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THERMAL TOLERANCES AND PREFERENCES OF FISHES OF THE VIRGIN RIVER SYSTEM (UTAH, ARIZONA, NEVADA)

James E. Deacon¹, Paul B. Schumann², and Edward L. Stuenkel³

ABSTRACT.—Critical thermal maxima (CTM) and thermal preferenda of the common fishes of the Virgin River were examined. Differences in final temperature preferenda and CTM for species with low thermal lability (speckled dace, spinedace, roundtail chub) correspond well with differences in their distribution and abundance in the river. These species shifted their acute thermal preferences relatively little as acclimation temperature increased. For thermally labile species (woundfin, red shiner, desert sucker, and flannelmouth sucker), the final preferendum is a less precise indicator of probable distribution. The woundfin, an endangered fish, has a high CTM (39.5 C at 25 C acclimation) and a labile acute preferendum (slope nearest 1) compared to other species in the system. The introduced red shiner likewise has a high CTM and a labile acute preferendum. In cooler temperatures, its acute preferendum shifts more rapidly than does that of the woundfin. At higher temperatures (above 15 C), the red shiner does not shift its acute preferendum as rapidly as does the woundfin. The red shiner, however, has a higher final preferendum. For thermally labile species, influence of acclimation temperature on mean preferendum, together with CTM, provides a better insight into distributional relationships within the system.

In recent years, agricultural, municipal, and industrial water uses in arid regions of the southwestern United States have reduced both stream flows and water quality. The consequent alterations in thermal, chemical, and flow regimes, coupled with the discharge of various effluents and the introduction of non-native fishes, have seriously reduced many native fish stocks (Deacon and Minckley 1974, Deacon 1979, Pister 1979, 1981).

The Virgin River in Utah, Arizona, and Nevada is an example of such a system. Its shifting, sandy bottoms, steep gradients, high sediment loads, variable flows, large daily and seasonal fluctuations in temperature, and other physical and chemical characteristics are typical of desert streams (Cook 1960, Deacon and Minckley 1974, Naiman 1981). Below Zion National Park, Utah, several natural physicochemical and geographic barriers disrupt the continuity of the biotic communities. These include Pah Tempe Springs, a series of over 100 saline hot springs emerging along the Hurricane Fault in Utah; and the Virgin River Gorge in Arizona where, during much of the year, the entire flow seeps below ground and reemerges in springs above Littlefield, Arizona (Sandberg and Sultz 1982).

The fish fauna of the Virgin River consists of

only six native species: speckled dace (*Rhinichthys osculus*); flannelmouth sucker (*Catostomus latipinnis*); desert sucker (*Catostomus [Pantosteus] clarki*); Virgin spinedace (*Lepidomeda mollispinis mollispinis*) and Virgin roundtail chub (*Gila robusta seminuda*), the latter two of which are endemic subspecies; and woundfin (*Plagopterus argentissimus*), which is an endemic species. The woundfin is listed as endangered (U.S. Fish and Wildlife Service 1986), the Virgin roundtail has been recommended for endangered status, and the Virgin spinedace has been recommended for threatened status (Deacon 1979, Deacon et al. 1979). The red shiner, *Notropis lutrensis*, was introduced into the Colorado River system as a bait fish in the early 1950s (Hubbs 1954). Of the 13 introduced fish species recorded from the lower Virgin River (Cross 1985), only the red shiner has become well established (Williams 1977, Cross 1978a).

Agricultural diversion and groundwater use since 1900 have reduced flows in the mainstream to the extent that long stretches may be dry during summer months. Following completion of the Quail Creek Reservoir project early in 1985, an unanticipated, dramatic increase in discharge of Pah Tempe Springs

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caused increases in both temperature and salinity throughout the downstream segment of the Virgin River in Utah (Deacon, in press). Summer river temperatures fluctuate by 15–20 C daily, reaching 36 C in some areas (Cross 1975, Deacon 1977, Schumann 1978). However, except for the roundtail (Schumann 1978) and Virgin spinedace (Espinosa and Deacon 1978), the temperature responses of the native fishes have not been examined.

This paper reports preliminary investigations of the temperature tolerances and preferences of the native fishes and the introduced red shiner.

