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finding may suggest a profitable avenue of experimentation for further studies on the maintenance of the Burns polymorphism.

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THERMAL SELECTION IN THE HELLBENDER, *CRYPTOBRANCHUS ALLEGANIENSIS*, AND THE MUDPUPPY, *NECTURUS MACULOSUS*

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ABSTRACT: After acclimation to 5°, 15°, and 25°C (AT) hellbenders had corresponding mean preferred temperatures (PT) in a laboratory thermal gradient of 11.6° ± 0.12°C, 17.7° ± 0.18°C and 21.7° ± 0.21°C. At the same AT the corresponding PT of mudpuppies were 9.1° ± 0.07°C, 16.1° ± 0.12°C and 20.21° ± 0.19°C. Increased AT thus resulted in significant elevations of PT in both species. Previous studies showed either no significant increase of PT with increased AT in salamanders or an inverse relationship. The generally low PT of *Cryptobranchus* and *Necturus* may reflect their strictly aquatic habitats.

MOST of the data on amphibian thermoregulation arise from measurements of temperatures in the field (reviewed by Strübing, 1955 and Brattstrom, 1963). Since such temperature values often represent the only temperature available at the time of measurement they may not reflect the abilities of the animals for thermal selection (Heath, 1975). This difficulty led to the conclusion that most amphibians do not appear to select a preferred temperature (PT) and that they are active at any temperature within their range of activity; this has been particularly applied to salamanders (Brattstrom, 1963, 1970). More recent work with experimental thermal gradients has demonstrated that many adult amphibians possess an ability for temperature selection (Claussen, 1973; Feder and Pough, 1975; Heath, 1975; Licht and Brown, 1967; Lillywhite, 1971; Spotila, 1972). The ability of amphibian larvae to regulate body temperature

through thermal selection is well established (Brattstrom, 1962; de Vlaming and Bury, 1970; Lucas and Reynolds, 1967; Workman and Fisher, 1941).

Since the range of temperatures is more limited in aquatic than in terrestrial environments, the ability of aquatic amphibians to thermoregulate by thermal selection has been questioned (Brattstrom, 1963; Heath, 1975). Thus, we undertook this study to determine the role of thermal acclimation on temperature selection in two strictly aquatic North American salamanders which were available. The mudpuppy, *Necturus maculosus*, and the hellbender, *Cryptobranchus alleganiensis*, are both strictly aquatic throughout their life cycle. The mudpuppy is primarily lacustrine and is generally limited to permanent bodies of water. The hellbender is strictly fluvial. The primarily branchial respiration of *Necturus* and the predominantly cutaneous gas exchange of *Cryptobranchus*

may limit both forms to fairly cool environments with well oxygenated water (Guimond and Hutchison, 1972, 1973).

MATERIALS AND METHODS

Necturus maculosus maculosus were obtained from a commercial supplier in central Wisconsin. The *Cryptobranchus alleganiensis bishopi* were collected on the North Fork of the White River, Ozark County, Missouri. Animals were maintained in aerated aquaria and acclimated at 5°, 15°, and 25° ± 1°C for periods of 2–6 weeks prior to use in experiments. A photoperiod of LD 12:12 (12-h scotophase alternating with 12-h photophase centered at 1200 h) was maintained throughout the acclimation and experimental periods. The animals were fed live crayfish and earthworms during the acclimation period but were not fed for 3 days prior to use in experiments.

Tests in the experimental gradient were conducted in October and November between 1300 and 1700 h to lessen any possible influence of seasonal (Feder and Pough, 1975) or diel (Claussen, 1973; Spotila, 1972) cycles on PT. The thermal gradient has been fully described and figured by Hill et al. (1975). Aerated, heated and cooled water were introduced into small tubelets at opposite ends of a 183 × 15.2-cm acrylic plastic tube to produce a gradient from 4° to 38°C. Thermometers were placed every 7.6 cm along the tube. Valves on cold and heated water inlets allowed maintenance of a stable gradient and stratification of water within the tube was prevented by a bar with small paddles which were rotated at 100 rpm. The gradient was uniformly lighted.

