



Energetics of Reproduction in a Neotropical Frog, *Physalaemus Pustulosus*

Michael J. Ryan, George A. Bartholomew, A. Stanley Rand

Ecology, Volume 64, Issue 6 (Dec., 1983), 1456-1462.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at <http://www.jstor.org/about/terms.html>, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Ecology is published by The Ecological Society of America. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Ecology

©1983 The Ecological Society of America

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

ENERGETICS OF REPRODUCTION IN A NEOTROPICAL FROG, *PHYSALAEMUS PUSTULOSUS*¹

MICHAEL J. RYAN²

Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14850 USA and
Smithsonian Tropical Research Institute, Apdo. 2072, Balboa, Panama

GEORGE A. BARTHOLOMEW

Department of Biology, University of California, Los Angeles, California 90024 USA

AND

A. STANLEY RAND

Smithsonian Tropical Research Institute, Apdo. 2072, Balboa, Panama

Abstract. The rate of oxygen consumption ($\dot{V}O_2$) of male *Physalaemus pustulosus* (mean mass 1.51 g) during 30 min of forced activity was 1.76 mL/h. The $\dot{V}O_2$ sustained by males (mean mass 1.84 g) during ≈ 3 min of intense activity was 3.34 mL/h. Formation of a foam nest by a pair, which includes oviposition and fertilization, involved consumption of 2.64 mL O_2 . In terms of ATP yield, the energy contributions of anaerobiosis account for only 2–7% of the total energy expended during calling, nest building, and sustained forced activity. The energy content of nests plus eggs averaged 3.96 kJ.

By combining the metabolic data with data on the reproductive pattern of the species, we estimate the total aerobically supported energy expenditure for reproduction by each sex over a breeding season. Females expend an order of magnitude more energy for reproduction than do males: 40.96 vs. 3.25 kJ. There are few comparative data available, but female *Physalaemus* expend slightly more energy per gram than do female lizards (*Uta stansburiana*) but slightly less energy than the lizards when energy expenditure is adjusted for the length of the breeding season. Male *Physalaemus* use much less energy for reproduction than male lizards (*Uta stansburiana*). Male *Physalaemus* also use less energy for reproduction per gram than do males of two species of Australian frogs (*Ranidella signifera* and *R. parinsignifera*).

Key words: aerobic metabolism; Amphibia; anaerobic metabolism; Leptodactylidae; Neotropics; *Physalaemus pustulosus*; predation risks; reproductive behavior; reproductive energetics.

INTRODUCTION

The "cost" of reproduction is important in understanding life history patterns (e.g., Williams 1966, Stearns 1976) and sexual selection (e.g., Trivers 1972). Two reproductive "costs" which have been examined are energy expenditure and predation risk (Stearns 1976).

In oviparous species, estimates of energy expended for reproduction are usually based on some measure of the energetic content of the eggs (e.g., Tinkle et al. 1970), but energy is also spent on other aspects of reproduction, such as sexual display, nest building, copulating, and egg laying. Direct measures of the energy expended by a vertebrate for these behaviors are only available from measurements of oxygen consumption during male sexual displays and nest construction by mated pairs of the neotropical frog *Physalaemus pustulosus* (Bucher et al. 1982).

The risk of predation is usually inferred from ob-

servations of predation on animals engaged in reproductive behaviors (e.g., Emlen 1976, Haas 1976, Howard 1978), or from differences in rates of mortality between breeding and nonbreeding animals or between males and females (e.g., Trivers 1976, Howard 1981, Schoener and Schoener 1982). Recently, Ryan et al. (1981) quantified the amount of predation on chorusing males of *P. pustulosus* and suggested that reduced predation risk and increased mating success in larger choruses favored the aggregation of males of this species when attracting mates. Predation by the frog-eating bat *Trachops cirrhosus* probably also influences the types and amount of displays by frogs (Ryan et al. 1982, Tuttle et al. 1982).

The purposes of the present study are: (1) to provide a more detailed analysis of energy expenditure during nesting, (2) to measure the anaerobic component of energy metabolism during nesting and calling, and (3) to estimate the total energy expended for reproduction by males and females during a breeding season.

NATURAL HISTORY

Physalaemus pustulosus (Leptodactylidae) is a small (1–2 g) frog common throughout Central America. It

¹ Manuscript received 26 April 1982; revised 8 November 1982; accepted 9 November 1982.

