

OXYGEN CONSUMPTION DURING RESTING, CALLING, AND NEST BUILDING IN THE FROG *PHYSALAEMUS* *PUSTULOSUS*¹

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Males (mean mass 1.7 g) called and amplexing pairs built foam nests in respirometer chambers. Mean oxygen consumption ($\dot{V}O_2$) of resting males during the day was 0.26 ml h⁻¹, and at night it was 0.53 ml h⁻¹. Mean $\dot{V}O_2$ of males that could hear other males calling but that were not themselves calling was 0.70 ml h⁻¹. Mean $\dot{V}O_2$ of calling males was 1.13 ml h⁻¹. The energy cost per call (whine) decreases as whine rate increases. Mean $\dot{V}O_2$ per frog during nest building was 2.03 ml h⁻¹. The individual energy cost incurred by male and female during nest building could not be separated. The data on oxygen consumption during sustained calling and nest building offer an opportunity for measuring voluntarily sustained elevated levels of aerobic metabolism in anurans. During calling and nest building mean aerobic metabolic scope was 1.23 and 1.67 ml h⁻¹, respectively. The corresponding factorial scope of about 5.7 is within the range of published values for anurans undergoing forced activity. Because there is a high energy cost associated with reproductive activities in *Physalaemus*, and presumably in other anurans, any interpretations of aerobic and anaerobic metabolic patterns in frogs and toads should take into account reproductive, as well as predatory and escape, behavior.

INTRODUCTION

An understanding of the costs, as well as the benefits, associated with sexual display is central to theories of animal communication. In view of the large number of species in which males or females attract members of the opposite sex by sexual advertising, surprisingly few attempts have been made to measure its most obvi-

¹ The possibility of measuring the energy cost of vocalization in *Physalaemus pustulosus* was originally suggested to us in 1979 by A. Stanley Rand on the basis of his extensive work with the species. Problems of scheduling unfortunately made it impossible for him to participate directly in the study. This research was supported in part by National Science Foundation grants DEB 78-03471 (GAB) and DEB 79-08893 (MJR), and a Smithsonian Predoctoral Fellowship (MJR), and were carried out using the facilities of the Smithsonian Tropical Research Institute.

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ous costs—enhanced risk of predation and increased energy expenditure. Some quantitative information is available on the increased risk of predation incurred by advertising male frogs (see Ryan, Tuttle, and Taft [1981] for a review), but to our knowledge no direct measurements of the energy costs of sexual display in vertebrates have hitherto been published, although there are some data for insects (Bennet-Clark 1970; McNally and Young 1980).

We have measured the energy expenditure associated with the male sexual display of a small Neotropical frog, *Physalaemus pustulosus*, and compared this expenditure with other aspects of energy metabolism in these animals, including the energy cost of nest building.

NATURAL HISTORY

Physalaemus pustulosus, a small, nocturnal, leptodactylid frog common in the

lowlands of tropical America from central Mexico to northern Colombia, offers an unusually favorable opportunity for studies of sexual advertising and its associated costs. During the rainy season the males form choruses in bodies of standing water. Their calling starts at dusk and usually subsides around midnight, but sometimes continues until dawn. Females visit a chorus and choose a male (Ryan 1980).

The mating call of the male has two components, a single whine and from zero to six chucks. The frequency of the whine is modulated by changes in the tension of the vocal cords. The chuck results from changes in the contours of the laryngeal wall which cause a special fibrous structure associated with the vocal cords to vibrate. The air stream that vibrates the laryngeal structures is ejected from the lungs into the vocal sac which becomes greatly inflated. The air from the sac is then reinjected into the lungs and the process of moving air from lungs, to air sac, to lungs may be repeated every few seconds for several hours (Drewry, Heyer, and Rand, in press). When other individuals are vocalizing nearby, males characteristically increase the complexity of their calls by adding chucks to the whine. This provides the female with information about the male's size (Ryan 1980) and may provide locational cues to the females (Rand and Ryan 1981).

The male mounts the female that has been attracted by his calls, and the pair remain in amplexus until oviposition and nest construction have been completed. However, the amplexing pair may temporarily leave the breeding site prior to nest building. During nest building the female extrudes eggs a few at a time. The male seizes the eggs with his hind feet, moves them past his cloaca, fertilizes them, and then whips the jelly matrix of the eggs into a foam with rapid kicks of his hind legs. The process, which requires from 30 min to more than 2 h, continues until all the eggs are enclosed in a foam nest. The nest floats on the water but is

anchored to some solid object (Heyer and Rand 1977).

