RELATION OF BODY SIZE AND SURFACE AREA
TO GAS EXCHANGE IN ANURANS[1]

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THE skin, lungs, and buccal cavity may all serve as respiratory surfaces in adult terrestrial amphibians. The relative role of these respiratory surfaces has been shown to be an important consideration in the ecology, geographic distribution, and phylogenetic relationships of caudate amphibians (Whitford and Hutchison, 1963, 1965, 1966, 1967). Respiration in anurans has been reviewed by Foxon (1964). Information on the comparative importance of the various respiratory surfaces in anurans has been based primarily on the anatomical studies of vascularization of respiratory surfaces (Czopek, 1955a, 1955b; Czopek and Czopek, 1959; Bieniak and Watka, 1962). Physiological studies dealing with the role of these respiratory surfaces in anurans have been limited to the classical studies of Krogh (1904) and Dolk and Postma (1927) on the European frogs, *Rana esculenta* and *R. temporaria*, and the recent study of Vinegar and Hutchison (1965) on the green frog, *R. clamitans*.

As Foxon (1964) has indicated, the interpretation of anatomical studies is difficult because breathing habits are particularly important in the renewal of

lung air on which gas exchange with the lung capillaries is dependent and because environmental conditions, particularly temperature, affect the respiratory exchanges and relative role of the respiratory surfaces. Our studies were designed to evaluate the effect of temperature on the role of the skin, pulmonary, and buccopharyngeal surfaces in the respiratory exchanges of a number of anurans representing several families from a variety of habitats; to obtain quantitative measurements of ventilation of the pulmonary surfaces to aid in the interpretation of gas exchange patterns; and to evaluate body size and metabolic rate relationships in anurans. These data are used to evaluate the adaptive significance of differences in respiratory patterns observed with regard to geographic distribution, ecology, and phylogenetic relationships of the forms studied.

MATERIAL AND METHODS

All animals were acclimated in constant temperature-photoperiod environmental chambers to the test temperatures and a 16-hr photoperiod for a minimum of 1 week prior to the experiments. Pulmonary (lung and buccopharyngeal) and cutaneous gas exchange were measured separately and simultaneously in constant volume respirometers by a direct manometric method. Details of the methods were given by Whitford and Hutchison (1963).

The carbon dioxide released through the pulmonary and cutaneous surfaces

was absorbed in beakers containing sodium hydroxide. The sodium hydroxide was titrated with standardized 1 N sulfuric acid to determine the amount of carbon dioxide released. Respiratory exchanges of each animal were measured for 5 consecutive hours between 0800 and 1600 EST.

The surface area of a number of anurans was measured by removing the skin in pieces and tracing the outline of the pieces of skin with an integrating polar planimeter. Distances between spots and other distinctive features were measured before and after skinning to determine the degree of shrinkage or stretching. These data were used to calculate the regression of $\log_{10}$ surface area on $\log_{10}$ body weight and to compare the regression of $\log_{10}$ metabolic rate with $\log_{10}$ body weight. Regression lines were calculated by the method of least squares.

<div align="center">RESULTS</div>

<div align="center">EFFECTS OF TEMPERATURE ON PULMONARY
AND CUTANEOUS GAS EXCHANGE</div>

The effect of temperature on pulmonary and cutaneous gas exchange in four temperate zone bufonids is shown in Figures 1–4 and Tables 1 and 2. The pattern of gas exchange at different temperatures was similar in *Bufo americanus*, *B. cognatus*, and *B. terrestris*. In these species pulmonary oxygen uptake increased linearly between 5 C and 25 C; cutaneous oxygen uptake increased between 5 C and 15 C but did not increase significantly between 15 C and 25 C. In *B. boreas* cutaneous oxygen consumption was almost constant at all temperatures, and pulmonary uptake was not significantly different at 5 C and 15 C. In *B. boreas* there was a marked increase in pulmonary oxygen consumption between 15 C and 25 C. *Bufo boreas* also had a significantly higher total oxygen consumption at 5 C than the other temper-

ate zone bufonids at that temperature (Figs. 2 and 14). Cutaneous release of carbon dioxide increased with temperature in all four species. In these species approximately 70–80% of the total carbon dioxide release was through the skin at all temperatures except at 5 C in *B. americanus* where 91% of the carbon dioxide was eliminated through the cutaneous surface. With the exception of *B. boreas*, the elimination of carbon dioxide through the pulmonary surfaces was lower at 5 C than at the other two temperatures (Table 2).

There was little difference in the gas exchange patterns of the temperate zone hylids (Figs. 5 and 6, Table 1). In *Hyla gratiosa* and *H. versicolor* pulmonary oxygen uptake increased linearly with temperature. Cutaneous oxygen consumption was essentially constant at 5 C and 15 C and increased between 15 C and 25 C. The pattern of cutaneous carbon dioxide release was similar to cutaneous oxygen consumption, being essentially equal at 5 C and 15 C and increasing between 15 C and 25 C. In *H. gratiosa* only 7.3% of the total carbon dioxide elimination was through the pulmonary surfaces, at 5 C, as compared with 15.1% in *H. versicolor* at that temperature.

In *Rana pipiens* both pulmonary and cutaneous oxygen consumption increased between 5 C and 25 C, but the rate of increase of pulmonary oxygen uptake was greater than that of cutaneous (Fig. 7). There was a marked increase in pulmonary oxygen consumption between 15 C and 25 C. The lungs accounted for 54% of the total oxygen consumption at 15 C and 68% of the total at 25 C. At 5 C and 15 C approximately 75% of the carbon dioxide release was cutaneous, but at 25 C only 47% was through the skin. Data at 25 C are not available for *R. catesbeiana* and *R. sylvatica*. The gas exchange pattern at 5 C and 15 C is similar to *R. pipiens* (Fig. 8). However, in *R.*
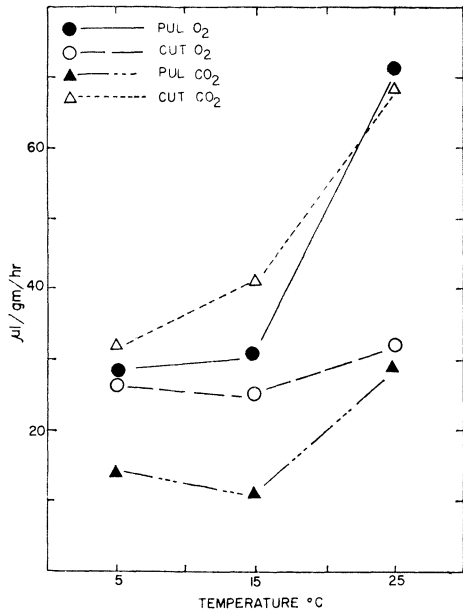
PUL O₂
CUT O₂
PUL CO₂
CUT CO₂

FIG. 1.—Pulmonary and cutaneous gas exchange in *Bufo boreas* at different temperatures.

FIG. 2.—Pulmonary and cutaneous gas exchange in *Bufo americanus* at different temperatures.

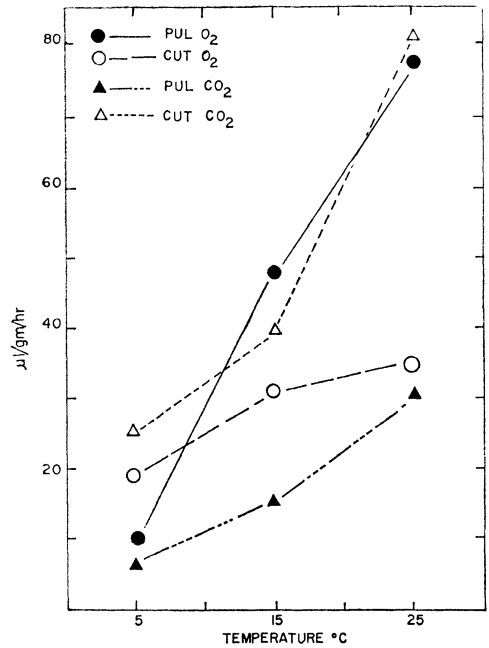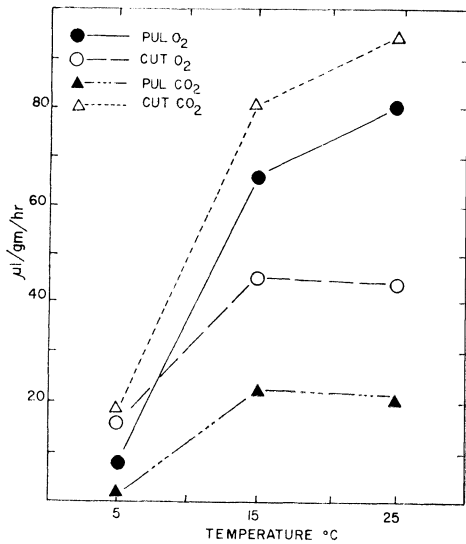FIG. 3.—Pulmonary and cutaneous gas exchange in *Bufo terrestris* at different temperatures.