² Present address: Museum of Vertebrate Zoology, University of California, Berkeley, California 94720 USA.

breeds mostly during the rainy season, which is from April to December on Barro Colorado Island, Panama, where most of this study was conducted. Males usually remain stationary while calling at the breeding site. They maintain interindividual distances but do not defend resource-based territories. Females come to the chorus and select a mate by making physical contact with a calling male. The male then clasps the female from above (Ryan 1980, 1983). Shortly thereafter, the amplexed pair leaves the breeding site and returns after chorusing has subsided, typically after 2400, and constructs a foam nest. While the pair is amplexed the female passes several eggs at a time from her cloaca. The male takes them with his hind feet and beats the jelly surrounding the eggs into the foam that constitutes the nest (Heyer and Rand 1977). Therefore, with the exception of sperm, it is assumed that all the constituents of the nest are contributed by the female. Fertilization presumably takes place when the male brings the eggs past his cloaca. The process continues for ≈ 1 h, until a clutch of ≈ 250 eggs has been fertilized and imbedded in foam.

METHODS

These studies were conducted during June and July 1981 at the Barro Colorado Island (BCI) station of the Smithsonian Tropical Research Institute in the Republic of Panama. Experimental animals were taken from two populations. All frogs that were killed for lactate determination were captured on the mainland in Gamboa. Animals that were used only for measurements of oxygen consumption were captured in the frog pond near Kodak House in the BCI laboratory clearing, and after measurement were released at the point of capture. All observations and experiments were conducted between 1900 and 0400.

Aerobic energy metabolism.—Measurements of oxygen were made with an S3A Applied Electrochemistry Oxygen Analyzer. The rate of oxygen consumption during nest building was measured, using a system similar to that described by Bucher et al. (1982). A measured volume of water was put in each of two cylindrical glass jars 9 cm in diameter and 14 cm tall. The jars were sealed with two-hole rubber stoppers equipped with Tygon tubing, three-way valves, and connectors. The jars were connected in series. Between 1730 and 1830 a female and male, which had been captured at a breeding pond in Gamboa the previous night, were placed in the upstream jar. The downstream jar (the blank) was used as a control. Air was drawn through the jars at 30 mL/s. After several hours the frogs usually amplexed. Thereafter they were watched continuously. About 50% of the amplexed pairs constructed nests. As soon as nest building started, the air pump was turned off. The valves to the respirometer jar and the blank jar were closed, converting them to closed systems, and a stopwatch started. As soon as nest building was completed and the

frogs separated, the time was noted and samples of air were withdrawn from the two jars with a 60-cm³ syringe equipped with a three-way valve. The syringes were placed in a Razel syringe pump, and the air they contained was pushed at a rate of 0.33 mL/s through a column containing desiccant (Drierite) and a CO₂ absorbant (Ascarite) and then through the oxygen sensor. Oxygen consumption ($\dot{V}O_2$) was calculated from the difference between the initial fractional concentration in the blank jar and the fractional concentration of oxygen in the respirometer jar at the end of the experiment.

$\dot{V}O_2$ during forced activity was measured in a similar manner, but the initial gas sample was room air taken into a syringe at the same time and place that the experimental respirometer was filled with air. The respirometer was a Plexiglas syringe (internal diameter, 5 cm) containing several drops of water to keep the air saturated. The frog was placed in the syringe, and the volume was adjusted to 100 mL. A stopwatch was started, and the syringe was rotated by hand, forcing the frog to move, or to right itself. At the end of the period of forced activity, the time was noted, a sample of the air in the syringe respirometer was transferred through a pair of valves into a 60-cm³ syringe, and fractional concentrations of oxygen in the blank and experimental syringes were determined. At the completion of nest building, and at the end of the period of forced exercise, the frogs were killed for lactate determination.

The rates of oxygen consumption ($\dot{V}O_2$) were calculated from the following formula and corrected to standard temperature and pressure (STP):

$$\dot{V}O_2 = \frac{V(FIO_2 - FEO_2)}{(1 - FEO_2)t},$$

where V is the volume of the dry air in the respirometer chamber, FIO_2 is the initial fractional concentration of oxygen in the blank respirometer, FEO_2 is the fractional concentration of oxygen in the experimental respirometer at the end of the run, and t is time.

