

Temperature-mediated feeding between spring-associated and riverine-associated congeners, with implications for community segregation

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Freshwater fish communities segregate along water temperature gradients attributed in part to temperature-mediated physiological processes that affect species fitness. In spring complexes of southwest USA, spring complexes with narrow range of water temperatures are dominated by a community of fishes (i.e., spring-associated fishes), whereas riverine habitats with wide-range of water temperatures are dominated by a different community of fishes (i.e., riverine-associated fishes). The purpose of this study was to test a prediction of the concept that temperature-mediated species performance is a mechanism in maintaining community segregation. We predicted that a spring-associated fish (Largespring Gambusia *Gambusia geiseri*) would feed first and more often in a pairing with a riverine-associated fish (Western Mosquitofish *Gambusia affinis*) at an average spring temperature (23°C) and that the riverine-associated fish would feed first and more often in a pairing with the spring-associated fish at a warm riverine temperature (30°C). Among four trials consisting of 30 pairings, at the spring complex temperature (23°C), Largespring Gambusia had a greater number of first feeds (mean \pm 1 SD, 5.0 ± 0.82) than Western Mosquitofish (2.5 ± 1.73) and had greater mean number of total feeds (1.9 ± 0.31) than Western Mosquitofish (0.81 ± 0.70). At the riverine environment temperature (30°C), Western Mosquitofish had a greater number of first feeds (5.25 ± 1.71) than Largespring Gambusia (2.5 ± 1.73) and had greater mean number of total feeds (2.78 ± 1.05) than Largespring Gambusia (0.94 ± 0.68). Our findings suggest that temperature-mediated species performance could be maintaining segregation between the two fish communities. This study benefits our understanding of distributional patterns and improves threat assessments of stenothermal aquatic organisms.

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2 **Temperature-mediated feeding between spring-associated and riverine-associated**
3 **congeners, with implications for community segregation**

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11

Abstract

12 Freshwater fish communities segregate along water temperature gradients attributed in part to
13 temperature-mediated physiological processes that affect species fitness. In spring complexes of
14 southwest USA, spring complexes with narrow range of water temperatures are dominated by a
15 community of fishes (i.e., spring-associated fishes), whereas riverine habitats with wide-range of
16 water temperatures are dominated by a different community of fishes (i.e., riverine-associated
17 fishes). The purpose of this study was to test a prediction of the concept that temperature-
18 mediated species performance is a mechanism in maintaining community segregation. We
19 predicted that a spring-associated fish (Largespring Gambusia *Gambusia geiseri*) would feed
20 first and more often in a pairing with a riverine-associated fish (Western Mosquitofish *Gambusia*
21 *affinis*) at an average spring temperature (23°C) and that the riverine-associated fish would feed
22 first and more often in a pairing with the spring-associated fish at a warm riverine temperature
23 (30°C). Among four trials consisting of 30 pairings, at the spring complex temperature (23°C),
24 Largespring Gambusia had a greater number of first feeds (mean \pm 1 SD, 5.0 ± 0.82) than
25 Western Mosquitofish (2.5 ± 1.73) and had greater mean number of total feeds (1.9 ± 0.31) than
26 Western Mosquitofish (0.81 ± 0.70). At the riverine environment temperature (30°C), Western
27 Mosquitofish had a greater number of first feeds (5.25 ± 1.71) than Largespring Gambusia ($2.5 \pm$
28 1.73) and had greater mean number of total feeds (2.78 ± 1.05) than Largespring Gambusia (0.94
29 ± 0.68). Our findings suggest that temperature-mediated species performance could be
30 maintaining segregation between the two fish communities. This study benefits our
31 understanding of distributional patterns and improves threat assessments of stenothermal aquatic
32 organisms.