With a uniform temperature (equal to acclimation temperature, AT) throughout the chamber, each test animal was placed in the gradient and left undisturbed for 1 h. The thermal gradient was then formed and the temperature of the water at the level of the head of each animal was recorded at 1-min intervals for periods of 20 to 30 min. The salamanders were ob-

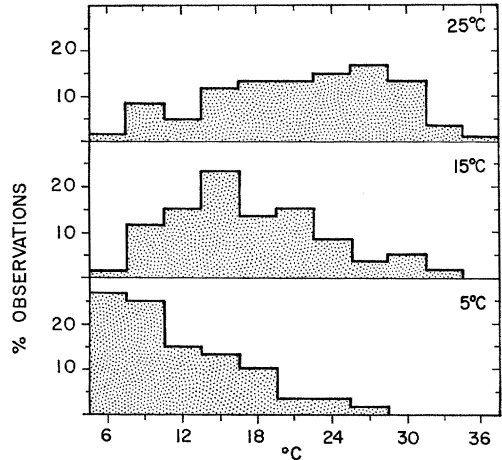


FIG. 1.—Frequency distribution of temperatures selected by *Cryptobranchus alleganiensis bishopi* in an experimental gradient after acclimation to 5°, 15°, and 25°C. Data grouped into 3°C intervals.

served from a distance with the aid of an inclined mirror. Fifteen different adults were used for each test at each acclimation temperature; each individual was used only once in the gradient.

There were no significant differences between sexes in each species and the data were grouped. Student's *t*-test, analysis of variance, and nonparametric methods (Siegel, 1956; Sokal and Rohlf, 1969) were used to test for significant differences between experimental groups.

RESULTS

Although the salamanders moved along the gradient during the observation periods they tended to concentrate about different temperatures, depending upon their previous thermal history (Table 1 and Figs. 1 and 2). Kolmogorov-Smirnov tests for goodness-of-fit showed that the observed data acclimations at 15° and 25°C for both species did not deviate significantly from a normal distribution. However, the distribution of data obtained for the groups acclimated at 5°C is abruptly truncated at the lowest temperature available in the

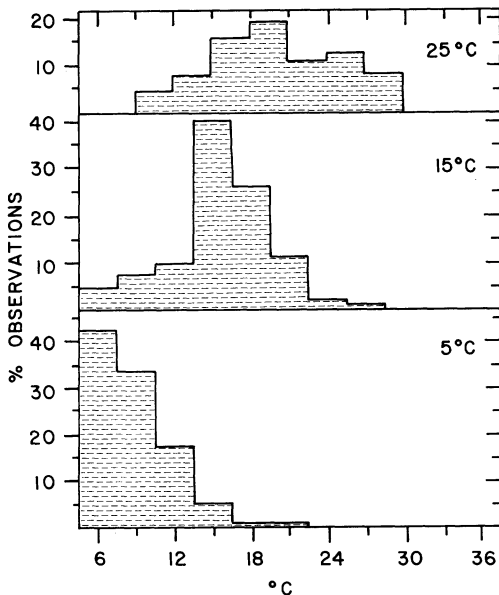


FIG. 2.—Frequency distribution of temperatures selected by *Necturus maculosus maculosus* in an experimental gradient. Plotted as in Fig. 1.

gradient. Comparisons of the 5°C data with results from the other acclimations were made with Wilcoxon two-sample tests.

In both species selection of a mean PT was strongest after acclimation to 5° and 15°C, with much greater dispersion around the means after acclimation to 25°C. Salamanders acclimated at 5°C tended to select the lowest temperatures available. In *Cryptobranchus* the PT after acclimation at 15°C was significantly higher ($t = 7.26$, $p < .001$) than after acclimation at 5°C; acclimation at 25°C increased the PT significantly ($t = 4.28$, $p < .001$) over the animals acclimated to 15°C. In *Necturus* there was no significant difference between the 15° and 25°C groups ($t = 1.95$, $.01 > p < .05$) but the 5°C group had a significantly ($p < .001$) lower PT. *Cryptobranchus* selected significantly higher ($p < .05$) temperatures than *Necturus* when both were acclimated to 5° ($t = 3.68$, $p < .001$), but there was no significant difference

($0.1 > p > .05$) between the two species acclimated at 15° and at 25°C.

The statistical parameters (Table 1) and the frequency distributions (Figs. 1 and 2) indicate that thermal selection is less variable in *Necturus* than in *Cryptobranchus*. No differences between the length of the acclimation period and thermal selection were observed.

The salamanders showed a strong tendency to follow the PT as the gradient was altered spatially by the adjustment of flow rates of the entering heated and cooled water, an indication that the position within the gradient was a response to temperature rather than to other stimuli.