METHODS

Our studies were conducted during August 1980 at the Barro Colorado Island Station of the Smithsonian Tropical Research Institute in the Republic of Panama. The experimental animals (mean mass = 1.7 g) were taken from a population of *Physalaemus* that breeds in the frog pond near Kodak House. After their oxygen consumption had been measured, the frogs were toe-clipped for future identification and released.

Oxygen consumption was measured in a closed system using an Applied Electrochemistry Oxygen Analyzer. The respirometer chambers were cylindrical glass jars 9 cm in diameter and 14 cm high, sealed with 2-hole rubber stoppers, equipped with Tygon tubing, three-way valves, and connectors (fig. 1).

All measurements were made in the dark at ambient temperature (25.0–27.5 C). Daytime resting measurements were made between 0800 hours and 1300 hours. All other measurements were made between 1930 and 0500 hours. Nighttime resting measurements were made in a laboratory where the experimental animals could not hear calling frogs.

Each measurement of $\dot{V}O_2$ (rate of oxygen consumption) was paired with a simultaneous measurement of the oxygen concentration in a control respirometer in which there was no frog. An hour or more before each run, a measured volume of water at ambient PO_2 was added to a pair of jars, and a frog was introduced into one of them. One to several hours later the jars were sealed, incurrent and excurrent valves were closed, and a timer started. The periods of measurement were approximately 0.5 h for calling and nesting frogs, 1 h for noncalling frogs at night, and 4 h for resting frogs in the daytime.

The fractional concentration of oxygen (FO_2) in air from each jar at the end of the period of measurement was determined by introducing a regulated flow of water (in

equilibrium with room air) from an overhead reservoir. This water displaced the air from the respirometer jars at a constant rate (usually 25 ml/min) and forced the air samples through a scrubber containing Drierite and Ascarite to remove water vapor and CO₂, through the oxygen sensor, and through a flow meter (fig. 1).

Rate of oxygen consumption was cal-

culated from the following formula and corrected to STP:

$$\dot{V}_{O_2} = \frac{V(F_{IO_2} - F_{EO_2})}{(1 - F_{EO_2})t}$$

where V is the volume of dry air in the respirometer chamber, F_{IO₂} is the initial