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Introduction

35 Aquatic species and communities are distributed along altitudinal, geographical, and
36 longitudinal gradients where habitats, food resources, predation, and water quality conditions
37 differ (Vannote et al., 1980; Taniguchi & Nakano, 2000). Among freshwater fishes, water
38 temperature is one of several described mechanisms regulating distributional patterns (Grossman
39 & Freeman, 1987). Temperatures can influence interspecific interactions within freshwater fish
40 communities when species temperature tolerances are overlapping (Taniguchi et al., 1998).
41 Temperature-mediated interactions and its influence on species distributions, though difficult to
42 quantify in nature (Gerking, 1994), are supported in laboratory experiments. Taniguchi et al.
43 (1998) and Taniguchi & Nakano (2000) compared water temperature tolerances and behaviors
44 among fishes distributed along an altitudinal gradient and found fish that inhabit cooler water at
45 higher altitudes was more aggressive, consumed more food, had faster growth, and greater
46 survival rate at cooler temperatures than lower altitude fishes. Conversely, fishes, which inhabit
47 warmer water at lower altitudes, were more aggressive, consumed more food, and had faster
48 growth at warmer temperatures than the higher altitude fish. Carmona-Catot, Magellan &
49 Garcia-Berthou (2013) quantified pairwise feeding performance at three temperatures (i.e., 19,
50 24, and 29°C) of an introduced warm-water cyprinodont and a native cool-water cyprinodont to
51 assess temperature-mediated interactions in non-native species range expansion and native
52 species extirpation potential. The invasive warm-water cyprinodont had a lower food capture rate
53 compared to the native cool-water cyprinodont at the coolest temperature. At warmer
54 temperatures, the invasive warm-water cyprinodont had a greater food capture rate compared to
55 native cool-water cyprinodont. Laboratory results of temperature-mediated interactions suggest
56 water temperature regulates fish distributions.

57 Spring complexes within limestone formations of southwest USA are evolutionary
58 refugia with stenocious water quality, including thermally-constant water temperatures (i.e.,
59 stenothermal habitat; range 21.0 - 23.3°C), and distinct fish communities consisting of spring-
60 associated fishes that have greater relative abundances and densities within spring complexes
61 (Craig et al., 2016). As spring complexes transition downstream into riverine environments with
62 less thermally-constant water temperatures (i.e., eurythermal habitat; range: 6 - 30°C) attributed
63 to ambient conditions and merging with higher order streams, relative abundances and densities
64 of spring-associated fishes are reduced and different species of fishes (i.e., riverine-associated
65 fishes) become dominant. Similar to altitudinal gradients (Taniguchi et al., 1998; Taniguchi &
66 Nakano, 2000), water temperature is a suggested mechanism in regulating richness, abundances,
67 and densities of spring-associated fishes and riverine-associated fishes (Hubbs, 1995; Kollaus &
68 Bonner, 2012) with spring-associated fishes being potentially more fit in stenothermal habitats
69 and riverine-associated fishes being potentially more fit in eurythermal habitats. Dissimilar to
70 altitudinal gradients, spring-associated fishes and riverine-associated fishes do not represent
71 previously researched cold-water and warm-water forms with overlapping tolerances, but both
72 are warm-water forms having similar temperature tolerances (Hagen, 1964; Brandt et al., 1993).
73 In marine systems, species in stenothermal habitats might select away from eurythermal enzymes
74 and proteins (Graves & Somero, 1982) and select for proteins and enzymes that are more energy
75 efficient within a narrow range of temperatures (Pörtner, Peck & Somero, 2007), whereas species
76 in eurythermal habitats are suggested to conserve temperature-dependent enzymes and proteins
77 that enable tolerance of wide-ranging water temperatures (Somero, Dahlhoff & Lin, 1996).
78 Differences in fitness between spring-associated fishes in stenothermal habitats and riverine-

79 associated fishes in eurythermal habitats could explain patterns in fish community segregation in
80 spring-river systems.