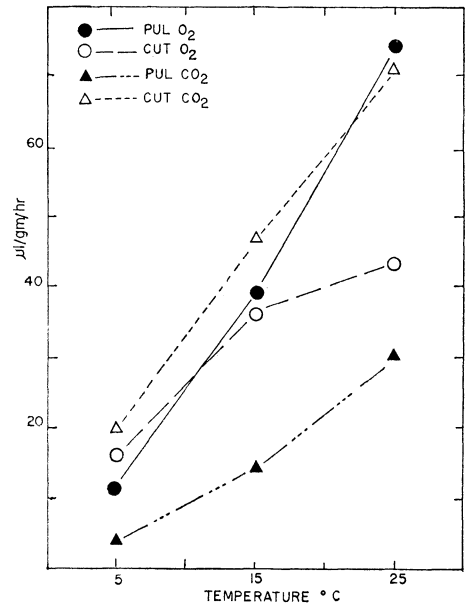FIG. 4.—Pulmonary and cutaneous gas exchange in *Bufo cognatus* at different temperatures.

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TABLE 1

PULMONARY AND CUTANEOUS OXYGEN UPTAKE IN ANURANS AT DIFFERENT TEMPERATURES[a]

Species	5 C					15 C					25 C				
	N	Pulmonary X̄	Pulmonary Range	Cutaneous X̄	Cutaneous Range	N	Pulmonary X̄	Pulmonary Range	Cutaneous X̄	Cutaneous Range	N	Pulmonary X̄	Pulmonary Range	Cutaneous X̄	Cutaneous Range
Bufo alvarius	...	...	...	...	...	7	46.43 (59.0)	12.0–100.2	32.27	17.1–52.4	...	...	...	...	...
B. americanus	7	7.95 (32.8)	4.2–9.5	16.18	8.3–23.6	10	64.98 (59.0)	30.5–120.1	45.20	16.0–65.4	10	79.31 (66.0)	52.5–167.9	43.31	8.5–84.6
B. boreas	10	29.41 (52.0)	18.3–41.9	26.86	7.5–43.7	10	30.80 (55.6)	11.2–47.5	25.54	10.3–47.1	8	71.2 (68.6)	45.1–98.4	32.54	13.8–67.9
B. cognatus	9	12.0 (42.6)	9.5–15.3	16.30	10.5–26.6	10	39.50 (51.9)	21.6–77.0	36.70	22.2–59.9	10	43.50 (63.3)	18.7–73.3	30.10	5.1–69.1
B. marinus	...	...	...	...	...	10	27.05 (72.3)	15.6–44.5	10.33	6.4–16.8	10	49.63 (69.4)	22.6–74.1	21.90	5.6–54.6
B. terrestris	9	10.77 (35.3)	5.1–18.2	19.73	11.5–30.0	10	48.95 (60.9)	20.2–84.3	31.53	8.7–44.3	10	78.05 (68.9)	27.2–95.0	35.21	20.2–51.1
Hyla cinerea	...	...	...	...	...	8	84.64 (59.5)	65.7–103.9	41.87	33.1–58.2	...	...	...	...	...
H. gratiosa	8	16.42 (30.9)	6.3–25.0	35.35	25.4–71.7	10	57.10 (64.1)	41.2–75.8	31.93	12.3–55.3	7	99.93 (67.9)	77.3–183.0	47.33	23.5–67.4
H. versicolor	8	28.17 (39.1)	18.4–21.7	44.08	28.4–104.9	10	65.59 (63.0)	35.7–118.9	38.56	19.4–76.1	9	135.30 (67.4)	81.2–223.3	65.39	34.7–117.4
Rana catesbeiana	9	17.02 (41.0)	5.3–39.4	24.56	18.3–36.6	4	29.36 (50.1)	22.5–33.2	27.74	22.5–33.2	...	...	...	...	...
R. palustris	...	...	...	...	...	6	42.12 (65.8)	23.7–54.5	21.91	16.4–27.0	...	...	...	...	...
R. pipiens	12	12.46 (43.3)	6.4–17.9	15.64	6.5–24.5	13	26.76 (54.2)	17.4–32.7	24.91	12.6–34.2	10	82.24 (67.9)	58.6–103.1	38.88	28.9–53.6
R. sylvatica	10	18.83 (34.9)	8.5–27.8	35.19	16.7–57.3	8	59.15 (59.8)	20.0–102.3	39.75	16.2–71.2	...	...	...	...	...
Scaphiopus bombifrons	...	...	...	...	...	4	94.06 (67.6)	70.4–138.4	45.11	36.7–48.0	...	...	...	...	...
S. couchi	...	...	...	...	...	9	51.53 (61.3)	29.0–88.9	32.52	23.5–50.3	...	...	...	...	...
S. hammondi	...	...	...	...	...	11	51.90 (55.2)	28.0–80.3	42.01	17.7–73.9	...	...	...	...	...
S. holbrooki	...	...	...	...	...	10	45.30 (54.1)	26.3–69.3	38.36	24.1–54.2	...	...	...	...	...
Microhyla carolinensis	...	...	...	...	...	5	33.90 (51.3)	23.6–50.3	32.23	21.8–42.0	...	...	...	...	...
Eleutherodactylus portoricensis	...	...	...	...	...	3	53.33 (76.8)	31.0–74.7	16.03	15.1–20.6	...	...	...	...	...
Xenopus laevis	...	...	...	...	...	6	14.05 (41.5)	13.7–20.1	19.78	8.7–30.6	...	...	...	...	...
Ceratophrys calcarata	...	...	...	...	...	8[b]	32.27[b]	20.3–69.2[b]	21.19[b]	6.4–56.9[b]	8[c]	48.72[c]	22.1–80.5[c]	20.28	10.3–31.7[c]

[a] Values given are in microliters per gram-hour. Figures in parentheses below each mean pulmonary value give the percentage of total oxygen uptake by the pulmonary and buccopharyngeal surfaces; the remaining percentage represents oxygen uptake by cutaneous surfaces.

[b] This species at 25 C.

[c] This species at 35 C.

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TABLE 2

PULMONARY AND CUTANEOUS CARBON DIOXIDE RELEASE IN ANURANS AT DIFFERENT TEMPERATURES[a]

Species	5 C Pulmonary $\bar{X}$	5 C Pulmonary Range	5 C Cutaneous $\bar{X}$	5 C Cutaneous Range	5 C $\bar{R}$	15 C Pulmonary $\bar{X}$	15 C Pulmonary Range	15 C Cutaneous $\bar{X}$	15 C Cutaneous Range	15 C $\bar{R}$	25 C Pulmonary $\bar{X}$	25 C Pulmonary Range	25 C Cutaneous $\bar{X}$	25 C Cutaneous Range	25 C R
Bufo alvarius						18.66	2.0-61.1	46.84	20.2-79.9	0.84	19.9	6.2-44.1	94.07 (82.6)	65.4-142.5	0.98
B. americanus	1.92	0.1-6.0	18.51 (90.7)	9.3-25.4	0.83	22.38	5.0-59.4	84.32 (79.0)	33.6-118.4	0.95	29.88	7.5-45.8	69.87 (69.4)	52.4-90.5	0.98
B. boreas	14.70	4.8-26.9	32.20 (68.7)	17.4-41.5	0.84	11.04	2.7-26.0	41.60 (79.0)	21.3-71.8	0.96	30.10	5.1-69.1	71.50 (70.0)	39.1-102.4	0.84
B. cognatus	4.60	2.2-12.4	19.90 (82.3)	15.5-23.8	0.86	14.70	0.0-28.8	47.01 (76.2)	28.9-90.8	0.81	15.66	1.3-30.7	49.52 (76.0)	27.8-61.3	0.94
B. marinus						11.16	3.0-20.0	23.7 (68.0)	13.8-36.5	0.86					
B. terrestris	7.28	3.6-10.2	25.91 (78.0)	15.6-34.7	0.88	16.14	3.2-28.6	39.56 (71.0)	23.7-79.5	0.78	29.09	3.6-53.7	86.31 (75.0)	38.1-100.3	0.92
Hyla cinerea						31.89	13.6-42.9	87.00 (73.0)	71.9-99.2	0.86					
H. gratiosa	3.06	0.0-7.4	38.90 (92.7)	30.1-70.0	0.79	15.44	7.2-28.5	42.54 (73.4)	32.0-53.4	0.72	23.92	0.0-89.6	102.61 (81.1)	84.5-142.6	0.85
H. versicolor	10.55	0.0-25.2	54.48 (84.9)	37.0-56.1	0.86	21.16	7.8-53.6	58.98 (73.6)	34.5-87.2	0.79	27.39	7.6-46.3	142.23 (83.9)	97.3-243.2	0.81
Rana catesbeiana	9.61	4.3-25.8	31.84 (76.8)	22.3-57.5	0.89	12.04	10.2-14.0	25.04 (67.5)	21.2-30.9	0.73					
R. palustris						17.63	13.7-23.7	49.72 (73.8)	29.9-66.3	0.92					
R. pipiens	4.08	0.0-13.7	12.09 (76.0)	3.7-16.8	0.72	11.62	1.3-28.0	34.78 (76.0)	15.5-62.6	0.97	36.84	17.9-55.5	50.43 (57.0)	23.4-83.5	0.58
R. sylvatica	10.31	1.7-17.8	33.13 (76.0)	18.6-46.6	0.78	22.21	7.3-41.1	71.51 (72.4)	30.9-148.0	0.84					
Scaphiopus bombifrons						32.20	13.5-42.0	90.35 (74.3)	83.2-112.0	0.88					
S. couchi						16.21	2.3-25.1	63.85 (79.7)	16.8-84.0	0.91					
S. hammondi						14.42	4.9-26.0	65.05 (77.8)	41.0-90.9	0.87					
S. holbrooki						13.12	3.3-27.1	48.70 (78.8)	35.3-64.5	0.85					
Microhyla carolinensis						7.97	0.0-14.8	53.52 (87.0)	24.8-63.3	0.92					
Eleutherodactylus portoricensis						15.20	0.0-17.7	66.27 (80.3)	53.1-82.2	1.14					
Xenopus laevis						2.81	0.9-4.7	26.25 (90.3)	17.1-36.2	0.87					
Ceratophrys calcarata						7.06[b]	1.6-14.1[b]	33.75[b] (82.7)	20.6-74.3[b]	0.82[b]	13.30[c]	4.4-23.9[c]	49.49[c] (78.9)	26.7-66.7[c]	0.94