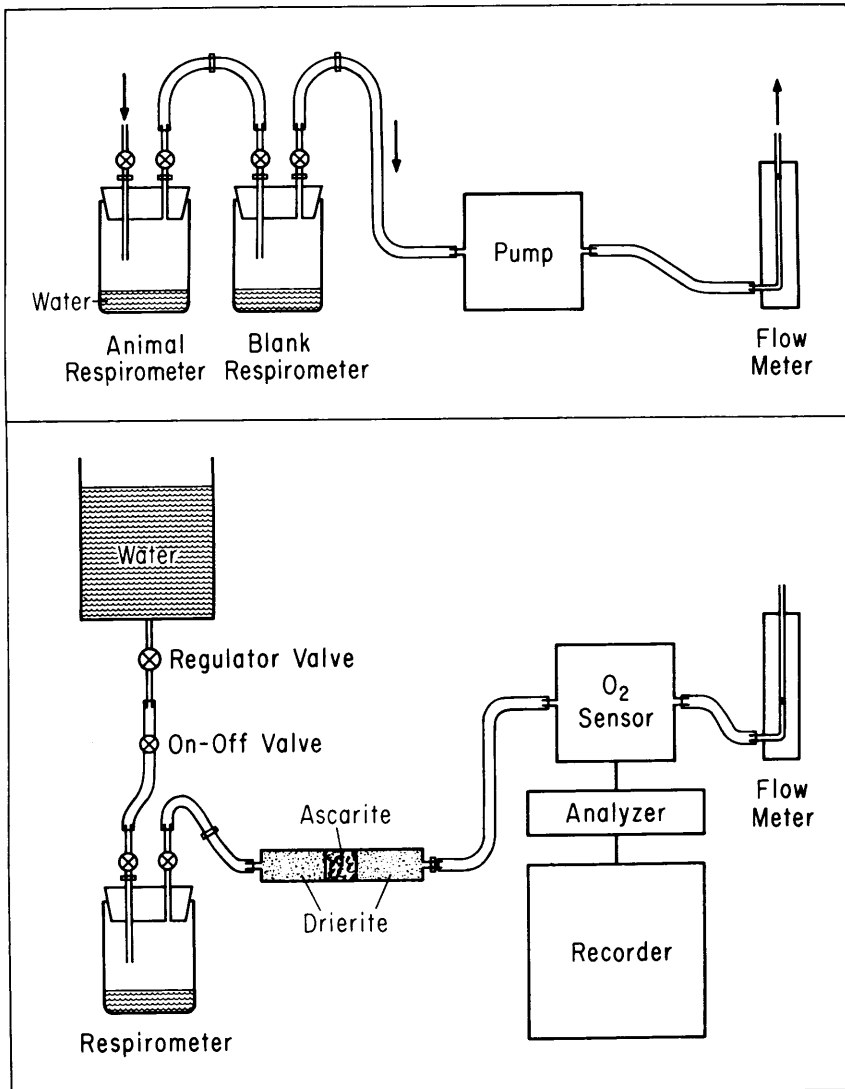


FIG. 1.—Apparatus used for measurement of \dot{V}_{O_2} by *Physalaemus pustulosus* (see Methods).

fractional concentration of oxygen in the air as determined from the sample in the blank respirometer, FEO_2 is the fractional concentration of oxygen in the air at the end of the run, and t is time.

The procedure described above was modified to obtain metabolic measurements from calling frogs. Twenty-four hours or more before measurement several frogs were taken from the well-established chorus in the frog pond adjacent to Kodak House on Barro Colorado Island and put into the respirometer jars. The jars were filled with water to a depth of 2.5 cm, covered with a wire mesh screen, and placed on a visually shielded bench approximately 3 m from the pond. Thus the frogs could hear the calls of the chorus from which they had been removed and were subject to the same environmental temperatures and photoperiod as the animals in and around the frog pond. At dusk three or four jars with the frogs in them were sealed and attached in series with a control jar, and air was drawn through the system at a rate of 650 ml/min. At this flow rate no measurable reduction in FO_2 developed in the respirometer jars, and FO_2 in the control respirometer was, therefore, indistinguishable from that in the experimental respirometers.

The respirometer jars containing the calling frogs were located from 0.2 m to 1.0 m from a speaker continuously broadcasting a tape-recorded mating call. The recorded call, a whine plus one chuck, was repeated at various intensities at 2-sec intervals, using a Nagra tape recorder and a Kudelski Pandex speaker.

As soon as one of the frogs inflated itself, floated in the water, and began to call, its respirometer and the blank respirometer jar were connected in series with pump and flow meter as shown in fig. 1. A Sepnheiser MKH 815T or a MKH 104 microphone was placed adjacent to the respirometer jar containing the frog, and the vocalizations of the calling male in the jar were recorded on a Nagra tape recorder. Because the microphone was immediately adjacent to the respirometer, the calls

produced by the experimental frog were clearly distinguishable from those of the playback tape and the background chorus. After a few minutes of auditory stimulation from the speaker and the nearby frog chorus, the frog in the respirometer usually resumed calling. When it did so, the incurrent and excurrent valves to the paired experimental respirometer jars were closed, converting them into two separate systems. The time was noted, and the tape recorder was turned on. After 30 min, the tape recorder was turned off, the respirometer jars were taken to an adjacent laboratory, and FO_2 was determined as previously described. The tapes were later analyzed to determine both the number and the type of calls produced during the experiment. Some of the frogs never resumed calling after their respirometers were sealed and remained inactive throughout the experimental periods. Later analyses showed that these frogs had elevated $\dot{V}O_2$. These noncalling animals supplied the data for $\dot{V}O_2$ stim (see Results, below).

Unless otherwise stated, means were considered significantly different if Student's t -test yielded values of $P \leq .05$. Regression equations were fitted by the method of least squares.

RESULTS

Rates of oxygen consumption of adult *Physalaemus pustulosus* were measured in five ecologically relevant behavioral circumstances: at rest during the day ($\dot{V}O_2$ day), at rest during the night ($\dot{V}O_2$ night), while stimulated at night by the sound of the chorus but not calling ($\dot{V}O_2$ stim), while calling ($\dot{V}O_2$ call), and while building a nest ($\dot{V}O_2$ nest). Unless otherwise specified all statements refer to males.

Mean $\dot{V}O_2$ day was 0.26 ml h^{-1} . Mean $\dot{V}O_2$ night was more than twice the daytime value. Noncalling frogs that could hear the chorus but were not themselves calling had increased rates of oxygen consumption; $\dot{V}O_2$ stim was 2.4 times $\dot{V}O_2$ day and 1.3 times $\dot{V}O_2$ night. Frogs that were

calling had significantly higher rates of oxygen consumption than those that were not; $\dot{V}O_2$ call was 4.4 times $\dot{V}O_2$ day, 2.1 times $\dot{V}O_2$ night, and 1.6 times $\dot{V}O_2$ stim (table 1).

