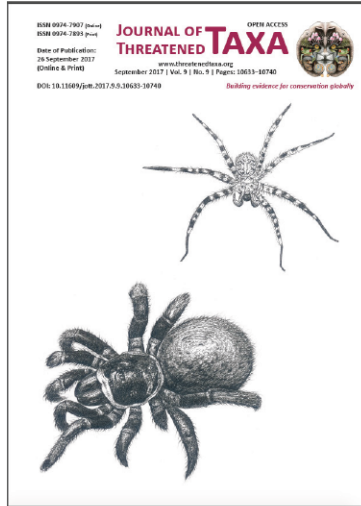


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EFFECTS OF THE INVASIVE TILAPIA ON THE COMMON SPINY LOACH (CYPRINIFORMES: COBITIDAE: *LEPIDOCEPHALICHTHYS THERMALIS*) - IMPLICATIONS FOR CONSERVATION

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Abstract: The introduction of invasive species leading to decline of freshwater fauna is a major concern for conservation biologists. In this study we examined the effect of introduced Tilapia on the survival of the loach *Lepidocephalichthys thermalis* via predation experiments with Tilapia and a native predator, the Snakehead fish *Channa gachua*. Examining the chemoecology of prey-predator interactions, we found that *L. thermalis* failed to detect water-borne cues from Tilapia but did recognize cues from *C. gachua*, indicating innate predator recognition. We also observed that *L. thermalis* can learn to associate kairomones with Tilapia when conditioned with kairomones and injured conspecific cues. Trained *L. thermalis* showed higher survival during Tilapia predation trials. Thus under experimental conditions the vulnerability of *L. thermalis* to Tilapia predation due to failure to detect chemical cues can be reduced via associative training. It remains to be determined how useful this behavioral plasticity can be in wild *L. thermalis* populations exposed to introduced Tilapia.

Keywords: Behavior, chemical cues, invasion, kairomones, *Oreochromis mossambicus*, predator recognition.

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Author Details: SANDIP D. TAPKIR is working on the prey predator interactions in aquatic organisms, gut microbiome of the animals and also interested in freshwater fish diversity. SANJAY S. KHARAT is working on diversity and distribution of freshwater fishes in the northern Western Ghats of India. PRADEEP KUMKAR is working on diversity, distribution, ecology and evolution of freshwater fishes. SACHIN M. GOSAVI is a PhD student, conducting his doctoral study in Department of Zoology, Modern College, Ganeshkhind. He works on behavior biology and ecology of aquatic animals.

Author Contribution: SDT and SMG designed the experiments with the help of SSK. SDT, SMG and PK performed experiments and wrote the manuscript with inputs from SSK.

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INTRODUCTION

More than 2,000 freshwater fish species are known to occur in India (Devi 2003; Dahanukar et al. 2004; Raghavan et al. 2013), with many new species described from the Western Ghats (Dahanukar et al. 2015), a global biodiversity hotspot (Myers et al. 2000). Unfortunately, endemic species are declining at high rates, which has been attributed to several factors including the introduction of invasive species (Molur et al. 2011). In the Western Ghats 324 invasive fish species have been identified, and this invasion has been linked to the loss of native populations (Johnson et al. 2014; Keskar et al. 2014). The Tilapia *Oreochromis mossambicus* (Peters, 1852), is one of the most harmful invasive species in aquatic ecosystems worldwide (Lowe et al. 2004) and it was introduced to India for aquaculture in 1952 (de silva et al. 2004). Tilapia now occupies wide variety of aquatic habitats (e.g., estuarine and free-flowing, lakes, watercourses and wetlands) shared with a range of endemic freshwater fish, including loaches. The Western Ghats harbors 43 loach species, of which 39 are endemic (Dahanukar & Raghavan 2013). Loach populations are declining in several areas, where a major factor is the introduction of invasive species (Paingankar & Dahanukar 2013; Keskar et al. 2014), including Tilapia. The chemoecology of prey-predator interactions in fish has been extensively investigated (Ferrari et al. 2010). While prey species often possess innate abilities to recognize native predators via water-borne chemical cues (Ferrari et al. 2010), they often fail to recognize predators with which they do not share an evolutionary history (Polo-Cavia et al. 2010; Gomez-Mestre & Diaz-Paniagua 2011). Thus invasive predators can exploit novel ecological contexts where prey populations lack sufficient anti-predator adaptations to limit predation pressure (Shea & Chesson 2002). It is, however, sometimes possible for prey to learn to recognize invasive predators under experimental conditions (Ferrari et al. 2010), suggesting that given sufficient opportunities they may be able to adapt to invaders in the wild.

