further evidence for the distinctive nature of the vocalization muscles can be found in histochemical and morphometric analyses. The trunk muscles of *Hyla versicolor* consist 100% of fast oxidative fibers, whereas the leg muscles of these animals comprise primarily (75%) fast glycolytic fibers. Nearly 20% of the total volume of the trunk muscles is mitochondria (Marsh and Taigen 1987).

The relations between the biochemical characteristics of anuran trunk muscles and the activity patterns of the muscles are similar in many ways to those documented for other vertebrate classes (see chapter 11). The catabolic capacities of mammalian muscles can be altered by training regimes, and these physiological changes are accompanied by changes in the biochemistry and anatomy of muscles. In a similar way, the very high aerobic capacity of the pectoral muscles in small passerine birds reflects the high levels of sustained
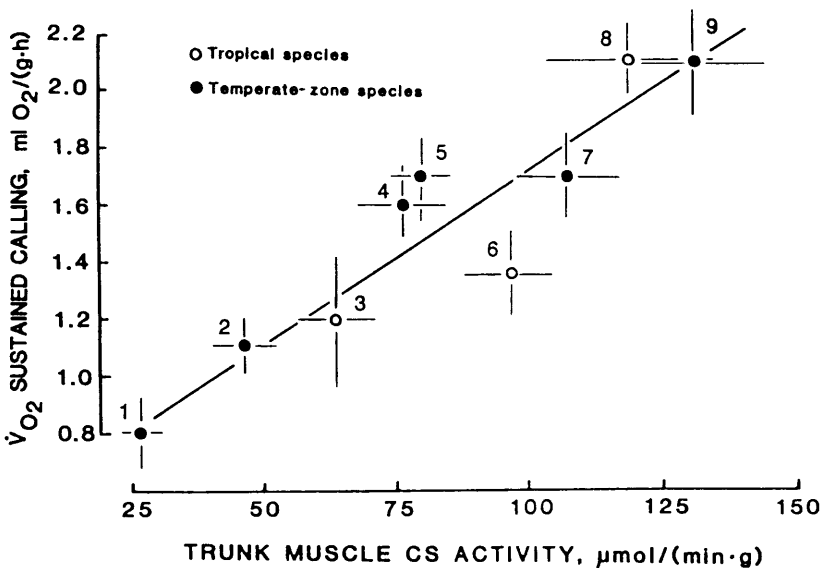

Fig. 14.17 Rate of oxygen consumption during sustained calling versus citrate synthase (CS) activity in trunk muscle. Rates of oxygen consumption were estimated from regression equations in figures 14.12, 14.13, and 14.16 using average field calling rates of males in a sustained chorus. Temperatures refer to the conditions under which metabolic performances were estimated and enzyme activities assayed. *1, Hyla crucifer*, 5°C; *2, H. crucifer*, 10°C; *3, Physalaemus pustulosus*, 25°C; *4, H. crucifer*, 15°C; *5, H. versicolor*, 20°C; *6, H. ebraccata*, 25°C; *7, H. crucifer*, 20°C; *8, H. microcephala*, 25°C; *9, H. crucifer*, 25°C.
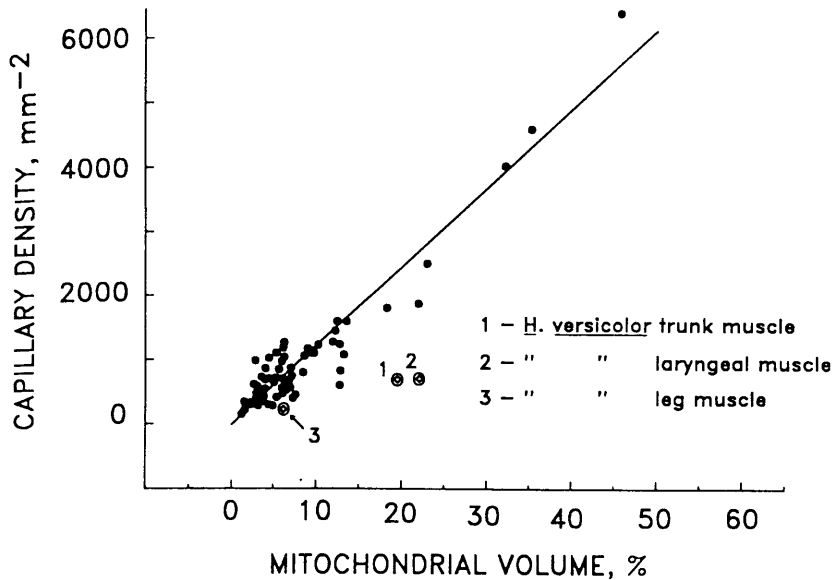
Fig. 14.18 Capillary density versus mitochondrial volume density. ●, data from a large range of mammalian species and muscle types from Hoppeler et al. 1981. ⊘, data for leg, trunk, and laryngeal muscles of *Hyla versicolor* from Marsh and Taigen 1987.)

activity in these animals during flight and thermogenesis (Marsh 1981). However, anuran muscles differ structurally from those of birds and mammals in the relationship between mitochondrial density and capillary density (fig. 14.18). The leg and trunk muscles of *Hyla versicolor* have capillary densities only one-third of those found in endothermic tissue of similar mitochondrial densities. Two nonexclusive hypotheses could explain this disparity: (1) If ectothermal vertebrates possess mitochondria with intrinsically lower oxidative capacity for ATP production and oxygen consumption, the number of capillaries per unit mitochondrion would be lower than those characteristic of endotherms. (2) Alternatively, the structural features of anuran trunk muscles may reflect the thermal environment within which the muscles are active. Because mitochondrial function is likely to be affected more profoundly by changes in temperature than by oxygen delivery (at least within the tissue), it is possible to identify a temperature for every combination of mitochondrial density and capillary density for which the system can be described as maximally designed. Such a calculation can be made for *H. versicolor* muscles by assuming that the temperature of maximum efficiency in the mammalian mitochondria-capillary relationship is 37°C and by assuming that mitochondrial function in anuran muscles decreases with temperature according to normal van't Hoff kinetics ($Q_{10} = 2$; see McKay 1989). The temperature for maximum efficiency under these assumptions in *H. versicolor* muscles is 19°, 20°, and 20°C for the trunk, laryngeal, and leg muscles, respectively. These calculations agree well with the environmental conditions in which this species vocalizes. In fact, gray treefrogs rarely call at ambient temperatures below 15°C, and our field observations over the past several years indicate that the choruses are generally at their peak activity at air temperatures between 18° and 22°C (Taigen and Wells 1985; Wells and Taigen 1986). A prediction from this analysis is that species that call in warmer climates, such as tropical anurans, will have higher capillary densities per unit mitochondria than species that call and reproduce in colder climates. A test of this prediction must await further data on the relationship between mitochon-

drial and capillary density in anurans from very different thermal enviroments.

Substrate Oxidation The high costs of vocalization appear to be met by the oxidation of fats and carbohydrates. Fat oxidation is indicated in two ways, a decline in the amount of fat found in the trunk muscles of some species as described perviously, and high activity of enzymes involved in fatty acid oxidation (Taigen, Wells, and Marsh 1985; Marsh and Taigen 1987). Measurements of the activity of 3-hydroxyacyl-CoA dehydrogenase (HOAD), an indicator of tissue capacity for fatty acid oxidation, shows that trunk muscles of *Hyla crucifer* and *H. versicolor* rely extensively on fat oxidation to support muscle contraction during calling. These enzymatic data are consistent with observations of structural characteristics of the laryngeal and trunk muscles of *H. arborea* and *H. versicolor* in which lipid droplets are distributed through the muscle fibers, immediately adjacent to mitochondria (Eichelberg and Schneider 1973; Marsh and Taigen 1987). By comparison, the hindlimb muscles of these species are nearly devoid of lipid.

A more detailed analysis of trunk muscle enzyme profiles reveals differences among species in substrate oxidizing capacity that appear to correlate with differences in reproductive behavior. The relative capacity for fatty acid oxidation, calculated as the ratio of HOAD to CS activity, is high for temperate zone species, such as *H. crucifer* and *Rana sylvatica,* that breed early in the year when insect prey are unavailable or present only at low densities (Taigen, Wells, and Marsh 1985; M. T. Lawrence and T. L. Taigen unpublished data). Temperate zone species that breed later in the year, such as *H. versicolor* and *Bufo americanus,* have lower HOAD activities relative to the total aerobic capacity of their muscle tissue and appear to rely less on stored fats to fuel calling activity (Marsh and Taigen 1987; M. T. Lawrence and T. L. Taigen unpublished data).