Anaerobic energy metabolism.—The contributions of anaerobic metabolism to calling, nest building, and forced activity were determined by assays of lactic acid in whole-animal homogenates. Immediately after each experiment, the frog was decapitated and homogenized in a Waring blender in a volume of chilled perchloric acid (0.6 mol/L) equal to 10 times its mass. A sample of each homogenate was kept chilled in a sealed vial. After being returned to the University of California, the sample was centrifuged. The supernatant was processed using a Calbiochem-Behring lactate kit, and the lactate concentration was determined at 300 nm with a Beckman model 35 spectrophotometer.

Calling.—Male *Physalaemus* captured in Gamboa, were put in screen-covered jars 9 cm in diameter and

14 cm tall, containing water 3–4 cm deep. The jars were then placed on a bench ≈ 3 m from the Kodak House frog pond where the experimental males could hear the nocturnal frog chorus. Air and water temperatures for the experimental males and for the males in the nocturnal chorus were the same, and always between 24° and 26°C. After they had been calling for 3–4 h, experimental males were killed for lactate determination.

A Sennheiser MKH 104 microphone and a Nagra IV-D tape recorder were used to record the calls produced by the experimental males. The output of the tape recorder was monitored by a type 1521 Graphic Chart Sound Level Recorder (General Radio), the printout from which allowed us to count the number of calls produced by the experimental males.

We counted the total number of calls a frog produced in a night by placing an individual in a plastic bucket (≈ 15 cm diameter) with a screened top. The bucket was then placed near the frog chorus at Kodak House. We used the tape recorder and the chart recorder to count the total number of calls produced in one night (1900–0200). This procedure was conducted on five nights, with a different frog each night.

Bomb calorimetry.—Nests produced by four of the experimental pairs and one nest collected in the field were weighed and dried in a forced-air oven at $\approx 50^\circ\text{C}$ for at least 24 h. After return to Cornell University, the energy content of the dried eggs and nests were determined with an oxygen bomb calorimeter (Parr Instruments).

RESULTS

Rate of oxygen consumption

Half-hour forced activity.—Different schedules with alternating periods of forced activity and rest were tested on male *Physalaemus* to determine the schedule yielding the maximum level of activity that could be sustained for at least 30 min. Of the schedules tested, this was one righting every 2 s, i.e., the respirometer cylinder was rotated through 180° during a period of 0.2 s, held motionless for 1.8 s, then rotated again through 180°. The frog usually clung to the wall of the rotating cylinder until it was nearly upside down, then dropped to the floor of the cylinder, righting itself as it did so. The frog remained motionless for $\approx 90\%$ of

the time and was forced to be active for $\approx 10\%$ of the time. This schedule was maintained until the frog did not attempt to right itself. The mean period that the frogs continued to right themselves on this exercise schedule was approximately one half-hour (Table 1). However, at the time when the frogs failed to right themselves, they were not completely exhausted. If touched they immediately took a series of vigorous evasive hops. During the 35-min period, $\dot{V}\text{O}_2$ averaged $1.16 \text{ mL}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$.

Continuous activity.—Shorter rest periods led to higher rates of oxygen consumption and an earlier cessation of righting attempts. For example, when the respirometer was rotated continuously once per second, a rate at which the frogs had no opportunity to rest, they stopped righting themselves after <3 min (Table 1). $\dot{V}\text{O}_2$ under this regime averaged $1.8 \text{ mL}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$.

Nest building.—The time required for building a nest averaged just over 60 min. During nest building, periods of intense activity lasting 3 or 4 s alternated with 15- or 20-s periods of inactivity. Mean $\dot{V}\text{O}_2$ per individual frog during nest building (Table 1) was $0.77 \text{ mL}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$, which was $\approx 66\%$ of the rate achieved during a half-hour of forced activity and 41% of the highest aerobic rate measured. The total combined oxygen consumption of a pair while building a nest averaged 2.64 mL.

Lactic acid production

Measurable concentrations of lactic acid were present in homogenates of entire bodies of all animals sampled. The values were lowest in resting animals, highest in animals that had been forced to remain active for a half-hour and intermediate in animals that had built a nest or had engaged in prolonged calling (Table 2). The resting animals were killed between 1800 and 2000. Each had been isolated and undisturbed for the previous 24 h. The lactate concentrations of resting males and resting females did not differ significantly and were typical of the published values available for other amphibians at rest (Bennett and Licht 1974, Cushman et al. 1976, Carey 1979, Hutchinson and Miller 1979).

