TEMPERATURE AND THE BALANCE BETWEEN AERIAL AND AQUATIC RESPIRATION IN LARVAE OF RANA BERLANDIERI AND RANA CATESBEIANA[1]

WARREN W. BURGGREN, MARTIN E. FEDER,[2] AND ALAN W. PINDER

Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003; and Department of Anatomy and Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois 60637

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Tadpoles of the frogs *Rana berlandieri* and *Rana catesbeiana* increased total oxygen uptake through lungs, gills, and skin as temperature increased. However, the partitioning of oxygen uptake among lungs, gills, and skin was similar at all experimental temperatures (15, 25, and 33 C), with the skin being the major site of O_2 uptake. This constancy of partitioning in tadpoles differs from the increased predominance of pulmonary respiration with rising temperatures reported for many other amphibious vertebrates. We suggest that neither the costs nor the physical constraints of aquatic O_2 exchange limit its predominance at high temperatures in tadpoles and perhaps in other forms.

INTRODUCTION

Fluctuations in environmental temperature produce changes in the metabolic rate of poikilotherms as well as alter the oxygen capacitance of the respiratory media (Dejours 1981). Therefore, adjustments in respiratory and circulatory convection through the gas-exchange organs must occur to support the appropriate level of oxygen uptake in the face of changes in temperature. Further complexities in maintaining adequate oxygen uptake may develop in animals that simultaneously use both water and air for gas exchange. With a given change in temperature (Dejours 1981), water varies much more in O_2 content than air. Thus, the relative rates of ventilation and perfusion of the two or three gas-exchange organs (usually gill, skin, and lung or gas bladder) may also change disproportionately to maintain the necessary oxygen uptake.

Considering the great thermal variability of the environments inhabitated by many bimodal breathers, it is surprising that relatively few studies of air- and water-breathing vertebrates have examined specifically the effects of temperature change on the balance between aquatic and aerial oxygen uptake (Johansen, Hanson, and Lenfant 1970; Lenfant, Johansen, and Hanson 1970; Rahn et al. 1971; Whitford 1973; Guimond and Hutchison 1976; Hutchison and Miller 1979; Miller and Hutchison 1979). A common finding for air-breathing fishes and amphibians is that, as temperature increases and the oxygen capacitance of water decreases, metabolic rate rises. Below a species-specific "threshold" temperature, aquatic oxygen uptake alone occurs, whereas above that temperature animals breathe air to supplement aquatic O_2 uptake. This pattern is common but by no means universal (see below). It is not clear from these studies whether aquatic respiration in a comparatively O_2-poor medium *cannot* be increased sufficiently to meet the metabolic demands of bimodal breathers at high temperatures, thus *requiring* aerial respiration, or whether the costs of increasing aquatic respiration to the necessary levels is simply higher than the cost of increasing lung ventilation.

This study on the effects of temperature on oxygen uptake and its partitioning in tadpoles of ranid frogs was stimulated by the findings that, even at moderately warm temperatures (20–25 C), the larvae

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[2] Present address: Department of Anatomy, University of Chicago, 1025 East 57th Street, Chicago, Illinois 60637.

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of anuran amphibians use a combination of the gills and skin to achieve as much as 80% of their total oxygen uptake at rest; the small remainder comes from oxygen uptake by the well-developed lungs (Feder 1981, 1983; Burggren and West 1982). The intent of this investigation was to determine whether an increase in aerial respiration is an inevitable consequence of any temperature-induced rise in metabolic rate in amphibians in which aquatic gas exchange normally predominates, or whether the partitioning of oxygen uptake may remain loosely fixed in spite of temperature-induced fluctuations in metabolic rate.

MATERIAL AND METHODS

Experiments were performed on a total of 25 *Rana catesbeiana* tadpoles (mean mass 5.74 g) and 26 *Rana berlandieri* tadpoles (mean mass 3.65 g). All were between developmental stages I–XIV (Taylor and Kollros 1946). Tadpoles were purchased from animal suppliers and maintained at 25 ± 1 C on a 14:10 photoperiod centered at 1400 EST for at least 10 days before experimentation. All tadpoles were fed boiled lettuce ad libitum but were not fed during the 24–48-h period of experimentation.

Two experimental procedures were used for each species. In the first procedure, a tadpole was anesthetized in MS-222 (1:10,000, buffered to pH 7.0) and weighed. The opercular spout was then cannulated with PE tubing (OD 1.9 mm, ID 1.5 mm) according to the techniques described in detail by Gradwell (1970) and Burggren and West (1982). The animal was allowed to recover from the anesthesia and then placed in a respirometer that allowed simultaneous measurement of total oxygen uptake ($\dot{V}O_{2\,TOTAL}$, in $\mu l\ O_2 \cdot g \cdot h^{-1}$), partitioned among the skin, gills, and lungs (see Burggren and West [1982] for a detailed description of the respirometer system).