In this study we performed chemoecology experiments using the Common Spiny Loach *Lepidocephalichthys thermalis* as prey, and the Snakehead fish *Channa gachua* and Tilapia as a native and invasive predator respectively. Our aim was to determine: (1) Does *L. thermalis* innately recognize the native and/or invasive predator species? (2) In the absence of an innate response, can *L. thermalis* learn to recognize predators? (3) Can such learning enhance the survival of *L. thermalis* in predator encounters?

MATERIALS AND METHODS

Animal collection and maintenance

Live *L. thermalis* (n = 63; hereafter test fish) were collected from a local fish market at Lonawala (18.747 N & 73.449 E), Maharashtra (Fig. 1). Fish were transported in plastic bags filled with dechlorinated oxygenated water to the laboratory, where they were maintained in large aerator-equipped aquariums (120 x 60 x 60 cm) filled with dechlorinated tap water (20 L) at 25°C under a natural photoperiod (12L : 12D). Live specimens of Snakehead (n = 2) and Tilapia (n = 20) were acquired from the same fish market and housed in separate aquaria under the same conditions. Water was renewed thrice weekly and fish were fed twice daily with artificial fish food/blood worms. All animals were allowed to acclimate for 20 days prior to experimentation.

Preparation of chemical stimuli

According to Peacor et al. (2006), water-borne cues last for 2–4 days. Predator chemical cues were prepared by filling aquaria with dechlorinated tap water and introducing either Snakehead or Tilapia; after 48hr of occupancy the fish were removed and the conditioned water was frozen in 50mL aliquots (Gomez-Mestre & Diaz-Paniagua 2011). Conditioned water was collected both from starved fish, which were not fed for two days prior to transfer (to clean their gut) nor during occupancy, and from satiated fish that were fed with *L. thermalis* once a day for two days prior to and during occupancy. A negative control was prepared using distilled water following the same procedure without exposure to fish (Woody & Mathis 1998).

Prey alarm cues were collected from *L. thermalis* donors (n=3) that were euthanized using highly concentrated MS-222 (Tricane methane sulphonate) solution, washed thoroughly in distilled water and snap-frozen in liquid nitrogen. Skin pieces (1cm²) were removed from both sides of the body and placed in 10ml chilled distilled water prior to homogenization and straining (Manek et al. 2013). This solution was diluted to 10L and frozen in 50ml aliquots (Woody & Mathis 1998).

Prey response to predator cues

The response of *L. thermalis* to water-borne chemical cues was measured using the well-established protocol of Batabyal et al. (2014). Briefly, individual fish were introduced to a testing chamber (100 × 12 × 6 cm) with 10 equal sections of 10cm length denoted by line markings. The chamber was cleaned and filled with 2L

