Evolutionary history and developmental plasticity interact to shape the feeding responses of prey under predation threat
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by

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ABSTRACT

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Many prey species display behavioral responses to environmental cues from predators. Organisms can inherit fixed behavioral responses to certain predators as a result of evolutionary history with a predator. Developmental plasticity allows individuals to associate predation risk with environmental cues experienced in their lifetimes and respond behaviorally. However, the interactive effects of evolution and plasticity on shaping immediate antipredator behavior is not well known. Here we show that evolution and developmental plasticity affect antipredator behavior of western mosquitofish (Gambusia affinis) through altered food intake in response to predation risk imposed by largemouth bass (Micropterus salmoides). Results show that the effects of evolutionary history and developmental plasticity are substitutive – mosquitofish show a similar level of feeding if they originated from ponds with largemouth bass (evolutionary history) or if they originated from ponds lacking largemouth bass but have been exposed to bass cues during development (developmental plasticity). Mosquitofish lacking both evolutionary history and developmental cues from the predator did not show a behavioral response. For populations lacking an evolutionary history with bass, developmental exposure to the predator was required to induce a behavioral response. In contrast, populations with
an evolutionary history with bass displayed antipredator behavior regardless of
whether they had been exposed to bass cues during development. Our results suggest
a progression of anti-predator feeding responses of prey from no behavioral response,
to an inducible response, to a fixed response. This sequence may shift the cascading
ecosystem effects of predators introduction from density-mediated to behaviorally-
mediated via plasticity to behaviorally mediated via evolution over time.
INTRODUCTION

Many prey species show behavioral responses to environmental cues from predators. Behavioral responses can be immediate, consistent responses displayed multiple times over an individual’s life in response to familiar environmental cues associated with predators (Foster 2013). If an individual fails to recognize and respond to environmental cues from predators, the consequence may be death. Environmental cues can manifest as visual (prey visually detects predators) or chemical triggers (prey recognizes predator and/or conspecific alarm cues), both of which have the potential to impact antipredator response (Lehtiniemi 2005). Both inherited behavioral traits (evolutionary history) and an individual’s past experience with certain predator species (developmental plasticity) can modify the immediate antipredator behavioral response (Sih et al. 2004). One such antipredator response is to adjust food intake. For example, an individual may reduce the time it spends feeding in response to the presence of a predator (Lima & Dill 1990). Extensive research has demonstrated the independent effects of evolutionary history and developmental plasticity on antipredator behavioral response (O’Steen et al. 2002; Reznick et al. 1990; Trussell & Smith 2000; Arnett & Kinnison 2016). Yet, studies rarely explore how evolution and plasticity interact to shape immediate antipredator behavior.

Organisms can inherit fixed behavioral responses to certain predators as a result of evolutionary history with a predator. Specifically, individuals from populations that have evolved in the presence of specific predators may display adaptive behavioral
responses to that predator, even if they had never directly encountered it. Adaptive behavioral responses to specific predator species are common across a diversity of prey species (e.g., guppies (*Poecilia reticulata*): (Seghers 1974; Magurran & Seghers 1990); European minnow (*Phoxinus phoxinus*): (Magurran 1990); damselflies: (Stoks et al. 2003). Studies examining adaptive behavioral responses to predators have also found evidence for a loss of antipredator behavior when predators are absent (O’Steen et al. 2002) suggesting a fitness trade-off.

Developmental plasticity allows individuals to associate predation risk with environmental cues experienced in their lifetimes and respond behaviorally. An individual with previous experience with a certain predator may alter its behavioral response, increasing its likelihood of survival. In contrast, naïve prey may not respond accordingly and thus be at greater risk of predation (Rehage et al. 2005) until they are able to associate predation risk with the appropriate cues. In aquatic systems, chemical cues can be reliable in determining predation risk (Brown 2003). Exposure to a combination of predator cues and damage released conspecific alarm cues during development allows aquatic prey to reliably acquire predator recognition and display antipredator behavior to increase survival (Magurran 1989; Brown 2003). Developmental plasticity can therefore result in behavioral shifts in individuals within a generation, in contrast to behavioral adaptation which requires multiple generations of evolutionary history with a predator.