Data for tropical anurans that breed when prey are readily available are largely consistent with the above pattern. *H. microcephala* and *H. ebraccata* both have trunk muscles with
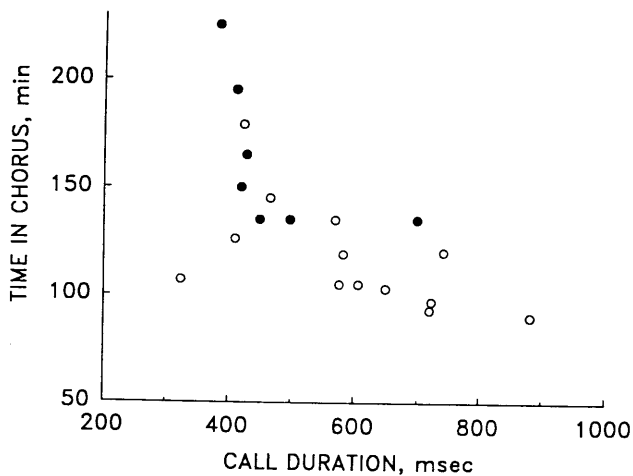
Fig. 14.19 Average duration of calls given by male *Hyla versicolor* versus the length of time the male called during an evening. Vocal behavior was assessed every 15 min. All males ceased calling of their own volition, and none was observed in amplexus at the end of the evening. Data from 2 years are shown by open and closed symbols. Correlations are significant for both years analyzed independently and when combined. (Data from Wells and Taigen 1986 and Walker 1989.)

low HOAD to CS ratios (Taigen and Wells unpublished). *Physalaemus pustulosus* is an apparent exception to this pattern; although it is a tropical species, its HOAD to CS ratio is similar to that of *H. crucifer*. However, the reproductive pattern of *P. pustulosus* consists of relatively short visits to the breeding pond, punctuated by long periods of absence during which the animals appear to be foraging in preparation for return to the chorus (Ryan 1985a). Hence, any behavior that entails a regular sequence of lipid storage and depletion might engender muscle biochemical profiles conducive to fatty acid oxidation, regardless of the thermal environment in which the behavior is performed.

Carbohydrate oxidation, especially in the form of glycogen utilization, is also important when frogs are vocalizing. Glycogen depletion has been observed in the laryngeal muscles of the discoglossid frog *Bombina bombina* (Eichelberg and Obert 1976) following 4 h of electrical stimulation, and measurements of trunk muscle glycogen content of calling *Hyla versicolor* indicate that glycogen depletion occurs during an evening of calling activity (Walker 1989). Males collected after 2 to 3 h of calling had glycogen levels in their trunk muscles that were approximately 50% of the levels found in males collected early in the evening as the chorus was forming. These results suggest that glycogen serves as a short-term energy store, perhaps undergoing a circadian cycle of depletion during a period of calling followed by replenishment the subsequent day. In fact, cessation of calling may occur when glycogen stores reach a critical low level. This hypothesis is like that describing human athletes in which depletion of intramuscular glycogen stores is associated with reduced muscle performance (Hollozsy and Booth 1976).

Variation in substrate levels may account for individual variation in patterns of activity and behavior in male *H. versicolor* (Wells and Taigen 1986). The vocal behavior of males in a dense chorus consists of long calls given at low rates, whereas males in more isolated situations produce short calls at high rates (fig. 14.14). The total calling efforts, calculated

as the product of call duration and rate, appear to be the same, as do the total energy costs (fig. 14.15). Females overwhelmingly prefer males that produce long calls at low rates (Klump and Gerhardt 1987). Wells and Taigen (1986) proposed that differential rates of glycogen depletion may account for these patterns. The vocal behavior that is most attractive to females is also the most costly in terms of the rate at which glycogen is used. This prediction is confirmed by an analysis of the length of time male *H. versicolor* spend calling each night. Individuals that produce relatively long calls at low rates remain in the chorus for shorter periods than individuals producing short calls at high rates (fig. 14.19). However, additional measurements of tissue substrate concentrations are needed to determine the degree of individual variation in patterns of substrate oxidation and the role that variation plays in constraining the behavior and reproductive success of male frogs.

COSTS OF REPRODUCTION
Michael J. Ryan

A central concern of studies of behavioral energetics is the pattern of acquisition and utilization of energy that supports reproductive behaviors. All behaviors have a physiological cost that potentially can be measured as energy expended. Animals cannot reproduce without expending energy, and measuring the energetics of reproduction has been an important endeavor of physiological ecologists (e.g., Calow 1981). A different kind of cost associated with reproduction has concerned evolutionary biologists because it is so closely tied to the measure used to quantify evolutionary effects of selection—fitness. Reproducing today has some effect on an individual's ability to reproduce in the future (e.g., Pianka and Parker 1975). Thus, costs of reproduction can be estimated in the context of physiology (energy expended) or evolution (decreased fitness). Other costs of reproductive behaviors include the time that would otherwise be spent in other important activities (e.g., foraging) and the loss of a benefit of those activities (e.g., reduced energy intake).

"Cost" often is used without definition, not always due to confusion but because, rightly or wrongly, physiological cost is thought to necessitate evolutionary cost. Presumably, on average and over sufficiently long periods of time, any energetic expenditure should decrease fitness. This assumption, for example, is central to optimal foraging theory (MacArthur and Pianka 1966; Stephens and Krebs 1986). The equality of physiological and fitness costs has not been documented in most studies, and this is a serious omission.

My purpose is to consider the costs of reproduction for amphibians, but few data are available for taxa other than anurans. Ecologists and behaviorists have employed a variety of measures of reproductive costs, and I will not attempt to catalogue all of these. Instead I will discuss why measurements of this physiological characteristic are critically important in evaluating behavioral, ecological, and evolutionary hypotheses. Of course, not all of the costs of reproduction are physiological. Indeed, the risk of predation is a conspicuous cost associated with reproductive behavior, and I will discuss how to relate physiological and behavioral costs in an evolutionary context.

Amphibians, and especially anurans, have emerged as tractable models for investigating both evolutionary and physiological aspects of reproduction (e.g., Wilczynski and Ryan 1988b). Evolutionary studies have documented relations between variance in male traits and variance in male reproductive success. Because anuran fertilization is usually external and mating behaviors are conspicuous, some studies of anuran mating systems have even estimated lifetime fitness (Howard 1979). Studies have also elucidated the relation between variation in male courtship behavior, especially vocalizations, and both male mating success (Gerhardt 1988; J. G. M. Robertson 1986a; Ryan 1980, 1983; Sullivan 1983; Wells 1988) and susceptibility to predation (Ryan, Tuttle, and Taft 1981, Tuttle and Ryan 1982). At the physiological level, measures of the number, size, and caloric content of eggs have been used to estimate energetic costs of reproduction by female amphibians (Crump and Kaplan 1979; Salthe and Duellman 1973).

In addition, reproductive behavior has a substantial physiological cost for males, and this cost has been difficult to measure in most animals. However, for most anurans the major reproductive behavior is vocalization, and Bucher, Ryan, and Bartholomew (1982) and Ryan, Bartholomew, and Rand (1983) were the first to estimate both the aerobic and anaerobic support of calling for a frog (*Physalaemus pustulosus*). These measures, which have now been made for several other anurans (described earlier this chapter), estimate energetic costs of male reproductive behavior. Reproductive behaviors can be costly in terms of survivorship because they attract predators (Tuttle and Ryan 1982), and anurans provide perhaps the best examples of the two most obvious costs associated with male courtship: energy and predation.

Energetic Costs of Reproduction

This section reviews the energetic costs of reproduction of amphibians, focusing on anurans because few data are available for salamanders and caecilians. Energetic costs incurred by both sexes have been measured or estimated, and I will consider their consequences for future reproduction. This analysis provides a basis for speculation about the potential evolutionary significance of these costs.