81 Purpose of this study was to test predictions of the concept that stenothermal habitat of
82 spring complexes is a factor in maintaining community segregation between spring-associated
83 and riverine-associated fishes. The study objective was to quantify feeding (i.e., first feed and
84 number of total feeds) as a measure of performance between spring-associated and riverine-
85 associated fish pairs at two water temperatures and determine if water temperatures favored one
86 species over the other. Water temperatures selected were 23°C, a typical water temperature in
87 spring complexes, and 30°C, a typical summertime temperature in riverine environments. We
88 used two congeneric species (spring-associated Largespring Gambusia, *Gambusia geiseri* and
89 riverine-associated Western Mosquitofish, *Gambusia affinis*; Hubbs, Edwards & Garrett, 2008)
90 with similar thermal tolerances (Hagen, 1964) and mostly abutted distributions in spring-river
91 systems (Watson, 2006; Behen, 2013). If water temperature mediates feeding and therefore
92 potential interactions, we predict *G. geiseri* will eat first and eat more food items than *G. affinis*
93 at 23°C and *G. affinis* will eat first and eat more food items than *G. geiseri* at 30°C. Ability to
94 identify stenothermic aquatic organisms and quantify temperature-mediated segregation will
95 benefit our understanding of distributional patterns and improve threat assessments.

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Materials and methods

99 Laboratory specimens were collected with a seine from the Guadalupe River drainage
100 basin under Texas Parks and Wildlife Scientific Research Permit No. SPR-0601-159. *Gambusia*

101 *geiseri* were collected from a site (29°53'22.2"N, 97°56'03.7"W) on the San Marcos River.
102 *Gambusia affinis* were collected from a site (29°54'43.8"N, 97°53'50.3"W) on the Blanco River
103 approximately 13 river kilometers away from the *Gambusia geiseri* collection site. Sexually-
104 mature *Gambusia* >20 mm in total length (TL) (Stevens, 1977; Haynes & Cashner, 1995) were
105 retained. Fishes were transported to a laboratory at Texas State University Freeman Aquatic
106 Biology Building and were drip acclimated to 23°C with well water from the Edwards Aquifer,
107 which is the same water source as the San Marcos and Blanco rivers (Groeger et al., 1997) and
108 followed approved Texas State University Institutional Animal Care and Use Committee
109 protocol (approval number: 201658034). Fishes were separated by species and placed into 35-L
110 glass aquaria submersed in a LS-700 Living Stream (Frigid Units, Inc.). Each aquarium was
111 equipped with a sponge filter. The Living Stream utilized a dual feedback heating and cooling
112 system to maintain desired temperature within $\pm 0.5^\circ\text{C}$. Photoperiod was 14 h light:10 h dark. To
113 maintain water quality, 50% water changes by volume were completed every 48 h. Fishes were
114 fed high protein BioDiet Grower 1.2 mm (Bio-Oregon) daily *ad libitum*. To avoid any learned
115 feeding behaviors, fishes were fed at varying times throughout the day and various locations of
116 the aquaria. For 23°C feeding trials, food was withheld 24 h prior to feeding trials. For 30°C
117 feeding trials, water temperature was adjusted 1°C per day for 7 d (Carmona-Catot, Magellan &
118 Garcia-Berthou, 2013). Fishes remained at 30°C for 48 h before use in feeding trials, and food
119 withheld 24 h prior to feeding trials.

120 For pairwise feeding trials, one *G. geiseri* and one *G. affinis* were visually size and sex
121 matched (Carmona-Catot, Magellan & Garcia-Berthou, 2013), placed into a 1.25-L opaque
122 container (23 x 15 cm area), and allowed to acclimate for 1 hour. The container was immersed
123 in the Living Stream to maintain the target temperature within $\pm 0.5^\circ\text{C}$. Five natural prey items

124 (Order Trichoptera, Family Hydroptilidae; Sokolov & Chvaliova, 1936) were placed into the
125 center of the container using a plastic pipette. The species of the individual feeding (i.e., strikes
126 that consumed all, part, or none of the prey) first was recorded and total feeds were recorded for
127 both individuals. Each pairwise trial was limited to five minutes or until all food items were
128 consumed. After completion, fishes were euthanized in MS-222 (Tricane-S) and preserved in
129 10% formalin; therefore, a fish was used only once in a feeding trial. For a no feed trial, the two
130 individuals were given an additional 30 minutes to acclimate and tried for an additional trial.
131 Four independent test batches were conducted at 23°C and 30°C. A test batch was defined as all
132 successful feeding trials at a certain temperature conducted within a 4 – 6 h period. All test
133 batches were conducted between May 2017 and July 2017. Targeted number of pairwise
134 matches was 10 to 11 per batch, but fish jumped out of the container on four occasions, and
135 neither fish eating after 30 minutes occurred on 16 occasions. For both instances, the pairwise
136 trial was ended and recorded observations were discarded.

