

THERMAL DEPENDENCE OF BEHAVIOURAL PERFORMANCE OF ANURAN AMPHIBIANS

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Abstract. The thermal dependence of performance capacity was assessed in two anuran amphibians: *Bufo boreas* (western toad) and *Rana pipiens* (leopard frog). Quantitative measurements of performance showed that *Bufo* could sustain slow rates of walking for 10 min and cover greater distances than *Rana*, which initially jumped more vigorously but fatigued within 5 min. Changes in performance with changes in body temperature were virtually instantaneous, and performance exhibited no acclimation over 7 days. Within the range of temperatures studied, performance capacity increased with increasing body temperature and reached a maximum at 28 C in *Bufo* and 20 to 29 C in *Rana*. Performance capacity and the underlying metabolic processes had a similar thermal dependence within a species. The behavioural capacity for activity is apparently maximal for both species at body temperatures normally encountered in the field. Anuran behaviours requiring sustained activity (migration to breeding sites, mating, foraging) must therefore be markedly temperature-sensitive.

Many amphibians experience wide daily variations in body temperature. Despite evidence for behavioural thermoregulation in amphibians (for review see Brattstrom 1979), the high rates of evaporative water loss (Tracy 1979), the need to maintain water balance, and the nocturnal habits of many amphibians limit the degree to which they can maintain a constant body temperature. Body temperatures of high-altitude toads have been measured from 0 to 35 C (Carey 1978), and variations in body temperature of 10 to 15 C are common in other amphibians (Brattstrom 1963; Lillywhite 1970; Lillywhite et al. 1973). These fluctuations in body temperature can have serious effects on physiological processes. In general, the rate of biochemical reactions doubles with every 10-C increase in temperature, so rate processes in amphibians have the potential to vary from two- to eight-fold over the course of a day. In terms of behaviour, changes of this magnitude in the rates of metabolic systems, rates of muscle contraction, or rates of nerve conduction could affect the ability of an amphibian to successfully reproduce, forage, or escape predators. It therefore is of interest to determine the thermal dependence of locomotory behaviour and performance in amphibians.

Anuran amphibians employ a variety of locomotory forms during activity, including walking, hopping, jumping, and swimming. While on land, many ranid frogs employ a sit-and-wait foraging strategy and avoid predation by jumping into the water and submerging themselves

(Hedeen 1972; Gregory 1979). Bufonids rely on more static defence mechanisms (lung inflation and poisonous skin secretions; Bennett & Licht (1973)) and may forage widely in the field (Karlstrom 1962). Seasonally, anurans can be highly active, as during spring migration to breeding sites (Martof 1953; Bragg & Brooks 1958; Oldham 1966, 1967; Fitzgerald & Bider 1974) or during territorial struggles and searching for mates (Brown & Pierce 1967; Wiewandt 1969; Wells 1977). The effect of temperature on 'burst' activity (distance jumped in a single jump) has been investigated in ranids (Huey & Stevenson 1979; Tracy 1979), but no comparable investigation exists of the effect of temperature on behavioural performance capacity over longer periods of time.

The purpose of this study is to determine the effect of temperature on behavioural performance capacity in order to assess the degree to which variation in body temperature in the field would impair an anuran's ability to engage in prolonged bouts of activity. Two anuran amphibians with different patterns of activity were used in this study. *Bufo boreas* (western toads) are slow-moving, fatigue-resistant anurans. Activity usually involves a slow walk that is supported by aerobic metabolism, dependent on oxygen delivery to the tissue (Bennett & Licht 1973). *Rana pipiens* (leopard frogs) engage in rapid activity, involving vigorous jumping, but fatigue quickly. This activity is supported by the anaerobic production of lactic acid in the muscles (Bennett & Licht 1974;

Carey 1979; Putnam 1979). Not only do these anurans exhibit widely different patterns of activity, but the underlying metabolic bases for those activities are also different. Therefore, the degree to which performance capacity is limited by metabolic capacities can be assessed.