The respirometer consisted of a sealed Plexiglas chamber irrigated in a flow-through fashion with air-saturated water at 15, 25, or 33 C. At the top of the chamber was a small funnel, filled with a known volume of gas, from which the tadpole could breathe freely. Measurement of changes in gas volume and P_{O_2} (measured with an IL μ13 blood gas analyzer thermostated at the appropriate temperature) per unit time allowed calculation of pulmonary $\dot{V}O_2$ ($\dot{V}O_{2\,LUNG}$). The opercular cannula was led out through the lid of the respirometer. The flow rate and P_{O_2} of water flowing from the gills could be measured by collecting water from this cannula, allowing calculation of branchial $\dot{V}O_2$ ($\dot{V}O_{2\,GILL}$), percentage of O_2 extracted, and branchial stroke volume. Water flowing into the respirometer and past the skin of the tadpole was collected from an outlet tube. The flow rate and P_{O_2} of this water yielded cutaneous $\dot{V}O_2$ ($\dot{V}O_{2\,SKIN}$). The sum of the pulmonary, branchial, and cutaneous $\dot{V}O_2$ was regarded as total $\dot{V}O_2$. Branchial ventilation rate (f_{GILL}, in beats·min^{-1}) was observed visually.

In the second set of experiments, 0.015-mm-diameter copper wires, insulated but for 0.5 mm at their tips, were sewn into the skin on the ventral surface of anesthetized tadpoles (West and Burggren 1982). One pair of electrodes was implanted near the heart to record the heart rate (f_{HEART}, beats·min^{-1}) and a second pair near the buccal cavity to record gill ventilation frequency (f_{GILL}). Electrodes were connected to high-gain preamplifiers in a Narco Biosystems Mark IV recording system. Each animal was placed in a 500-ml Erlenmyer flask containing air-equilibrated water at 15, 25 or 33 C.

Air-breathing frequency (f_{LUNG}) was determined in cannula- and electrode-free larvae by visual inspection for 1 h. Animals were held in 500-ml Erlenmeyer flasks filled with air-equilibrated water.

EXPERIMENTAL PROTOCOL

All tadpoles were allowed 12–24 h at 25 C to recover from anesthesia and to acclimate to the experimental conditions. At the end of this period, measurements were taken, after which the temperature was adjusted during a 2-h period to a new experimental temperature. After 1 h at this temperature, a second data set was collected; after that, adjustment to the next experimental temperature was begun. With the exception of the acclimation periods at 25 C, no tadpole remained at any given experimental temperature for

more than 3–4 h. We therefore view all of the data as responses to acute temperature change. In most experiments, the tadpoles were exposed to the following temperatures in sequence: (*a*) 25 C, (*b*) 33 C, (*c*) 15 C, and (*d*) 25 C. In some experiments the initial measurement at 25 C was omitted, while in several others only measurements at 25 C were obtained.

STATISTICAL ANALYSES

To minimize size-related variation, experimental animals of similar size were chosen. Preliminary analyses of covariance for each species established that body size had no significant effect on any of the respiratory variables under study in larvae of *R. catesbeiana* ($P > .10$) but significantly affected $\dot{V}O_2$ in *R. berlandieri*. Because analysis of covariance and one-way analysis of variance yielded similar results in every case, we employed the latter (and more simple) procedure to test for temperature effects on respiratory variables.

The Q_{10}'s of respiratory variables were computed from the mean values of these variables at 15, 25, and 33 C.

All proportions (e.g., percentage extraction and the percentages of oxygen uptake due to lungs, gills, or skin) were transformed as their logits (base *e*) before statistical analyses were performed. Although we have retained the actual values of the proportions in the tables and figures, the results of the statistical tests are for the transformed values. Transformed and untransformed proportions yielded the same statistical result in every case.