[a] Values given are in microliters per gram-hour. Figures below each mean cutaneous value give the percentage represents carbon dioxide release by the cutaneous surfaces; the remaining percentage represents carbon dioxide released by pulmonary and buccopharyngeal surfaces. $\bar{R}$ = mean respiratory exchange ratio (respiratory quotient) for total gas exchange at each temperature. Sample sizes are given in Table 1.

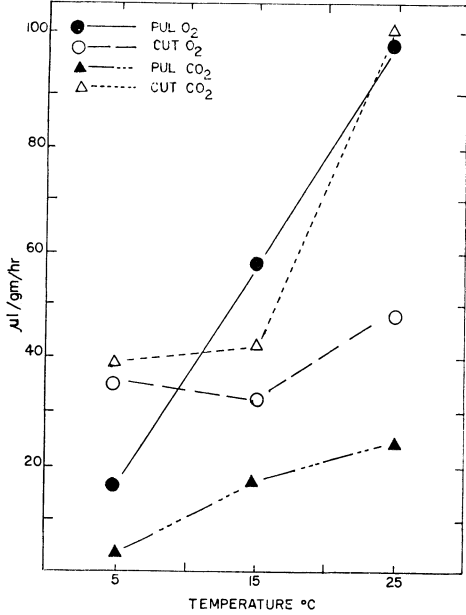[b] This species at 25 C.

[c] This species at 35 C.

FIG. 5.—Pulmonary and cutaneous gas exchange in *Hyla gratiosa* at different temperatures.
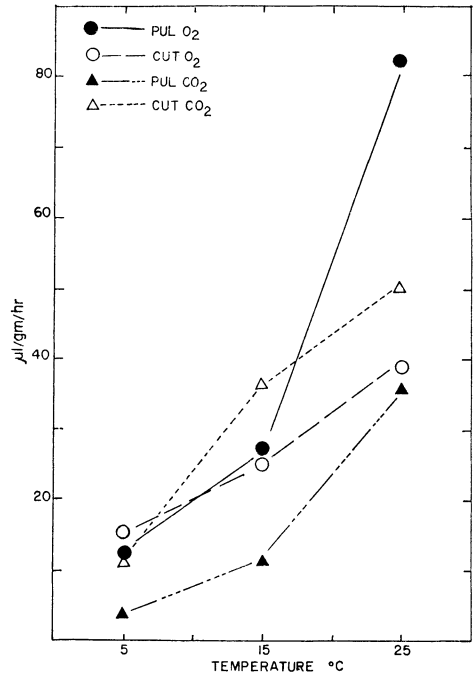

FIG. 7.—Pulmonary and cutaneous gas exchange in *Rana pipiens* at different temperatures.
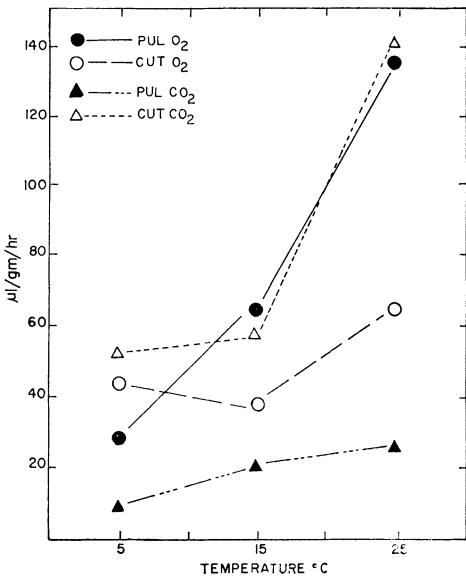

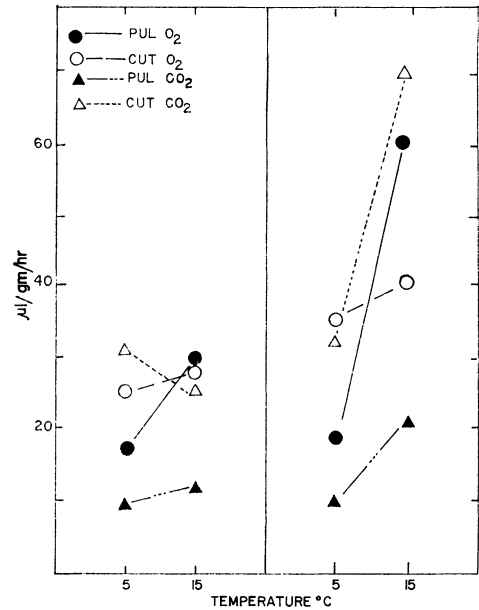FIG. 6.—Pulmonary and cutaneous gas exchange in *Hyla versicolor* at different temperatures.

FIG. 8.—Pulmonary and cutaneous gas exchange in *Rana catesbeiana* (left) and *R. sylvatica* (right).

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sylvatica the pulmonary surfaces supplied less of the total at 5 C (35%) than in the other ranids (42%). In the ranids, the skin accounted for between 60% and 70% of the total carbon dioxide elimination except as noted above.

The gas exchange patterns of two tropical anurans were studied at different temperatures for a comparison with pulmonary surfaces supplied more of the total oxygen requirement at both 25 C and 15 C than most of the temperate zone forms at either of these temperatures (Fig. 9 and Table 1). The skin accounted for 68–75% of the total carbon dioxide elimination in both tropical species (Table 2), which is similar to the pattern in temperate forms.
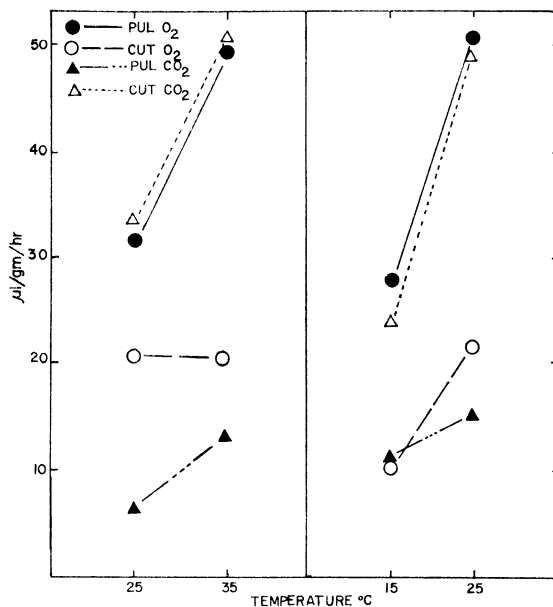

FIG. 9.—Pulmonary and cutaneous gas exchange in *Ceratophrys calcarata* (left) and *Bufo marinus* (right)

the temperate zone forms. *Ceratophrys calcarata* did not survive acclimation to 15 C, and *B. marinus* was unable to survive acclimation at 5 C. In *Ceratophrys* the pulmonary surfaces accounted for 60% of the total oxygen consumption at 25 C and 71% at 35 C (Fig. 9 and Table 1). At 25 C the pulmonary surfaces of *Ceratophrys* accounted for approximately the same portion of the total oxygen uptake as most of the temperate zone anurans at 15 C. At 35 C, however, slightly more of the total oxygen requirement was supplied by the pulmonary surfaces of *Ceratophrys* than was supplied by the lungs of temperate zone anurans at 25 C. In *B. marinus* the

The mean values for the relative importance of the pulmonary and cutaneous surfaces in gas exchange are not indicative of the great variability in the gas exchange pattern observed at the various temperatures. The range of variation in the percentage of the total oxygen requirement supplied by these respiratory surfaces is important in comparisons between the species of anurans studied. Since the activity of the animals in the respirometer could not be completely controlled, being limited only by the fastening of the legs to a hardware cloth base, there were differences in the degree of activity during the experiments among individuals of the same species.