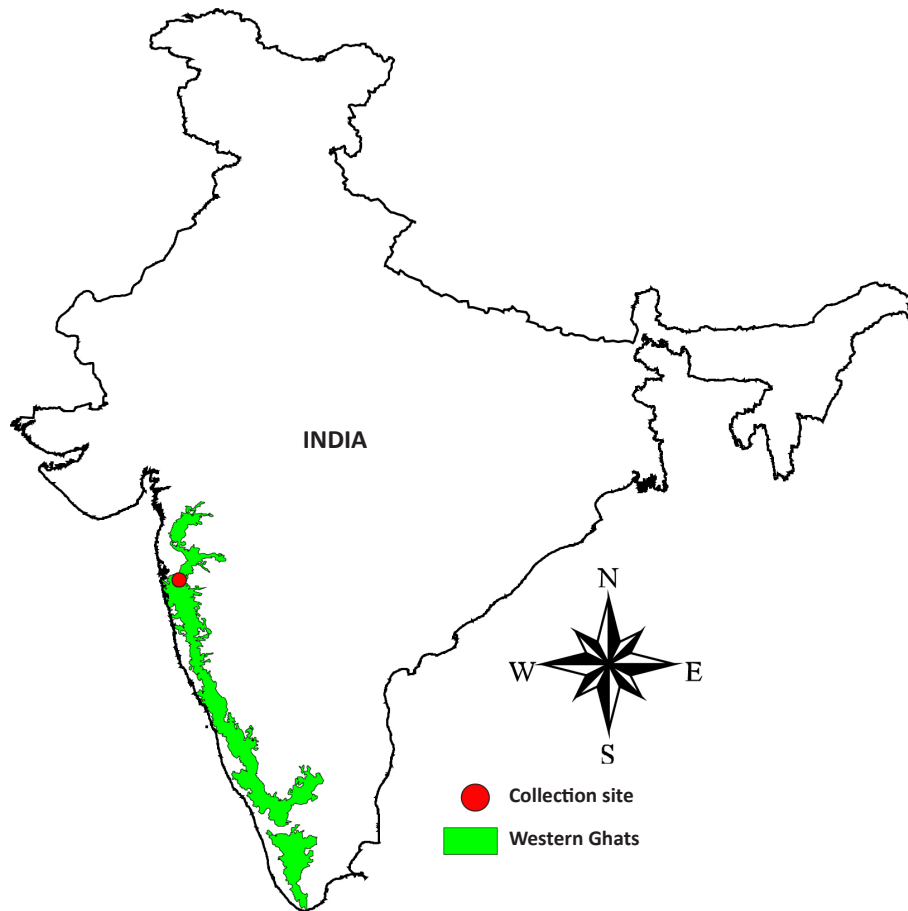


Figure 1. Location map for collection site of prey (*L. thermalis*) and native (Snakehead *Channa gachua*) as well as invasive predator (*Tilapia Oreochromis mossambicus*).



Image 1. *Lepidocephalichthys thermalis* (Prey fish) in life.

of dechlorinated tap water prior to introduction of a test fish, which was allowed to acclimate for 20 min. Pre-stimulus activity was measured by counting the number of lines crossed by the test fish during a period of four minutes. 5ml aliquots of test solution were then added to each end of the testing chamber, and any chemical cues present were allowed to diffuse for five minutes (determined via a dye test using KMnO_4 per Batabyal et al. 2014). Post-stimulus activity was then recorded for four minutes. Stimulus response was calculated by

subtracting pre-stimulus from post-stimulus readings; a negative value indicated reduced activity, a positive value increased activity. In total, 20 individual fish across five different treatments were used. Observers were blinded as to the test solution used in each trial.

Prey conditioning

L. thermalis individuals (n= 40) were randomly assigned to two groups in separate aquaria. Each aquarium received 10ml of starved Tilapia-conditioned solution, and one aquarium ("conditioned") also received 10ml of *L. thermalis* alarm cue solution. After 24h, fish from both aquaria were tested for response to Tilapia predator cues or distilled water as described above.

Prey survival

Fish from conditioned and non-conditioned aquaria (above) were randomly sorted into pairs (n = 20 pairs), whose members identified by distinctive morphological features. Pair members were simultaneously introduced to separate aquaria filled with 20L of dechlorinated tap water containing one Tilapia that had been starved for

48h. The time was recorded until one fish was eaten or killed by the Tilapia, and the identity of the survivor was recorded.

Data analysis

Shapiro-Wilks test for normality revealed non-normal distribution of data. Therefore, to compare the swimming activity of test fish in presence of different chemical cues for both Expt. 1 and Expt. 2, we used a Kruskal–Wallis H test followed by Mann-Whitney U-test for multiple pairwise comparison with Bonferroni correction. In Expt. 3, survival in predation trials was analyzed using Fisher's exact test. All results were considered significant at $\alpha = 0.05$. The statistical analysis was carried out using PAST 3.13 (Hammer et al. 2001).