The mean lactate concentration of calling males (mean duration of calling was 3.6 h) did not differ significantly from that of resting males ($t = 1.28, .2 <$

TABLE 1. Oxygen consumption in relation to type of behavior in *Physalaemus pustulosus*.

Behavior	Sex	N	Mass (g)		Duration (min)		$\dot{V}\text{O}_2$ ($\text{mL}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)	
			Mean	SD	Mean	SD	Mean	SD
Nest building	♂ + ♀	8*	1.71	0.52	60.6	5.33	0.77	0.05
Half-hour sustained activity	♂	6	1.51	0.09	34.9	3.73	1.16	0.21
Maximum activity	♂	10	1.84	0.09	2.9	0.27	1.82	0.37

* Eight pairs of ♂♂ and ♀♀; mass and $\dot{V}\text{O}_2$ are for an individual of the pair, i.e., one-half the measured value for the chamber.

TABLE 2. Lactic acid concentrations of whole-body homogenates in relation to type of behavior in *Physalaemus pustulosus*.

Behavior	Sex	N	Mass (g)		Lactate (mg/g)	
			Mean	SD	Mean	SD
Resting	♂	4	1.70	0.25	0.32	0.22
Resting	♀	4	1.71	0.38	0.34	0.31
Nest building	♂	4	1.49	0.20	0.65	0.24
Nest building	♀	4	1.60	0.22	0.44	0.13
Continuous calling	♂	5	2.18	0.28	0.50	0.21
Half-hour sustained activity	♂	4	1.39	0.10	0.67	0.25

$P < .4$), even though the calling males had been stimulated to call at a rate 50% higher than normal (see below). After both nest building and 35 min of forced activity, however, lactate concentrations of males were significantly higher than those of resting animals ($t = 2.04$, $.05 < P < .10$ and $t = 2.13$, $.01 < P < .02$, respectively). The lactate concentrations for nesting frogs, calling frogs, and frogs forced to be active for a half-hour did not differ significantly from each other (nesting vs. calling, $t = .99$, $.2 < P < .4$; nesting vs. forced activity, $t = .73$, $.4 < P < .5$; calling vs. forced activity, $t = 1.61$, $.1 < P < .2$).

Despite the elevated lactate levels of the active animals, the energy contributions of anaerobiosis to total energy expenditure during calling, nesting, and sustained activity are negligible. They accounted for only 2–7% of the total energy input in terms of ATP yield (Table 3; see Discussion).

Calling rates

Of the five males monitored for total amount of calling per night (1900–0200), one male called for 7 h, four males discontinued calling during the 6th h, and one stopped after 5 h. While males called, the mean number of calls per hour was 830.6 (SD = 274.7). The means ($t = .28$, $P > .50$) and variances ($F = 3.21$, $P > .10$) of calling rates of this study and Bucher et al. (1982) do not differ significantly.

Bomb calorimetry

The mean dry mass of the five nests, including eggs, analyzed was 0.17 g (SD = 0.04). The mean energy

content was 3.96 kJ/nest (SD = 1.09) or 22.91 kJ/g (SD = 1.20). The energy content of the field nest (3.76 kJ) was within range of values of the experimental nests.

Energy expended for reproduction by males and females during one breeding season

The laboratory measures of energy expended during certain reproductive behaviors can be extrapolated to energy expended for reproduction over an entire breeding season, by estimating such variables as: the time spent by males sexually advertising, the rate of mating by males, female clutch size, and the number of clutches produced by females each season. At least some *P. pustulosus* breed during every month of the year, but most breeding takes place during the rainy season. We estimate that the rainy season, and thus the frogs' breeding season, on BCI is 259 d (1 April–15 December). Predation of *P. pustulosus* at the breeding site is high (Ryan et al. 1981), and many males probably do not survive an entire season. However, for comparative purposes we estimate the total amount of energy expended by a male during an entire breeding season.