Thus, the extremes noted are probably fairly indicative of the role of the pulmonary and cutaneous surfaces in gas exchange in active and relatively sedentary individuals in nature, whereas the means are probably more indicative of the pattern of gas exchange for average activity at a particular temperature.

In the bufonids, with the exception of *B. boreas*, as much as 40–50% of the total gas exchange may be pulmonary in an active individual at 5 C, and in *B. boreas* 77% of the total oxygen uptake may be pulmonary at 5 C (Table 1). At 15 C and 25 C, active bufonids, hylids, and ranids may obtain as much as 70–85% of their total oxygen requirement via the pulmonary surfaces. The tropical toad, *B. marinus*, may obtain as much as 89% of its total oxygen through the lungs at 25 C. *Ceratophrys* had a much lower maximum pulmonary oxygen uptake, even at 35 C, than did *B. marinus* (Table 1) but was considerably more quiescent in the respirometer than *B. marinus*. The tropical frog, *Eleuthrodactylus portoricensis*, had a maximum pulmonary oxygen uptake of 83% at 15 C, which was greater than all of the species studied at that temperature except the southern tree frog, *H. gratiosa* (Table 1). The minimum contribution of the pulmonary surfaces to the total oxygen requirement at 5 C was between 13% and 24% in the ranids, *H. gratiosa* and *B. americanus*. In the other temperate zone anurans, the lowest percentage of pulmonary oxygen consumption at 5 C was 34% or greater.

SPECIES COMPARISON AT 15 C

Sufficient numbers of some species were not available for experiments at all three temperatures. These species were all studied at 15 C, a moderate temperature for most amphibians and for comparison with similar data obtained from salamanders (Whitford and Hutchison, 1965).

There was little difference in the role of the pulmonary and cutaneous respiratory surfaces in gas exchange in the four species of *Scaphiopus* studied (Fig. 10). In *Scaphiopus* approximately 55–60% of the total oxygen demand was supplied by the pulmonary surfaces. The maximum percentage of oxygen uptake in *Scaphiopus* was between 66% and 76% (Table 1). Approximately 75–80% of the total carbon dioxide elimination was through the skin. The data for several other species are summarized in Figure 11. There was little difference in the respiratory exchanges in *Bufo alvarius*, *Rana palustris*, and *Hyla cinerea* and the other temperate zone bufonids, ranids, and hylids, respectively. In *Microhyla carolinensis* approximately 50% of the total oxygen consumption was pulmonary. In *Xenopus laevis* the pulmonary surfaces supplied a smaller portion of the total oxygen requirement than any of the other anurans studied at 15 C. In addition, *X. laevis* exhibited the greatest range (15–69%) in the role of the pulmonary surfaces in respiration. Approximately 90% of the total carbon dioxide release was cutaneous in *X. laevis*; and in three of the six animals studied, the lungs accounted for less than 5% of the total carbon dioxide elimination (Tables 1 and 2).

RESPIRATORY QUOTIENTS

Respiratory quotient (RQ) values are given in Table 2. The RQ ranged between 0.53 and 1.26 with most of the values falling between 0.80 and 0.86.

VENTILATION RATES AND TIDAL VOLUMES

In salamanders the buccopharyngeal oscillations can be distinguished easily from the deep inspirations which resulted in air exchange in the lungs; in anurans
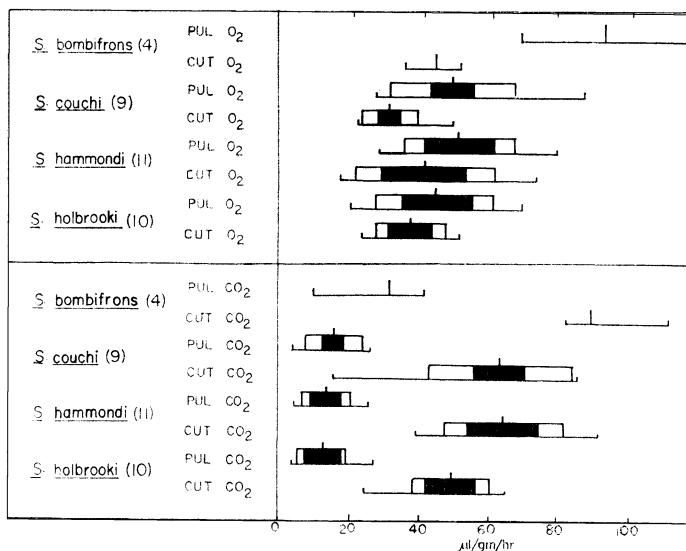
FIG. 10.—Pulmonary and cutaneous gas exchange in four species of *Scaphiopus* at 15 C. Numbers in parentheses, sample size; horizontal line represents range; thin vertical line, mean; one black and one white rectangle on each side of the mean, 1 standard deviation; a black rectangle on each side of the mean, 2 standard errors.
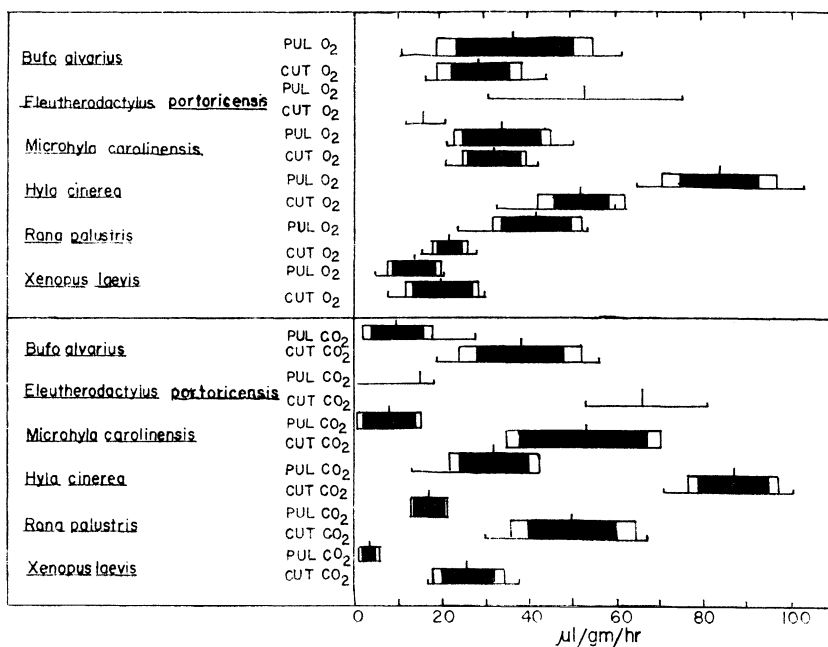

FIG. 11.—Pulmonary and cutaneous gas exchange in six species of frogs at 15 C. Method of presentation is the same as in Fig. 10.

it was extremely difficult to distinguish between these movements.

In some species we were unable to make separate counts of buccopharyngeal and lung inspirations. In anurans like *Bufo marinus*, movements of the flanks were fairly regular and were used as the criteria for determining the rate of rate of strong flank movements and constriction of the nares decreased from 38 per minute immediately following an active period to 4 per minute at rest. It is unlikely that the normal lung ventilatory rate in this species at 25 C is only 4 per minute; this low rate may have been a result of hyperventilation during

TABLE 3

VENTILATION RATES IN ANURANS AT DIFFERENT TEMPERATURES

SPECIES	MEAN WT. GRAMS	5 C				15 C				25 C			
		L^a	BP^b	Total	K^c	L^a	BP^b	Total	K^c	L^a	BP^b	Total	K^c
Bufo americanus	25.2	20	67	87	3.3	50	86	136	1.7	....	....	131	....
B. boreas	71.3	37	30	67	0.8	40	28	68	0.7	68	99	167	1.45
B. cognatus	45.2	20	48	68	2.4	29	59	88	2.0	....	....	93	....
B. marinus	112.3	....	....	....	....	17	82	109	0.2	....	....	78	....
B. terrestris	21.3	15	7	22	0.5	68	46	114	0.68	....	....	....	....
Hyla gratiosa	12.2	....	....	62		....	....	120		....	....	173	....
H. versicolor	8.0	30	15	45	2.0	44	133	177	3.0	....	....	228	....
Rana catesbeiana	74.8	14	24	38	1.7	....	....	....	....				
R. palustris	14.5	....	....	....	....	....	....	94					
R. pipiens	25.0	....	....	....	....	....	....	119					
R. sylvatica	9.1	23	46	69	1.5	38	80	118	1.7				
Scaphiopus bombifrons	13.3	....	....	....	....	....	....	106					
S. couchi	26.9	....	....	....	....	....	....	75					
S. hammondi	23.6	....	....	....	....	....	....	73					
S. holbrooki	14.0	....	....	....	....	....	....	86					
Microhyla carolinensis	3.0	....	....	....	....	109	80	189	0.73	....	....		
Eleuthrodactylus portoricensis	3.7	....	....	....	....	....	....	111					
Xenopus laevis	63.6	....	....	....	....	6	11	17	0.54				
Ceratophrys calcarata	55.0	....	....	....	....	16	74	90	4.6	12	39	51	3.25

a Respiratory movements which resulted in air exchange in the lungs.
b Respiratory movements which resulted in no lung air exchange.
c Ratio of buccopharyngeal oscillations:lung inspirations.