DISCUSSION

Although use of the term "preferred temperature" has been questioned by Regal (1966, 1967) and Templeton (1970), we have followed Licht et al. (1966) and Lillywhite (1971) in using the term for results obtained only from laboratory gradients. This concept of "PT" is also more consonant with the widest usage in a large body of literature (See Precht et al., 1973 for a review). "Preferred body temperature" has been restricted to behavioral thermoregulation in ectothermic animals and approved by the International Union of Physiological Sciences and the International Commission for Thermal Physiology (Bligh and Johnson, 1973).

Feder and Pough (1975) found an inverse relationship between AT and PT in the salamander *Plethodon cinereus*. After acclimation to high temperatures, *Taricha rivularis* tended to avoid high body temperatures by thermoregulatory behavior (Licht and Brown, 1967). In several species of plethodontids no significant differences were found between conspecifics acclimated at different temperatures (Spotila, 1972). Thus, our finding that increased AT increases PT (except from 15 to 25°C in *Necturus*) differs from previous observations on adult salamanders. An increase in the PT of salamanders with an increase

TABLE 1.—Thermal selection of *Necturus maculosus* and *Cryptobranchus alleganiensis* in a laboratory thermal gradient. Fifteen separate individual animals were used for each group. N = number of observations, $\bar{x} \pm SE$ = mean \pm one standard error, SD = standard deviation, CV = coefficient of variation $C_{.68}$ = range of central 68%.

	Acclimation temperature ($^{\circ}\text{C}$)		
	5 $^{\circ}$	15 $^{\circ}$	25 $^{\circ}$
<i>Cryptobranchus</i>			
N	300	301	300
$\bar{x} \pm SE$	11.6 \pm 0.12	17.7 \pm 0.18	21.7 \pm 0.21
SD	2.05	3.06	3.72
CV	17.67	17.33	17.13
Range	5–27	6–34	7–35
$C_{.68}$	9.6–13.7	14.6–20.7	18.0–25.4
Median	16	20	21
Mode	7	15	27
<i>Necturus</i>			
N	225	225	225
\bar{x}	9.1 \pm 0.07	16.1 \pm 0.12	20.2 \pm 0.19
SD	1.00	1.82	2.87
CV	11.04	11.31	14.21
Range	4–22	6–27	9–32
$C_{.68}$	8.1–10.1	14.3–17.9	17.3–23.1
Median	13	16.5	20.5
Mode	8	15	15

in AT, at least up to some final preferendum, would not be unexpected since such a change has been widely observed in animals including adult and larval anurans. Thus, all salamanders do not have stable thermal preferences; the change in PT for each 10 $^{\circ}\text{C}$ change in AT in *Cryptobranchus* and *Necturus* is equivalent to the lability of PT observed in many fishes (Fry, 1967).

The PT of *Cryptobranchus* and *Necturus* at an AT of 5 $^{\circ}\text{C}$ is lower than that reported for any amphibian; at an AT of 15 $^{\circ}\text{C}$ lower or similar PT values have been observed only in four plethodontid salamanders. The PT at 25 $^{\circ}$ is similar to several adult plethodontids (Spotila, 1972) and larval amphibians (Lucas and Reynolds, 1967).

The critical thermal maxima (CTM) of *Cryptobranchus* and *Necturus* are also relatively low compared to other salamanders (Hutchison et al., 1973; Hutchison and Rowlan, 1975). In all cases, the range of PT is well below the CTM for each corresponding AT. The rate of acclimation

of the CTM to different temperatures in *Cryptobranchus* is appreciably slower than that of other amphibians (Hutchison et al., 1973) and, in *Necturus*, is similar to many other species (Hutchison and Rowlan, 1975).

Ecritic temperature data from field studies are not available for comparisons with our laboratory data. *Cryptobranchus alleganiensis bishopi* inhabits the relatively cool and larger streams of the Black River System and the North Fork of the White River in southeastern Missouri and adjacent Arkansas. The water temperature measured over a period of 15 months at the collection sites of the hellbenders used in this study ranged from 9.8 $^{\circ}\text{C}$ in February to 22.5 $^{\circ}\text{C}$ in July (Nickerson and Mays, 1973). The mudpuppy is less stenoeccious than the hellbender and will on occasion occupy diverse aquatic habitats (Bishop, 1941).

The generally lower PT and CTM of *Cryptobranchus* and *Necturus* may reflect

their strictly aquatic habitats and distribution in generally cooler waters.

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