The rate of whining, the chuck rate, and $\dot{V}O_2$ call varied widely among the calling frogs (table 2). The energy cost associated with calling in *P. pustulosus*, the incremental cost of calling ($\dot{V}O_2$ icc), can be estimated from the increment of oxygen consumption of a calling frog above its nighttime resting level ($\dot{V}O_2$ call - $\dot{V}O_2$ night). The rate of increase of this quantity decreases as whine rate increases (fig. 2). Multiple regression analysis indicates that

inclusion of body mass and chuck rate as additional variables does not account for significantly more of the variability in $\dot{V}O_2$ icc than does whine rate alone.

Both male and female are involved in nest building. The individual energy costs incurred by the male and female during nest building cannot be isolated. Therefore, we have arbitrarily partitioned the measured $\dot{V}O_2$ equally between the members of a pair. This procedure necessarily underestimates the oxygen consumption of the more active member of the pair. Mean $\dot{V}O_2$ nest for six frogs was 2.03 ml h^{-1} , which is 5.6 times the mean $\dot{V}O_2$ day of the same six individuals (table 3).

TABLE 1
OXYGEN CONSUMPTION IN "P. PUSTULOSUS" AS A
FUNCTION OF TIME OF DAY AND BEHAVIORAL
CIRCUMSTANCES

	MASS	OXYGEN CONSUMPTION			
	(g)	(ml h ⁻¹)			
	Mean±SE	Mean±SE	Max	Min	N
$\dot{V}O_2$ day	1.72±.06	.26±.01	.47	.15	22
$\dot{V}O_2$ night . . .	1.66±.08	.53±.03	.66	.37	10
$\dot{V}O_2$ stim . . .	1.76±.10	.70±.07	.96	.28	10
$\dot{V}O_2$ call	1.67±.06	1.13±.13	1.94	.62	9

NOTE.—All mean $\dot{V}O_2$'s are significantly different from each other ($P \leq .05$). The equality of the means of $\dot{V}O_2$ stim and $\dot{V}O_2$ call was tested with the Mann-Whitney U Test because a normal distribution could not be assumed for $\dot{V}O_2$ call.

TABLE 2
VOCALIZATION RATES AND MINIMAL AND CALLING
RATES OF OXYGEN CONSUMPTION OF
INDIVIDUAL "P. PUSTULOSUS"

Mass	Whine Rate	Chuck Rate	$\dot{V}O_2$ Call	$\dot{V}O_2$ Day
(g)	(h ⁻¹)	(h ⁻¹)	(ml h ⁻¹)	(ml h ⁻¹)
1.57	844	0	1.18	.23
1.51	797	267	.92	.21
1.64	1,232	1,108	1.94	.27
1.57	78	8	.62	.24
2.05	76	20	.67	.47
1.81	922	786	1.31	.26
1.60	396	140	1.02	.20
1.77	1,268	1,904	1.30	.30
1.48	1,354	574	1.24	.22

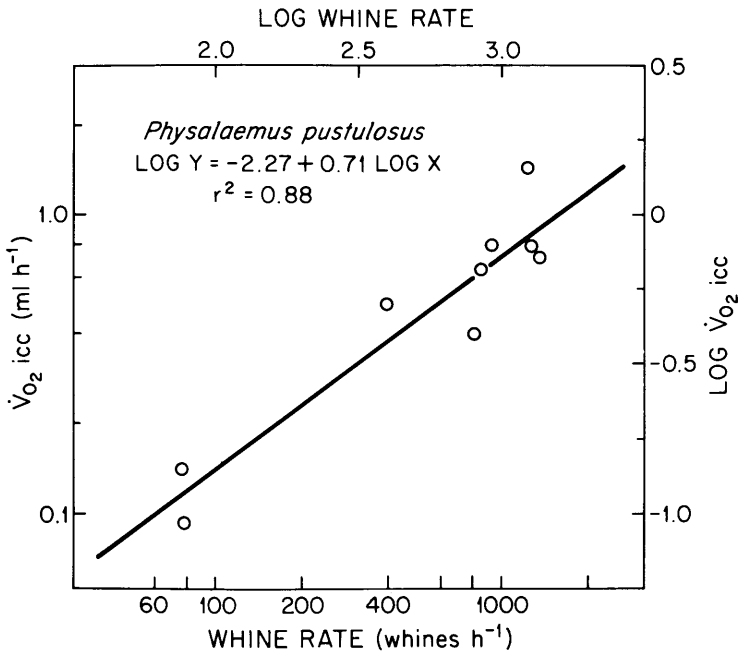


FIG. 2.—The relationship between the log-transformed values for the incremental cost of calling (\dot{V}_{O_2} night - \dot{V}_{O_2} call) and whine rate in *Physalaemus pustulosus*. The slope is significantly different from 1.0, $t = 2.91$, $P < .05$.