137 Number of first feeds and mean number of total feeds were calculated for each species by
138 target temperature. Number of first feeds was calculated by summing the number of first feeds
139 by species per batch. Mean number of total feeds was calculated by summing of total feeds by
140 species in each batch and dividing by the number of pairwise trials. One tailed two sample t-tests
141 (SAS Institute, Cary, North Carolina) were used to detect differences in first feeds and mean
142 number of total feeds between species at 23°C and 30°C. Use of one tailed t-tests were justified
143 by the a priori prediction that the spring-associated fish would outperform at 23°C and the
144 riverine-associated fish would outperform at 30°C.

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Results

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Discussion

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At 23°C, 30 pairwise first feeds and 82 total feeds were observed out of 150 food items offered between *G. geiseri* and *G. affinis* pairs among four batches. Number of first feeds was greater ($t = 2.61$, $df = 6$, $P = 0.02$) for *G. geiseri* than *G. affinis* (Table 1). Mean number of total feeds was greater ($t = 2.82$, $df = 6$, $P = 0.02$) for *G. geiseri* than *G. affinis*.

At 30°C, 31 pairwise first feeds and 111 total feeds were observed out of 160 food items offered between *G. geiseri* and *G. affinis* pairs among four batches. Number of first feeds was greater ($t = 2.26$, $df = 6$, $P = 0.03$) for *G. affinis* than *G. geiseri*. Mean number of total feeds was greater ($t = 2.94$, $df = 6$, $P = 0.01$) for *G. affinis* than *G. geiseri*.

Our predictions that spring-associated *G. geiseri* has greater feeding performance than riverine-associated *G. affinis* at a temperature typical of a spring complex, and conversely, *G. affinis* has greater feeding performance than *G. geiseri* at a temperature typical of a summertime riverine environment were supported by pairwise trials. These results are similar to temperature-mediated feeding performances among families, genera, and species reported by others (De staso & Rahel, 1994; Taniguchi et al., 1998; Taniguchi & Nakano, 2000; Carmona-Catot, Magellan & Garcia-Berthou, 2013). This study, however, is novel in that it documents temperature-mediated performance between a spring-associated fish and a riverine-associated fish with similar thermal tolerances (Hagen 1964). Greater feeding performance of *G. affinis* at a water temperature of 30°C corresponds with the reported fastest growth rates and greatest natality rates of *G. affinis* at 30°C when compared to 20 and 25°C (Vondracek, Wurtsbaugh & Cech, 1988). Our results and

170 the findings of Vondracek Wurtsbaugh & Cech (1988) suggest that a warmer water temperature
171 increases physiological and feeding performance of *G. affinis*, which corresponds with
172 distributions of *G. affinis* during summertime in riverine environments. Conversely, a water
173 temperature typical of spring complexes increases feeding performance for *G. geiseri*, which
174 corresponds with distributions of *G. geiseri* during summertime in spring complexes. Growth
175 rates, natality rates, and other measures of physiology are not known at this time for *G. geiseri*.