Methods

Bufo boreas were collected in southern California and *Rana pipiens* were purchased from Graska Biological Supplies, Oshkosh, Wisconsin. Ten adult *Bufo* weighing $69.1 \text{ g} \pm 1.6 \text{ SE}$ (range 61.8 to 75.9) and 10 *Rana* weighing $43.3 \pm 2.8 \text{ g}$ (range 26.8 to 55.2) were used in the performance experiments. Animals were maintained in the laboratory for a week to a month at 20 to 22 C, before experiments began. Throughout the experiments, animals were maintained with available free water and mealworms ad lib on a 12–12 light–dark cycle centred on noon. We performed the experiments in June through August 1979.

We measured distance performance in an activity track made from two inflatable rubber swimming pools, of diameters 150 cm and 110 cm, one placed inside the other. The gap between them formed a circular track 12 cm wide, 4.12 m in average circumference, and 30 cm high. A small amount of water was placed in the bottom of the track to prevent dehydration of the animals during activity. Animals were manually prodded to continuous activity. Distance travelled was measured every minute for 5 min (*Rana*) or 10 min (*Bufo*). *Rana* were near fatigue after 5 min. *Bufo* were exercised for 10 min to assure that they attained a constant rate of locomotion. Total distance moved during these time periods will be defined as performance capacity. Cloacal temperature was measured before and after activity with a Schultheis quick-registering thermometer.

All animals were initially acclimated to 20 C for 5 days with ad lib food and water and a 12–12 light–dark cycle. Performance was measured at this temperature on 2 consecutive days. *Rana* were then tested at 3, 15, 32.5, and 9 C consecutively, each test being preceded by 5–12 days' acclimation. *Bufo* were sequentially acclimated to and tested at 9, 30, 3, and 15 C. Performance was measured once for each animal at each temperature. All animals died within 4 days in response to a constant acclimation temperature of 37 C.

To test the rate of acclimation, separate groups of *Rana* and *Bufo* were acclimated to

10 C for 12 days. Performance was measured on days 5 and 12. On day 13, the animals were transferred to 20 C for an additional 7 days, and we measured performance within 1 h of when the frogs' body temperature attained 20 C. Performance was also measured on days 14 and 19.

Comparisons of performance at different temperatures and of the mean performance on different days at the same temperature were made using a Wilcoxon signed-rank test (WSRT) (Siegel 1956). Comparisons of rank scores of individuals at different temperatures were made by calculating a coefficient of concordance and testing for differences from zero with an *F*-test (Festinger & Katz 1953). The level of significance was 0.05 for all tests, and all values are reported as the mean \pm one standard error of the mean (SE).

Results

Activity

Bufo maintained a constant rate of walking after the initial 1 to 2 min of activity. *Rana* initially jumped vigorously but were fatigued by the end of the activity period (Fig. 1). Perfor-

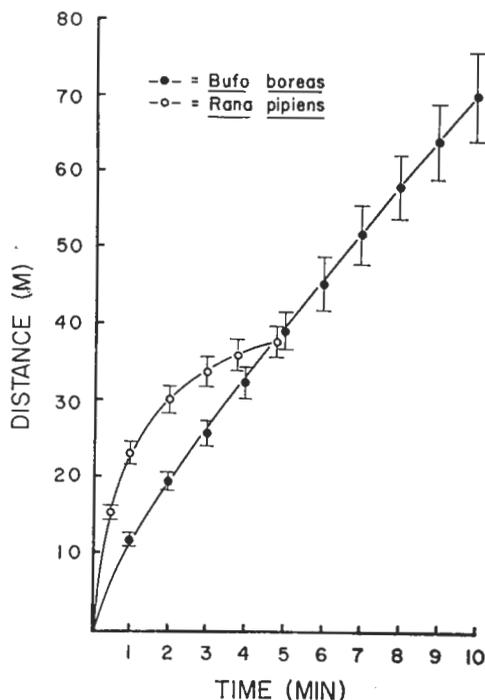


Fig. 1. Distance moved (in metres) by *Rana pipiens* and *Bufo boreas* as a function of time at 20 C. Points are means $\pm 1 \text{ SE}$.

mance capacity for a species was the same when measured at 20 C on 2 consecutive days ($P > 0.36$, WSRT) (Table I). This indicates that the measure of performance capacity in this study is repeatable.