RESULTS

EXPERIMENTAL TECHNIQUES

The data were first analyzed to assess the effects of restraint, cannulation, and placement of electrodes on the respiratory variables under study. Five tadpoles (three *Rana berlandieri* and two *R. catesbeiana*) in which the operculum was cannulated were measured at 25 C both before and after exposure to 15 C and 33 C (table 1). Repeated measurement and exposure to temperatures other than 25 C in

TABLE 1

METABOLIC RATES AND CARDIORESPIRATORY FREQUENCIES AT 25 C BEFORE AND AFTER EXPOSURE TO 33 C AND 15 C

	NO.	MEASUREMENT AT 25 C 1[a]	MEASUREMENT AT 25 C 2[a]	DIFFERENCE	*P* OF DIFFERENCE
Larvae with operculum cannulated:[b]					
$\dot{V}O_{2\,LUNG}$ ($\mu l \cdot g^{-1} \cdot h^{-1}$)	5	26.2 ± 10.3	20.6 ± 4.1	5.6 ± 10.5	.62
$\dot{V}O_{2\,GILL}$ ($\mu l \cdot g^{-1} \cdot h^{-1}$)	5	37.4 ± 9.5	37.6 ± 11.0	−.2 ± 16.7	.99
$\dot{V}O_{2\,SKIN}$ ($\mu l \cdot g^{-1} \cdot h^{-1}$)	5	114.6 ± 21.9	98.8 ± 9.0	15.8 ± 19.0	.83
$\dot{V}O_{2\,TOTAL}$ ($\mu l \cdot g^{-1} \cdot h^{-1}$)	5	178.2 ± 36.7	157.0 ± 15.2	21.2 ± 30.7	.69
Extraction %	5	45.4 ± 4.5	48.4 ± 3.5	−3.0 ± 5.1	.59
Gill flow ($ml \cdot min^{-1}$)	5	1.62 ± .22	1.33 ± .43	.29 ± .54	.62
f_{GILL} ($\cdot min^{-1}$)	5	106.8 ± 5.9	104.4 ± 9.9	2.4 ± 11.6	.85
Gill stroke vol (μl)	5	15.7 ± 1.6	14.3 ± 4.6	1.4 ± 4.5	.77
Larvae with electrodes (f_{GILL} and f_{HEART}) and unrestained (f_{LUNG}) larvae:					
Rana berlandieri:					
f_{GILL} ($\cdot min^{-1}$)	8	89.8 ± 6.6	79.1 ± 13.6	10.6 ± 12.4	.42
f_{HEART} ($\cdot min^{-1}$)	8	54.0 ± 8.3	42.1 ± 10.4	11.9 ± 13.8	.42
f_{LUNG} ($\cdot h^{-1}$)	8	2.2 ± 1.4	1.3 ± .8	.9 ± 1.6	.59
Rana catesbeiana:					
f_{GILL} ($\cdot min^{-1}$)	9	91.4 ± 5.2	93.3 ± 5.3	−1.9 ± 5.4	.74
f_{HEART} ($\cdot min^{-1}$)	6	66.8 ± 4.6	64.3 ± 4.3	2.5 ± 4.7	.62
f_{LUNG} ($\cdot h^{-1}$)	8	1.7 ± .9	1.8 ± .9	−.1 ± 1.1	.92

[a] Measurement 1 refers to initial measurement at 25 C. Measurement 2 refers to second measurement at 25 C after intervening measurements at 33 C and 15 C.

[b] Three *R. berlandieri* and two *R. catesbeiana*.

general did not affect these measurements at the reference temperature, 25 C. In no case did mean values differ significantly between the two sets of measurements at 25 C for any respiratory variable (P = .42–.99; t-test for paired comparisons). For 10 variables the means were less in the second set of measurements; in four cases the means were greater in the second set of measurements. The second set of measurements at 25 C for "cannulated" animals was compared to the first set of measurements for all animals (i.e., both those that were measured at 25 C a second time and those that were measured at 25 C only once). None of the differences between these two sets of measurements was significant (P = .12–.99; one-way analysis of variance).

The differences between the f_{GILL}'s of larvae that were cannulated and larvae that were fitted with electrodes were not significant for *R. berlandieri* at 33 C and for *R. catesbeiana* at 25 and 33 C ($P > .2$; t-test). However, at 25 C cannulation resulted in a 22% increase above the f_{GILL} of *R. berlandieri* tadpoles fitted with electrodes ($P < .05$; t-test).

Feder (1981, 1982) presented equations relating the $\dot{V}O_{2\,TOTAL}$ and the body size of unrestrained ranid tadpoles as follows:

$$M_D = 0.047\ M_W^{1.06}$$

$$\dot{V}O_{2\,TOTAL} = 2.5\ M_D^{0.878},$$

where $\dot{V}O_{2\,TOTAL}$ is in $\mu l\ O_2 \cdot h^{-1}$, M_D is dry mass, and M_W is wet mass (both in mg). We have used these equations to compare $\dot{V}O_{2\,TOTAL}$ of the larvae in the present study with the $\dot{V}O_{2\,TOTAL}$ reported previously for unrestrained animals that were neither cannulated nor fitted with electrodes (Feder 1981, 1982).