Female Reproduction Female amphibians devote a large amount of energy to reproduction, mostly in the form of egg production. The ability to acquire energy is assumed to be an important determinant of a female's ability to produce progeny (Pianka 1981), although this relationship has been documented for only a few species. However, most interest in variation of anuran female investment in reproduction has concerned its relation to interspecific differences in reproductive mode. At the intraspecific level, investigation of variation in reproductive investment has been restricted mostly to size-related fecundity (e.g., Howard 1979). No data yet show that variation among female anurans in any behavioral or physiological trait influences the amount of energy that can be devoted to reproduction.

The size and number of eggs produced per clutch provides an estimate of the energy devoted to reproduction by female amphibians (Salthe and Duellman 1973). Duellman and Trueb (1986) summarize such data for eighty-four species of anurans and show that clutch sizes range from 4 to 15,000 eggs.

That variation suggests a correspondingly large interspecific variation in energy investment. A more direct estimate of energy costs of female reproduction comes from measures of the caloric content of eggs. The total energy per clutch for nine species of tropical frogs varied from 1.49 kJ to 8.17 kJ, and the mass-specific energy ranged from 14.36 to 25.90 kJ $\cdot$ g^{-1} (Crump and Kaplan 1979). Females of larger species devoted more energy to reproduction absolutely, but not relative to body mass. Energy invested in eggs did not differ between females of species that deposit their eggs in standing water versus those that deposit their eggs in overhanging vegetation. However, the partitioning of energy differed among reproductive modes: species that deposit eggs in standing water have more and smaller eggs than species that use overhanging vegetation for oviposition sites.

These limited data indicate that physiological constraints might impose a ceiling on energy expended per clutch. To confirm this hypothesis, one would have to determine the number of clutches produced per lifetime (a difficult measure to obtain) or at least the number of clutches produced per season.

Females of the frog *Physalaemus pustulosus* partition the energy they devote to reproduction into a somatic contribution to eggs and into behaviors associated with reproduction (Ryan, Bartholomew, and Rand 1983; Ryan 1985a). Females produced an average of 234 eggs per clutch, and the average total caloric content of the clutch was 3.96 kJ (= 22.92 kJ $\cdot$ g^{-1}).

Female *P. pustulosus* have another energetic cost involved in reproduction—nest construction. As the female extrudes eggs from her cloaca, the male beats the jelly matrix of the egg into a foam with his hind legs. The foam nest may provide protection from desiccation if the temporary pools used by these frogs dry during periods without rain. It was not possible to measure rates of oxygen consumption of each sex during nest construction. Therefore, Ryan, Bartholomew, and Rand (1983) measured this rate for a pair of frogs and assumed that each individual expended the same amount of energy (table 14.10). This assumption probably underestimates male expenditure and overestimates female. During the approximately 1 h of nest construction, the pair expended 0.26 kJ. Aerobic metabolism is not the only source of energy for nest building; an accumulation of lactic acid indicates that some of the behavior is supported anaerobically. However, anaerobic metabolism contributes only about 4% of the total ATP yield.

Besides knowing the total amount of energy that females invest in reproduction, it would be instructive to evaluate the magnitude of this energy allocation relative to the total energy budget. This proportion, rather than total calories, might give a more accurate indication of the effects of reproductive investment on future reproduction and survivorship. Calculations for the salamander *Desmognathus ochrophaeus* (Plethodontidae) indicate that reproductive activities, which in this species include both egg production and parental care, comprise 48% of the female's energy flow (Fitzpatrick 1973a). The largest single category of energy expenditure for this species appears to be the production and care of offspring.

Females of species with extended breeding seasons may produce more than one clutch of eggs annually, and energy investment can vary substantially within a season (Crump

1974; Duellman and Trueb 1986; Davidson and Hough 1969). For example, female *P. pustulosus* exhibit a synchronous pattern of oogenesis at the beginning of the breeding season and then switch to a pattern of asynchronous oogenesis (Davidson and Hough 1969). Early in the season, when favorable breeding conditions are more predictable, clutch size is large but interclutch interval is long. As the breeding season progresses, favorable conditions become less predictable, and females have asynchronous oogenesis resulting in smaller clutches that can be deposited at shorter intervals. This mechanism may allow females to exploit favorable breeding conditions as they arise.

Partitioning the annual reproductive energy investment of a female anuran into multiple clutches could have potentially important effects on mating systems, operational sex ratios, and the intensity of sexual selection on male traits (Wade and Arnold 1980). When females partition their energy among several clutches in a season, in contrast to producing only one clutch, the breeding season is extended and the opportunity for a few males to monopolize breeding increases (Emlen and Oring 1977). This hypothesis parallels the expectation that variance in male mating success should be greater in species with prolonged breeding seasons relative to explosive breeders (Wells 1977; Woolbright 1983). Kluge (1981) and Ryan (1985a) have compared variance in male mating success for species with prolonged versus explosive breeding seasons. Contrary to expectation, the variance was not higher in species with prolonged breeding seasons.

The activity associated with choosing a mate is a potential cost of reproduction for females that is crucial to some theories of sexual selection, but it has not been documented. In many species of amphibians, especially frogs, females select mates with minimal interference from other males. For example, female *P. pustulosus* do this by moving among males in the chorus, often sitting directly in front of one male for several minutes before moving on to the other males (Ryan 1985a). This behavior occurs in other anurans such as the bullfrog, *Rana catesbeiana* (Emlen 1976; Howard 1978a), and the red-groined toadlet, *Uperoleia laevigata* (formerly *U. rugosa*), a myobatrachid (J. G. M. Robertson 1986b). The energetic cost of this behavior could affect fitness (e.g., Kirkpatrick 1987a), or it could have a trivial impact on the female's energy budget with virtually no evolutionary consequence. However, exposure to predation is likely to be a more important cost of mate selection. A chorus of males not only attracts members of the opposite sex but also advertises a resource concentration to predators (Tuttle and Ryan 1982). Both calling males and silent females increase their predation risk as they increase their time and movements at a chorus.

Mate selection by female anurans can include additional energy costs and even a risk of injury or death as a result of the behavior of conspecific males. Noncalling males of some species clasp females that are moving toward calling males, and the females struggle vigorously to escape (e.g., Sullivan 1982a). Also, unmated males of many species attempt to disrupt mated pairs (e.g., Howard and Kluge 1985). In both situations females probably expend energy while attempting to escape. The most vigorous struggles might result in substantial lactate concentrations, and some females drown (Ryan 1985a). Some of these costs of mate choice would have im-

mediate evolutionary consequences, and their documentation would be worthwhile.

A significant evolutionary cost associated with exercising mate choice would have important implications for theories of sexual selection. Female preference for a male trait can result in an increase in the frequency of both the trait and the preference (Fisher 1958; Kirkpatrick 1982; Lande 1981); the phenomenon is called "runaway sexual selection." For example, assume that choosy females prefer males with long tails. If there is a heritable component to the preference and to the trait itself, choosy females will produce sons with longer tails and daughters that prefer males with longer tails. As a result the trait and the preference will become genetically correlated. The trait increases in frequency due to the preference, and, because of the genetic correlation, the preference increases in frequency as a correlated response to selection acting on the trait. The process causes the frequencies of the preference and trait to increase at an ever-accelerating rate. This process can occur even if the male trait reduces survivorship.

A critical assumption of models of runaway selection is that there is no cost to the female in exercising a choice. A recent model suggests that if there is a cost to female choice, female preference will evolve to favor the male trait that is optimum for his survival (Kirkpatrick 1987a). This prediction is an important departure from those of models that assume no cost of female preference.

Parental care can incur a reproductive cost. Only a minority of anuran species exhibit parental care, although the phenomenon is phylogenetically widespread (McDiarmid 1978), but it is more common in salamanders (Forester 1979) and occurs in caecilians, some of which also nourish the fetus with oviductal secretions (Wake 1977b). Parental care surely enhances the survivorship of immediate progeny, but at what cost to future progeny? Undoubtedly, there are energetic costs from reduced energy intake during parental care (e.g., males of the leptodactylid frog *Eleutherodactylus coqui;* Townsend 1984). These costs should be investigated systematically.

Perhaps the most interesting form of parental care among anurans is the provisioning of offspring by female dart-poison frogs, *Dendrobates pumilio* (Dendrobatidae; Brust 1990; Weygolt 1980). Females of this species carry larvae that hatch from terrestrial eggs and release them individually in small pools of water that accumulate in the leaf axils of plants. For some weeks the female returns to these sites and deposits unfertilized eggs that her larvae eat. Similar obligate oophagy has been described for the larvae of other species of frogs (see chapter 16). The costs and benefits of enhancing the survivorship of immediate offspring at the cost of future fitness invite analysis.