Acclimation of Behavioural Performance

Figure 2 shows the time course of acclimation of performance. Changes in performance in response to a temperature change were rapid and were completed within 1 or 2 h. No acclimation in performance was exhibited over the next 5 to 7 days. Performance capacity after 1 or 2 h exposure to a temperature change (acute effects) was the same as after several days at that temperature (chronic effects). Therefore, the performance capacity measured in response to chronic temperature exposure in this study will reflect changes in the performance capacity of these anurans exposed to acute temperature changes in the field.

Temperature during Activity

Animals were placed at constant environmental temperatures of 3, 9, 15, 20, plus either 30 C (*Bufo*) or 32.5 C (*Rana*). Body temperatures before activity were 3.8 ± 0.1 C, 8.8 ± 0.1 C, 14.1 ± 0.1 C, 20.6 ± 0.1 C and 27.9 ± 0.4 C for *Bufo* and 4.4 ± 0.1 C, 9.2 ± 0.1 C, 14.4 ± 0.1 C, 20.2 ± 0.2 C and 29.1 ± 0.3 C for *Rana*. Activity led to an average increase of 1.2 C regardless of initial body temperature.

Temperature Effects on Performance

Figure 3 shows the effect of initial body temperature on performance in *Bufo*. At all temperatures, toads walked about twice as fast during the first minutes of activity and maintained a slower, constant walking speed during the last 5 to 7 min of activity. Cold temperatures led to near incapacitation. At 9 C toads were sluggish. At 4 C, walking was noticeably

laboured and uncoordinated. Increasing temperature increased performance capacity in toads up to 20 C. From 20 to 28 C there was a smaller increase in performance. At 28 C, *Bufo* frequently began hopping during the initial phase of activity. The distance walked varied significantly at all test temperatures ($P < 0.05$, WSRT) after both 1 min and 10 min. At all temperatures, individual performance varied nearly twofold. The ranges of individual performance in *Bufo* varied from 6 to 13 m in 10 min at 4 C to 70 to 120 m in 10 min at 28 C. One toad covered 20.6 m in the first minute of activity, a rate similar to some *Rana* at 20 to 30 C.

The effect of temperature on performance in *Rana* is shown in Fig. 4. During the initial phases of activity, *Rana* moved rapidly with long jumps. Activity became progressively less intense until most frogs were fatigued and capable of only infrequent jumps or slow crawling after 5 min. Many frogs were unable to maintain normal posture by 5 min and were unable to right themselves when placed on their back, although

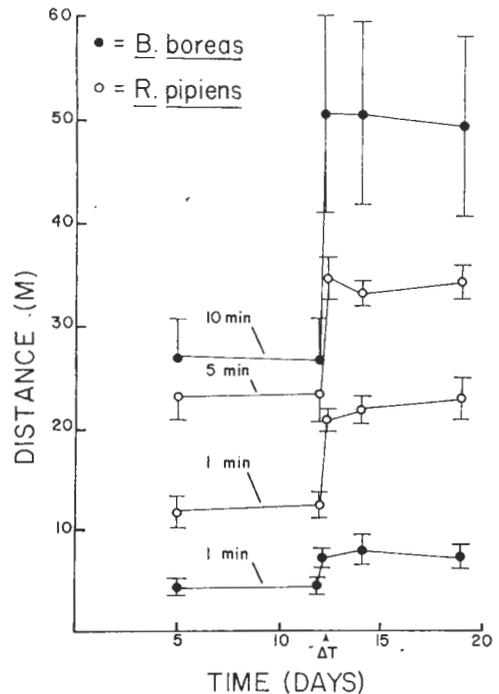


Fig. 2. Distance moved (in metres) before and after a 10-C temperature change. For each species, distance moved initially (after 1 min) and total distance moved (5 min for *R. pipiens* and 10 min for *B. boreas*) are reported. Points are means ± 1 SE.