Figure 1 presents the $\dot{V}O_{2\,TOTAL}$ for all "cannulated" tadpoles during the first set of measurements at 25 C and also the $\dot{V}O_{2\,TOTAL}$ expected for unrestrained larvae of *R. berlandieri* at 25 C. The $\dot{V}O_{2\,TOTAL}$ of cannulated tadpoles of *R. catesbeiana* ranged from 83% to 159% of expected routine levels (mean = 121%) and did not differ significantly from expected routine levels (P = .14; t-test for paired comparisons). By contrast, the $\dot{V}O_{2\,TOTAL}$ of cannulated *R. berlandieri* ranged from 161% to 379% of expected routine levels (mean = 266%) and was significantly greater than expected routine $\dot{V}O_{2\,TOTAL}$ ($P < .001$; t-test for paired comparisons). Thus larvae of the two species differ substantially in the consequences for metabolic rate of cannulation and confinement.

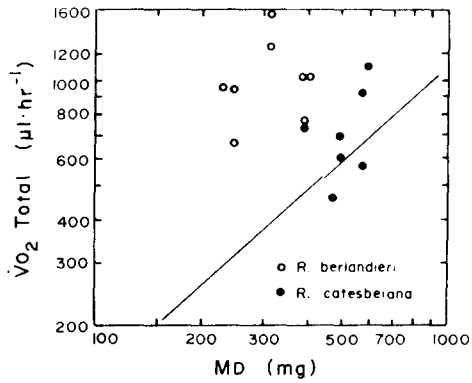


FIG. 1.—Effect of body size on rates of oxygen consumption in cannulated *Rana berlandieri* and *R. catesbeiana* larvae at 25 C. Solid line shows routine rates of oxygen consumption expected for unrestrained larvae without cannulae (Feder 1982).

OXYGEN UPTAKE AND ITS PARTITIONING AMONG GILLS, SKIN, AND LUNGS

With the exception of the $\dot{V}O_{2\,TOTAL}$, which was approximately twice as great in *R. berlandieri* as in *R. catesbeiana*, the patterns of change in gas-exchange partitioning and respiratory and cardiac rates in response to acute temperature change were very similar in both species. Figure 2 and figure 3 present these data for *R. berlandieri* and *R. catesbeiana*, respectively. Values of Q_{10} were calculated from the means of the experimental variables shown in figures 2–3 and are presented in table 2.

Although at all three experimental temperatures $\dot{V}O_{2\,TOTAL}$ was greater in *R. berlandieri* than in *R. catesbeiana*, in both species $\dot{V}O_{2\,TOTAL}$ increased significantly with temperature (fig. 2), with Q_{10}'s ranging from 1.8 to 2.4 (table 2). In both species the increase in the $\dot{V}O_{2\,TOTAL}$ resulted primarily from an increase in $\dot{V}O_{2\,SKIN}$, which had a Q_{10} of about 1.5–1.7 in the two species between 15 and 25 C, and 2.2–2.8 between 25 and 33 C. However, temperature did not significantly af-

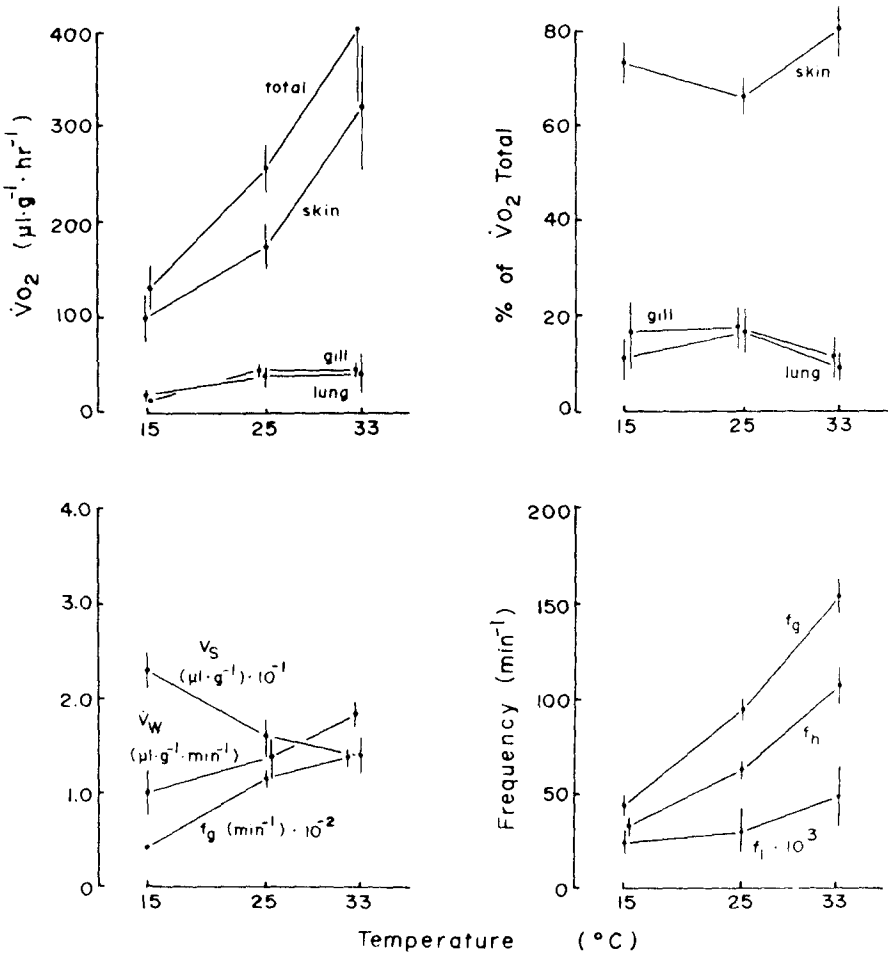
... the relative importance of the gills, lungs, and skin as organs of oxygen uptake in either species. The skin, gills, and lungs consistently contributed approximately 70%, 20%, and 10%, respectively, of $\dot{V}O_{2\,TOTAL}$.