lung ventilation. In *Hyla versicolor* movements of the flanks were accompanied by a constriction of the nares, indicating that air was being forced into the lungs by the contraction of the buccal floor during the nares constriction phase. In some species, like *B. cognatus* at 25 C, the animals became inflated, and it was impossible to visually correlate movements of the buccal floor with ventilation of the lungs (Table 3). In other anurans extreme lung ventilation could be distinguished from other buccal movements only when the frogs were active. In one active *H. gratiosa* at 25 C, the activity, with a subsequent decrease in ventilation upon cessation of the activity. It seems probable that the deep buccal movements accompanied by flank contraction and nares constriction are associated with the large tidal volumes measured in some individuals (Table 4). Because the frogs were masked during the tidal volume measurements, a constriction of the nares associated with the extreme tidal movements could not be observed. However, a strong flank contraction was observed when large tidal volumes were measured.

In species where both ventilatory

movements could be distinguished visually, the ratio of buccopharyngeal movements to lung inspirations was calculated and is shown in Table 3 as the "K value" proposed by Das and Srivastava (1957). The K values, representing the ratio of buccopharyngeal to lung oscillations, ranged from a low of 0.47 in *B. terrestris* at 5 C to 4.63 in *Ceratophrys* at 25 C.

The K values were not constant for the same species at different temperatures, as suggested by Das and Srivastava (1957) (Table 3).

In general, there was an inverse relationship between the average size of a species and the mean ventilatory rate (Table 3).

There was a direct relationship be-

TABLE 4

LUNG AND BUCCOPHARYNGEAL TIDAL VOLUMES IN ANURANS AT VARIOUS TEMPERATURES[a]

SPECIES	5 C TIDAL VOLUME (cm³)		15 C TIDAL VOLUME (cm³)		25 C TIDAL VOLUME (cm³)	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Bufo americanus	.06	.03-.15	.07	.03-.15	.11	.03-.19
	.39	.25-.88	.70	.25-1.87	.62	.34-1.41
B. boreas	.12	.05-.17	.07	.03-.25	.13	.03-.20
	.37	.34-.44	.31	.19-.40	.99	.40-1.3
B. cognatus	.05	02-.11	.03	.01-.06	.12	.12-.24
	.47	.17-1.36	.51	.20-1.50	.66	.30-1.65
B. marinus	....	....	.07	.03-.15	.11	.04-.25
	....	....	1.04	.37-4.0	1.04	.58-3.5
B. terrestris	.04	.02-.06	.05	.01-.09	.05	.02-.13
	.30	.10-.58	.52	.25-1.19	.68	.30-1.37
Hyla cinerea	....	....	.03	.01-.04	....	....
	....	....	.32	.21-.46	....	....
H. gratiosa	.05	.02-.19	.09	.04-.19	.12	.03-.60
	.23	14-.44	.56	.30-1.12	.37	.28-1.13
H. versicolor	.02	01-.05	.04	.01-.06	.05	.01-.09
	.23	.10-.49	.28	.14-.53	.45	.15-.86
Rana catesbeiana	.05	.03-.08	....	....		
	.63	.25-1.8	....	....		
R. palustris	....	....	.04	.02-.05	....	....
	....	....	.25	.17-.40	....	....
R. pipiens	.05	.03-.07	.06	.01-.13	.05	.03-.08
	.28	.21-.40	.24	.17-.31	.37	.14-1.00
R. sylvatica	.03	.02-.05	.03	.02-.05	....	....
	.21	.16-.34	.22	.12-.27	....	....
Scaphiopus bombifrons	....	....	.05	.01-.11		
	....	....	.29	.17-.56		
S. couchi	....	....	.07	.03-.11		
	....	....	.49	.23-1.39		
S. hammondi	....	....	.08	.02-.12		
	....	....	.29	.12-.60		
S. holbrooki	....	....	.04	.01-.08		
	....	....	.39	.20-1.50		
Microhyla carolinensis	....	....	.003	.001-.005		
	....	....	....	....		
Eleuthrodactylus portoricensis	....	....	.01	.005-.02	....	....
	....	....	.03	....	....	....
Xenopus laevis	....	....	.13	.09-.18	....	....
	....	....	.96	.70-1.25	....	....
Ceratophrys calcarata	....	....	.11	.02-.19	....	....
	....	....	.67	.39-1.0	....	....

[a] Buccopharyngeal tidal volumes are given in the first line and the lung tidal volumes in the second line for each species.

tween mean lung tidal volume and body size. This relationship was not easily demonstrable in some animals acclimated to 5 C and 15 C where the small sample size was not sufficient to determine a reliable mean when the variation in the individual measurements was so great. The mean lung tidal volumes for individuals of several species of anurans at 15 C, where we were able to obtain fairly reliable and consistent measurements of tidal movements, were used to

by the pulmonary surfaces was paralleled in the variability observed in the tidal volume measurements.

TEMPERATURE, BODY SIZE, AND METABOLIC RATE

The relationship between body size and metabolic rate in anurans at all temperatures studied may be expressed by the general equation $M = KW^{0.71}$, where M = metabolic rate in cm^3 of oxygen per hour, K is a constant for each
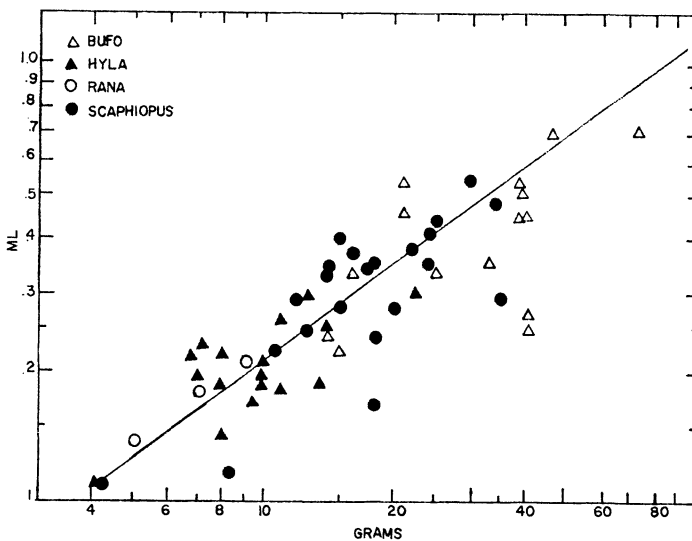

FIG. 12.—The relationship between body weight and tidal volume in species of four genera of frogs

calculate the regression of $\log_{10}$ tidal volume on $\log_{10}$ body weight (Fig. 12). This relationship may be expressed by the equation: $V_T = 0.423W^{0.73}$.