Male Reproduction   In general, secondary sexual characteristics associated with male reproduction appear to be costly in two ways: a physiological cost of providing energy for growth of epigamic structures and for the support of often extravagant courtship behaviors and an evolutionary cost because these characters seem to shorten the life span of their bearers.

Male amphibians, especially anurans, have structures associated with reproduction, such as the enlarged teeth of

some male salamanders (Arnold 1977), the keratinized spines used in battles by gladiator frogs (Kluge 1981), and the larynxes of some male anurans that dwarf the size of the homologous structures in females (Martin 1972). Presumably the growth and maintenance of such structures require an energy expenditure that is unique to males, but these costs have not been measured.

The importance of vocalization in anuran reproduction has long been recognized (Dickerson 1906). Species-specific differences in advertisement calls (Blair 1958; Gerhardt 1988) and the neural mechanisms underlying acoustically mediated species recognition (Capranica 1976a; Fuzessery 1988; Walkowiak 1988b) have been especially important focuses in anuran biology. It is now clear that calls also exhibit variation that influences aggressive interactions among conspecific males (Davies and Halliday 1978; Wells 1988) and female choice of mates from individuals of the same population (Ryan 1980; Gerhardt 1988) or nearby populations (Ryan and Wilczynski 1988). Studies of anuran vocalization have allowed direct measurements of energy expenditure and predation risk associated with male secondary sexual characters and behaviors.

An indirect energetic cost of calling is decreased food intake (Jenssen and Klimstra 1966; Martof 1956; Ryan 1985a; Woolbright 1985c; Woolbright and Stewart 1987). Male coquís (*Eleutherodactylus coqui* [Leptodactylidae]) are smaller than females, as is true for most anurans despite demonstrations of sexual selection favoring larger male body size number of species (Shine 1979). Male coquís grew more slowly than females in the field where they engaged in their normal reproductive behavior, whereas males and females grew at the same rate in captivity where reproductive behavior was not exhibited (Woolbright 1985c; Woolbright and Stewart 1987). This observation is consistent with the hypothesis that male reproductive behavior might reduce the growth rate or ultimate adult body size in this species.

Either sex can incur a physiological cost of reproduction during parental care. Again, studies of *E. coqui* suggest that significant costs of parental care are due to decreased energy intake. Males guard eggs that are deposited terrestrially. Males guarding eggs ate less than calling males, perhaps because they did not leave the eggs to go to places where they were likely to encounter prey (Townsend 1984). Similarly, males of the frog *Cophixalus parkeri* (Microhylidae) that were brooding eggs had lower intakes, smaller fat bodies, and less carcass fat than did nonbrooding males (Simon 1983).

Does Energy Constrain Reproductive Behavior?

Evolutionary biologists have been concerned with reproductive energetics for two reasons: the amount of energy available for reproduction might influence reproductive success, and costs of mate choice by females and displaying by males have implications for hypotheses of sexual selection (e.g., Halliday 1987; Kirkpatrick 1987a; Ryan 1988b).

Energetic constraints on male reproductive behavior could be manifested in the short term or in the long term. In the short term, the amount of energy a male invests in calling might be limited by energy stores. In the long term, energy expenditure could influence the number of nights that a male

spends at the chorus. All of these factors could affect the fitness of an individual male frog. If energy does constrain male reproductive behavior, another question arises: do males perform energy-demanding behaviors to indicate their physical vigor (and perhaps their genetic quality) to females? In other words, do females rely on these behaviors to select physically and genetically superior mates?

Acoustic Energy of Vocalization Intraspecific call variation influences mate choice by females of some anuran species, and often the males that emit the most acoustic energy attract females preferentially (Gerhardt 1988). Several call variables are correlated with acoustic energy, and females may prefer calls with more components, longer duration, greater intensity, or greater repetition rate, all of which have more energy than their counterparts (i.e., fewer components, shorter duration, lower repetition rate—see Ryan 1988a, 1988b, and above). Therefore, selection might favor males that can increase the energy in the call. This could be done by increasing both the metabolic energy used for calling and the efficiency with which metabolic energy is converted to acoustic energy (Ryan 1988a, 1988b).

Selection acts on morphological and physiological aspects of calling to increase call energy content (Ryan 1988a, 1988b, and above). The transformation of metabolic energy to acoustic energy (energetic efficiency of calling) is quite low for most animals, and frogs are no exception (Ryan 1985b, 1988b; Prestwich, Brugger, and Topping 1989). The energetic efficiency of vocalization by *P. pustulosus* ranged from 0.55 to 1.2% depending upon the number of components in the call (Ryan 1985b). This value is similar to estimates for the bladder cicada (0.8%, MacNally and Young 1981), a cockerel (1.6%, Brackenbury 1977), and humans (1%, Wood 1962). Presumably, the greater the amount of energy devoted to calling, the greater the amount of acoustic energy emitted by a male. However, this relation rests on the untested assumption that individual variation in the energetic efficiency of calling is trivial.

The low efficiencies of anuran vocalization probably result from a mismatch between the dominant wavelengths used in communication and the size of the resonating and radiating structures of the animal (MacNally and Young 1981; Prestwich, Brugger, and Topping 1989; Ryan 1985b, 1986a; Wiley and Richards 1982). In general, animals use wavelengths that are too long to be either resonated or radiated at maximum efficiency. Some species probably could produce shorter wavelengths. For example, males of some species of frogs can shorten the wavelength of their call (increase the frequency) by using the laryngeal muscles to deform the shape of the larynx, thus increasing the tension and the frequency of vibration of the vocal cords (Drewry, Heyer, and Rand 1982; Martin 1972). In some species of frogs, such as *Leptodactylus albilabris* (Leptodactylidae) and *Acris crepitans* (Hylidae), males change the frequency of the call in response to social situations (Lopez et al. 1988; Wagner 1989).

Several factors may counteract any advantage of increasing the energetic efficiency of calling by producing calls with shorter wavelengths (fig. 14.20). Generally, shorter wavelengths are attenuated more rapidly than sounds of longer wavelengths. This attenuation results from heat loss through
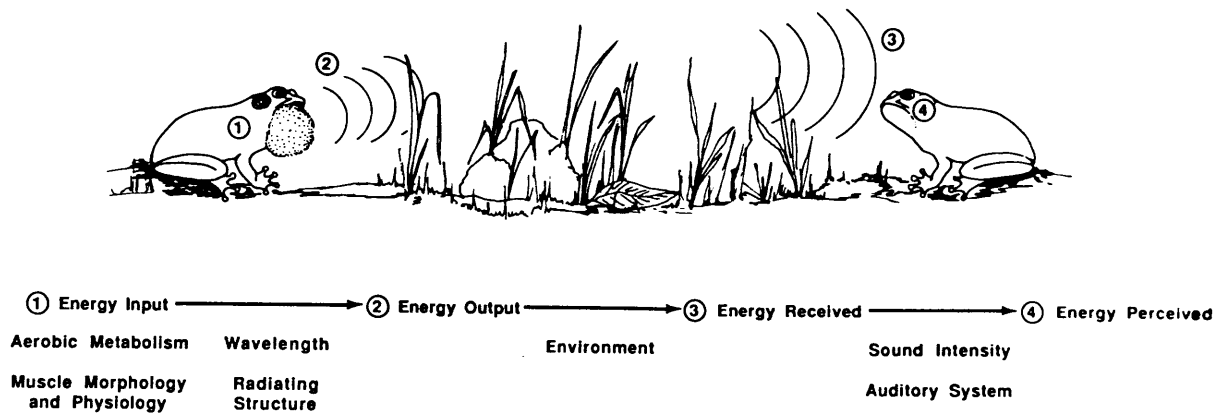
Fig. 14.20 Major factors influencing the amount of acoustic energy in the male's advertisement call that is perceived by females. (Reprinted, by permission, from Ryan 1988b.)

molecular interactions, and interference from small objects in the sound path (Marten, Quine, and Marler 1977; Morton 1975; Wiley and Richards 1982). Differential attenuation of frequencies has been demonstrated for a variety of animal sights, including frog calls (Ryan 1986a). Thus, the efficiency with which metabolic energy is converted to short wavelength acoustic energy might not be realized at the receiver because of the greater attenuation of short wavelengths.