METHODS AND MATERIALS

Collection and Maintenance of Specimens

Suckers, spinedace, speckled dace, woundfin, and red shiners were collected during May and June using 10-m nylon seines with 6.4-mm mesh. Virgin roundtail adults were collected between April and October. Captured fish were acclimated in aerated and filtered 450-liter and 1100-liter aquaria, containing aged tap water maintained at temperatures of 10, 15, and 25 ± 1 C, for at least two weeks before testing (Otto 1973, Feldmeth and Baskin 1976, Otto and Rice 1977). Fish were maintained on a 12-hour photoperiod and fed Purina Trout Chow daily. Food was withheld for 25 hours prior to experimentation. All experiments were conducted between June and August to avoid the influences of seasonality and aging (McCauley et al. 1977).

Critical Thermal Limits

Tolerance of high temperature was measured as critical thermal maximum (CTM) (Lowe and Heath 1969, Fry 1971, Feldmeth and Baskin 1976). The CTM was determined for six individuals of each species at each acclimation temperature in an aerated 13-liter glass chamber immersed in a Masterline 2095 water bath. Fish were introduced into the chamber at their acclimation temperature. After a 60-minute adjustment period, the chamber was heated at a constant rate of 0.24 C/minute until the animal lost equilibrium. At that point the fish was immediately returned to its acclimation temperature. No more than three fish were used in a single test. The temperature at which loss of equilibrium is

observed is an unambiguous endpoint, ecologically equivalent to death in a natural situation where the animal would then be unable to escape lethal conditions (Fry 1971). CTMs were not measured for 15-C-acclimated suckers of either species (see next section).

Thermal Preferendum

Acute preferred temperatures (Reynolds and Casterlin 1979) were determined for six individuals of each species (except the suckers and the roundtail chub) at all acclimation temperatures. Testing was done in a horizontal gradient consisting of three 20-liter aquaria joined lengthwise and partitioned to give six small chambers, each $16 \times 20 \times 21$ cm. One end was cooled by plastic-coated copper coils through which refrigerated water was circulated, while the other end was heated with 100-W aquarium heaters. Aeration in each cell prevented gas supersaturation and temperature stratification. Fish could thus choose temperatures between approximately 8 C and 35 C. Tests were observed from behind a blind, and temperatures were measured by mercury thermometers in each chamber.

Preliminary tests without a thermal gradient demonstrated that selection was not spatially influenced in any of the species. This was further avoided during the course of the experiments by a slight shift of temperatures along the gradient.

Two or three individuals of a single species were introduced into the chamber closest to their acclimation temperature and left undisturbed for 30 minutes. Chamber temperatures and the distribution of the animals in the gradient were then recorded at 10-minute intervals for one hour, and at 20-minute intervals for the next two hours. The fish were then removed and their length and weight recorded (Table 1).

Time and resource constraints prevented our collecting enough suckers (of either species) to provide complete acclimation groups. Therefore, preferenda are reported for fewer than six individuals at most acclimation temperatures (Table 2). Likewise, insufficient numbers of Virgin roundtail adults small enough to fit the apparatus were available at the time of the tests. Consequently, young-of-the-year roundtails spawned in captivity from adults captured from the nearby Moapa River in Nevada were acclimated to 8 C, 22 C, 25 C,

TABLE 1. Critical thermal maxima (CTM) at three acclimation temperatures for the common fishes of the Virgin River. Each number is the mean \pm 1 standard deviation for six fish, except that only three desert suckers were used at 25 C and three flannelmouth at 10 C. A range in length is shown for roundtail.

Species	T _{accl} (°C)			Length (mm)	Weight (gr.)
	10	15	25		
Roundtail chub	27.90 \pm 0.22	32.30 \pm 1.39	36.41 \pm 0.66	120 - 233	62.60 \pm 47.60
Speckled dace	30.47 \pm 1.60	32.57 \pm 0.46	36.82 \pm 0.63	72.17 \pm 12.70	3.73 \pm 1.86
Virgin spinedace	30.25 \pm 0.40	32.90 \pm 0.30	37.02 \pm 0.44	95.79 \pm 7.66	8.54 \pm 1.99
Woundfin	30.70 \pm 0.21	33.58 \pm 1.01	39.47 \pm 0.21	71.27 \pm 10.56	3.35 \pm 1.35
Red shiner	30.10 \pm 1.05	33.07 \pm 0.59	38.80 \pm 0.71	61.47 \pm 6.43	2.92 \pm 1.06
Desert sucker	32.30 \pm 0.64	—	37.17 \pm 0.50	124.60 \pm 22.89	16.35 \pm 7.33
Flannelmouth sucker	31.22 \pm 1.08	—	36.98 \pm 0.29	155.60 \pm 20.94	27.57 \pm 9.48