In most species there was a positive correlation between lung tidal volume and the role of the pulmonary surfaces in respiration (Table 3). For example, in B. boreas there was essentially no difference in the lung tidal volume at 5 C and 15 C and no difference in the percentage of pulmonary oxygen uptake at these two temperatures (Tables 1 and 4). In addition, variation in the percentage of the total oxygen consumption supplied

temperature condition, W = weight in grams, and 0.71 the average exponent calculated from the regression of $\log_{10}$ oxygen consumption on $\log_{10}$ body weight for anurans of the same family (Figs. 13–17). There was no significant difference in the relationship between body size and metabolic rate in the anurans studied with the exception of Bufo boreas (Fig. 13) and the tropical Ceratophrys and Eleuthrodactylus (Figs. 16 and 17). The oxygen consumption of B. boreas was excluded from the calculation of the regression of metabolism–body weight in the Bufonidae at 5 C because of the un-
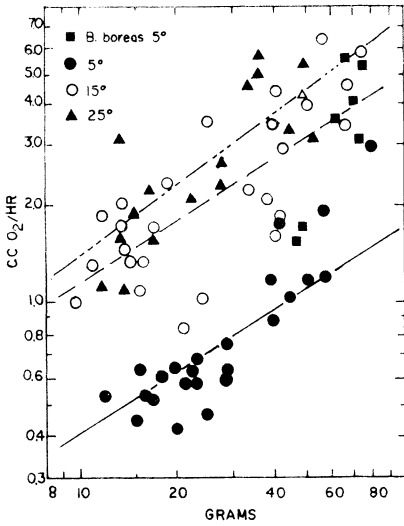
FIG. 13.—The relationship between body weight and metabolic rate in *Bufo americanus*, *B. boreas*, *B. cognatus*, and *B. terrestris* at different temperatures. Lower regression line, 5 C; middle, 15 C; upper, 25 C. The metabolic rate of *B. boreas* at 5 C was significantly different from the other species, and these points are shown separately.
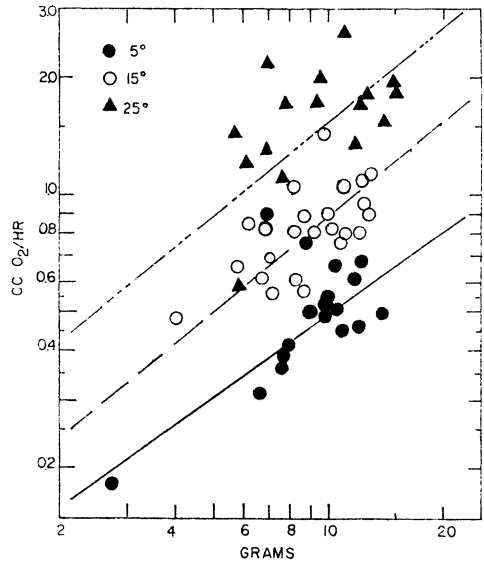
FIG. 14.—The relationship between body weight and metabolic rate in frogs of the family Hylidae at different temperatures. Regression lines are same as in Fig. 13.
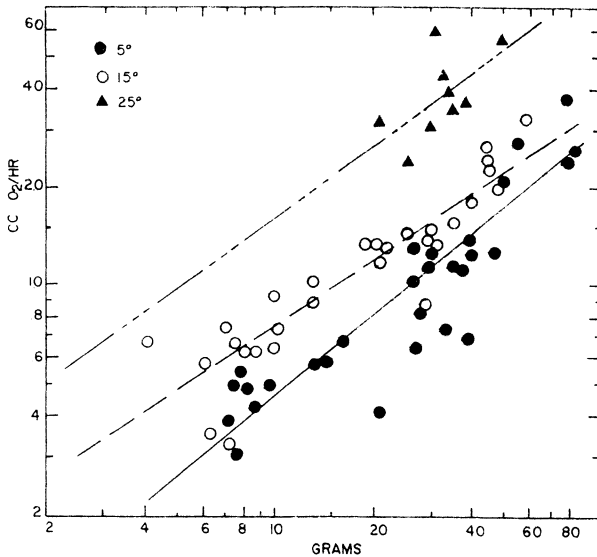
FIG. 15.—The relationship between body weight and metabolic rate in frogs of the family Ranidae. Regression lines are same as in Fig. 13.
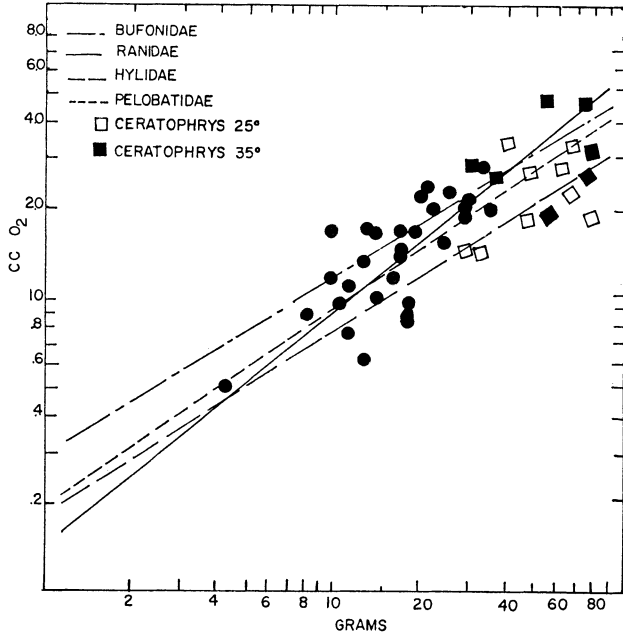
FIG. 16.—The relationship between body weight and metabolic rate in temperate zone species of three families compared with that of a tropical species (*Ceratophrys calcarata*) at 25 C and 35 C. Regression lines shown are from Figs. 13–15 and represent measurements made at 5 C, 15 C, and 25 C.
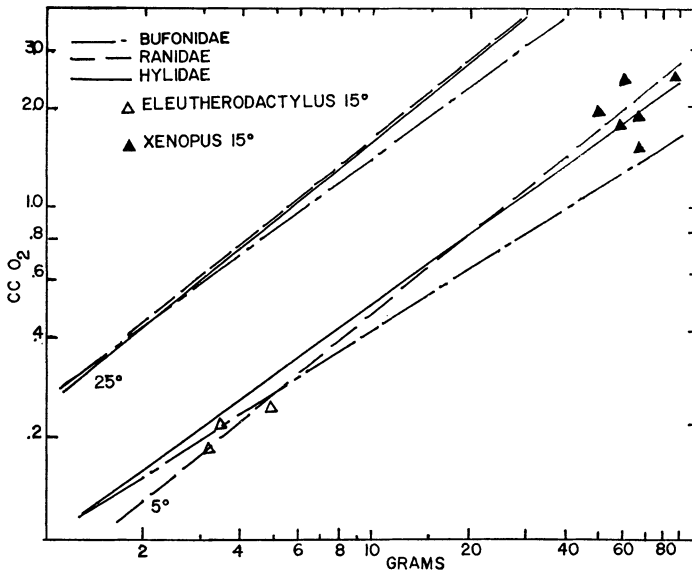

FIG. 17.—The relationship between body weight and metabolic rate in temperate zone families of frogs compared with that of a tropical species (*Eleuthrodactylus portoricensis*) at 15 C. Regression lines are the same as in Fig. 16.

usually high metabolic rate of this species at 5 C. The data for the oxygen consumption of *B. boreas* at 5 C more nearly fit the line calculated for the Bufonidae at 15 C and are plotted separately (Fig. 13). The following are the regression equations for oxygen consumption and body weight for the families studied:

Bufonidae:
$$5\ C \dots \dots M = 0.009W^{0.61}$$
$$15\ C \dots \dots M = 0.471W^{0.59}$$
$$25\ C \dots \dots M = 0.410W^{0.73}$$
Hylidae:
$$5\ C \dots \dots M = 0.002W^{0.72}$$
$$15\ C \dots \dots M = 0.132W^{0.82}$$
$$25\ C \dots \dots M = 0.683W^{0.52}$$
Ranidae:
$$5\ C \dots \dots M = 0.157W^{0.82}$$
$$15\ C \dots \dots M = 0.244W^{0.64}$$
$$25\ C \dots \dots M = 0.456W^{0.75}$$
Pelobatidae:
$$15\ C \dots \dots M = 0.072W^{0.94}$$

Ceratophrys had a lower metabolism at 25 C and 35 C than temperate zone anurans at 25 C (Fig. 16). The oxygen consumption of *Ceratophrys* at 25 C was similar to the temperate ranids at 15 C, and at 35 C was similar to the temperate hylids at 15 C. At 15 C *E. portoricensis* had a metabolic rate similar to temperate zone anurans at 5 C (Fig. 17). However, the oxygen consumption of the tropical bufonid, *B. marinus*, was not significantly different from that of temperate toads at the same temperature, and the data for *B. marinus* was included in the calculation of the regression equations (Fig. 13).

The Q_{10} values based on oxygen consumption of *B. boreas* between 5 C and 15 C was 0.98, indicating no significant difference in metabolic rate between these two temperatures (Table 5). The other temperate zone bufonids exhibited a Q_{10} greater than 2.0 between 5 C and 15 C. *Rana pipiens* had a Q_{10} greater than 2.0 between 15 C and 25 C. The

tropical anuran *Ceratophrys* had a Q_{10} of 1.31 between 25 C and 35 C, indicating a lower rate of metabolic change with an increase in temperature than in the temperate zone anurans.

The oxygen consumption of the bufonids in general was more variable than the other anurans with the exception of *Scaphiopus sps.* (Figs. 13–17). There was considerable overlap in the oxygen consumption of bufonids at 15 C and 25 C (Fig. 13), and the data for *Scaphiopus sps.* at 15 C showed considerable overlap with the regression lines for other anurans at 25 C (Fig. 16). There was some overlap in the oxygen consumption of the Ranidae and Hylidae even between different temperatures. This scattering of the oxygen consumption data is probably a reflection of the variation in activity of the individual animals, a factor impossible to control in whole undrugged animals.