BRANCHIAL PERFORMANCE, HEART RATE, AND LUNG VENTILATION

Both f_{GILL} and the gill flow rate increased with temperature, while the branchial stroke volume declined slightly in both species. However, the means at the three experimental temperatures did not differ significantly (table 2) in *R. berlandieri*, while only the change in f_{GILL} was significant in *R. catesbeiana*.

Oxygen extraction from the gills was not significantly affected by temperature in either species and ranged from 24% ± 6% ($\bar{X}$ ± SE) at 15 C in *R. catesbeiana* to 43% ± 5% in *R. berlandieri*.

The f_{HEART} increased at approximately the same rate as the f_{GILL} in both species,



R. berlandieri

FIG. 2.—Effect of temperature on rates of oxygen consumption, cardiorespiratory frequencies, and partitioning of oxygen consumption among lungs, gills, and skin in larvae of *Rana berlandieri*. Means ± SE are plotted. See table 2 for significance of differences. Rates in the bottom right graph are for animals with electrodes (f_{GILL} and f_{HEART}) and unrestrained animals (f_{LUNG}); other panels represent rates for cannulated animals.

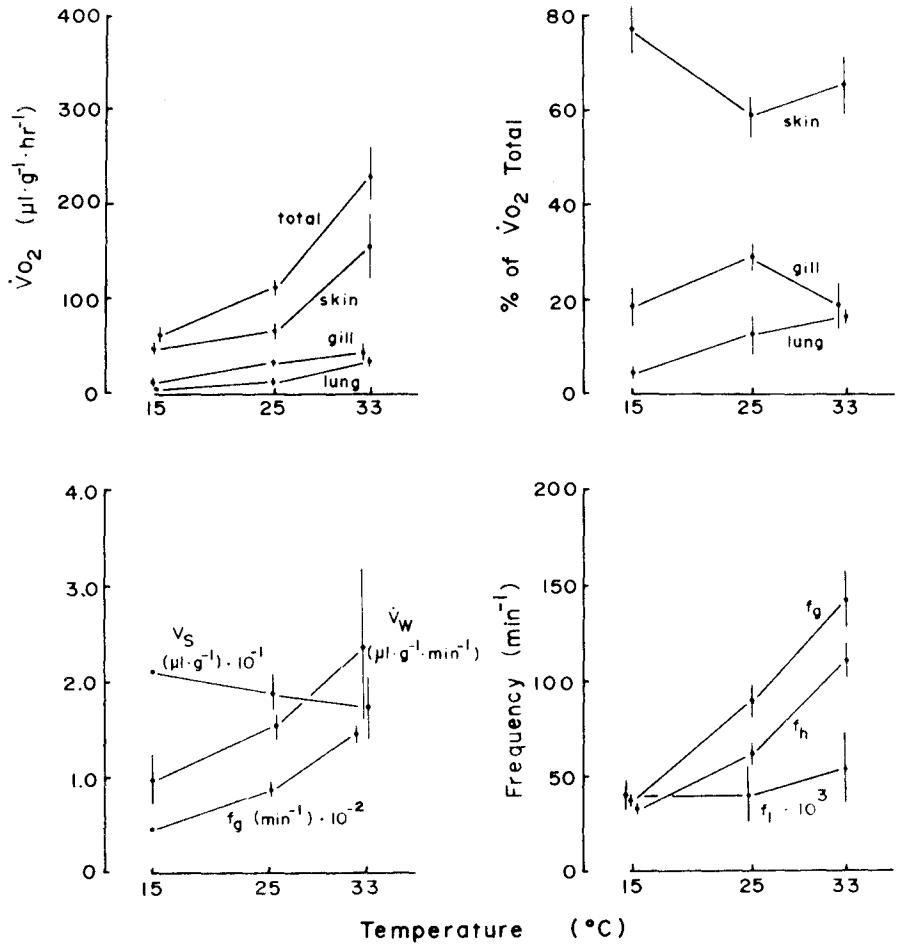
with a Q_{10} of between 1.8 and 2.1. There was no evidence of heart/gill phase coupling in either species at any temperature, nor were there any significant changes with temperature in the ratio of f_{GILL} to f_{HEART}.