The number of nights on which males visit the breeding site is quite variable. Breeding activity was monitored for 152 consecutive nights (30 June–2 December 1979; Ryan 1983). Individual males were present for an average of 7.2 nights over the mean span of 43 d (SD = 40.0) during which they were known to be alive (i.e., first capture to last sighting). Thus males were present at Kodak Pond 17% of the time they were known to be alive during the breeding season. Al-

TABLE 3. Comparison of calculated ATP* yield of aerobic and anaerobic metabolism in total energy input during nest building, calling, and prolonged forced activity in *Physalaemus pustulosus*; body mass normalized to 1.5 g.

Behavior	Mass (g)	VO ₂ (mL)	Lactic acid production (mg)	ATP yield (mmol)		Aerobic ATP (% of total)
				Aerobic	Anaerobic	
♂ + ♀ building nest†	3.0	2.32	1.64	0.67	0.03	96
♂ calling for 3 h	1.5	3.04‡	0.76†	0.88	0.01	99
♂, half-hour sustained activity†	1.5	0.87	1.01	0.25	0.02	93

* Assumes that production of 1 mg of lactic acid yields 0.0167 mmol ATP, and consumption of 1 mL O₂ yields 0.290 mmol.

† Data from Tables 1 and 2.

‡ Data from Bucher et al. 1982.

TABLE 4. Estimates of aerobic energy expenditure (kilojoules) for reproduction during one breeding season by male and female *Physalaemus pustulosus*.

Males (mean mass 1.7 g)							
No. days present	No. hours at breeding site	Energy for calling males (kJ)	Energy for silent males (kJ)	No. nights mated	Energy for nesting (kJ)	Total energy/season (kJ)	
						Silent + mating	Calling + mating
44	264	3.12	0.88	8.4	0.13	1.02	3.25
Females (mean mass 1.8 g)							
Energy per nest (kJ)	Energy for nesting (kJ)	Total energy/season (kJ)					
3.96	0.13	41.0					

though males might have been at other breeding sites when not at Kodak Pond, surveys of nearby sites indicate strong fidelity to Kodak Pond.

Ryan (1983) showed that there was a significant correlation between the amount of time a male spent at the breeding site and the amount of calling ($r = .91$, $N = 617$, $P < .001$). This suggests that the amount of calling by any male is determined primarily by the amount of time he is at the site. For males whose calling was quantified in this study, the modal number of hours spent calling was six. For comparative purposes, we also estimate the energy expenditures of males that are present at the pond but not calling, although there probably are almost no totally silent males in the population. We use the mean increase in $\dot{V}O_2$ due to calling (i.e., $\dot{V}O_2$ calling - $\dot{V}O_2$ nocturnal resting) of 0.60 mL/h to estimate energy expended for calling. Likewise, we use mean $\dot{V}O_2$ increase due to males being at the pond but not calling ($\dot{V}O_2$ nocturnal stimulated - $\dot{V}O_2$ nocturnal resting) of 0.17 mL/h to estimate the energy expended by a silent male.

The average male mated on 19% of the nights he was at the pond. We use this percentage and the mean number of nights present per season to estimate the number of times a male engaged in nest-building activity. The $\dot{V}O_2$ for nesting was determined for the nesting pair, and for our estimates we divide this quantity equally between the male and female, which undoubtedly underestimates the contribution of the male to nest building (Heyer and Rand 1977). The mean $\dot{V}O_2$ for nesting was 0.80 mL/h above the nocturnal resting rate for an individual, and nesting took ≈ 1 h.

We do not have adequate data to determine the interclutch interval in the field. However, Davidson and Hough (1969) reported that *Engystomops* (= *Physalaemus*) *pustulosus* has an interclutch interval of 4–5 wk in the laboratory. Four weeks appears to be more consistent with the limited field data we have. We estimate that a female should nest 10 times during a season, and we use the mean chemical potential energy content (in kilojoules per clutch) to estimate the energy cost of egg production over a season.

We converted oxygen consumption to joules by as-

suming that the consumption of 1 cm³ of O₂ yields 20.10 J. We consider the energy contribution of anaerobiosis during normal behavior to be negligible and have ignored it.

An average male living through an entire breeding season should expend 3.25 kJ/season above normal maintenance and growth for calling and mating (Table 4). Although there were not totally silent males in the population (Ryan 1983), if a male were to remain silent at the breeding site and mate at the normal rate he would expend 1.02 kJ/season above the resting level for reproduction.