TABLE 3
MINIMAL (\dot{V}_{O_2} day) AND POSTNESTING RATES OF OXYGEN CONSUMPTION OF INDIVIDUAL "P. PUSTULOSUS" AND MEAN NESTING RATES OF OXYGEN CONSUMPTION OF THE INDIVIDUALS IN A PAIR

	Mass (g)	\dot{V}_{O_2} Day (ml h ⁻¹)	\dot{V}_{O_2} Post Nest (ml h ⁻¹)	\dot{V}_{O_2} Nest (ml h ⁻¹)
Pair 1:				
Male	1.92	.27	
Female	1.98	.44	.99	1.29
Pair 2:				
Male	2.17	.35	...	
Female	1.63	.39	.58	2.15
Pair 3:				
Male	1.80	.28	...	
Female	2.69	.45	.77	2.65
\bar{x}	2.03	.36	.78	2.03

NOTE.—The means are significantly different ($P \leq 0.05$). Due to the small sample size, comparison of means was made using a Mann-Whitney U test. Total \dot{V}_{O_2} during nesting was arbitrarily partitioned equally between members of a pair to calculate \dot{V}_{O_2} nest.

DISCUSSION

COSTS AND BENEFITS OF CALLING

Our data indicate that the mean energy expenditure of male *Physalaemus pustulosus* while calling is about twice that of males at rest at the same time in their daily activity cycle (table 1). Data are available on a cost of another sort associated with sexual advertisement by the males—enhanced risk of predation.

Female *P. pustulosus* are most strongly attracted to those males that produce complex calls (many chucks per whine), probably because calls with chucks provide information about male body size, and the chucks may offer short-range locational cues. However, the production of complex calls also increases the risk of predation. The bat, *Trachops cirrhosus*, which feeds on *P. pustulosus* and locates them acoustically, is attracted preferentially to male frogs that are producing the more complex calls (Ryan, Tuttle, and Rand 1981).

Ryan, Tuttle, and Taft (1981) have suggested that male *P. pustulosus* should join as large a chorus as possible to maximize the probability of mating and minimize the probability of being preyed upon. If so, reproductively active males should be strongly attracted to large choruses, and as a result of the stimulus from the chorus, would have elevated rates of oxygen consumption even if they themselves were not calling. Mean mass-specific $\dot{V}O_2$ of such males is 1.2 times mean mass-specific $\dot{V}O_2$ night. Calling further increases oxygen consumption. Mean mass-specific $\dot{V}O_2$ of calling frogs is 2.1 times $\dot{V}O_2$ night. Joining a chorus, even without calling, has at least two costs—increased energy expenditure and increased risk of being preyed upon, particularly by nonacoustic hunters—and no apparent benefits unless noncalling males sometimes mate, an occurrence for which there is no evidence in this species. Figures 2 and 3 show that the actual energy cost of vocalization per whine ($\dot{V}O_2$ icc/whine) decreases by a factor of about four, from a high of $1.9 \mu\text{l O}_2$ whine⁻¹ to a low of 0.49

$\mu\text{l O}_2$ whine⁻¹, as whine rate increases about twentyfold. Chuck rate (call complexity) is not significantly correlated with $\dot{V}O_2$ icc.

We assume that the more often a male calls, the more likely he is to be selected by a female and to mate. However, *Trachops* preys preferentially on males with high calling rates (Tuttle and Ryan 1981). As the rate of whining increases, the probability of predation increases, the energy cost per whine declines, and the probability of mating increases. If a male calls at all, he usually calls continuously. This suggests that the probability of mating increases rapidly enough with increasing whine rate to offset both the increased danger of predation and the increased absolute energy expenditure.