176 In order to show ubiquity of temperature-mediated performance as a mechanism for
177 segregation among species distributions, feeding comparisons in addition to quantification of
178 other temperature-mediated performance measures (e.g., growth and swimming performance)
179 can be assessed for several other closely related taxa with similar distributions as *G. geiseri* and
180 *G. affinis* within spring-river systems, such as spring-associated *Etheostoma lepidum* (Hubbs,
181 1985) and riverine-associated *E. spectabile*, *E. fonticola* (Bonner & McDonald, 2005) and *E.*
182 *proeliare*, *Cyprinella proserpina* (Hubbs, 1995) and *C. lutrensis*, *Dionda argentosa* (Garrett,
183 Hubbs & Edwards, 2002) and *D. diaboli*, and *Ictalurus lupus* (Sublette, Hatch & Sublette, 1990)
184 and *I. punctatus*. In addition, spring-associated fishes and riverine-associated fishes maintain
185 segregation during the winter when water temperatures of riverine environments are colder than
186 water temperatures of spring complexes (Kollaus & Bonner, 2012). Assessments of feeding
187 performance among spring-associated fishes and riverine-associated fishes at typical winter time
188 temperatures would complete the range of conditions in which segregation is maintained.
189 Ultimately, quantification of genetic, physiological, and biochemical mechanisms will be
190 necessary to describe underlying temperature-mediated performance of spring-associated and
191 riverine-associated species (see review in Somero, Dahlhoff & Lin, 1996). At a minimum,
192 known mechanisms for stenotherm radiation and maintenance can serve as a basis for

193 understanding evolutionary origins and maintenance of segregation among spring-associated and
194 riverine-associated fishes.

195 Ability to identify stenothermic aquatic organisms and to quantify temperature-mediated
196 segregation will benefit our understanding of distributional patterns and improve threat
197 assessments. Stenothermic organisms are potentially more sensitive to temperature changes
198 related to physical habitat alterations and global climate change than eurythermic organisms
199 because of the lack of gene product selection associated with eurythermic organisms (Somero,
200 Dahlhoff & Lin, 1996). Physical habitat alterations include instream or riparian modifications
201 that manipulate the energy budget or thermal capacity of the surface water (Poole & Berman,
202 2001), such as discharge of heated effluents (Langford, 1990; Olden & Rahel, 2008), removal of
203 riparian vegetation (Moore, Spittlehouse & Story, 2005), stream channel modification (Nelson &
204 Palmer, 2007), dams and diversions (Olden & Naiman, 2010), and reduction of discharge
205 through groundwater pumping (Sinokrot & Gulliver, 2000). Groundwater sources supporting
206 spring complexes of southwest USA are commodities (Loaiciga, 2003), and groundwater harvest
207 is linked to the loss of spring complexes and associated biota (Craig & Bonner, unpublished data
208 ; Winemiller & Anderson, 1997). Continued climate change in North America is predicted to
209 alter stream flow patterns, increasing storm events, decreased dissolved oxygen, and increases in
210 groundwater temperatures (Poff, Brinson & Day, 2002; Ficke, Myrick & Hansen, 2007). As with
211 physical habitat alterations, stenothermic aquatic organisms are predicted to follow isoclines of
212 suitable habitat (Ficke, Myrick & Hansen, 2007), remain in place and wait for better times, adapt
213 to changes, or become extinct (Clarke, 1996).

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Conclusions

217 In conclusion, this study supports a prediction that temperature mediates species distribution of a
218 spring-associated and a riverine-associated fish through laboratory trials. Novel results of this
219 study show temperature-mediated feeding performance of two species with similar temperature
220 tolerances that inhabit spring-river systems. Although further work is needed to test for the
221 ubiquity among other fishes, this study suggests temperature to be a structuring mechanism for
222 organisms in spring-river systems.

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Table 1 (on next page)

Number of first feeds and mean number of total feeds by batch for *Gambusia geiseri* and *Gambusia affinis* at 23°C and 30°C.

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Temperature	Batch	N of pairs	Number of first feeds		Mean number of total feeds	
			<i>G. geiseri</i>	<i>G. affinis</i>	<i>G. geiseri</i>	<i>G. affinis</i>
23°C	1	7	5	2	2.29	0.29
	2	6	4	2	2.00	0.83
	3	6	5	1	1.60	0.33
	4	11	6	5	1.70	1.80
	Mean		5.00	2.50	1.90	0.81
	SD		0.82	1.73	0.31	0.70
30°C	1	9	3	6	1.44	2.11
	2	7	4	3	1.43	2.71
	3	7	0	7	0.00	4.29
	4	8	3	5	0.88	2.00
	Mean		2.50	5.25	0.94	2.78
	SD		1.73	1.71	0.68	1.05

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