Females expended much more energy than did males. A female that mated and nested only once expends 4.10 kJ for reproduction, which is more energy than an average male expends in an entire season for reproduction. This difference would hold even if the entire energy cost of nest building were attributed to the male. Females that have 10 clutches per season expend an order of magnitude more energy per season for reproduction than do males (Table 4). Even if a male were present at the breeding site on every night of the season, which seems unlikely since stomach analysis indicates that males probably do not eat when at the breeding site (M. J. Ryan, *personal observation*), and still nested at the normal rate, they would expend 24.90 kJ/season for reproduction, still considerably less than a female.

DISCUSSION

Comparison with other amphibians and reptiles.—There are few comparative data on reproductive energetics of anurans. The mass-specific energy content of eggs of nine species of neotropical hylids (Crump and Kaplan 1979) was slightly higher than those we obtained for *Physalaemus pustulosus* (24.71–25.73 kJ/g vs. 22.92 kJ/g for *P. pustulosus*).

We know of no previously published direct measures of the energy expended by male anurans for reproductive behavior. However, for some species energy stores of a male frog are depleted during the breeding season (e.g., Smith 1976). MacNally (1981) measured depletion of energy reserves in somatic tis-

TABLE 5. Comparisons of total energy expended for reproduction by three species of ectotherm: two frogs and a lizard.

Species	Sex	Energy expended (kJ)			Length of breeding season	Mass (g)	Reference
		Per season	Per gram per season*	Per gram per day*			
<i>Physalaemus pustulosus</i>	♂	3.25	2.19	0.008	259	1.7	This study
<i>Physalaemus pustulosus</i>	♀	40.96	26.43	0.102	259	1.8	This study
<i>Ranidella signifera</i> †	♂	2.22	2.88	0.047	60	0.7	MacNally 1981
<i>Ranidella parinsignifera</i> †	♂	2.30	2.99	0.024	120	0.7	MacNally 1981
<i>Uta stansburiana</i>	♂	21.50	8.78	0.075	117	3.3	Nagy 1982
<i>Uta stansburiana</i>	1-yr ♀	44.80	23.96	0.204	117	2.3	Nagy 1982
<i>Uta stansburiana</i>	2+-yr ♀	45.40	21.52	0.186	177	2.7	Nagy 1982

* Mass-specific energy expenditures were determined by dividing by mass.⁷⁵ in grams.

† Masses of *Ranidella* are not given in MacNally (1981), but the average snout to vent length for both species was 21.5 mm. We calculated mass, using the equation: $M = 6.0 \times 10^{-2} SV^{3.24}$, where SV is snout to vent length in centimetres (from Pough 1980).

sue, fat bodies, and liver during the breeding season in males of *Ranidella signifera* and *R. parinsignifera*. He estimated that these males expend 2.22 and 2.30 kJ during breeding seasons of 60 and 120 d, respectively (Table 5). Over an entire breeding season, *Physalaemus* males expended more energy for reproduction than did either of the *Ranidella*. However, the *Ranidella* are smaller (0.72 vs. 1.7 g, Table 5: footnote †) and have a much shorter breeding season (60 and 120 d vs. 259 d) than *Physalaemus*. Adjusting for body size (dividing by mass⁷⁵, in grams), the *Ranidella* expended ≈ 1.3 times more energy per gram per season and 3–6 times more energy per gram per day for reproduction than *Physalaemus* (Table 5). MacNally (1981) did not present data on energy expended by females for reproduction.

Many studies have represented "reproductive effort" of lizards as the energy contents of eggs (e.g., Tinkle and Hadley 1975). However, Nagy (1982) has measured metabolic rates of *Uta stansburiana* in the field, using doubly labeled water, and from these data estimated the energy above growth and maintenance that was devoted to reproduction. He reported that 1st and 2nd-yr females devote 44.8 and 45.4 kJ/season, respectively, to reproduction. Female *Uta* utilize a similar, but slightly lower, mass-specific amount of energy for reproduction than do female *Physalaemus* (Table 5) but devote more energy per day to reproduction during the breeding season than do frogs (Table 5). Male *Uta* devote much more energy to reproduction per gram than do male *Physalaemus*, on both a seasonal and a daily basis (Table 5). Female *Uta* used ≈ 3 times more energy than males per gram per season or 2.6 times more energy per gram per day, but the female frogs used 12 times more energy per gram per season and 12.7 times more energy per gram per day than did the male frogs.