A female's choice of mates is influenced by the energy her auditory system receives. The auditory system adds another layer of complexity because it can be differentially sensitive to frequencies (Fuzessery 1988; Zakon and Wilczynski 1988). Consequently, the sound energy perceived is not necessarily proportional to the sound energy received, and only the former influences a female's evaluation of mates. The production, transmission, reception, and perception of the acoustic energy that influences mate choice are of obvious evolutionary significance. Investigation of this problem must integrate various levels of biological investigation, including muscle biochemistry, morphology, environmental acoustics, and sensory physiology for a complete understanding of sexual selection and communication by anurans.

Energy Stores and Chorus Tenure Another short-term effect of energetics on male behavior is the degree to which available energy influences a male's ability to engage in particular activities. Vocal advertisement, as energetically expensive as it may be, is the most common behavior male anurans use to attract females. However, some males in many species may adopt noncalling behaviors (Howard 1984). Some noncalling males, referred to as satellite males, wait near calling males and attempt to intercept females as they approach calling males (e.g., Perrill, Gerhardt, and Daniels 1978). Other noncalling males actively but quietly search for females (e.g., Wells and Taigen 1984). The energetic costs of any aspect of noncalling behavior are unknown but are probably less than those of calling. Thus, the energy available to a male might dictate its choice of mating behaviors.

Some evidence supports this hypothesis: calling territorial males in a breeding chorus of Uperoleia rugosa (= U. laevigata [see Davies and Littlejohn 1986], Myobatrachidae) lost weight, whereas noncalling satellite males gained weight

(J. G. M. Robertson 1986a). A weight loss could have important fitness consequences because fighting ability is related to weight and heavier males win more encounters. MacNally (1981b) reported depletion of energy reserves during the breeding season for male Ranidella signifera and R. parinsignifera (Myobatrachidae) at the population level. He suggested a considerable expenditure of energy for reproduction, although he did not document either weight loss of individuals or correlated shifts in behavior. Small male Rana clamitans spend less time in territories and lose less weight during the breeding season than do large males (Wells 1977, 1978). Rana virgatipes provides the clearest demonstration of a trade-off between growth and calling effort (Given 1988). Small males call less than large males, and within small males calling effort and growth rate were negatively correlated after the effect of initial mass was removed.

No correlation between individual variation in physiological capacity and mating behavior has yet been demonstrated. The aerobic capacity of male Bufo americanus that call is the same as those that search (Wells and Taigen 1984), and the calling rates of male B. woodhousii are not correlated with their aerobic capacities (Sullivan and Walsberg 1985). Aerobic capacity was estimated by locomotory performance in these studies, however, and the muscles used for vocalization are anatomically and physiologically distinct from the muscles used during locomotion (see above). Consequently, measurements of the aerobic capacity for locomotion probably have little relevance to the capacity for vocalization.

Energy constraints that limit male reproductive behaviors might have long-term effects. An important determinant of male mating success is the number of nights a male spends at the breeding site (chorus tenure). This correlation has been demonstrated for Bufo calamita (Arak 1983a), B. woodhousii (B. Woodward 1982), Hyla chrysoscelis (Godwin and Roble 1983), H. cinerea (Gerhardt et al. 1987), H. rosenbergi (Kluge 1981), the centrolenids Centrolenella fleischmanni and C. prosoblepon (Greer and Wells 1980; Jacobson 1985), and the leptodactylid Physalaemus pustulosus (Ryan 1983, 1985a). Because males often do not forage at the breeding site (e.g., Ryan 1985a), energy stores might influence the number of nights an individual spends at the breeding site. Green (1990) investigated the relation between energy intake and male chorus tenure and vocalization in P. pustulosus by

feeding one group of males and starving a second group. He measured the amount of calling by each group, released the males, and then determined which males returned to the chorus site. The starved and fed groups did not differ in the amount of calling while they were in captivity or in chorus attendance after they were released. Thus, the energy stores of these males did not influence their reproductive behavior.

Only J. G. M. Robertson's (1986a) study of *Uperoleia laevigata* and Given's (1988) study of *Rana virgatipes,* both conducted over an entire breeding season, suggest that the reproductive behaviors of male frogs are constrained by their energy stores. The other studies that have addressed this question examined species with short breeding seasons, and Green's experiments were restricted to a relatively short period in a long breeding season. Energetic constraints may operate over longer time periods.

Favorable Genes and Runaway Selection

Documentation of physiological costs of male courtship behavior has confirmed the notion of Darwin (1871) and many others that these behaviors incur serious energy expenditures that may eventually reduce the survival ability of males relative to females (Halliday 1987). One of the important questions remaining in sexual selection is why females have evolved preferences for males bearing such apparently maladaptive traits. The potential costs incurred by females in choosing males and the amount of energy invested in displays as an indicator of differences in heritable true fitness among males are important and controversial issues that need further exploration to evaluate seriously many of the hypotheses of the evolution of female mate choice.

The possibility that physiological costs of male behavior indicate heritable differences in true fitness among males has been a contentious issue in sexual selection (e.g., Kirkpatrick 1987b). Behavioral differences among males clearly can reflect differences in the amount of energy devoted to behavior. Even without evidence that these differences among males indicate differences in physiological abilities to support behavior, a number of authors have suggested that females prefer energetically expensive behaviors because they allow females to evaluate underlying genetic differences among males. This favorable genes hypothesis has been developed and advocated by several authors in slightly different contexts (e.g., Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Zahavi 1977) and applied to female call preference in *Hyla versicolor* by Klump and Gerhardt (1987).

Sexual Differences in Energy Devoted to Reproduction

Sexual differences in rates of growth, longevity, and age at first reproduction (e.g., Pianka and Parker 1975; Stearns 1976) and in the time and energy invested in parental care (e.g., Trivers 1972; Williams 1966) are of great interest in evolutionary ecology. Some of the theories proposed to explain these differences are based on differences in costs of reproduction. Energy expended for production of gametes is the primary reproductive investment for species with no parental care, and eggs contain more energy than sperm. A female has relatively few ova, whereas a male might have enough sperm to fertilize a substantial fraction of the female population. Increasing the number of mates will have little or no influence on a female's reproductive success, whereas the number of mates will be the most important determinant of a male's success. Consequently, females usually are the limiting sex and have low variance in reproductive success, whereas males are the limited sex and have a much higher variance in reproductive success. As a result, sexual selection has a more important influence on males than on females.

One important issue of parental investment theory is the degree to which the energy cost of forming gametes limits an individual's ability to reproduce. The costs of spermatogenesis (in time and energy) are not known, but sperm production is not the only reproductive cost for a male. Comparisons of energy invested in reproduction by males and females have been hampered by a difference in the form of the investment: the energy invested by females can be estimated by determining the energy content of their eggs, whereas much of the energy invested by males is used for reproductive behavior.

The energy invested in reproduction by both sexes has been estimated for only a few species of amphibians. Sexual differences in reproductive energy expenditures for *Physalaemus pustulosus* were compared by estimating the energy invested in eggs by females, in calling by males, and in nest building by both sexes. These estimates were combined with a detailed study of the phenology of both sexes throughout a breeding season. Based on average values for the amount of time males spent at the breeding site, the amount of that time they called each night, the number of times they mated and constructed nests, and the interclutch interval of females (Ryan 1985a), Ryan, Bartholomew, and Rand (1983) estimated the amount of energy devoted to reproduction by each sex (table 14.14). During an average breeding season of 152 days, males were present at the breeding site for 264 h over 44 days and mated about eight times. Females mated ten times per season. An average male expended 3.25 kJ for re-

TABLE 14.14   Total Energy Expended for Reproduction by Three Species of Ectothermal Vertebrates

| | Sex | Body Mass | Breeding Season (days) | Energy (kJ) | | |
				Total	Total per g	Daily per g
Physalaemus pustulosus	M	1.7	259	3.25	2.19	0.008
Physalaemus pustulosus	F	1.8	259	40.96	26.43	0.102
Ranidella signifera	M	0.7	60	2.20	2.88	0.047
Ranidella parinsignifera	M	0.7	120	2.30	2.99	0.024
Uta stansburiana	M	3.3	117	21.50	8.78	0.075
First year	F	2.3	117	44.80	23.96	0.204
>1 year	F	2.7	117	45.50	21.52	0.186

Source: Data from Ryan 1985a.

production if he always called when present at the breeding site, and only 1.02 kJ if he remained silent. A female, on the other hand, invested 40.96 kJ in reproduction, mostly for egg production. Unfortunately, the annual food intake for this species was not determined.