Table I. Distance Performance of Frogs and Toads at 20 C on 2 Consecutive Days*

	<i>Bufo boreas</i>		<i>Rana pipiens</i>	
	1 min	10 min	1 min	5 min
Day 1	10.84 ± 0.57	69.26 ± 3.70	23.32 ± 1.73	36.50 ± 2.50
Day 2	11.76 ± 0.57	69.86 ± 5.39	23.03 ± 1.23	37.70 ± 1.78

*Values are distance travelled in metres (mean ± 1 SE).

righting response is a strong reflex in anurans. *Rana* were able to move well at all temperatures and did not show the incapacitation in the cold that was exhibited by *Bufo*. Frogs jumped not only farther, but also higher, with increasing temperature. After 0.5 min, performance in-

creased significantly at higher temperatures ($P < 0.01$, WSRT). After 5 min, performance increased up to 20 C ($P < 0.01$, WSRT) but was not improved significantly between 20 and 29 C.

The effect of body temperature on performance in the two species is more easily seen in

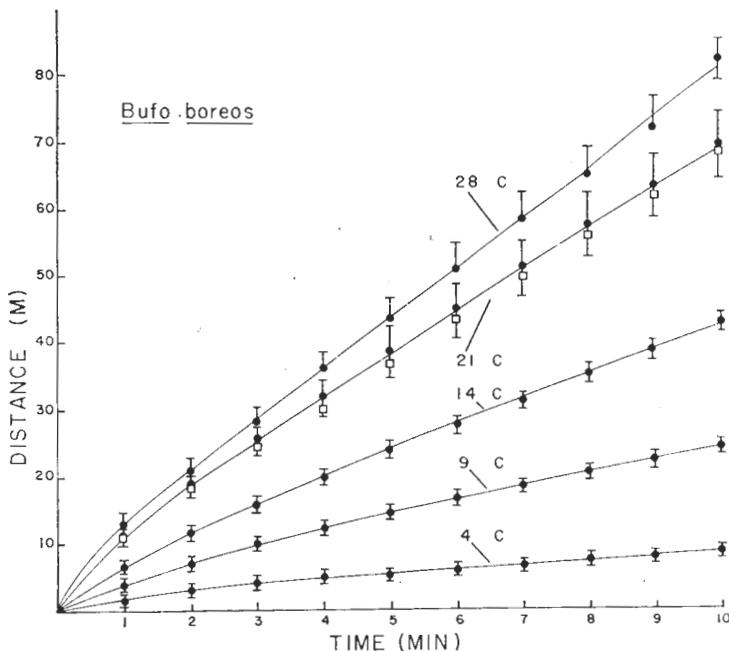


Fig. 3. Distance moved (in metres) during 10 min at various initial body temperatures by *Bufo boreas*. The empty boxes and filled circles at 20 C represent distance moved on 2 consecutive days. Curves are drawn by eye. Points are means \pm 1 SE.

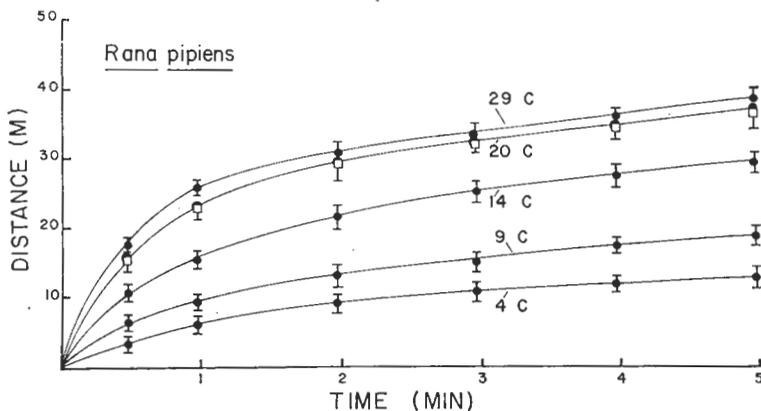


Fig. 4. Distance moved (in metres) during 5 min at various initial body temperatures by *Rana pipiens*. All symbols as in Fig. 3.

Fig. 5. The distances moved during 5 min are similar in the two species, although *Rana* were fatigued at this time while *Bufo* were capable of further sustained activity. The shapes of the curves of the effect of temperature on performance are similar in the two species, although quantitatively temperature has a greater effect on performance in *Bufo*. It would be interesting to have performance measurements at body temperatures of 32 to 35 C (near thermal maximum) to see whether performance would decline or increase further.