TABLE 2. Distribution of native and introduced fishes of Virgin River in a thermal gradient. Fish were acclimated to 10, 15, and 25 C. Data for the Virgin roundtail are in Schumann (1978).

Species	Accl. temp.	# fish	# obs.	Temperature				
				Max.	Min.	Mean	σ	Mode
Speckled dace	10	6	77	20	10	14	4.4	9.5 - 10.5
	15	6	78	26	14	16	2.8	14 - 15
	25	6	71	27	9	16	4.2	15 - 16
Virgin spinedace	10	6	68	26	10	19	3.8	18.5 - 19.5
	15	7	86	31	15	21	3.7	21.5 - 22.5
	25	6	78	29	15	23	3.4	24 - 25
Woundfin	10	6	78	20	10	11	2.3	10 - 11
	15	6	69	23	14	16	3.6	14 - 15
	25	6	72	32	13	24	4.8	23.5 - 24.5
Red shiner	10	6	78	22	10	12	3.8	10 - 11
	15	6	50	31	15	23	4.9	23 - 24
	25	6	75	34	10	27	5.0	30 - 31
Desert sucker	10	6	80	28	10	13	4.3	10 - 11
	25	3	36	30	10	22	3.5	20 - 21
Flannelmouth sucker	10	3	46	25	10	14	5.0	10 - 11
	25	6	65	34	15	26	2.8	26 - 27

and 30 C and tested in the same manner as the other species (Schumann 1978). As with the 15-C-acclimated suckers, results were not compared statistically with the other fish but are presented here to complete the picture for the native species.

Analysis of Data

CTM data were analyzed by Welch's unequal-variance analysis of variance (ANOVA) and Bonferroni paired comparisons. Regression lines for CTMs were constructed and compared by covariance analysis (Dixon 1981).

Significance of temperature selection was verified by chi-square tests for each species. Differences between species and between acclimation temperatures were tested by

Welch's unequal-variance ANOVA and Bonferroni paired comparisons (Dixon 1981). These were verified by two-way ANOVA (Burr 1974) and two-way Friedman's test (Tate and Clelland 1957) of the means for each group. Nonlinearity of preference curves was verified by regression analysis (Dixon 1981).

RESULTS

Temperature Tolerance

CTM increased in a linear fashion with acclimation temperature for all species examined. Within any given species, mean CTM values differed significantly ($p < .05$) at different acclimation temperatures (Table 1). CTMs were not significantly different ($p > .05$) between species in either the 10-C- or

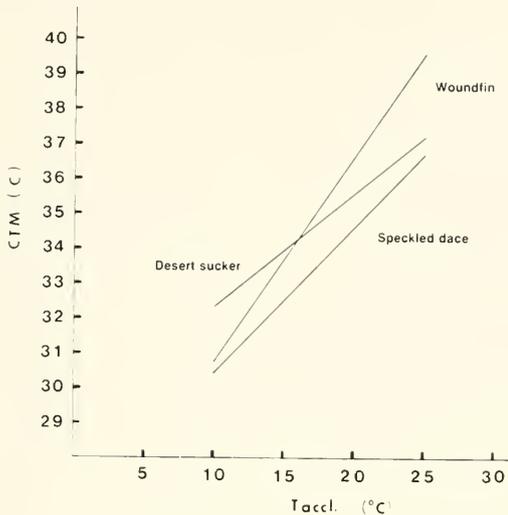


Fig. 1. The effect of acclimation temperature on critical thermal maximum in three Virgin River fishes. Regression lines are presented for one representative species of each group described in the text.