The large difference in energy devoted to reproduction between male and female *P. pustulosus* is due to the large amount of energy invested in eggs. However, if females reproduced only once per season, they would still invest more energy in reproduction than would males. And if males were present at the breeding site on every night of the season, called on each of those nights, and nested at the same rate, they would invest 24.9 kJ per season, which is only about half that of the average female. Males of this species probably never invest more energy in reproduction than do females, because producing eggs costs much more than calling.

Nagy's (1983b) study of the lizard *Uta stansburiana* suggests a pattern of energy investment in reproduction that is similar to that of *P. pustulosus*. Female lizards expend about the same amount of energy as female *P. pustulosus* even when adjusted for differences in body mass (table 14.14). Male lizards, on the other hand, expend more energy than the male frogs after adjusting for differences in body mass. The high energy investment of male lizards results from their defending territories every day during the breeding season, whereas male frogs are present at the breeding site on only 17% of the nights. Thus, *U. stansburiana* are similar to *P. pustulosus* in that males expend much less energy in reproduction than females do.

In contrast are the reproductive energetics of the Puerto Rican leptodactylid frog *Eleutherodactylus coqui* (Woolbright 1985c). Both sexes have higher energy intakes during the wet season (July) than during the dry season (January), and in each season females acquire more energy than do males: average seasonal totals of 1.60 kJ versus 0.60 kJ during the wet season, and 0.62 kJ versus 0.26 kJ during the dry season. Female *E. coqui* expend 45.99 kJ per year, similar to the 40.96 kJ for female *P. pustulosus*. Woolbright's (1985c) estimate of the energy invested in reproduction by male coquís is extraordinarily high: 78.84 kJ per season versus 3.25 kJ for *P. pustulosus*. However, these figures include energy forfeited by not feeding during vocalization. This cost was not included in the estimate for *P. pustulosus*. Even without this cost, however, *E. coqui* males were estimated to expend 36.35 kJ per season.

The large difference between energy expended in reproduction by the males of *E. coqui* and *P. pustulosus* seems to be due to differences in male reproductive behavior. Like the lizards, male *E. coqui* do not leave the breeding site. Furthermore, they call on 50% of the nights of the breeding season. If the energetic cost of reproduction is adjusted for these differences in the number of nights at the breeding site, as well as for body mass, the expenditures are similar: 0.030 kJ · g^{-1} · day^{-1} for *E. coqui* and 0.043 kJ · g^{-1} · day^{-1} for *P. pustulosus*. Data for *Ranidella parinsignifera* and *R. signifera* (Myobatrachidae) indicate similar mass-specific daily energy expenditures for males. Like *P. pustulosus*, this is a pond-breeding species that is not always present at the breeding site. By measuring the depletion of energy reserves in males throughout the breeding season, MacNally (1981b) estimated that male *R. parinsignifera* and *R. signifera* expended 2.30 kJ (0.024 kJ · g^{-1} · day^{-1}) and 2.22 kJ (0.047 kJ · g^{-1} · day^{-1}), respectively.

An interesting aspect of Woolbright's (1985c) study is the estimated energy expended relative to estimated energy gained. During the dry season energy gained and energy expended by females are similar, whereas during the wet season gain exceeds expenditure. Males in the dry season, on the other hand, have a balanced energy budget if they do not call and a negative energy balance if they call. In the wet season, calling results in a balanced energy budget; if males abstain from calling, their energy gain exceeds their expenditure.

These energy budgets indicate that a male's decision to call or not to call should have importance consequences for its future reproductive effort. If males call in the wet season, they must use energy that has been stored during the same season on nights when they did not call. In the dry season their energy budgets are balanced at best—there is no excess energy for storage or growth.

Predation as a Cost of Reproduction

The importance of predation in the evolution of reproductive traits was invoked by Darwin (1871) in his theory of sexual selection. The general notion is that courtship is usually ostentatious and that by engaging in courtship individuals expose themselves to an increased risk of predation. In addition, the foraging associated with accumulating energy reserves or meeting the demands of reproduction may increase the risk of predation.

Foraging and mate selection are behaviors that probably expose female amphibians to predators, but no data demonstrate that female amphibians increase their chances of survival by forsaking reproduction. The possibility of investigating this problem exists because some species of anurans, especially in the tropics, breed several times per season, so that mortality during breeding and nonbreeding cycles could be compared.

Also, the risk of predation to females could be measured as a function of the time they spend sampling males at the breeding site. Females are less conspicuous than males while at the breeding site prior to amplexus. However, the contrast of interest is not between males and females but among individuals within the sexes: do different individuals have different risks of predation as a result of their behavior at a breeding site? For example, some females spend more time than others selecting a mate; does that increase their risk of predation? Predators such as snakes, turtles, and crocodilians can be plentiful at amphibian breeding sites, and the movement of females should increase their susceptibility to those predators. It seems likely, but needs to be documented, that females are in more danger at a breeding site than away from it and that the risk increases in proportion to the time spent at the breeding site. Kirkpatrick (1987a) suggested that the most important contribution that empirical research can make to sexual selection theory is documentation of the selection forces acting on female mate choice. This goal might be achieved with some anurans.

Male anurans greatly increase their conspicuousness while advertising for mates, and the risk of predation has been mea-
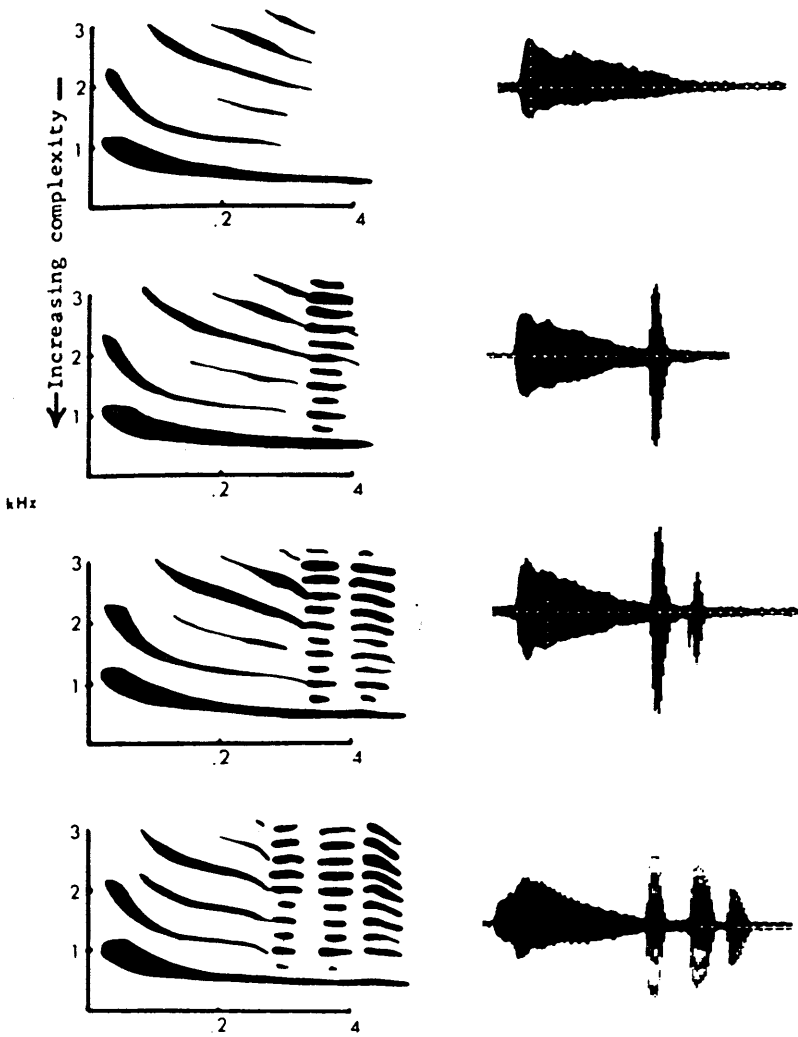
Fig. 14.21 Sonograms (*left*) and oscillograms (*right*) of the call complexity series of *Physalaemus pustulosus*. Each call contains a whine with zero (*top*) to three (*bottom*) chucks. (Reprinted, by permission, from Rand and Ryan 1981.)

sured for some species. Male bullfrogs (*Rana catesbeiana*) that defended territories in the middle of a pond were susceptible to predation by snapping turtles (Emlen 1976; Howard 1978a). Marine toads (*Bufo marinus*) have been observed to orient toward a chorus of *Physalaemus pustulosus,* apparently attracted by the calls of their potential prey (Jaeger 1976). Predators of *P. pustulosus* include a crab (*Potamocarcinus richmondi*), a snake (*Leptodeira annulata*), a leptodactylid frog (*Leptodactylus pentadactylus*), an opossum (*Philander opossum*), and a bat (*Trachops cirrhosus;* reviewed in Ryan 1985a). *Leptodactylus* and the mammals use the frogs' advertisement calls as a localization cue. Males increase their predation risk while calling, and the risk to noncalling males increases when predators are attracted to a breeding site.