RESULTS

Prey response to predator cues

A Kruskal–Wallis H test showed that there was a statistically significant difference in swimming activity of test fish between predator cue treatments ($\chi^2 = 31.36$, $P < 0.0001$). Post-hoc tests revealed that test fish reduced their swimming activity significantly in the presence of starved Snakehead cues, compared to their activity in distilled water (Mann-Whitney U-test = 50.5; $P = 0.0005$; Fig. 2). Test fish reduced activity even further when exposed to cues from satiated Snakehead that had fed on conspecific prey ($U = 48$; $P = 0.0004$; Fig. 2). The test fish, however, did not reduce their activity level in the presence of chemical cues from invasive Tilapia, regardless of whether Tilapia were satiated ($U = 184$; $P = 1$; Fig. 2) or starved ($U = 182$; $P = 1$; Fig. 2).

Prey conditioning

A statistically significant difference was observed in the swimming activity of test fish ($\chi^2 = 15.52$, $P = 0.0014$; Fig. 3) between conditioned and non-conditioned treatment. Multiple pair-wise comparisons showed that, test fish conditioned with conspecific alarm cues added in combination with Tilapia cues significantly reduced swimming activity in the presence of Tilapia cues compared to distilled water ($U = 66.5$; $P = 0.0019$; Fig. 3), whereas activity of non-conditioned test fish did not vary in the presence of Tilapia cues compared to distilled water ($U = 189.5$; $P = 1$; Fig. 3). In addition, swimming activity of conditioned and non-conditioned test fish did not differ significantly in distilled water ($U = 160$; $P = 1$; Fig. 3), but conditioned test fish were comparatively less active than non-conditioned test fish

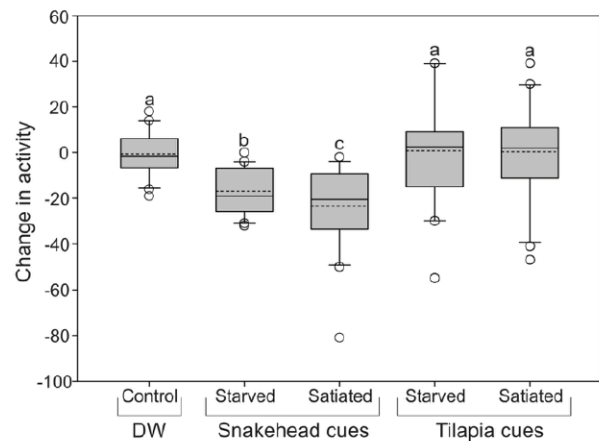


Figure 2. Change in activity of the *L. thermalis*, in trials with the distilled water, chemical cues from native predator (Snakehead, satiated and starved) and chemical cues from invasive predator (Tilapia, satiated and starved). Different letters indicate significant difference between treatment groups at $P \leq 0.05$. Horizontal dotted line and continuous line within each box indicates mean and median value respectively.

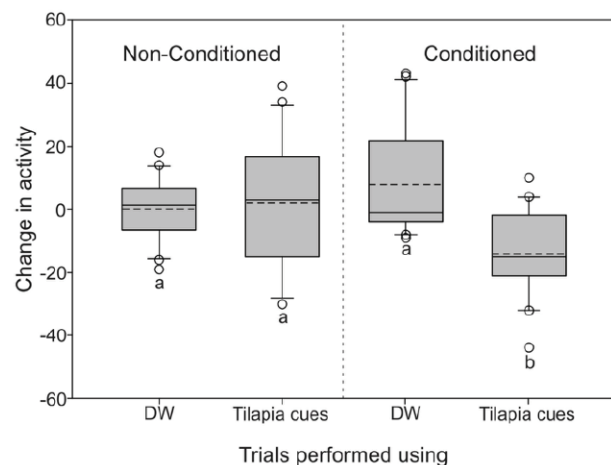


Figure 3. Change in activity of the *L. thermalis*, either in distilled water (gray bars) or in presence of water borne chemical cues from invasive Tilapia (black bars). Test fishes were either exposed to the mixture of chemical cues from Tilapia with conspecific alarm cues (conditioned) or mixture of chemical cues from Tilapia with distilled water (non-conditioned). Different letters indicate significant difference between treatment groups at $P \leq 0.05$. Horizontal dotted line and continuous line within each box indicates mean and median value respectively.

in presence of Tilapia cues ($U = 104$; $P = 0.05$; Fig. 3).