15-C-acclimation groups. However, at 25 C acclimation, the mean CTMs of woundfin and red shiner each differed significantly from all other species ($p < .05$), although they were not significantly different from each other ($p > .05$).

The lines relating CTM to acclimation temperature have slopes ranging from 0.28 (desert sucker) to 0.59 (woundfin). These are illustrated in Figure 1 along with that of the speckled dace, which is intermediate at 0.42. The flannelmouth sucker (0.38), Virgin spinedace (0.45), Virgin roundtail (0.48), and red shiner (0.58) also fall between the extremes. An increase in slope indicates that acclimation temperature has an increased effect on CTM.

Thermal Preference

The frequency distribution of each species in the thermal gradient (Table 2) suggests that variation and skewness were associated with some experimental groups (Richards et al. 1977). For any given species, the mean acute preferred temperature observed at one acclimation temperature differed significantly at the .05 level from the mean preferendum at any other acclimation temperature, with one exception: no significant difference ($p > .05$) was found between acute preferenda of 15-C- and 25-C-acclimated speckled dace. In all

other cases, an increase in acclimation temperature shifted thermal preferenda upward (Figs. 2 and 3). Mean acute preferenda equaled or exceeded acclimation temperature for all species acclimated to 10 C and 15 C. At 25 C acclimation, however, this was true only for the flannelmouth sucker and the red shiner. Modal preferred temperatures likewise equaled or exceeded temperature of acclimation for all species acclimated to 10 C and for all species except woundfin at the 15-C-acclimation level. As was found for the means, modal preferenda in the 25-C-acclimation group were greater than or equal to acclimation temperature for only flannelmouth suckers and red shiners.

DISCUSSION

Despite the large body of information on the physiological performance of organisms with respect to temperature, surprisingly few studies relate this clearly to the organism's ecology (Ferguson 1958, Gift 1977, Richards and Ibara 1978, Huey and Stevenson 1979, Beitinger and Fitzpatrick 1979, Calhoun et al. 1982, Matthews 1986). Only recently have formalized attempts been made to define a "thermal niche" for ectotherms and to apply concepts of niche theory and competition to the thermal resource (Fry 1971, Alderdice 1972, Hutchinson 1978, Magnuson et al. 1979). The Virgin River's considerable spatial and temporal variation in water temperature places greater value on eurythermal species that can operate as "thermal generalists" under suboptimal conditions, but respond opportunistically when preferred thermal situations are encountered. This is the established pattern for desert spring and stream fishes for such factors as food and space (Deacon and Minckley 1974).

Magnuson et al. 1979 state that lethal temperatures are so extreme as to say little about the "fine tuning" of an organism's utilization of its thermal resource. However, these set the outermost limits of the thermal niche and form the bounds of the thermal resistance zone (Reynolds and Casterlin 1979). Our CTM values (Table 1) illustrate the eurythermality of these desert species. This is shown further by the ranges associated with the acute thermal preferences (Table 2). We recorded observations between 10 C and