The f_{LUNG} was unaffected by temperature in both *R. berlandieri* and *R. catesbeiana*.

DISCUSSION

EXPERIMENTAL METHODS

In larval amphibians, as in adult amphibians and many other vertebrates, minor surgery, the implantation of cannulae or electrodes, and even the stress of handling or confinement can lead to marked and prolonged departure from the physiological state of a resting and undisturbed animal (Hughes and Knights 1968; Holeton 1974; Miller and Hutchison 1979; Feder 1981; Kanwisher, Gabrielson, and Kanwisher 1981; Wassersug, Paul, and Feder 1981). Thus, in amphibians, minor differences in experimental procedures may result in major differences in the $\dot{V}O_{2\,TOTAL}$ (Feder 1976; Hillman et al. 1979; see also the contrasting results of



R. catesbeiana

FIG. 3.—Effect of temperature on rates of oxygen consumption, cardiorespiratory frequencies, and partitioning of oxygen consumption among lungs, gills, and skin in larvae of *Rana catesbeiana*. Means + SE are plotted. See table 2 for significance of differences. Rates in the bottom right graph are for animals with electrodes (f_{GILL} and f_{HEART}) and unrestrained animals (f_{LUNG}); other panels represent rates for cannulated animals.

Hutchison and Hutchison [1972] and Miller and Hutchison [1979]). In the present study, the attachment of opercular cannulae, or electrodes to larvae of *Rana berlandieri* resulted in significant differences in the $\dot{V}O_{2\,TOTAL}$ and the f_{GILL}. Unrestrained *R. catesbeiana* in the present study breathed air regularly, while confined and cannulated conspecifics of similar size and developmental stage did not (Burggren and West 1982). None of the animals in the present study showed cardiorespiratory synchrony, which occurs in undisturbed tadpoles (Wassersug et al. 1981). Clearly, detailed studies of respiratory and cardiovascular physiology are impossible without surgery, the implantation of instrumentation, and some degree of stress in experimental animals. However, as the results of the present study and many others demonstrate, investigators should bear in mind the possibility of experimental artifact if invasive techniques are used and, whenever possible, perform parallel studies with noninvasive techniques to examine the consequences of "experimental stress."

To a large extent, the behavioral and morphological characteristics of a species may affect its suitability for invasive instrumentation (Hughes and Knights 1968) and its susceptibility to experimental stress. For example, in the present study *R. catesbeiana* larvae were far more refractory to disturbance than *R. berlandieri* larvae and underwent hardly any increase in their $\dot{V}O_{2\,TOTAL}$. Cannulated *R. catesbeiana* tadpoles calmed quickly when placed in the respirometer, while cannulated *R. berlandieri* larvae often struggled vigorously for extended periods. Also, cannulated but otherwise unrestrained *R. catesbeiana* larvae did not differ significantly in blood pH, blood lactate, or muscle lactate concentration from conspecific larvae that were unrestrained (Quinn 1982). These interspecific differences may reflect other aspects of species' biology. For example, predatory fish eat tadpoles of *R. catesbeiana* much less readily than other ranid larvae (Kruse and Francis 1977); hence larvae of *R. catesbeiana* may have relatively poorly developed capabilities for escaping predators through intense activity (Bennett and Licht 1974).