Western mosquitofish (*Gambusia affinis*) is a widespread freshwater fish that may alter their behavior in response to predation risk by decreasing food intake. An
individual’s evolutionary history and developmental experience may result in a shift in their antipredator behavioral response through shifts in food intake. Mosquitofish are prey for a number of larger predatory fish, including largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis macrochirus*). Bass act as a strong predator on mosquitofish whereas bluegill are intermediate predators on mosquitofish as well as competitors (Nowlin & Drenner 2000). In response to a predator, mosquitofish will typically decrease food intake and activity and increase refuge use; however, when facing a novel predator western mosquitofish may fail to reduce food intake (Rehage et al. 2005) resulting in a higher risk of predation. Other work has found evidence of behavioral shifts of mosquitofish in response to predator exposure during rearing, favoring both reduced activity and increased boldness in two species of mosquitofish (Arnett & Kinnison 2016). Evolutionary history and developmental plasticity can individually affect behavioral response through changes in food intake, however the interaction between evolution and development on behavioral response is unknown. By understanding the interaction between evolutionary history and developmental experience we can better predict the food intake of individuals and, further, predict the ecological impact of a population.

We tested how evolutionary history and developmental plasticity interact to influence mosquitofish behavioral response (in terms of food intake) to environmental cues from a predator. Evolutionary history and developmental plasticity may interact in three possible ways to enhance survival in the presence of predators: (1) additively – evolutionary history and developmental plasticity independently reduce food intake,
and both together reduce food intake in an additive way; (2) synergistically –
evolutionary history and developmental plasticity independently reduce food intake,
and both together reduce food intake in a synergistic (more than additive) way or (3)
substitutively – evolutionary history and developmental plasticity reduce food intake,
but both together do not reduce food intake beyond each factor alone. Alternatively, if
evolutionary history and developmental plasticity do not influence food intake,
mosquitofish would have the same food intake regardless of evolutionary history and
direct exposure to predator cues.

METHODS

Source populations

Mosquitofish have been spread worldwide to reduce mosquito larvae
abundance (Pyke 2005). In 1922, Western mosquitofish were introduced into
California from sites in Texas and spread throughout the state (Dill and Cordone,
1997). We selected 12 ponds geographically isolated from each other in California
that differed in predator regime: (1) no fish predators (n=5), (2) bluegill predators
(n=3), or (3) largemouth bass predators (n=4). Within these treatments, ponds with
largemouth bass represent high predation risk sites, ponds with bluegill represent
intermediate predation risk sites, and ponds with no predators represent low predation
risk sites.
We measured mosquitofish density at each pond during July and August of 2015. We estimated mosquitofish density for each sample site using the known surface area sampled. Fish were collected using a beach seine and dip net, and a random subsample of mosquitofish was euthanized with an overdose of MS-222 and frozen. Standard length was later measured for a maximum of 50 adult fish per site. Predator community surveys were conducted at each site using a beach seine during June, July, and August of 2016. At one sample site (Furnace Creek) we were unable to use beach seines and instead conducted a visual predator survey (this was a reliable method due to very high water clarity at this site).

**Common rearing**

Our aim was to test how evolutionary history and developmental plasticity interact to shape the immediate behavioral response of mosquitofish to a largemouth bass predator. In our experiment, evolutionary history is represented by the predation regime of each mosquitofish source pond: no predators, bluegill, or largemouth bass. We collected wild (F0) Gambusia from June – August, 2016 with seine and dip nets and transported them to cattle tanks (1135L, Rubbermaid Co.) located at the University of California-Santa Cruz Coastal Campus for common rearing. In our experiment, developmental plasticity was manipulated through the presence or absence of largemouth bass predator cues in the rearing environment. Offspring of wild mosquitofish (F1) from each population were collected twice daily and immediately transferred into tanks representing treatments with either largemouth
bass predator cues present or cues absent. Common rearing occurred from August to October, 2016. Largemouth bass predator cues were added by suspending clear plastic enclosures containing one largemouth bass in each predator treatment cattle tank. Largemouth bass were fed mosquitofish twice per week, so predator cues represented a combination of largemouth bass cues and mosquitofish conspecific alarm cues. Previous studies have found that the pairing of predator cues with conspecific alarm cues allows previously naïve prey to associate predator cues with predation risk (Brown & Smith 1998). Each predator enclosure had mesh-covered holes in the sides to allow for water flow between the bass container and the mosquitofish in the cattle tank.