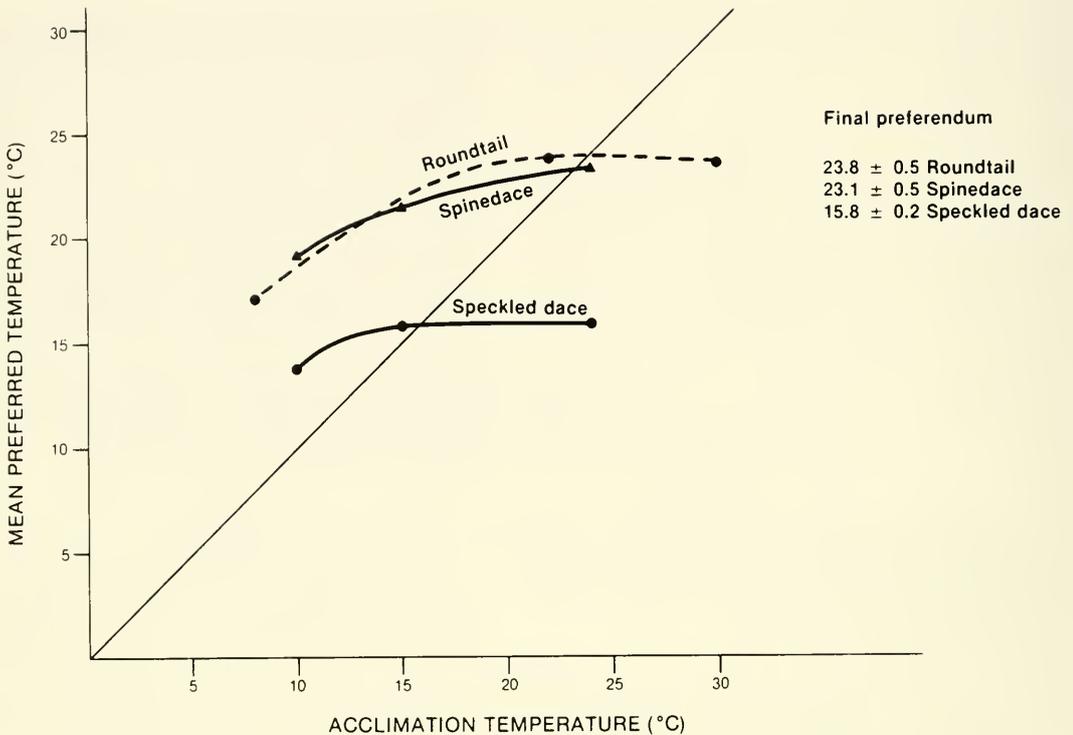


Fig. 2. Influence of acclimation temperature on mean preferred temperature in Virgin River fishes of low thermal lability. Lines fitted by eye.

32–34 C for all species except the desert sucker and speckled dace. Further, when Magnuson et al.'s (1979) operational definition of thermal niche breadth (i.e., mean preferred temperature \pm one standard deviation) is applied to Figure 2, all species exhibit ranges 5–10 C in breadth at all acclimation temperatures. This implies that desert fishes tend to have broader thermal niches than most temperate freshwater fishes previously considered (Reutter and Herdendorf 1974, Beitinger et al. 1975, Coutant 1977, Magnuson et al. 1979).

Nearly all species tested exhibited skewed preferred temperature distributions (Table 2). This resulted in differences between the various measurements of central tendency used to describe them. The skewed patterns may be partly attributable to the design of the apparatus, but similar findings have been reported by De Witt (1967), Reynolds and Casterlin (1976, 1979), and others using a variety of designs. This widespread phenomenon and its possible causes and effects have been re-

viewed in detail by De Witt and Friedman (1979).

Fry (1947) defined the final thermal preferendum, in part, as being the point where preferred temperature equals acclimation temperature. He considered this a largely species-specific phenomenon, independent of the animal's previous thermal history. This concept has garnered considerable attention in recent years, although, surprisingly, its potential for bridging the gap between thermal physiology and ecology has remained relatively unexplored (Reynolds 1977).

The results of our attempts to define the final thermal preferendum of the Virgin River fishes are shown in Figures 2 and 3. Each curve was fitted by eye to the mean acute preferendum values according to the method of Reynolds and Casterlin (1979) (see also Otto and Rice 1977, Garside et al. 1977, Richards and Ibara 1978). This gave approximate final preferenda of 27.0 C for the red shiner, 25.9 C for the flannelmouth sucker, 23.8 C for the roundtail, 23.1 C for the spinedace, 19.5 C for