This decrease in the incremental cost per whine with increasing whine rate surprised us. Its ecological advantages are clear (see below), but the mechanism which causes it is not. The limited data available allow us to suggest a simple hypothesis. Part of the increased metabolic rate of calling frogs results from the stimulus of being in a chorus, hearing and seeing other calling male frogs and seeing females. The energy expenditure associated with this stimulated state ($\dot{V}O_2$

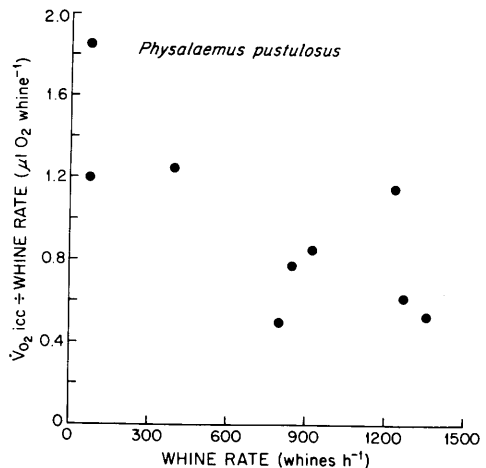


FIG. 3.—The relation of oxygen consumption per whine ($\dot{V}O_2$ icc ÷ whine rate) to whine rate in *Physalaemus pustulosus*.

stim) may not change with calling rate. If we assume that it remains constant, then the actual mechanical cost of producing a whine, which is represented by $\dot{V}O_2$ call - $\dot{V}O_2$ stim rather than $\dot{V}O_2$ icc, decreases with increasing calling rate. To account for this decreased cost, we propose that the energy cost to the frogs of initially inflating themselves by buccal pumping against tissue compliance is greater than the energy cost of transferring the air back and forth between lungs and vocal sac after inflation during calling. The elastic recoil of the vocal sac and the tissues of the thorax and lungs provides some of the mechanical force necessary for moving air back and forth.

Thus the more calls a frog can produce by passing the same air back and forth between lungs and vocal sac, the less energy it spends per call. If a frog can complete a large number of calls on a single inflation before it must renew its air supply for either metabolic or mechanical reasons, its energy cost per whine should decline as whine rate approaches the maximum these frogs can achieve.

The data presently available suggest that natural selection should favor the following program for breeding male *P. pustulosus*: (1) Join as large a chorus as possible (this will increase the probability of attracting females while decreasing the attendant risk of predation). (2) Call as continuously as possible (energy cost per call decreases and probability of mating increases with increasing rate of calling; these advantages apparently outweigh preferential predation on males with high calling rates). (3) Produce calls more complex than those of adjacent males, but not very much more complex (this will attract females away from nearby males with a minimal enhancement of the risk of predation by *Trachops*).

The $\dot{V}O_2$ call averaged 4.4 times $\dot{V}O_2$ rest in the sample as a whole. For the three frogs which called most continuously (table 2), $\dot{V}O_2$ call \div $\dot{V}O_2$ rest was 5.7 (table 4). The only other published data on the energy cost of calling are for insects. The

relative cost of calling in these insects (8 to 20 times $\dot{V}O_2$ rest) is substantially greater than in *P. pustulosus*. Insects which warm up significantly during singing (*Neconocephalus*, *Euconocephalus*, and *Cystosoma*) show substantially higher relative costs of calling than either the frog or the crickets, which do not warm up substantially. The relative costs of calling for the insects shown in table 4 may be underestimates, because the values for $\dot{V}O_2$ rest were obtained at times of day which were probably during the active phase of their daily cycles.

CALLING, NESTING, AND AEROBIC METABOLIC SCOPE FOR ACTIVITY

We know of no previously published data on $\dot{V}O_2$ during voluntarily sustained, intense activity in amphibians except those of Seymour (1973b) on burrowing in *Scaphiopus*. The calling and nest-building activities during which we measured $\dot{V}O_2$ were voluntary. Consequently, the data on energy metabolism which we obtained offers an excellent opportunity for estimating the magnitude of voluntarily sustained elevated aerobic metabolism in anurans.

The mass-specific $\dot{V}O_2$'s which we measured in *P. pustulosus* during calling by the three males which called most continuously and during nest building for periods of 19-29 min were the highest values we obtained. These data yield an average factorial scope ($\dot{V}O_2$ nest \div $\dot{V}O_2$ day) of 5.7. The highest scope ($\dot{V}O_2$ nest - $\dot{V}O_2$ day) of any individual frog (pair 3 male, see table 3) was 1.32 ml O_2 $g^{-1}h^{-1}$. The corresponding maximal factorial scope was 9.5 (table 3).