The reasons for the substantial differences in energy expended for reproduction by male *Uta* and male *Physalaemus* are both methodological and biological. The measurements on *Uta* include all behaviors as-

sociated with reproduction, including territorial defense. In our study, we measured only the two most conspicuous behaviors associated with reproduction: sexual display and nesting. However, the difference in energy expenditure for reproduction by the male frogs and male lizards is probably due primarily to qualitative differences in reproductive behavior. Male *Uta* set up territories in February, and these territories are defended continuously for the next 3 mo. This contrasts with the reproductive behavior of male *Physalaemus*. They do not stay continuously at the breeding site, and while there they do not defend territories.

Energy expenditure, predation risk, and sexual dimorphism.—As with other anurans (Shine 1979), in *P. pustulosus* there is a positive correlation between size of the female and the number of eggs per clutch (Ryan 1983). This implies that there should be selection for large body size in females. Among many species of frogs, including *P. pustulosus* (Ryan 1980, 1983), larger males are more likely to acquire mates than are smaller males (Shine 1979). This implies that there should be selection for large male body size. Given these two inferences it is surprising that in 90% of the > 500 species surveyed by Shine (1979), females were larger than males. This size sexual dimorphism has been explained by sexual differences in age at first reproduction and in rates of mortality (Howard 1981), and in rates of energy expenditure and acquisition (Woolbright 1983).

Differences in absolute energy expenditure do not explain the observed differences in size between male and female *P. pustulosus*; females are larger and expend more energy for reproduction. However, the proportion of total energy expenditure devoted to reproduction is not known. Woolbright (1983) suggested that females might have more time to forage than males engaged in time-consuming reproductive behaviors. Increased foraging by females, however, might lead to higher mortality away from the breeding site, but this would tend to skew the size distribution toward males (see below). Tentatively, we suggest that energy con-

siderations probably do not account for the larger size of females in *P. pustulosus*, although this possibility must be considered when investigating sexual dimorphism in other animals.

There is intense predation at breeding sites of *P. pustulosus* (Ryan et al. 1981). Males have a higher risk of predation than females because they spend more time at the breeding site (Ryan 1983) and because calling males are more easily located by acoustically foraging predators (Tuttle and Ryan 1981). This is consistent with the hypothesis that females are larger than males because they live longer. It is also possible that although females preferentially select larger males as mates, there may not be a heritable component to male body size and thus no evolutionary response of male body size to sexual selection (Ryan 1983).

All the data needed to evaluate hypotheses of sexual selection and life history patterns rigorously (e.g., female growth rates in breeding and nonbreeding seasons, nonbreeding mortality and total energy budgets for both sexes, heritability of male characters selected by females) are not available. Nevertheless, the present study, despite its incompleteness, is a first step in a quantitative evaluation of the relative roles of, and interrelations among, energy expenditure, predation risk, body size, and mating success in shaping the reproductive patterns of a species.

ACKNOWLEDGMENTS

We thank K. Adler, T. Bucher, R. Howard, and H. Pough for their comments on the manuscript. We are also grateful to the Smithsonian Tropical Research Institute for the opportunity to conduct this work on BCI. This research was supported by a Smithsonian Predoctoral Fellowship to M. J. Ryan and National Science Foundation Grants DEB-79-08893 to M. J. Ryan and DEB-81-03513 to G. A. Bartholomew.