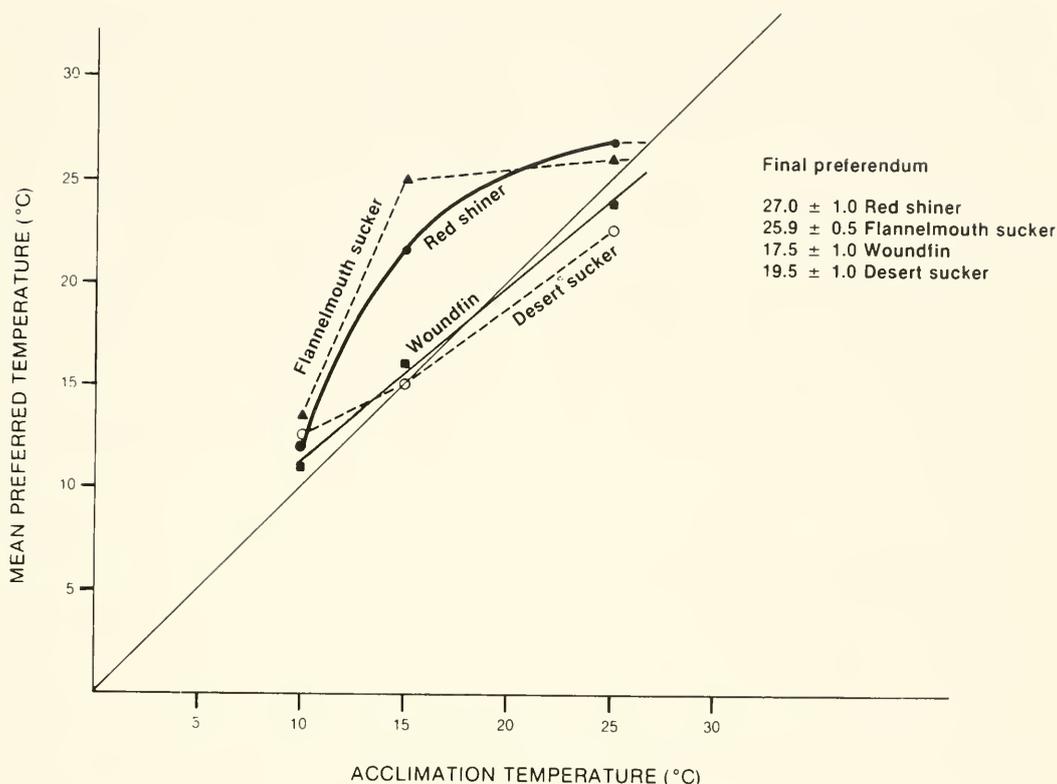


Fig. 3. Influence of acclimation temperature on mean preferred temperature in thermally labile Virgin River fishes. Dashed curves are hypothesized from responses of a single 15-C-acclimated specimen (see text). Lines fitted by eye.

the woundfin, 17.5 C for the desert sucker, and 15.8 C for the speckled dace. Final preferenda of 30.0 and 23.3 C have been determined for populations of red shiner in two distinctly different habitats in Texas (Calhoun et al. 1982).

Three types of curves are represented in Figures 2 and 3. The curves most closely approximating the line of equality (Fig. 3) indicate a maximally thermally labile species. This situation, represented most strongly by the woundfin, suggests that the species prefers the temperature in which it finds itself. This may be adaptive for a fish subjected to widely varying thermal conditions. As long as it can acclimatize successfully to ambient conditions, it probably operates near peak physiological efficiency throughout much of the range of seasonal variation encountered (Beitinger and Fitzpatrick 1979). The curves diverging most strongly from the line of equality (Fig. 2) characterize species whose pre-

ferred temperature remains nearly unchanged despite wide variations in acclimation temperature (Brett 1952, McCauley et al. 1977). The curves for the red shiner and flannelmouth sucker (Fig. 3) differ from both of the above two types. At cooler temperatures, rising acclimation temperatures shift preferenda upward rapidly, while at warmer temperatures, acclimation temperature has relatively little influence on preferred temperature. These three apparently different types of curves provide interesting insight into the ecology and distribution of fishes in the Virgin River.

The woundfin has a high CTM, relatively low final preferendum, and the most labile acute preferendum of any of the species examined. It is the dominant native species in the moderately altered sections of the middle and lower mainstream where temperature variability is extreme (Cross 1978a, Deacon and Hardy 1984). The thermal lability of the

woundfin is most strikingly demonstrated by the ability of acclimation temperature to influence preferred temperature. This capability, however, becomes somewhat reduced at higher temperatures as the thermal selection curve diverges from the line of equality (Fig. 3). At higher temperatures, then, the red shiner may have an advantage over woundfin, while at lower temperatures (below 25 C), the reverse may occur.

The thermal selection curve for the desert sucker suggests that it, too, is thermally labile. It diverges more from the line of equality at both higher and lower temperatures than does the woundfin; however, the final preferendum is also somewhat lower, suggesting a more upstream (cooler) pattern of distribution and abundance than woundfin. The desert sucker is in fact the most widely distributed species in the Virgin River system, reaching greatest abundance in middle and lower tributaries and the upper mainstream. Abundance drops in the lower, warmer mainstream and in the upper, cooler tributaries (Cross 1975, 1985).