Studies of predation by the bat *T. cirrhosus* on *P. pustulosus* revealed the interaction of mate attraction and predation. Male *P. pustulosus* produce a call that consists of whine and from zero to six chucks (fig. 14.21). A male calling in isolation usually produces only a whine, but males add chucks to their calls when they are in a chorus. Females are attracted to calls with only whines, but they prefer calls with chucks. Thus, by adding chucks to the call, a male can increase his ability to attract mates (Rand and Ryan 1981). Why, then, do

males not always produce the calls that are most attractive to females? Energetic cost does not limit the production of chucks: male *P. pustulosus* increase their metabolic rate severalfold while calling, but the number of chucks in the call does not appear to affect the rate of oxygen consumption (Bucher, Ryan, and Bartholomew 1982). Instead, predation by bats (*T. cirrhosus*) appears to be an important factor.

T. cirrhosus is unusual among microchiropteran bats so far studied in its ability to perceive and localize the relatively low frequencies that are characteristic of frog calls (Ryan, Tuttle, and Barclay 1983; Ryan and Tuttle 1987). *T. cirrhosus* is attracted to the calls of a variety of frog species, although they tend to avoid calls of species that are unpalatable or too large for them to eat (Tuttle and Ryan 1982). Among the many calls to which they are attracted is the simple whine (i.e., without chucks) call of *P. pustulosus*. However, *T. cirrhosus* is attracted preferentially to calls with chucks, just as female *P. pustulosus* are (Ryan, Tuttle, and Rand 1982). Thus, males vary their ability to attract mates and their predation risk in parallel when they change the number of components in the call. Male *P. pustulosus* are not completely at the mercy of the predators; they can detect and escape bats on all but the darkest nights, and they vary the intensity of

their escape behavior from merely becoming silent to submerging and swimming away depending on the proximity of the bat (Tuttle, Taft, and Ryan 1982).

A chorus of calling male anurans should be especially prone to bat predation. One possible explanation for such aggregations is the selfish herd hypothesis, which suggests that the per capita risk of predation decreases with increasing size of aggregations (Hamilton 1971). This prediction is supported by observations of *P. pustulosus*: males in large choruses were less likely to be eaten than those in small choruses (Ryan, Tuttle, and Taft 1981). Furthermore, this benefit was not achieved at the cost of reduced mating success, because larger choruses attracted proportionally more females than did small choruses, and the per capita mating success of males was higher in larger choruses (Ryan 1985a; Green 1990).

Another frog, *Smilisca sila* (Hylidae), produces calls with varying numbers of components and frequently falls prey to *T. cirrhosus*. The bats are attracted preferentially to multicomponent calls, and *S. sila* are able to detect an approaching bat on all but the darkest nights. In darkness, when the bats are difficult to detect, the frogs produce calls with fewer components than they do in bright light (Tuttle and Ryan 1982). The frogs also alter their calling sites, calling from the tops of exposed rocks in the middle of streams on bright nights and from under vegetation on dark nights. The frogs also call near small waterfalls that produce a broad frequency band of background noise. When given a choice, bats are attracted preferentially to calls farther from such noisy sources.

Integrating Predation Risk and Energetic Costs of Reproduction

The cost of predation to male reproductive behavior is perhaps better documented for anurans than for any other animal. However, few data indicate that exposure to predation has anything more than a short-term effect on the behavior of male anurans, that differences in predation levels within and among populations or species of anurans have caused the evolution of differences in reproductive behavior, or that predation affects the age or size structure or the degree of sexual dimorphism within populations. If this apparent absence of effects of predation is correct, studies of reproductive energetics can treat the risk of predation as a cost of reproduction that does not interact with the energetics of reproductive behavior. Experimental confirmation of that assumption would require detailed comparisons of the reproductive behaviors of individuals from populations that are known to have had different predation intensities for many generations (cf. Endler's [1980] studies of guppies). However, the apparent absence of long-term effects of predation on the activities of primary interest to physiological ecologists suggests that studies of the behavioral energetics of anuran reproduction may lead to demonstration of a link between individual variation in physiology and Darwinian fitness.

BEHAVIORAL ENERGETICS AND THE ECOLOGY OF AMPHIBIANS
F. Harvey Pough

The topics reviewed in this chapter demonstrate the contributions that investigations of amphibians can make to understanding patterns of biological variation, and they emphasize the many opportunities for integrative studies. The importance of these investigations extends well beyond increasing our understanding of the biology of amphibians, fascinating as that goal is, because these studies contribute to a general understanding of mechanics of natural selection and evolution. As Emerson (1988) has emphasized, the independent evolution of similar character complexes in unrelated phylogenetic lineages provides the best evidence for a direct role of morphological and physiological characters in determining fitness. Information about amphibians can be used to test the generality of hypotheses derived from studies of other taxa, such as lizards, and data from amphibians can generate hypotheses that can be tested in their turn with comparative studies. Even among amphibians, anurans and salamanders are independent radiations that can fruitfully be compared and contrasted.

The goal of behavioral energetics is to understand patterns in nature, and studies of amphibians have emphasized two sets of natural patterns: one in foraging and the other in reproductive behavior. Studies of the relation of foraging mode to community structure and to the morphological and physiological characteristics that are correlated with different foraging modes were among the earliest attempts to merge the perspectives of physiological and community ecologists. Examples of correlations among physiology, morphology, and foraging ecology of anurans are widespread and so familiar that we take them for granted. For example, the general body form of a frog provides a basis for an informed prediction of its behavior and diet. Furthermore, patterns of body form and diet can be extended to include exercise physiology: species that forage widely have higher capacities to sustain aerobic metabolism than sit-and-wait predators. These subjective impressions are supported by statistical analyses (Taigen, Emerson, and Pough 1982; Emerson 1985, 1988).

The emergence of intelligible patterns from descriptive studies is satisfying, but the next step in the analysis, understanding the mechanistic basis of the patterns, has so far proven intractable. We currently have little understanding of why the patterns we see in foraging biology appear so robust. Correlations are widespread, especially at the whole-animal level, and these can be extended to elements of the oxygentransport system, but mechanistic links tracing variation in foraging behavior to variation in the structure, physiology, or biochemistry of muscle tissue are rare, especially at the level of individual variation (table 14.15). Furthermore, current evidence indicates that the normal foraging behavior of anurans does not require rates of energy input that approach the maximum values measured in laboratory tests, so no theoretical basis for the correlations can be suggested. Perhaps, as Walton (1988) has proposed, the aerobic capacities of widely foraging anurans represent excessive construction that provides a margin of safety for rare, critical events in the lives of individuals. Testing hypotheses will be difficult, as will be the search for mechanistic links between individual variation in performance and fitness during rare events. Alternatively, the observation of elevated levels of lactic acid in freeranging animals engaged in apparently low levels of activity may indicate that extrapolation of laboratory measurements to the field is more complicated than we appreciate. In that event, mechanistic links between variation in physiology and foraging behavior might yet be demonstrated.