TABLE 2

TEMPERATURE COEFFICIENTS (Q_{10}'s) FOR RESPIRATORY VARIABLES OF ANURAN LARVAE[a]

	Species					
	Rana berlandieri			*R. catesbeiana*		
	P	Q_{10} 15–25 C	Q_{10} 25–33 C	*P*	Q_{10} 15–25 C	Q_{10} 25–33 C
$\dot{V}O_{2\,LUNG}$	.48	2.28[b]	1.13[b]	<.01	5.35	3.19
$\dot{V}O_{2\,GILL}$	.09	3.26[b]	.88[b]	.04	2.72	1.28
$\dot{V}O_{2\,SKIN}$	<.01	1.74	2.16	<.01	1.46	2.83
$\dot{V}O_{2\,TOTAL}$	.93	1.97	1.76	<.01	1.87	2.41
% Lung $\dot{V}O_2$ (%)	.80	1.58[b]	.46[b]	.14	2.76	1.39
% Gill $\dot{V}O_2$ (%)	.11	1.06[b]	.61[b]	.11	1.59[b]	.57[b]
Skin $\dot{V}O_2$ (%)	<.01	.90[b]	1.26[b]	.05	.76	1.14
Extraction (%)	.13	1.64[b]	.94[b]	.04	1.65	1.02
Gill stroke vol.	.47	.68[c]	.82[b]	.80	.89[c]	.90[b]
Gill flow rate	.08	1.36[b]	1.45[b]	.14	1.56[b]	1.72[b]
f_{GILL} (cannulated)	.12	2.74[c]	1.26[b]	<.01	1.84	2.04
f_{GILL} (electrode)	<.01	2.24	1.85	<.01	1.95	1.84
f_{HEART}	<.01	1.89	1.89	<.01	1.80	2.08
f_{LUNG}	.89	1.31[b]	1.87[b]	.31	.96[b]	1.66[b]
f_{GILL}/f_{HEART}	.76	1.08[b]	1.09[b]	.71	1.12[b]	.84[b]

[a] The *P* refers to result of one-way analysis of variance. Sample sizes for cannulated animals: five at 15 and 33 C (both species), eight at 25 C (*R. berlandieri*), seven at 25 C (*R. catesbeiana*). Sample sizes for uncannulated animals: five to 11.

[b] Temperature had no significant effect on indicated variable according to one-way analysis of variance. The Q_{10} should be considered not significantly different from 1.0.

[c] The f_{GILL} was not observed in these larvae at 15 C. The Q_{10} was calculated from the mean f_{GILL} for electrode larvae at 15 C.

Larvae of both species resembled conspecifics in previous studies (Burggren and West 1982; West and Burggren 1982; Feder 1983) in their partitioning of O_2 uptake among lungs, gills, and skin. The Q_{10}'s of total $\dot{V}O_2$ were also similar to previous results for related species and other tadpoles (Parker 1967; Marshall and Grigg 1980; Noland and Ultsch 1981). However, the total $\dot{V}O_2$ for *R. berlandieri* was significantly elevated above levels expected for resting larvae (Feder 1982).

TEMPERATURE AND THE PARTITIONING OF O_2 UPTAKE

The present investigation of gas-exchange partitioning among the lungs, gills, and skin of *R. berlandieri* and *R. catesbeiana* has clearly demonstrated that the balance between aerial and aquatic respiration is unaffected by acute temperature change. This finding is in contrast to studies of many other bi- or trimodal breathers. In the air-breathing fishes *Amia* (Johansen et al. 1970) and *Lepisosteus* (Rahn et al. 1971), the contribution of air breathing increases from 0% to 12% of total O_2 uptake at 10 C to 60%–80% of total O_2 uptake at 25–30 C. Similar patterns are evident in the aquatic salamanders *Ambystoma, Amphiuma,* and *Siren* (Lenfant et al. 1970; Guimond and Hutchison 1976), the aquatic frog *Xenopus* (Hutchison and Miller 1979), and many adult anurans and salamanders measured entirely in air (Hutchison, Whitford, and Kohl 1968; Whitford 1973). The general implication of these studies is that at low temperatures such animals are facultative air breathers while at high temperatures they become obligate air breathers, although this has been substantiated in relatively few cases (Das 1927; Hutchison and Dady 1964; Burggren 1979).

At least two explanations have been advanced for the changes in respiratory partitioning with temperature in bimodal breathers. We suggest that neither of these explanations is entirely or exclusively satisfactory for several reasons.