**Feeding experiment**

We conducted feeding trials to test the effects of evolutionary history, development plasticity, and behavioral plasticity on antipredator behavior by measuring changes in food intake (Figure 1). We ran feeding trials using 12 female F1 fish from each population, if we did not have 12 mature female fish in a given population, we used immature fish. We identified females as being larger than the average male size from that population and lacking any sign of a gonopodium (Pyke 2005). Fish smaller than the smallest male in the population and lacking a gonopodium were classified as immature.

The experimental setup consisted of two separate trial arenas (127x64x45cm), one containing largemouth bass and the other lacking predators. Prior to the start of each
trial, mosquitofish were placed into holding tanks (30x15x20cm) with filtered water from the corresponding cattle tank to keep predator cues consistent. Prior to feeding trials, mosquitofish were not fed for two days. Bass were placed in the predator treatment trial arena and not fed for one to two days before the trial start; in between trials, bass were fed mosquitofish in the trial arena.

Six clear plastic trial tanks (27.5x17x17cm), each containing one mosquitofish and zooplankton prey, were placed into each trial arena and left for one hour before being removed. Feeding behavior was measured using the mass of zooplankton consumed during a trial as a proxy for food intake. Mosquitofish are primarily pelagic predators (Pyke 2005) and, due to this, we chose to use zooplankton as the prey source during the experiment. Zooplankton were collected daily using a zooplankton net (80 µm mesh) at a nearby pond (Antonelli Pond). Contents from the tows were homogenized into 30L of water and a zooplankton sample from each trial was preserved in 80% ethanol to identify prey abundance and composition.

We started each trial by placing one mosquitofish and 100mL of zooplankton water from the homogenized 30L of water mixed previously into each trial tank. An 80 µm mesh filter was secured on the lid of each trial tank to prevent zooplankton escape during the trial, each trial tank was then sunken into a trial arena. At the end of one hour the containers were removed, the mosquitofish euthanized with an overdose of MS-222 and frozen for preservation. We ran a total of 24 trials, with 4 groups of 3 populations run together. Each group was run in 6 consecutive trials and consisted of
three random populations of varying predator regimes. We later measured standard length for each fish using ImageJ.

We examined prey availability during the trials by counting and measuring a subset of zooplankton from each trial. Samples were split using a plankton splitter to obtain a minimum of 150 individuals. Each individual was identified down to genus when possible and 20 individuals from each genus were measured. There was some variation in zooplankton prey abundance and composition between trials however there was high enough abundance of zooplankton in all trials that they were never depleted.

We calculated gut content mass for each fish by removing the gut content, identifying each prey item down to genus when possible, and measuring each prey item. When we were unable to measure the length of a prey item, the average body length measured in the corresponding zooplankton sample was used. To obtain individual fish gut content mass, we calculated crustacean zooplankton mass using length-mass regressions (Bottrell et al, 1976; Dumont et al, 1975) excluding other prey items (principally terrestrial insects) since their presence in the feeding trials was rare and sporadic. The effect of excluding non-zooplankton prey items from gut content mass calculations was minimal as they made up only 0.9% of the total number of prey items across all the diets. In order to standardize gut content mass by mosquitofish body mass, we calculated mosquitofish gut fullness using gut content mass / (fish mass - gut content mass).
**Data analysis**

There was a negative correlation between mosquitofish length and gut fullness since larger fish have a smaller stomach volume for their length. In order to standardize for fish standard length (SL) and normalize the data, we took the residuals of the best fit model, which was an exponential 2 parameter model: \( a \cdot \text{Exp}(b \cdot \text{SL}) \) where \( a = 0.002 \) and \( b = -0.184 \). We refer to these residuals as mosquitofish food intake throughout the rest of the paper. These residuals conformed to the assumption of normality. We then ran a linear mixed model to test the effects of evolutionary history (by predator regime: no predator, bluegill, bass), developmental plasticity (by predator rearing cue: present or absent), trial condition (by predator trial cue: present of absent), and all 2-way interactions, with population included as a random factor. We ran this model using the lme4 package in R and the car package to run ANOVA (R core team, 2015): \( \text{lmer}(\text{residuals} ~ \text{trial cue} + \text{rearing cue} + \text{evolutionary history} + \text{rearing cue*evolutionary history} + \text{rearing cue*trial cue} + \text{trial cue*evolutionary history} + (1|\text{population}). \)