Individual Performance

On the 2 consecutive days of activity at 20 C, individual performance ranks were similar for

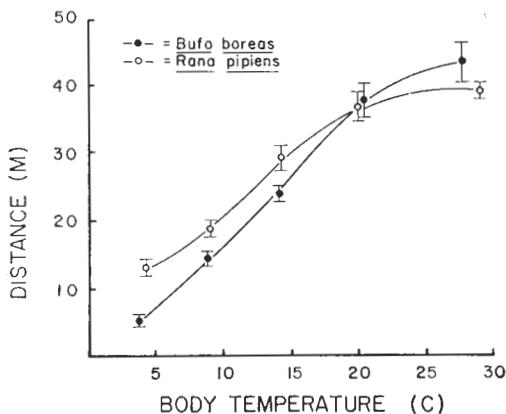


Fig. 5. Distance moved (in metres) after 5 min at various initial body temperatures in *Rana pipiens* and *Bufo boreas*. Curves are drawn by eye. Points are means \pm 1 SE.

both species ($P > 0.36$, WSRT). The rank for each animal during activity at different temperatures is shown in Table II. The rank is not related to body mass. Analysis of coefficient of concordance of individual rank at various temperatures indicates rank is conserved in both species (*Bufo*: $W = 0.51$, $F = 5.22$, $P < 0.001$; *Rana*: $W = 0.51$, $F = 5.22$, $P < 0.001$).

Discussion

The fact that anurans undergo sustained activity in the field is generally not appreciated. Anurans engage in sustained activity during mating and during seasonal migrations. Fighting for territories or mates has been observed to last for 30 min in some anurans (Wiewandt 1969). Migrations of 2 km to breeding sites have been reported for toads (Oldham 1966; Fitzgerald & Bider 1974) and frogs (Martof 1953; Oldham 1967). Exceptional cases of mass migrations have been reported for *Bufo cognatus* (Great Plains toad) (Bragg & Brooks 1958), with toads walking 3 to 5 km per day (30 m/10 min). Anurans are also often found considerable distances from the nearest available free water (Karlstrom 1962), suggesting that they forage widely. The effect of temperature on these breeding and foraging behaviours can be inferred from the thermal dependence of the sustained activity measured in this study.

Previous quantitative studies of the thermal dependence of performance in anurans have dealt only with maximal jumping distance in *Rana* spp. (Huey & Stevenson 1979; Tracy 1979). These measurements are most relevant to the ability of *Rana* to escape predators, since ranids

Table II. Ranks of Individual Performance at Various Temperatures*

Animal No.	<i>Bufo boreas</i>						<i>Rana pipiens</i>					
	4	9	14	20†	20**	28	4	9	14	20†	20**	29
1	4	6	7	9	10	10	3	1	4	1	1	4
2	1	1	1	1	1	1	4	2	6	6	4	3
3	2	7	8	2.5	5	3	1	3	2	4	8	5
4	10	10	4	6	2	2	6.5	7	10	7	9	8
5	7	4	2	8	7	7	5	5	3	2	7	1
6	3	5	10	5	6	8	10	8	9	8	10	2
7	6	3	5	7	3	6	8	9	5	5	6	9
8	5	2	3	2.5	4	5	2	—	1	3	2	—
9	9	8.5	6	10	9	9	6.5	4	7.5	10	5	7
10	8	8.5	9	4	8	4	9	6	7.5	9	3	6

*A rank of 1 indicates the individual that walked the farthest distance during a trial, while a rank of 10 indicates the individual that walked the shortest distance.

†Rank performance on day 1 at 20 C.

**Rank performance on day 2 at 20 C.

employ one to several jumps (Hedeem 1972; Gregory 1979) when confronted by a predator. The 0.5-min performance data for *Rana* in this study represent the sums of about 15 to 25 jumps and may be correlated with maximal jumping distance. However, on the basis of morphological evidence, Emerson (1978) argues that 'quickness of movement' (acceleration) is an important component of predator avoidance. Furthermore, in terms of interspecific comparisons, the significance of maximal distance jumped in *Bufo boreas* is questionable, since this species rarely jumps, relying instead on static defence mechanisms for predator avoidance. Therefore, while the measure of total performance capacity used here may not directly relate to burst activities such as predator avoidance or prey capture, it does give information about an anuran's ability to sustain activity.