TABLE 5

Q_{10} VALUES BASED ON OXYGEN CONSUMPTION AT DIFFERENT TEMPERATURES

Species	5 C–15 C	15 C–25 C	25 C–35 C
Bufo americanus	4.5	1.10	....
B. boreas	0.98	1.87	....
B. cognatus	2.70	1.56	....
B. marinus	....	1.91	....
B. terrestris	2.63	1.41	....
Hyla gratiosa ..	1.67	1.65	....
H. versicolor ...	1.44	1.92	....
Rana catesbeiana	1.37	....	....
R. pipiens	1.72	2.45	....
R. sylvatica	1.83	....	....
Ceratophrys calcarata	....	....	1.31

BODY WEIGHT–SURFACE AREA RELATIONSHIPS

There was no significant difference in the relationship between body weight and external (not including lung and buccopharyngeal surface areas) body surface area in any of the anurans studied (Fig. 18). This relationship may

be expressed by the equation $SA = 1.131W^{0.579}$. Thus, in anurans metabolism does not appear to be closely related to external body surface area. The following are the regression equations calculated for some individual species and families of anurans and shown graphically in Figure 18:

Bufonidae . . . . $SA = 0.966W^{0.645}$
   Bufo boreas . . . . $SA = 1.713W^{0.266}$
   B. cognatus . . . . $SA = 1.017W^{0.580}$
   B. terrestris . . . . $SA = 1.037W^{0.582}$
Hylidae . . . . $SA = 1.129W^{0.610}$
   Hyla arenicola . . . . $SA = 1.276W^{0.410}$
   H. arborea . . . . $SA = 0.905W^{0.823}$
   H. cinerea . . . . $SA = 1.462W^{0.273}$
   H. versicolor . . . . $SA = 1.218W^{0.511}$
Ranidae . . . . $SA = 1.056W^{0.666}$
   Rana catesbeiana . . . . $SA = 0.953W^{0.725}$
   R. clamitans . . . . $SA = 0.997W^{0.712}$
   R. pipiens . . . . $SA = 1.107W^{0.606}$
   R. palustris . . . . $SA = 0.991W^{0.705}$
   R. sylvatica . . . . $SA = 1.117W^{0.683}$
Pelobatidae:
   Scaphiopus couchi . . . . . . $SA = 0.833W^{0.714}$
Anura (regression line in
   Fig. 18) . . . . $SA = 1.131W^{0.579}$

DISCUSSION

The most important factor in the respiratory exchanges of anurans appears to be the ventilation of the lungs. In general, ventilatory rate was inversely proportional to size, whereas the tidal volume was directly proportional to size, with a proportionality factor of $W^{0.73}$. This is similar to the factor of metabolism to weight, $W^{0.71}$. The exceptions to these general relationships are associated with differences in the respiratory exchange patterns. The ventilatory rates and tidal volumes of *Bufo boreas* at 5 C and 15 C were essentially the same, and the percentage of total oxygen consumption supplied by the pulmonary surfaces at those temperatures was equal. Since the mixing and renewal of air in the lungs is a function of the rate and depth of breathing, the gradient between the pO_2 of the lung air and the pO_2 of the blood in pulmonary capillaries is largely dependent on lung ventilation.
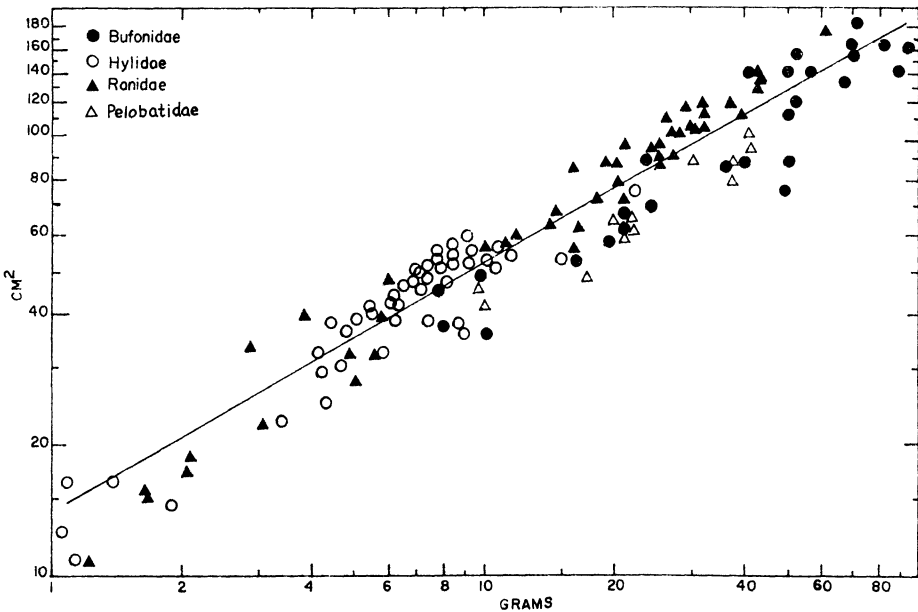

FIG. 18.—The relationship between body weight and surface area in four families of anurans

DeLong (1962) demonstrated that in *Rana pipiens* blood in the pulmocutaneous artery contained partially oxygenated blood. Assuming that similarities in vascularity of skin and surface area-mass relationships result in a similar degree of cutaneous oxygenation of blood returning to the heart, renewal of air in the lungs of anurans would be the single most important factor in establishing a concentration gradient favorable for the diffusion of oxygen from the lungs into pulmonary capillaries. The extremes noted in the percentage of pulmonary oxygen consumption in anurans are probably directly correlated with increased rate of pulmonary ventilation and high tidal volumes. As mentioned above, in some frogs the number of strong lung ventilatory movements was found to increase markedly during and immediately following activity. Thus, the analysis of the role played in respiration by the various respiratory surfaces is incomplete without a consideration of the rate and depth of lung ventilation.

Since the ratio of buccopharyngeal oscillations to lung inspirations (K value) does not remain constant for the same species at different temperatures, as suggested by Das and Srivastava (1957), we see no reason to retain the term "k value," as it is essentially meaningless; the volume of air moved into the buccopharyngeal cavity and lungs is not only a function of breathing rate, as suggested by Das and Srivastava (1957), but also of tidal volume. The tidal volume varies widely in the same species and must be determined separately for each temperature.

The anatomical studies of Czopek (1955a, 1955b), Czopek and Czopek (1959), and Bieniak and Watka (1962) have shown that there is little difference in the percentage of total respiratory capillaries of the skin and lungs in the hylids, bufonids, and ranids which they studied. The percentage of total respiratory capillaries in the lungs ranged from 62.5% in *R. temporaria* to 77.8% in *B. cognatus*. The small differences in vascularity of the respiratory surfaces are reflected in the similarity in gas exchange patterns observed in these groups with the exceptions previously noted. Although the major portion of the respiratory capillaries are in the lungs, the percentage that the lungs contribute to the total oxygen requirement as indicated by the degree of vascularization is reached only at a temperature of 15 C or higher. The rate and depth of pulmonary ventilation increased markedly between 5 C and 15 C, indicating that at temperatures below 15 C pulmonary ventilation was insufficient to establish a suitable pO_2 gradient between lung air and capillaries. Thus, in most temperate zone anurans, pulmonary ventilation appears to be a better measure of the effects of environmental differences on the role of the lungs and skin in respiration than capillary density per se, although capillary density is often correlated with the relative amounts of oxygen available to the animals in different environments (Szarski, 1964; Salthe, 1965).

Differences in the upper and lower extreme values of the percentage of the total oxygen requirement supplied by the lungs are probably better indicators of adaptations to the environment than are the mean values. Thus, in the grass frog, *R. pipiens*, and the wood frog, *R. sylvatica*, which extend into northern Canada, there is a higher maximum percentage of pulmonary oxygen consumption at 5 and 15 C than in *R. catesbeiana*, which ranges only as far north as southern Ontario (Conant, 1958). *Hyla versicolor* and *H. gratiosa* are sympatric over

most of the range of *H. gratiosa* (coastal plain from Mississippi to central North Carolina), but *H. versicolor* extends north to the Canadian border. The mean and extreme percentage of pulmonary oxygen consumption was different only at 5 C, where lower values were obtained for *H. gratiosa*. This reduced efficiency of the pulmonary surfaces of *H. gratiosa* at low temperatures could be a factor in limiting its distribution.

The higher percentage of pulmonary oxygen uptake and high metabolic rate in *B. boreas* at 5 C is probably an adaptation for activity at lower temperatures. *Bufo boreas* is found along the coast from the upper Baja peninsula to the Aleutian chain in Alaska, and east only to the eastern borders of the Rocky Mountains (Stebbins, 1954). Stebbins states that *B. boreas* was found to be active throughout the year as long as temperatures over 4 C prevailed in the toad's microclimate. Data on the respiratory exchanges in this toad suggest that its ability to be active at very low temperatures may be a result of its ability to obtain more oxygen at low temperatures than related species. This is probably correlated with shifts in the temperature optima of respiratory pigments and enzyme systems of the buccal musculature, allowing increased pulmonary ventilation at low temperatures. These data indicate that further studies on the adaptations of *B. boreas* to low temperatures are needed.