**RESULTS**

Mosquitofish density was highest in ponds with no fish predators (27.05 mosquitofish/m²), intermediate in ponds with bluegill predators (21.84 mosquitofish/m²), and lowest in ponds with largemouth bass predators (7.24 mosquitofish/m²). Wild mosquitofish from ponds with no predators and bluegill
predators had larger body size than those from ponds with largemouth bass predators (Table 1).

Consistent with an immediate behavioral response to predators, largemouth bass presence during the trial resulted in an overall decrease in mosquitofish food intake (p=0.0003). We found an marginally significant effect of evolutionary history on food intake when looking across all three predator regimes (p=0.089). Developmental plasticity had a significant effect on the food intake of mosquitofish (p=0.039), with exposure to bass cues in the rearing environment reducing food intake when bass were present (Fig 2).

We found a marginally significant interaction between evolutionary history and developmental plasticity (p=0.095). For mosquitofish sharing an evolutionary history with bass, experiencing bass cues during development resulted in higher food intake in feeding trials lacking bass. In the immediate presence of bass, mosquitofish had low food intake regardless of rearing cue (Fig. 2a). In contrast, mosquitofish from bluegill and no predator evolutionary histories showed overall higher food intake in the absence of bass. Furthermore, mosquitofish from bluegill predator and no predator histories did not decrease food intake in the presence of largemouth bass unless they had been exposed to largemouth bass predator cues during development (Fig 2b, c). Thus, in the presence of bass, mosquitofish with an evolutionary history with bass did not require the predator cue during development to display the antipredator response of decreased foraging, whereas mosquitofish with an evolutionary history lacking largemouth bass required predator cues during
development to show an antipredator response. In this way, exposure to bass cues during development appeared to compensate for an evolutionary history that lacked exposure to the predator.

**DISCUSSION**

Previous research has shown that both evolutionary history and developmental plasticity play roles in determining behavioral response to predators (Gosline & Rodd 2008); however, we know of no experimental studies to examine the interaction between evolution and plasticity. We explored the interaction between evolutionary history and developmental plasticity in shaping mosquitofish antipredator behavior. We found that the effects of evolutionary history and developmental plasticity are substitutive – mosquitofish show a similar level of feeding if they originated from ponds with largemouth bass or if they originated from ponds lacking largemouth bass but have been expose to bass cues during development (Fig 2). Mosquitofish with an evolutionary history with largemouth bass display increased food intake in no bass trials when reared with bass; however, mosquitofish displayed antipredator behavior in the presence of that predator regardless of their own developmental history (Fig 2a). In contrast, mosquitofish from ponds lacking largemouth bass required developmental experience with the predator to display a response (Fig 2b, c). Specifically, mosquitofish from populations with either no fish predators or with bluegill predators decreased food intake in the presence of bass only if they had been exposed to bass cues during development. If they were not exposed to bass cues
during development, mosquitofish with evolutionary histories lacking bass did not show an anti-predator response.

Our results demonstrate that evolutionary history with a specific predator species influences mosquitofish antipredator response. Our results support the idea that antipredator behavior can be inherited (Magurran 1990); however, the behavioral response we observed was species-specific for the predator. Mosquitofish from ponds with bluegill predators responded to largemouth bass in a similar way to mosquitofish from ponds lacking fish predators (Fig 2b, c). Thus, similar to other studies, we found that evolutionary history with one predator did not result in an advantageous response when facing a novel predator (Magurran & Seghers 1990). Our results indicate that decreased food intake in response to predator risk was depended on evolutionary history with that specific predator species. The behavioral response was not apparent in individuals with evolutionary history with a different predator. This suggests that chemical cues from predators may be specific to species or closely related species (Ferrari et al. 2007) and that recognition of one cue does not necessarily aid in recognition of other predator cues.