COMPARISON OF ENERGY METABOLISM OF *P. PUSTULOSUS* WITH THAT OF OTHER ANURANS

It is difficult to compare our data either on resting $\dot{V}O_2$ or on $\dot{V}O_2$ during activity with the values for anurans in the literature. The animals we measured were taken fresh from the field, measured at the same temperature they experienced in

TABLE 4

ENERGY METABOLISM DURING REST AND DURING CALLING IN SOME INSECTS AND A FROG

SPECIES	MASS (g)	METHOD OF SOUND PRODUCTION		$\dot{V}O_2$ CALL (ml O_2 h ⁻¹)	$\dot{V}O_2$ REST	$\dot{V}O_2$ CALL/ $\dot{V}O_2$ REST	SOURCE
		$\dot{V}O_2$ CALL	$\dot{V}O_2$ REST				
Katydid at 23 C (<i>Neoconocephalus robustus</i>)87	Wing stridulation	12.53	.70	18	Stevens and Josephson 1977, fig. 3	
Katydid at 25 C (<i>Euconocephalus nasutus</i>)83	Wing stridulation	10.8	.83	13	Stevens and Josephson 1977, fig. 1	
Bladder cicada at 23 C (<i>Cystosoma saundersii</i>)	1.2	Tymbal	8.32	.42	20	MacNally and Young 1980	
Cricketid at 24 C (<i>Anurogryllus arboreus</i>)377	Wing stridulation	1.53	.12	13	Prestwich and Walker (in press), tables 2 and 4	
Cricketid at 23 C (<i>Oecanthus celerinctus</i>)053	Wing stridulation	.212	.027	8	Prestwich and Walker (in press), tables 2 and 4	
Cricketid at 23 C (<i>Oecanthus quadripunctatus</i>)049	Wing stridulation	.214	.027	8	Prestwich and Walker (in press), tables 2 and 4	
Leptodactylid frog at 25 C (<i>Physalaemus pustulosus</i>)	1.63	Vocalization	1.49	.26	6	Present study (three frogs which called most continuously during period of measurement)	

NOTE.—Data from the literature are recalculated for consistency in units and conditions of measurement.

their natural environment, and, except for the periods of measurement during the day, were exposed to the ambient photoperiod. Aside from the three females involved in the nest-building experiments, all of our experimental animals were sexually mature males. There are no matching data in the literature.

Physalaemus pustulosus shows a strong daily rhythm in $\dot{V}O_2$. Every individual in our sample had a higher $\dot{V}O_2$ at night than during the day. Similar differences in $\dot{V}O_2$ as a function of time of day have been reported in other anurans (Weathers and Snyder 1977; Carey 1979a), but, in many studies, measurements made at different times of day are pooled, or time of day is not specified (see, e.g., Seymour 1973b; McClanahan, Stinner, and Shoemaker 1978; Hillman and Withers 1979).

Temperature acclimation has substantial effects on anuran energy metabolism, even when the time between capture and measurement is only a few days and even when the daily range of body temperatures of captive anurans approximates that of frogs in the field (Carey 1979b). Much of the published data on $\dot{V}O_2$ of anurans during activity are based on manometric measurements of electrically stimulated animals, and many of these measurements are unsatisfactory (Hillman et al. 1979).

Because our data on scope are based on voluntary activity, they may not represent maximum possible values. Nevertheless the factorial aerobic scope sustained by *P. pustulosus* during sustained calling and nest building is of the same general magnitude as that reported in the literature for other anurans. However, apparently because of differences in methodology, reported values for factorial scope vary greatly. Within the Ranidae and the Bufonidae the highest values for factorial scope are those reported by Carey (1979a). This is not surprising, because hers is the only study in which one may be sure that $\dot{V}O_2$ rest was measured at the low point in the daily metabolic cycle and that the animals were maintained outdoors exposed to natural temperature and photo-

period. Our measurements of the leptodactylid *P. pustulosus* (mean = 5.7, max = 9.5) are 60% of the mean of 9.5 reported by Carey for *Rana pipiens* and 26% of the value of 22.2 that she reported for *Bufo boreas*. Similar relative differences in factorial scope between the Ranidae and Bufonidae are reported by several authors. The only existing values for the Pipidae and Pelobatidae are either intermediate or close to the bufonids (see tables 3 and 5).

The data presently available on $\dot{V}O_2$ rest, at 25 C in anurans, are too variable to offer much support for additional comparative statements. The log-transformed data show only a weak correlation between $\dot{V}O_2$ rest (ml h⁻¹) and mass (g).²

$$\begin{aligned}\dot{V}O_2 \text{ rest} &= 0.166 \text{ mass}^{0.79}, \\ r^2 &= 0.32, \\ t &= 2.8, \\ n &= 19.\end{aligned}$$

Mean $\dot{V}O_2$ day for *P. pustulosus* is within 2% of the value predicted by this equation.