TABLE 14.15   Patterns of Variation in the Behavioral Energetics of Anurans

Pattern	Interspecific Comparisons	Intraspecific Comparisons
Predatory Behavior and Diet		
Ecology and behavior		
WF make more prey captures than SW.	Yes (30).	Yes (30, 54).
WF capture prey that occur in patches.	Yes (30).	Not tested.
WF travel at lower velocities than SW.	No (30).	Not tested.
WF feed on small prey.	Maybe, but spatial and seasonal variation is large (30, 46, 49, 50, 51).	Not tested.
WF are less territorial than SW.	No (30).	Not tested.
Morphology		
WF have slim bodies and small mouths.	Yes, but phylogenetic bias is large and *Bufo* is an exception (41, 50).	Not tested.
WF have short jaws.	Yes, but *Bufo* is an exception (10).	Not tested.
WF have short limbs.	Yes (11).	Not tested.
Fiber type of limb muscles parallels whole-animal performance.	Varies (25, 32, 40).	Not tested.
Physiology		
WF have greater aerobic capacity.	Yes (3, 4, 45).	No (54).
Heart mass and blood oxygen capacity parallel aerobic capacity.	Yes (20, 21).	Yes (29, 53).
Contractile properties of muscles parallel whole-animal performance.	Yes (27, 32).	Not tested.
Enzyme activities of limb muscles parallel whole-animal performance.	Varies (7, 55).	Yes (2, 3, 5, 31, 32).
Reproductive Behavior		
Ecology and Behavior		
Intensity of call is proportional to body size.	No (58).	Yes (1, 15, 17).
Loud calls are more costly.	Yes (58).	Yes (57, 58, 59).
Long or complex calls are more costly	Yes (58).	Varies (6, 36, 37, 47, 58)
Costly calls are more attractive to females.	Not applicable.	Yes (13, 24, 33).
Call characteristics are correlated with aerobic capacity for locomotion.	Not applicable.	No (44, 56).
Mating success is proportional to chorus tenure.	Not applicable.	Yes (1, 12, 14, 16, 17, 18, 19, 22, 23, 35, 39, 42, 43, 55, 58, 60).
Chorus tenure is limited by energy reserves.	Not applicable.	Varies (34, 58).
Morphology		
Mass of trunk muscles is proportional to calling effort.	Yes (47).	Yes (26, 47).
Mass of laryngeal muscles is proportional to calling effort.	Not tested.	Yes (52).
Structural properties of laryngeal muscles are correlated with calling effort.	Yes (8, 9, 28, 38).	Not tested.
Physiology		
Tetanic frequency of laryngeal muscles is proportional to pulse rate of call.	Yes (27).	Yes (27).
Metabolic substrates of calling muscles are related to reproductive behavior.	Yes (58).	Yes (48).
Enzyme activities of trunk muscles are proportional to calling effort.	Yes (26).	Yes (58).

Sources: (1) Arak 1983b; (2) Baldwin, Friedman, and Lillywhite 1977; (3) Bennett 1974; (4) Bennett, and Licht 1973; (5) Bennett and Licht 1974; (6) Bucher, Ryan, and Bartholomew 1982; (7) Cummings 1979; (8) Eichelberg and Schneider 1973; (9) Eichelberg and Schneider 1974; (10) Emerson 1985; (11) Emerson 1988; (12) Emlen 1976; (13) Forester and Czarnowsky 1985; (14) Gatz 1981; (15) Gerhardt 1975; (16) Gerhardt et al. 1987; (17) Given 1987; (18) Godwin and Roble 1983; (19) Greer and Wells 1980; (20) Hillman 1976; (21) Hillman 1980a; (22) Jacobson 1985; (23) Kluge 1981; (24) Klump and Gerhardt 1987; (25) Lannergren and Smith 1966; (26) McKay 1989; (27) Manz 1975; (28) Marsh and Taigen 1987; (29) Pough and Kamel 1984; (30) Pough and Taigen 1990; (31) Putnam 1979a; (32) Putnam and Bennett 1983; (33) Rand and Ryan 1981; (34) J.G.M. Robertson 1986a; (35) Ryan 1983; (36) Ryan 1988a; (37) Ryan 1988b; (38) Schneider 1977; (39) Sherman 1980; (40) Smith and Ovalle 1973; (41) Sperry 1981; (42) Strüssmann et al. 1984; (43) Sullivan 1982b; (44) Sullivan 1987; (45) Sullivan and Walsberg 1985; (46) Taigen, Emerson, and Pough 1982; (47) Taigen and Pough 1983; (48) Taigen and Wells 1985; (49) Taigen, Wells, and Marsh 1985; (50) Toft 1980b; (51) Toft 1980a; (52) Toft 1981; (53) Trewavas 1933; (54) Walsberg, Lea, and Hillman 1986; (55) Walton 1988; (56) Wells 1976b; (57) Wells and Taigen 1984; (58) Wells and Taigen 1989; (59) Wells and Taigen, this chapter; (60) B. Woodward 1982.

Notes: WF = widely foraging; SW = sit and wait.

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However, studies of the physiological correlates of foraging mode pose a second challenge that will be difficult to meet: foraging is a diffuse activity that integrates interactions with the physical environment, such as thermoregulation and hydroregulation, with the biological activities of defending territories, finding prey, and avoiding predators. Furthermore, daily and seasonal cycles affect the behavior of the study species and of its prey and predators simultaneously; complex interactions of factors are likely to occur.

Mechanistic aspects of the significance of physiological traits in evolution are best studied in behaviors that occupy an animal to the near exclusion of other activities, especially when a mechanistic link between performance and fitness can be demonstrated (Pough 1989b). Reproductive behavior appears particularly suited to studies of this sort, especially for species in which reproduction is separated in time and space from other activities (e.g., Clutton-Brock 1988). Anurans may be uniquely suitable for these investigations because their reproductive biology is more diverse at the species level than that of any other group of vertebrates except fishes (Pough, Heiser, and McFarland 1989).

The reproductive behavior of males of some species of anurans is energetically costly, and it excludes many other activities. Furthermore, males of some species reduce food intake during the breeding season, thereby increasing the chance that energy reserves may limit costly behaviors. The risk of predation during courtship, although it is large for males of some species of anurans, does not appear to confound the interpretation of energetic costs.

Studies of the reproductive behavior of anurans have described species-level correlations between behavior and energetics that appear to reflect mechanistic relationships (table 14.15). For example, male gray treefrogs, *Hyla versicolor* (Hylidae), employ the form of vocalization that maximizes nightly calling duration when they are calling in isolation. When they call in choruses, competing with other males for the attention of females, they shift to complex and energetically expensive calls that are more attractive, but these calls exact a price measured by a reduction in the total time spent calling during an evening (figs. 14.14 and 14.15).

Similarly, the biochemical and physiological characteristics of the trunk muscles of spring peepers, *H. crucifer*, that call at low body temperatures early in the spring are different from those of males that join the chorus later in the spring when it is warmer (McKay 1989). The ratio of females to males is most favorable in early spring, so males that call early probably obtain a disproportionately large number of matings. Studies of these frogs may provide direct evidence of a role of individual physiological variation among males in determining mating success.

The surprisingly short chorus tenures of males of many species of anurans with long breeding seasons may be another example of an energetic constant. Because vocalization is so expensive, males may leave choruses to replenish their energy stores at intervals during the season. If this is the case, the foraging abilities of an individual male (perhaps including its capacity to sustain activity at unfavorable combinations of body temperature and hydration state) might determine how quickly it could return and thus contribute directly to the total time it spent in a chorus during a year.

Although salamanders do not form choruses of vocalizing males, they may be equally useful subjects for study. Salamanders have been the focus of an enormous amount of ecological investigation (e.g., Hairston 1987), but the physiological and morphological correlates of their ecology have been less studied. The mass-specific cost of egg production by salamanders appears to be as great as that of frogs, and the brooding behavior of females of many species of plethodontid salamanders appears to impose the same limits on feeding as described for some frogs. Many salamanders are less vagile than frogs, and they may be correspondingly more tractable for studies that use habitat manipulations to link foraging behavior to energy intake and biomass production.

Experiments that test hypotheses drawn from detailed and specific information about diverse aspects of the biology of a study species appear to be the most productive way to address questions about the processes that lead to the patterns of physiology, morphology, ecology, and behavior revealed by descriptive studies. Reliance on interpretation of correlations revealed by a posteriori analyses is an inefficient experimental design, and it is beset with pitfalls because even the limited information currently available suggests that complex interactions of the phenomena we are investigating are likely to be the rule. For example, the role of energy stores in constraining chorus attendance and calling effort by male anurans may depend on the time of year a species breeds, the length of its breeding season, and the predictability of suitable conditions. The breadth of information needed to design and interpret studies that address questions about the relations between variation in performance and fitness reaffirms the traditional importance of the mechanistic and field-oriented perspective of physiological ecology.