Both *Bufo* and *Rana* experience wide variations in body temperatures in nature. Field temperatures range from 3 to 30 C (mean 21 C) and from 18 to 35 C (mean 24 C) for *Bufo boreas* and *Rana pipiens*, respectively (Brattstrom 1963). Toads may be found active with body temperatures as low as 0.4 C at high altitudes (3000 m) but are never active below 10 C at lower elevations (Carey 1978). Body temperatures as high as 34 C have been reported for active toads (Carey 1978). These extremes of field temperatures are close to the lethal temperatures for these species, reported as -2 to 38 C for *Bufo boreas*, and -1.6 to 35 C for *Rana pipiens* (Brattstrom 1968).

Temperature has a marked effect on the performance capacity of *Bufo* and *Rana* (Figs 3 and 4). At cold temperatures of 4 C, *Bufo* are incapacitated while *Rana* are capable of coordinated locomotion. Performance capacity increases with increasing temperature up to 20 C in *Rana* and 29 C in *Bufo*. Capacity does not increase in *Rana* between 20 and 30 C. Thus, at body temperatures normally encountered in the field (20 to 30 C) both species will apparently have maximal performance capacities (Figs 3 and 4). Over the temperature range of 5 to 30 C, performance capacity is more temperature-sensitive than is maximal jumping distance (Huey & Stevenson 1979; Tracy 1979), suggesting that while avoidance behaviours may not be particularly temperature-sensitive, behaviours requiring long-term activity (migrations, mating, foraging) will be.

The effects of changes in body temperatures on activity capacity are essentially instantaneous

(Fig. 2). Daily events such as basking, entering either cold or warm waters (Lillywhite 1970), and cold nights, therefore, can have a marked effect on performance capacity. The lack of an acclimation of performance capacity is surprising since anurans show acclimation of their maximal thermal limits (Hutchison & Ferrance 1970). It may be that capacity acclimation is not significant throughout a few days in animals which undergo wide daily variations in temperature (Carey 1978). However, seasonal changes in performance capacity cannot be discounted on the basis of the present data.

The thermal dependence of performance capacity in amphibians can be compared with that of other lower vertebrates. Fish exhibit a correlation between maximal sustained swimming speed and normally encountered field temperatures (Brett et al. 1958). Field temperatures, however, are low in these fish (15 C) and performance was actually shown to decrease at higher temperatures. In contrast to fish, performance in some reptiles is maximized at the highest test temperatures (40 C), even in species that behaviourally maintain body temperatures as low as 25 C (Bennett 1980). It would be of interest to study amphibians with low field body temperatures (10 to 15 C) such as *Hyla regilla* (Pacific treefrog) or *Desmognathus escholtzi* (Monterey salamander; Brattstrom 1963), to see whether they are more similar to fish or reptiles in their thermal dependence of performance capacity, and to study *Rana* and *Bufo* at their lethal thermal limits. That jumping ability declines above 30 C (Huey & Stevenson 1979; Tracy 1979) and that *Bufo exsul* (black toads) appear sluggish in the field above 30 C (Schuierer 1962) suggest that performance capacity also would decline above 30 C.

Despite the apparently good match between average field temperatures during activity and maximal capacity for performance, activity and high body temperatures are not always correlated in anurans. Hadfield (1966) reported basking behaviour and higher body temperatures in inactive *Bufo* than in active animals, suggesting that the maintenance of a high body temperature is unrelated to activity. Lillywhite et al. (1973) found that after feeding, juvenile *Bufo boreas* selected high body temperatures in a laboratory thermal gradient. Other functions that could be maximized by maintaining a high body temperature include growth rates (Lillywhite et al. 1973); digestive efficiency (Harlow et al. 1976); or behavioural capacities not related to loco-

motion such as speed, accuracy of strikes at prey (Greenwald 1974), or acceleration during a jump (Emerson 1978). The seasonal and nocturnal breeding habits of many amphibians may also dictate body temperatures. The selection of body temperature is undoubtedly a complex function of environmental and physiological factors that may be only partially related to maximizing activity capacity.