The thermal selection curves of the other native species are uniformly similar in shape, differing primarily in vertical displacement. All appear less labile than the woundfin and desert sucker. The speckled dace, with the lowest final preferendum, has the most upstream distribution. It achieves greatest abundance in middle and lower tributaries and the upper mainstream. In the middle and lower mainstream it is almost always associated with cool, clear inflowing tributaries or springs. The Virgin spinedace, with the next highest final preferendum, has a slightly more downstream distribution. It is most abundant in lower tributaries and the upper mainstream. More downstream occurrences are primarily associated with tributary and spring inflows. The flannelmouth sucker has the highest final preferendum, but reaches its greatest abundance in the upper mainstream. Its downstream distribution, however, is not as restricted to tributary and spring inflow as are those of the speckled dace and spinedace. In general, the distributional relationships of these three species (Cross 1975) correspond well with the thermal relationships illustrated in Figures 2 and 3. Note also that the flannelmouth sucker (which had the highest final preferendum of any native species) and the

woundfin (with the highest CTM) most often approach the Pah Tempe hot spring inflows more closely than other species (Cross 1975, Williams 1977).

The Virgin roundtail has a thermal selection curve very similar to that of the spinedace. It has the lowest CTM value of any native species in the river and an intermediate final preferendum. Acclimation temperature has relatively little influence on its preferred temperature. This species is confined to the middle and lower mainstream of the Virgin River below Pah Tempe Springs (Cross 1978b). The roundtail is no longer perennially abundant anywhere within its range, although there is evidence that it once was (Cross 1978b). Increased diversion of water for irrigation, increased irrigation return flow in the heat of the summer, clearing of streamside vegetation, overgrazing in the watershed, and other activities associated with man's use of the region may have increased summer temperatures within the range of the roundtail. Lack of suitable tributary streams, plus the barrier provided by Pah Tempe Springs, has perhaps prevented upstream displacement of roundtail populations. Their thermal relationships suggest a pattern of distribution and abundance in the Virgin River similar to that of the spinedace. The fact that most good spinedace habitat is unavailable to the roundtail may partly explain its present precarious status in the Virgin River.

The thermal selection curves for the red shiner and flannelmouth sucker are different from those of other native species. The red shiner has a high CTM, and a higher final preferendum than any native species. It occurs throughout the lower mainstream but, until 1985, was abundant only in the deeper water (> 8 cm) of the highly modified lower reach, where the flow is intermittent through a wide, shallow, braided channel. Here, summer temperatures appear to exceed 30 C more often, and for longer periods, than elsewhere in the river. The red shiner is the dominant species in this segment of the river and is often accompanied by fewer numbers of woundfin. Other native species occur sporadically. Occasionally woundfin reach numbers nearly equaling those of the red shiner (Cross 1975, Deacon and Hardy 1984, Deacon, in press).

Woundfin and red shiner shift their CTM

more markedly in response to increase in acclimation temperature than do other species. This apparently provides both species with an advantage over other native fishes in the warmer, more thermally variable, shallow waters of the lower river. The higher final preferendum exhibited by the red shiner suggests that that species may have a thermal advantage over the woundfin during the summer in this lower segment of the mainstream.

The flannelmouth sucker has only a slightly lower final preferendum than does the red shiner, but at an acclimation temperature of 25°C the sucker has a significantly lower CTM. This may partly explain the near absence of the flannelmouth sucker in Virgin River below Mesquite, Nevada.

Thermal tolerance and preference relationships are not the only factors involved in niche partitioning in the Virgin River. Preferred temperatures may be unavailable over large stretches of the river, or for long periods of time. Interactions influencing utilization of food, space, and other resources affect the fishes as well (Cross 1975, 1978a, 1978b, Deacon 1979, Deacon and Hardy 1983, Greger 1983). Temperature relations determined in the laboratory do not always correspond well to field distributions (Reynolds 1977, Magnuson et al. 1979, Reynolds and Casterlin 1979), but in the case of the Virgin River fishes, the correspondence is striking.

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