Prey survival

In real predation trials using starved Tilapia, conditioned test fish had significantly higher overall survival than non-conditioned test fish (Fisher exact test, $P = 0.0038$; Fig. 4). Non-conditioned test fish were often consumed before conditioned test fish due to their higher swimming activity. In total, 20 out of 40 test fish

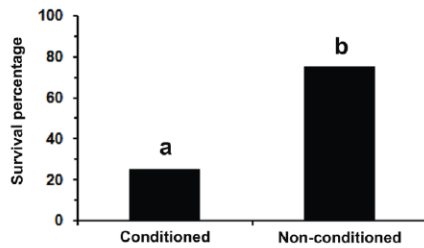


Figure 4. Showing survival percentage of the test fishes in real predation trails with the invasive Tilapia. Grey color bar indicates non-conditioned group whereas black color bar shows the conditioned group. Different letters indicate significant difference between treatment groups at $P \leq 0.05$.

were eaten, 15 (75%) of them non-conditioned and five (25%) conditioned.

DISCUSSION

Lepidocephalichthys thermalis possess innate predator recognition towards the Snakehead (native predator), since they detect water-borne chemical cues from starved Snakehead without prior experience and adaptively reduce activity. Several other aquatic species (freshwater snails, salmonoid fishes, larval toads and salamanders) are also known to display innate predator recognition wherein prior exposure to the predator is not essential (Ferrari et al. 2010). Furthermore, the anti-predator responses were much stronger when *L. thermalis* were tested against the chemical cue from satiated Snakehead, indicating a synergistic effect of Snakehead kairomones and dietary cues. In contrast, *L. thermalis* failed to discriminate chemical cues from invasive Tilapia, regardless of whether Tilapia was starved or satiated. There are two plausible reasons behind such lack of responses. Firstly, development of innate predator recognition requires a long evolutionary history between the prey and predator (Ecological coexistence theory; Kiesecker & Blaustein 1997). Invasive Tilapia was introduced in India in 1952 (de Silva et al. 2004), however, according to documentary evidences Tilapia was recorded from the study area for the first time in 2012 (Dahanukar et al. 2012). Previous investigations on fish fauna of Indrayani River by Sykes (1839), Suter (1944) and Yazdani & Mahabal (1976) showed no records for Tilapia occurrence in study area. This indicates that Tilapia was introduced in the study area after 1976. For instance, even if we consider that Tilapia was introduced in the study area in 1976, it is just 39 years after introduction of Tilapia, which may not be sufficient evolutionary time span to

develop innate predator recognition in *L. thermalis*. This suggests that the lack of innate recognition of invasive Tilapia likely to be common in other loach species such as *Acanthocobitis mooreh*, *Oreonectes evezardi*, *Nemachilichthys rueppelli*, *Noemacheilus anguilla*, *Schistura denisoni* inhabiting the study area. Similar study performed by Polo-Cavia & Gomez-Mestre (2014) on Western Spadefoot Toad *Pelobates cultripes* showed that tadpoles of the spadefoot toads fail to detect the chemical cues innately from the invasive Red Swamp Crayfish *Procambarus clarkii* even after 35 years of its introduction. Yet, some amphibian species are known to adapt to novel thermal regimes via behavioral plasticity within a 30-year time frame (Skelly & Freidenburg 2000; Freidenburg & Skelly 2004). Second plausible reason may be higher generation times of *L. thermalis*, but currently no data is available on its reproductive biology. Due to the higher generation time responses of *L. thermalis* to selection for innate recognition of introduced predators should be slow. We suggest that, detailed investigation of the reproductive biology of *L. thermalis* is needed to understand the role of higher generation time in shaping the lack of anti-predator responses against Tilapia.

Post-digestion or dietary cues are also known to elicit anti-predatory responses against the novel predators in aquatic prey (Ferrari et al. 2010; Nunes et al. 2013), but in case of the *L. thermalis* presence of even dietary cues may not be sufficient to trigger recognition of invasive predator. This could be explained in terms of the phylogenetic-relatedness theory. The 'Phylogenetic-relatedness theory' proposes that response of prey to alarm cues or dietary cues of closely related predator species should be stronger than such cues from distantly related ones (Sullivan et al. 2003; Schoeppner & Relyea 2005). Moreover, the chemical cues (Kairomones/dietary cues) released by related predator are more similar and identified by prey species (Ferrari et al. 2007). Phylogenetically, Snakehead and Tilapia are not closely related since both belong to two different families (Channidae and Cichlidae respectively). Therefore, despite of ecological coexistence of *L. thermalis* with Snakehead and Tilapia, *L. thermalis* only detect *Channa* dietary cues and fails to detect kairomones as well as dietary cues from Tilapia.