LITERATURE CITED

- Bennett, A. F., and P. Licht. 1974. Anaerobic metabolism during rest and activity in amphibians. *Comparative Biochemistry and Physiology A: Comparative Physiology* **48**: 319-327.
- Bucher, T. L., M. J. Ryan, and G. A. Bartholomew. 1982. Oxygen consumption during resting, calling and nest building in the frog *Physalaemus pustulosus*. *Physiological Zoology* **55**:10-22.
- Carey, C. 1979. Aerobic and anaerobic energy expenditure during rest and activity in montane *Bufo b. bufo* and *R. pipiens*. *Oecologia* (Berlin) **39**:213-228.
- Crump, M. L., and R. H. Kaplan. 1979. Clutch energy partitioning in tropical tree frogs (Hylidae). *Copeia* 1979: 626-635.
- Cushman, J. R., G. C. Packard, and T. J. Boardman. 1976. Concentrations of lactic acid in neonate and transformed tiger salamanders (*Ambystoma tigrinum*) before and after activity. *Journal of Comparative Physiology* **112**:273-281.
- Davidson, E. R., and B. R. Hough. 1969. Synchronous oogenesis in *Engystomops pustulosus*, a Neotropical frog suitable for laboratory studies: localization in the embryo of RNA synthesized in the lampbrush stage. *Journal of Experimental Zoology* **172**:25-48.
- Emlen, S. T. 1976. Lek organization and mating strategies in the bullfrog. *Behavioral Ecology and Sociobiology* **1**: 283-313.
- Haas, R. 1976. Sexual selection in *Nothobranchius guentheri* (Pisces: Cyprinodontidae). *Evolution* **30**:614-622.
- Heyer, W. R., and A. S. Rand. 1977. Foam nest construction in the leptodactylid frogs, *Leptodactylus pentadactylus* and *Physalaemus pustulosus* (Amphibia, Anura, Leptodactylidae). *Journal of Herpetology* **11**:225-228.
- Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* **32**:850-871.
- . 1981. Sexual dimorphism in bullfrogs. *Ecology* **62**: 303-310.
- Hutchinson, V. H., and K. Miller. 1979. Anaerobic capacity of amphibians. *Comparative Biochemistry and Physiology A: Comparative Physiology* **63**:213-216.
- MacNally, R. C. 1981. On the reproductive energetics of chorusing males: energy depletion profiles, restoration and growth in two sympatric species of *Ranidella* (Anura). *Oecologia* (Berlin) **51**:181-188.
- Nagy, K. A. 1982. *in press*. Ecological energetics in a lizard. In R. Huey, E. Pianka, and T. Schoener, editors. *Lizard ecology: studies of a model organism*. Harvard University Press, Cambridge, Massachusetts, USA.
- Pough, F. H. 1980. The advantages of ectothermy for tetrapods. *American Naturalist* **115**:92-112.
- Ryan, M. J. 1980. Female mate choice in a Neotropical frog. *Science* **209**:523-525.
- . 1983. Sexual selection and communication in a Neotropical frog, *Physalaemus pustulosus*. *Evolution* **37**: 261-272.
- Ryan, M. J., M. D. Tuttle, and A. S. Rand. 1982. Sexual advertisement and bat predation in a Neotropical frog. *American Naturalist* **119**:136-139.
- Ryan, M. J., M. D. Tuttle, and L. K. Taft. 1981. The costs and benefits of frog chorusing behavior. *Behavioral Ecology and Sociobiology* **8**:273-278.
- Schoener, T. W., and A. Schoener. 1982. The ecological correlates of survival in some Bahamian *Anolis* lizards. *Oikos* **39**:1-16.
- Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. *Copeia* 1979:297-306.
- Smith, G. C. 1976. Ecological energetics of three species of ectothermic vertebrates. *Ecology* **57**:252-264.
- Stearns, S. C. 1976. Life history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:3-47.
- Tinkle, D. W., and N. F. Hadley. 1975. Lizard reproduction: caloric estimates and comments on its evolution. *Ecology* **56**:427-434.
- Tinkle, D. W., H. M. Wilbur, and S. G. Tilley. 1970. Evolutionary strategies in lizard reproduction. *Evolution* **24**: 55-74.
- Trivers, R. L. 1972. Parental investment and sexual selection. In B. Campbell, editor. *Sexual selection and the descent of man, 1871-1971*. Aldine, Chicago, Illinois, USA.
- . 1976. Sexual selection and resource accrual ability in *Anolis garmanni*. *Evolution* **30**:253-269.
- Tuttle, M. D., and M. J. Ryan. 1981. Bat predation and the evolution of frog vocalizations in the Neotropics. *Science* **214**:677-678.
- Tuttle, M. D., L. K. Taft, and M. J. Ryan. 1982. Evasive behaviour of a frog in response to bat predation. *Animal Behaviour* **30**:393-397.
- Williams, G. C. 1966. *Adaptation and natural selection*. Princeton University Press, Princeton, New Jersey, USA.
- Woolbright, L. L. 1983. Sexual selection and size dimorphism in anuran amphibians. *American Naturalist* **121**: 110-119.