The underlying physiological mechanisms that mediate the thermal dependence of performance are unknown. The role of metabolic processes (aerobic and anaerobic) can be assessed by comparing their temperature coefficients (Q_{10} , the relative increase of some process corresponding to a 10-C increase in temperature) with the thermal dependence of performance (Table III). During activity, the slow-moving *Bufo* generate virtually all of the needed energy through aerobic metabolism (Bennett & Licht 1973; Seymour 1973). Therefore, activity should have a temperature dependence similar to aerobic metabolism. Conversely, the Q_{10} 's of performance in *Rana* should be similar to the thermal dependence of anaerobic metabolism, since the high level of activity exhibited in *Rana* is largely supported by the production of lactic acid (Bennett & Licht 1974; Carey 1979). In *Rana*, the low thermal dependence of performance is most similar to the Q_{10} 's of anaerobic meta-

bolism. In *Bufo* below 20 C, the Q_{10} 's of performance and aerobic metabolism are similar, although above 20 C performance has a lower thermal dependence than the aerobic systems. Above 20 C, physiological processes other than metabolism (nervous conduction, contractile systems) may limit performance. Despite the general agreement between temperature dependence of performance and metabolic processes in these anurans, performance is a complex behavioural process that involves motivation and the central and peripheral nervous system as well as metabolic and contractile systems. Caution should therefore be exercised in interpreting metabolism as the primary factor limiting performance capacity.

Body temperature clearly has a marked effect on performance capacity in anurans. Performance capacity is apparently maximal at average field body temperatures. The performance responses to temperature changes are virtually instantaneous and thus of significance on a daily basis. The underlying metabolic processes have a thermal dependence similar to the performance capacities in these two species of anurans.

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Table III. Q_{10} of Performance and Aerobic and Anaerobic Scopes during Activity

Temp. range	Aerobic*	Activity (1 min)	Anaerobic (1 min)†	Anaerobic (10 min)*	Activity (10 min)
<i>Bufo boreas</i>					
5-10	3.62	4.77	—	1.11	7.61
10-15	2.99	2.62	1.64**	1.21	2.94
15-20	2.46	2.25		1.19	2.09
20-30	1.84	1.23	1.53	1.16	1.21
<i>Rana pipiens</i>					
5-10	5.74	3.22	—	2.34	2.13
10-15	4.13	2.49	2.25	1.63	2.39
15-20	2.99	2.04	3.45	1.35	1.46
20-30	1.79	1.09	0.88	1.14	1.07

*Calculated from Carey (1979).

†Calculated from Bennett & Licht (1974).