In anurans maximum $\dot{V}O_2$ scales with body mass to the 1.0 power (Withers and Hillman 1981). Therefore mass-specific $\dot{V}O_2$ max should be independent of body mass, and both factorial and absolute scope will increase as mass increases. The fact that *P. pustulosus* is an extremely small frog makes its voluntarily sustained factorial scope impressively high. Our highest value for $\dot{V}O_2$ nest is approximately 80% of the value predicted by the regression of $\dot{V}O_2$ during forced activity on mass for anurans (Withers and Hillman 1981). This strongly suggests that during calling and nest building both the male and female *Physalaemus* must function at or close to the highest level of aerobic metabolism they can sustain. We have no information on the contributions of

² Data extracted or recalculated from Bentley and Shield 1973; Holzman and McManus 1973; Seymour 1973a, 1973b; Weathers and Snyder 1977; McClanahan, Stinner, and Shoemaker 1978; Carey 1979a; and Hillman and Withers 1979.

TABLE 5
AEROBIC METABOLISM AT 25 C IN SOME ANURANS

Species	Mass (g)	$\dot{V}O_2$ Rest (ml [g \cdot h] $^{-1}$)	$\dot{V}O_2$ Max (ml [g \cdot h] $^{-1}$)	Factorial Scope	Reference
<i>Rana pipiens</i>	34.8	.077	.729	9.5	Carey 1979a
<i>Bufo boreas</i>	40.2	.050	1.109	22.2	Carey 1979a
<i>Rana pipiens</i>	44.3	.128	.847	6.6	Hillman and Withers 1979
<i>Xenopus laevis</i>	29.3	.143	1.336	9.3	Hillman and Withers 1979
<i>Bufo boreas</i>	27.3	.098	1.364	13.9	Hillman and Withers 1979
<i>Rana pipiens</i>	38.4	.109	.421	3.9	Seymour 1973b
<i>Rana catesbetana</i>	43.5	.048	.195	4.1	Seymour 1973b
<i>Scaphiopus hammondi</i>	10.9	.090	.854	9.5	Seymour 1973b
<i>Bufo cognatus</i>	39.6	.129	1.334	10.3	Seymour 1973b
<i>Physalaemus pustulosus</i> : Calling	2.03	.179	1.000	5.6	Present study (values given are for nest pairs;
Nesting	1.63	.161	.916	5.7	see table 3 and the three males with the highest calling rates)

NOTE.—Data have been arranged by study to facilitate internal comparison (see Discussion).

anaerobic metabolism to calling or to egg laying and nest building.

Taigen, Emerson, and Pough (unpublished) have collected data for $\dot{V}O_2$ rest and $\dot{V}O_2$ max at 20 C for 17 species of anurans in seven families. They calculated the following equations:

$$\begin{aligned}\dot{V}O_2 \text{ rest} &= 0.089M^{0.75}, \\ \dot{V}O_2 \text{ max} &= 0.746M^{0.91},\end{aligned}$$

where $\dot{V}O_2$ is ml h^{-1} and M is body mass in grams. The exponents do not appear to differ either from the one which we compiled for $\dot{V}O_2$ rest or from that of Withers and Hillman for $\dot{V}O_2$ max. Both of the latter regressions have larger proportionality constants than reported by Taigen et al., presumably because of differences in experimental temperatures and methods of measurement. Factorial scopes calculated from Taigen et al. are highest in large bufonids and large microhylids and range from 6.6 to 26.8. Our values for *Physalaemus* (mean 5.7, max 9.5) are similar to their data on another small leptodactylid, *Eleutherodactylus coqui* (6.6), and less than their value for the larger *Odontophrynus americanus* (15.6).

It has been suggested that dependence on aerobic metabolism and high aerobic

scope in anurans are correlated with the static defense behavior associated with skin toxins and/or cryptic coloration, whereas dependence on anaerobic energy release and low aerobic scope are correlated with rapid escape movements (Bennett and Licht 1974; Hutchison and Miller 1979). Taigen et al. refute this simple dichotomy and suggest that the extent of dependence on aerobic metabolism is strongly influenced by patterns of predatory behavior: substantial aerobic capacity would be advantageous to active searchers and a major dependence on anaerobiosis would be likely in passive searchers. Our measurements of high, sustained levels of aerobic metabolism during nest construction in *Physalaemus* indicate that reproductive patterns also should be considered in evaluating the metabolic capacities of anurans.

Obviously in making fundamental functional and evolutionary interpretations of anuran energy metabolism one must consider all aspects of behavior and ecology. The metabolic capacities of anurans have probably resulted from selective pressures related to several aspects of their natural history including predatory, escape, and reproductive behavior.

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