Our results provide evidence that developmental plasticity also affects mosquitofish antipredator behavior when facing a predator. Specifically, individuals exposed to bass cues during development were more likely to behaviorally respond to the presence of bass by reducing food intake. Mosquitofish originating from no predator or bluegill ponds decreased food intake only when exposed to bass during development. Further, individuals reared in the presence of bass decreased food
intake regardless of whether their parents were from populations with bass, bluegill, or no predators. Thus, for populations lacking an evolutionary history with a specific predator, exposure to predator cues paired with conspecific alarm cues during development can allow individuals to recognize a novel predator (Brown & Smith 1998). In contrast, for populations with an evolutionary history of exposure to a predator, developmental cues appear to be unnecessary for immediate antipredator behavior. This finding is consistent with the idea of genetic assimilation, where a phenotype that is initially induced via plasticity becomes a fixed evolutionary response (West-Eberhard 2003).

Our results show that evolutionary history and developmental plasticity influence the behavioral response to a predator in a substitutive way. First, evolutionary history with a predator was enough to influence an individual’s behavioral response to that predator, regardless of previous exposure to that predator during development. Inherited antipredator behavior evolves across generations but allows individuals to respond to predators they have never individually encountered. Second, developmental exposure to a predator caused individuals to display a behavioral response to that predator regardless of their evolutionary history. Plasticity can, within a generation, allow individuals to respond behaviorally to predator risk providing they had previous experience with a predator (Magurran 1990). The strength of antipredator response was similar for all individuals with prior predator exposure, regardless of whether they had parents from populations that had evolved with or without bass. Furthermore, behavioral response to a predator, in terms of food
intake, was similar for mosquitofish that had developed with a predator and mosquitofish originating from populations that had evolved with a predator (regardless of rearing history). In other words, either evolutionary history or developmental plasticity alone are sufficient to cause an individual to display antipredator behavioral responses to specific predators. The recognition and antipredator response are similar regardless of the cause being evolutionary history or developmental plasticity and we did not see a stronger behavioral response in individuals that had both developmental and evolutionary experience with bass predators. This could suggest that additional antipredator behavior would fail to increase survival or result in decreased fitness due to the trade-off between time spent active or in cover.

Predators alter ecological processes through direct and indirect effects on their prey (Carpenter et al. 2001). High predation rates may initially result in reductions in prey density, which may cause a density-mediated trophic cascade, as predators consumes naïve prey with neither evolutionary history nor developmental exposure to that predator. As prey experience the predator during development, they will begin to show the appropriate behavioral response to the immediate risk of predation. This behavioral response is the foundation of behaviorally-mediated trophic cascades (Schmitz et al. 1997; Schmitz et al. 2004; Breviglieri et al. 2017). Finally, evolution appears to facilitate predation recognition, even in the absence of developmental experience with the predator. Thus, populations with evolutionary history with predators may be the most likely to show behaviorally-mediated trophic cascades, as
the behavioral response is no longer tethered to developmental experience. We expect that the ecosystem results of this sequence, upon the introduction of a novel predator, will be the general progression from stronger density-mediated trophic cascades and shifting towards stronger behaviorally-mediated trophic cascades.

CONCLUSIONS

Because prey species respond to a threat by reducing food intake (Lima & Dill 1990), predator recognition may have further implications for the whole ecosystem. We found that the interaction between evolutionary history and developmental plasticity is substitutive – evolution and plasticity independently reduce food intake, but both together do not further reduce food intake. Populations with evolutionary history with largemouth bass displayed antipredator behavior regardless of developmental experience with bass cues. In contrast, populations with an evolutionary history lacking largemouth bass required developmental experience with bass cues to display antipredator behavior. Individuals lacking both evolutionary history and developmental experience did not display antipredator behavior. Lastly, we found that evolutionary history, developmental plasticity, and the combination of both resulted in similar reductions of mosquitofish food intake and that experience with a different predator (bluegill) did not result in an advantage when facing a novel predator (bass). Because of the observed progression of prey behavioral responses, we expect that predator introductions will initially cause strong density mediated trophic cascades, as
 naïve prey are consumed. This initial period may be followed by a transition to behaviorally mediated trophic cascades, driven first by developmental plasticity and then, after many generations, by a fixed evolutionary response.
Figures

![Diagram showing the transition of wild caught fish from three predator regimes to the F1 fish that were reared with and without bass cues and then run in the feeding experiment with and without bass cues. Red circles indicate a treatment where mosquitofish were exposed to predator (largemouth bass) cues, gray circles indicate no predator treatments.]