The tropical anurans exhibited some significant differences in respiratory patterns in comparison with temperate forms. The high percentage of pulmonary oxygen consumption in *B. marinus* at 15 C is probably related to the higher ventilatory rate and tidal volumes than predicted on the basis of body size. In addition, there was little difference in the tidal volumes of *B. marinus* at 15 C and 25 C. This was directly correlated with

the similarity of the role of the pulmonary surfaces at 15 C and 25 C.

The metabolism-weight relationship for *B. marinus* was not different from the temperate zone bufonids at 15 C and 25 C. Tashian and Ray (1957) found that tropical anurans had lower respiratory rates than temperate forms at the same temperature. However, both *Ceratophrys calcarata* and *Eleutherodactylus portoricensis* fit the metabolic pattern of the tropical frogs studied by Tashian and Ray (1957). *Ceratophrys calcarata* had a total metabolism at 25 C and 35 C similar to temperate anurans at 15 C. Since *C. calcarata* did not survive acclimation to 15 C, it cannot be compared with other species at that temperature, but the pulmonary-cutaneous gas exchange pattern at 25 C was similar to temperate anurans at 15 C, and an overall metabolism at 25 C was similar to temperate forms at 15 C; this species appears to be a more narrowly specialized tropical anuran than *B. marinus*. Although *B. marinus* probably evolved in the tropics, its introduction into many parts of the world, including warm temperate zones, indicates its plasticity in acclimating to euryecious conditions. However, *C. calcarata* fits the concept proposed by Bullock (1955) that activity rates are greater at a given temperature in cold-blooded animals from northern latitudes when compared with closely related southern forms, and this species is limited to hot tropical environments; *B. boreas* also fits this concept, but *R. sylvatica* and *B. marinus* do not. Based on these data, it appears that generalizations dealing with temperate and tropical anurans must be evaluated carefully to include the degree of specialization in adaptation to different microclimatic conditions.

The data for *Xenopus laevis* indicate that in this tropical species the lungs are

less important in the respiratory exchanges than in other anurans studied at 15 C. Although *Xenopus* had a high tidal volume, the ventilatory rate was very low. Since *X. laevis* is aquatic, measurements of pulmonary and cutaneous respiration in air probably do not reflect the normal respiratory pattern. This is indicated by the wide variation in percentage of pulmonary oxygen consumption (15–69%). Charles (1931) estimated that in *X. laevis* the ratio of lung to skin intake would be 2.5–3.1. Our data do not support this view, although such a ratio might occur when the animal is in its normal aquatic environment. In only one individual did the ratio of pulmonary to cutaneous oxygen uptake exceed 2:1. In four of the six *Xenopus* studied, the lungs supplied less than 50% of the total oxygen requirement. During active periods, *Xenopus* could fill its large lungs with air and effectively supply the additional oxygen required as indicated by the high tidal volume. The total metabolism of *Xenopus* at 15 C was similar to temperate anurans at 5 C; thus, this species fits the pattern of metabolism predicted by Tashian and Ray (1957) for tropical anurans.

The relationship between body size and metabolic rate in animals has been a subject of considerable interest and discussion for many years. Although heat loss appears to be a satisfactory causal factor governing the so-called surface law in mammals and birds, there have been few satisfactory suggestions of causal factors governing the operation of the "surface law" in poikilotherms. Hemmingsen (1960) reviewed the data on metabolic studies of poikilotherms and concluded that the relationship between mass and metabolic rate is expressed by $KW^{0.75}$. Szarski (1964) presented the argument that in the process of evolution it is easier for an organism which changes size to adapt its cells to the new internal environment than to perfect new morphogenetic processes able to restore the formal equilibrium. Data from studies on the respiratory exchanges of amphibians add information useful in interpreting this relationship.

Whitford and Hutchison (1967) presented data showing that in salamanders with lungs, the metabolism-weight relationship is expressed by $M = 1.1W^{0.86}$, and in lungless salamanders by $M = 1.2W^{0.72}$. Although there was no difference in the external surface area–mass relationship between these two groups of salamanders, the differences in total respiratory surface area–mass relationship paralleled the metabolic differences. It was suggested that the total respiratory surface area available for gas exchange was an important factor in limiting metabolism.

Data from this study show a similarity in relationship between metabolism and body size and between tidal volume and body size. Since tidal volume in amphibians is a function of the volume of the buccal cavity due to the force-pump ventilating mechanism, there appears to be a relationship between metabolism and pulmonary ventilation. In anurans, body surface area $= KW^{0.58}$, indicating a decrease in the cutaneous respiratory surface per unit weight in larger frogs. Since both body surface area and buccal volume are power functions of the weight, it is reasonable to assume that larger anurans are able to supply less oxygen to the tissues per unit time for the same expenditure of ventilatory and circulatory energy than smaller frogs. A similar relationship appears to be operative in the metabolic relationships of the Caudata (Whitford and Hutchison, 1965).

These allometric relationships strongly suggest that metabolism in amphibians

is regulated to a considerable degree by the availability of oxygen to the tissues. The amount of oxygen available to a cell can regulate the metabolism of the cell, since the rate of oxidation of DPNH is dependent on the availability of oxygen as an electron acceptor. Salthe (1965) has shown that the substrate inhibition characteristics of lactic dehydrogenase found in the heart and skeletal muscle of amphibians show correlations with the availability of oxygen in the environment. Terrestrial species tend to have greater substrate inhibition than aquatic species, indicating greater dependence on oxidative metabolism.

If the increase in size of an organism is not accompanied by an equal increase in all body proportions, the value of n in the equation, structure size = KW^n will be less than one. Since the body surface area (which in amphibians is a respiratory surface) and the buccal volume in relation to the body weight of amphibians have n values less than one, it is reasonable to assume that larger individuals are able to supply less oxygen to the cells per unit time/unit work. These relationships support Szarski's contention that in evolution cells probably adapted to the new internal environment rather than the complex genetic changes necessary for perfect compensation in size of structures, organs, etc., to occur. These data also indicate that in amphibians the ability to obtain oxygen is the single most important factor regulating metabolic rate.

SUMMARY

Pulmonary and cutaneous gas exchange was measured separately and simultaneously in a number of species of anurans at different temperatures. In the temperate zone anurans, *Bufo americanus*, *B. cognatus*, *B. terrestris*, *Hyla gratiosa*, *H. versicolor*, *Rana catesbeiana*, *R. pipiens*, and *R. sylvatica*, the portion of the total oxygen uptake supplied by the pulmonary surfaces increased directly with temperature from approximately 35% at 5 C to 68% at 25 C. There were only slight changes in cutaneous oxygen consumption at different temperatures. At 5 C, *B. boreas* had a higher oxygen consumption and a higher percentage of pulmonary oxygen uptake (52%). Most of the carbon dioxide produced (70–95%) was released through the skin at all temperatures in the species studied.

The lungs of the tropical anuran, *Ceratophrys calcarata*, supplied 60% of the total oxygen requirement at 25 C and 71% at 35 C, which paralleled the role of the pulmonary surfaces in temperate anurans at 15 C and 25 C. The pulmonary surfaces of *B. marinus* accounted for a greater portion of the total oxygen uptake at 15 C and 25 C than temperate forms at these temperatures.

The role of the skin and lungs in gas exchange was similar in a number of temperate zone anurans, including four species of *Scaphiopus* studied for comparison at 15 C. In these species the pulmonary surfaces accounted for between 51% of the total oxygen consumption in *Microhyla carolinensis* and 67% in *Scaphiopus bombifrons*. The pulmonary surfaces of *Eleutherodactylus portoricensis* supplied significantly more of the total oxygen demand (77%) than the temperate anurans. Gas exchange in *Xenopus laevis* at 15 C was extremely variable, with between 15% and 70% of the total oxygen uptake via the pulmonary surfaces.

In general, there was an inverse relationship between body size and ventilatory rate and a direct relationship between tidal volume and weight. The relationship between tidal volume and weight in anurans was expressed by

$V_T = 0.42W^{0.73}$. The relationship between body size and metabolism in all anurans studied was expressed by $M = KW^{0.71}$. The relationship between body surface area and weight in anurans was expressed by $SA = 1.13W^{0.58}$. These allometric relationships suggest that the most important factor in the respiratory exchanges in anurans is the ventilation of the lungs and that the ability to obtain oxygen is the single most important factor regulating metabolism.

Differences in the upper and lower extreme values for percentage of oxygen uptake were more closely correlated with the habitat and distribution of anurans than were the mean values of oxygen consumption.

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