** Q_{10} for 10-20 C.

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REFERENCES

- Bennett, A. F. 1980. The thermal dependence of lizard behaviour. *Anim. Behav.*, **28**, 752-762.
- Bennett, A. F. & Licht, P. 1973. Relative contributions of anaerobic and aerobic energy production during activity in amphibia. *J. comp. Physiol.*, **87**, 351-360.
- Bennett, A. F. & Licht, P. 1974. Anaerobic metabolism during activity in amphibians. *Comp. Biochem. Physiol.*, **48A**, 319-327.
- Bragg, A. N. & Brooks, M. 1958. Social behavior in juveniles of *Bufo cognatus* Say. *Herpetologica*, **14**, 141-147.
- Brattstrom, B. 1963. A preliminary review of the thermal requirements of amphibians. *Ecology*, **44**, 238-255.
- Brattstrom, B. 1968. Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comp. Biochem. Physiol.*, **24**, 93-111.
- Brattstrom, B. 1979. Amphibian temperature regulation studies in the field and laboratory. *Am. Zool.*, **19**, 345-356.
- Brett, J. R., Hollands, M. & Alderidge, D. F. 1958. The effect of temperature on the cruising speed of young sockeye and Coho salmon. *J. Fish. Res. Bd Canada*, **15**, 587-605.
- Brown, L. E. & Pierce, J. R. 1967. Male-male interactions and chorusing intensities of the Great Plains Toad, *Bufo cognatus*. *Copeia*, **1967**, 149-154.
- Carey, C. 1978. Factors affecting body temperatures of toads. *Oecologia*, **35**, 197-219.
- Carey, C. 1979. Aerobic and anaerobic energy expenditure during rest and activity in montane *Bufo b. boreas* and *Rana pipiens*. *Oecologia*, **39**, 213-228.
- Emerson, S. 1978. Allometry and jumping in frogs: helping the twain to meet. *Evolution*, **32**, 551-564.
- Festinger, L. & Katz, D. 1953. *Research Methods in the Behavioral Sciences*. New York: Holt, Rinehart & Winston.
- Fitzgerald, G. J. & Bider, J. R. 1974. Seasonal activity of the toad *Bufo americanus* in Southern Quebec as revealed by a sand-transect technique. *Can. J. Zool.*, **52**, 1-5.
- Greenwald, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia*, **1974**, 141-148.
- Gregory, P. T. 1979. Predator avoidance behavior of the red-legged frog (*Rana aurora*). *Herpetologica*, **35**, 175-184.
- Hadfield, S. 1966. Observations on body temperature and activity in the toad *Bufo woodhousei fowleri*. *Copeia*, **1966**, 581-582.
- Harlow, H. J., Hillman, S. & Hoffman, M. 1976. The effect of temperature on digestive efficiency in the herbivorous lizard, *Dipsosaurus dorsalis*. *J. comp. Physiol.*, **111**, 1-6.
- Hedeon, S. E. 1972. Escape behavior and causes of death of the mink frog, *Rana septentrionalis*. *Herpetologica*, **28**, 261-262.
- Huey, R. B. & Stevenson, R. D. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.*, **19**, 357-366.
- Hutchison, V. H. & Ferrance, M. 1970. Thermal tolerances of *Rana pipiens* acclimated to daily temperature cycles. *Herpetologica*, **26**, 1-8.
- Karlstrom, E. L. 1962. The toad genus *Bufo* in the Sierra Nevada of California: ecological and systematic relationships. *Univ. Calif. Publ. Zool.*, **62**, 1-104.
- Lillywhite, H. B. 1970. Behavioral temperature regulation in the bullfrog, *Rana catesbeiana*. *Copeia*, **1970**, 158-168.
- Lillywhite, H. B., Licht, P. & Chelgren, P. 1973. The role of behavioral thermoregulation in the growth energetics of the toad, *Bufo boreas*. *Ecology*, **54**, 375-383.
- Martof, B. S. 1953. Territoriality in the green frog, *Rana clamitans*. *Ecology*, **34**, 165-175.
- Oldham, R. S. 1966. Spring movements in the American toad, *Bufo americanus*. *Can. J. Zool.*, **44**, 63-100.
- Oldham, R. S. 1967. Orienting mechanisms of the green frog, *Rana clamitans*. *Ecology*, **48**, 477-491.
- Putnam, R. W. 1979. The basis for differences in lactic acid content after activity in different species of anuran amphibians. *Phys. Zool.*, **52**, 509-519.
- Schuieler, F. W. 1962. Remarks upon the natural history of *Bufo exsul* Myers, the endemic toad of Deep Springs Valley, Inyo County, California. *Herpetologica*, **17**, 260-266.
- Seymour, R. S. 1973. Physiological correlates of forced activity and burrowing in the spadefoot toad, *Scaphiopus hammondi*. *Copeia*, **1973**, 103-115.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.
- Tracy, C. R. 1979. Further thoughts on anuran thermoregulation: discussion. In: *The Behavioral Significance of Color* (Ed. by E. H. Burt, Jr.), pp. 63-68. New York: Garland STPM Press.
- Wells, K. 1977. The social behaviour of anuran amphibians. *Anim. Behav.*, **25**, 666-693.
- Wiewandt, T. A. 1969. Vocalization, aggressive behavior, and territoriality in the bullfrog, *Rana catesbeiana*. *Copeia*, **1969**, 276-285.

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