The ability to learn to detect novel predators is always advantageous over an innate mechanism of predator detection since innate predator recognition has limitation for identification of number of predators (Batabyal et al. 2014). Therefore, learned predator recognition is known to be helpful in reducing the predation by invasive predators (Polo-Cavia & Gomez-

Mestre 2014). In the current study, we showed that *L. thermalis* can learn to recognize chemical cues from invasive Tilapia as a threat by associative learning, and modify their anti-predator responses adaptively based on their experience. Such associative learning through pairing of kairomones with alarm cues has been reported in different species (Ferrari et al. 2010). It includes, flatworms, mollusks, insects, crustaceans, fishes and amphibians (as reviewed in Ferrari et al. 2010). Most of these studies, however, have been conducted in the laboratory; learning through alarm cues is likely to happen in the wild too, since prey animals are constantly exposed to a combination of predator's kairomones and alarm cues released by attacked conspecifics (Ferrari et al. 2010). By cognitive association of these cues, prey animals adjust quickly to the surrounding environment and may dynamically adjust risk assessment, enhancing their ability to detect and avoid predators by responding plastically to new threats through changes in morphology and/or behavior. Furthermore, associative learning may provide substantial time for evolution of innate recognition of invasive predators in prey individuals.

Prior experience with predators is known to affect the prey fitness and survival. Unfortunately, most studies are only restricted to predator detection and learning. Very few studies till date have demonstrated adaptive value of learned predator recognition in direct encounters with predators (Mirza & Chivers 2000; Gazdewich & Chivers 2002; Lonnstedt et al. 2012; Polo-Cavia & Gomez-Mestre 2014). To our knowledge, this is the first study which provides empirical evidence of learned predator recognition in loaches and its effect on survival rates during direct encounters with an exotic, globally introduced predator, Tilapia. We found that, *L. thermalis* that learned to recognize the Tilapia by associative learning showed higher survival as compared to those that are not conditioned. Enhanced survival is likely to occur also in natural scenario, since experienced prey fishes might rapidly identify predatory Tilapia as threatening and exhibit avoidance behavior (Polo-Cavia & Gomez-Mestre 2014). Such ability to learn about the invasive predator might be important in case of the loach populations to persist in presence of invasive predators. Associative learning ability in loach populations helps to cope up with the immediate impact of invasions through behavioral plasticity and buy time for genetic variants to appear and respond to selection (Polo-Cavia & Gomez-Mestre 2014). Moreover, prey animals are also known to undergo certain changes in morphology induced by novel predators (Ferrari et al. 2010; Gomez-Mestre & Díaz-Paniagua 2011). These morphological changes

allow experienced prey individuals to effectively cope with the new selective challenge without necessarily or immediately leading to genetic shifts in populations (Huey et al. 2003; Gomez-Mestre & Díaz-Paniagua 2011). But in comparison with morphological responses, behavioral responses are quick and energetically less costly due to the unpredictable nature of predation risk. Therefore, learning is the best and rapid way towards adaptation to a novel invasive predator, whereas innate responses might evolve after substantial ecological coexistence with invasive predator (West-Eberhard 2003). Hence, evolution of behavioral plasticity in terms of activity reduction seems to be beneficial for native prey animals to adapt to selective impacts from introduced predators (Strauss et al. 2006).

In conclusion, our results show that despite lacking innate recognition of invasive Tilapia, *L. thermalis* can learn to recognize this invasive predator by associative learning when jointly receive Tilapia cues and alarm cues from injured conspecifics. This cognitive ability of *L. thermalis* increases their chance of survival in direct encounters with Tilapia, which might be important for native loach populations to endure predator invasions until they develop innate predator recognition against Tilapia. We suggest that, more work with consideration of the other loach species is needed to document and better understand the effect of invasive species on loach population. This will help in determining that which loach species is most likely to be the more vulnerable for extinction due to invasion and based on this knowledge, conservation strategies can be planned.

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