**Figure 1:** Experimental setup showing the transition of wild caught fish from three predator regimes to the F1 fish that were reared with and without bass cues and then run in the feeding experiment with and without bass cues. Red circles indicate a treatment where mosquitofish were exposed to predator (largemouth bass) cues, gray circles indicate no predator treatments.
**Figure 2:** Mean and SE for female mosquitofish reared with bass (red) and no predator (blue) cues from largemouth bass sites (A), bluegill sites (B), and no predator sites (C). Symbols are slightly displaced to better show error bars.
Table 1: Summary of environmental data for each population including mosquitofish density and wild caught length. Average values ± standard error (in parentheses) for each predator regime is showed in grey. At Neary Lagoon we were unable to catch any mosquitofish during the density survey.

<table>
<thead>
<tr>
<th>Population</th>
<th>Location</th>
<th>Background</th>
<th>Mosquitofish/m²</th>
<th>Avg. Female Length</th>
<th>Avg. Male Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antonelli Pond</td>
<td>N 36.956292, W 122.060251°</td>
<td>Bass</td>
<td>5.75</td>
<td>23.79</td>
<td>19.06</td>
</tr>
<tr>
<td>Furnace Creek</td>
<td>N 36.460371, W 116.872953°</td>
<td>Bass</td>
<td>18.89</td>
<td>25.08</td>
<td>19.33</td>
</tr>
<tr>
<td>Neary Lagoon</td>
<td>N 36.962687, W 122.029602°</td>
<td>Bass</td>
<td>0.00</td>
<td>23.52</td>
<td>17.91</td>
</tr>
<tr>
<td>Schwann Lake</td>
<td>N 36.965141, W 121.994765°</td>
<td>Bass</td>
<td>4.31</td>
<td>27.36</td>
<td>19.35</td>
</tr>
<tr>
<td>Bass Average</td>
<td>N/A</td>
<td>Bass</td>
<td>7.73 (4.07)</td>
<td>24.94 (0.88)</td>
<td>18.91 (0.34)</td>
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<tr>
<td>De Anza</td>
<td>N 36.951802, W 122.061420°</td>
<td>Bluegill</td>
<td>17.39</td>
<td>27.09</td>
<td>20.97</td>
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<td>Harkin Slough</td>
<td>N 36.911616, W 121.804411°</td>
<td>Bluegill</td>
<td>43.67</td>
<td>29.15</td>
<td>20.86</td>
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<tr>
<td>Spring Hills Pond</td>
<td>N 36.980468, W 121.756525°</td>
<td>Bluegill</td>
<td>4.45</td>
<td>25.39</td>
<td>19.17</td>
</tr>
<tr>
<td>Bluegill Average</td>
<td>N/A</td>
<td>Bluegill</td>
<td>21.84 (11.54)</td>
<td>27.21 (1.09)</td>
<td>20.33 (0.58)</td>
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<td>Artesian Well</td>
<td>Bishop, CA</td>
<td>No Predator</td>
<td>6.37</td>
<td>29.77</td>
<td>22.61</td>
</tr>
<tr>
<td>De Laveaga Pond</td>
<td>N 36.998071, W 121.999344°</td>
<td>No Predator</td>
<td>6.02</td>
<td>32.56</td>
<td>18.30</td>
</tr>
<tr>
<td>Keogh’s 2</td>
<td>Bishop, CA</td>
<td>No Predator</td>
<td>34.36</td>
<td>27.68</td>
<td>20.84</td>
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<tr>
<td>NBLM</td>
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<td>27.38</td>
<td>28.94</td>
<td>21.65</td>
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<td>Warm Springs Upper</td>
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<td>24.67</td>
<td>20.72</td>
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<td>27.05 (10.21)</td>
<td>28.73 (1.29)</td>
<td>20.82 (0.72)</td>
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</table>
References