The first explanation is that, although these animals could increase aquatic oxygen uptake by increasing ventilation, the energetic cost of doing so may be much greater than switching to aerial respiration. Because water is relatively dense and its oxygen content is low, the energetic cost of the gill convection requirement is high (Holeton 1980) and may become prohibitive as the temperature rises and the O_2 capacitance of water falls. Although this cost is certainly major, other costs may also be large and may offset the low energetic cost of ventilating the lungs. For example, Kramer and McClure (1981) have recently demonstrated in the air-breathing catfish, *Corydoras aeneus,* that the energetic and temporal costs of moving vertically through the water column to breathe at the surface are considerable and add substantially to the overall cost of aerial ventilation. Carrying gas underwater in the lungs increases a tadpole's buoyancy and decreases locomotor performance in some tadpoles, although not in ranids (Wassersug and Feder 1983). Finally, the air-water interface can be the site of intense predation (Kramer and Graham 1976), a risk that would increase as air breathing increased.

Continued aquatic respiration may be especially advantageous in tadpoles in that it is predominantly cutaneous, and cutaneous gas exchange usually does not require dedicated ventilatory movements. Hence it avoids the high costs and high risks associated with lung and gill ventilation.

The second common explanation for changes in respiratory partitioning with temperature suggests that the fall in aquatic O_2 capacitance as water temperature rises, concomitant with a rise in O_2 demand as body temperature increases, produces a situation in which extraction of O_2 from water alone cannot be raised sufficiently to meet oxygen demand. Consequently, aerial respiration must increase to prevent an oxygen deficit (Rahn et al. 1971). There have been surprisingly few studies that document inadequate performance of the aquatic gas exchangers at high water temperatures. In fact, most such studies suggest the opposite conclusions. Certainly, in strictly aquatic fish, in which air breathing is not an option, increases in gill ventilation in air-saturated water are more than adequate to compensate for temperature-induced increases in O_2 consumption (Hughes and Roberts

1965; Heath 1973; Randall and Cameron 1973; Butler and Taylor 1975; Cech, Campagna, and Mitchell 1979). However, the gills of many air-breathing fish are reduced (Randall et al. 1981), and no studies of the effect of temperature on gill performance in air-breathing fish are available to substantiate the possibility that reduced gill surface in these forms actually limits gill O_2 uptake at high temperatures.

Of course, gill performance need not limit aquatic oxygen uptake in tadpoles, since the largest portion of gas exchange is via the skin (Burggren and West 1982). Cutaneous gas exchange in amphibians is generally regarded as diffusion (and not perfusion) limited (Piiper, Gatz, and Crawford 1976; Moalli et al. 1980; Moalli 1981). Diffusion limitation is probably an adequate characterization of O_2 movement at the capillary level. However, even in such a system, mass transport of oxygen will increase if additional cutaneous capillaries are recruited. "Blushing" of particularly the ventral skin of many anuran larvae occurs following exercise (independent unpublished observations of M. Feder, D. Quinn, and R. Wassersug), suggesting that adjustments in cutaneous perfusion can occur when O_2 demand is high (see also Moalli et al. 1980; Moalli 1981; Smith et al. 1981). More to the point, adult plethodontid salamanders, which lack both lungs and gills, can increase O_2 uptake considerably with both temperature and activity (Whitford and Hutchison 1965; Feder 1976, 1978).

Although both explanations for a change in O_2 partitioning with temperature have merit, they do not stand independently because they ignore aspects of ecology and physiology that yield different predictions. Hence tadpoles, which show a fixed partitioning of oxygen uptake throughout a wide range of temperature, need not be viewed as departing from an "expected" pattern. Moreover, tadpoles are not unique in exhibiting a thermal stasis of O_2 partitioning between air and water. For example, the aquatic salamanders *Ambystoma tigrinum* (Whitford and Sherman 1968) and *Necturus maculosus* (Miller and Hutchison 1979), and the caecilian *Typhlonectes compressicauda* (Sawaya 1947) exhibit constant ratios of aerial and aquatic O_2 uptake throughout a wide temperature range.

In contrast to the relatively constant proportions of aerial and aquatic O_2 exchange at various temperatures, tadpoles respond to aquatic hypoxia with a dramatic increase in the proportion of pulmonary respiration (West and Bruggren 1982; Feder 1983). The responses to hypoxia may differ from responses to temperature because under aquatic hypoxia the P_{O_2} gradient across the aquatic O_2 exchangers is small, while the P_{O_2} gradient across the lungs remains high. Thus, aquatic O_2 uptake is clearly not favored under aquatic hypoxia, and in fact tadpoles lose O_2 to the water at low aquatic P_{O_2} (West and Burggren 1982; Feder 1983). Hence, when exposed to aquatic hypoxia, tadpoles maintaining constant levels of aerobic metabolism have little choice but to surface to breathe air. Tadpoles clearly can increase the $\dot{V}_{O_2 LUNG}$ when warranted during aquatic hypoxia but obviously do not exploit this excess capacity in response to temperature increases.

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