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Individual boldness traits influenced by temperature in male Siamese fighting fish



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HIGHLIGHTS

• The effect of ambient temperature on boldness responses of Siamese fighting fish was determined.

• Temperature changed boldness behaviors; latency to move, time in farthest area from release, and activity level.

• We inferred these behaviors to reflect an increase in general 'boldness' with increased temperature.

• Careful temperature control is needed when studying behavior in the fish.

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ABSTRACT

Temperature has profound effects on physiology of ectothermic animals. However, the effects on temperature variation on behavioral traits are poorly studied in contrast to physiological endpoints. This may be important as even small differences in temperatures have large effects on physiological rates including overall metabolism, and behavior is known to be linked to metabolism at least in part. The primary aim of this study was to determine the effects of ambient temperature on boldness responses of a species of fish commonly used in behavioral experiments, the Siamese fighting fish (*Betta splendens*). At 26 °C, subjects were first examined for baseline behaviors over three days, using three different (but complementary) 'open field' type assays tested in a fixed order. Those same fish were next exposed to either the same temperature (26 °C) or a higher temperature (30 °C) for 10 days, and then the same behavioral assays were repeated. Those individuals exposed to increased temperatures reduced their latency to leave the release area (area I), spent more time in area III (farthest from release area), and were more active overall; together we infer these behaviors to reflect an increase in general 'boldness' with increased temperature. Our results add to a limited number of studies of temperature effects on behavioral expective, our results indicate careful temperature control is needed when studying behavior in this and other species of fish.

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1. Introduction

Boldness or the propensity of individuals to take risks is a fundamental axis in animal behavior that has received a great deal of attention over the past decade [1,2]. Consistent individual differences in boldness has been identified in many taxa, including mammals [3,4], birds [5], reptiles [6], fish [7], and crustaceans [8]. The degree to which individuals display a specific behavior in a particular situation may have significant

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ecological and evolutionary consequences. For example, individual differences in boldness have been shown to affect migratory propensity [9], the likelihood to become dominant [10,11], success at foraging [12], and reproductive performance [13]. However, bold behaviors may also have fitness disadvantages, such as increased exposure to predation risk, which can reduce long-term survival [14,15].

As one of the main abiotic factors in aquatic ecosystems, temperature has immense impact on the energy budgets, growth, respiration, behavior, and locomotion performance of aquatic ectothermic species [16–19]. Fish as a major group of ectothermic animals, typically experience a wide range of temperatures across days and even within days; however, growth and reproduction only take place in a more limited temperature range [16]. Given that temperature has large direct effects on metabolic rates in fish (and indeed all ectotherms), it is likely to have

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large effects on physiology and behavior. For example, among year increases in temperature can lead to increases in activity and risk-taking in fish, which in turn are linked to elevated predation mortality [20]. Apart from the natural environment, fluctuating temperatures could be important in laboratory conditions, particularly when the behavioral performance of individuals should be considered [8,15,18,21]. Although several studies exist which examine individual responses to temperature variation, there is still relatively few and low taxonomic breadth among these studies, which limits our ability to generalize findings about the effects on animal behavior at both the population- and individual-level.

The effects of temperature on behavioral traits are poorly studied in fish in contrast to physiological endpoints (e.g. [22,23]). In this regard, the majority of studies on temperature dependence of the behavior of fish species have focused on swimming and foraging [24–26], which are closely related to growth and survival indices. In recent years, however, there has been a rapid growth of interest in the fitness consequences of changes in temperature in a number of aquatic organisms, especially fish (e.g. personality traits in *Pomacentrus moluccensis* [18], risk assessment in *Pomacentrus chrysurus* [27], escape ability in *Daphnia* [28], stability of social hierarchy in *Apistogramma agassizii* [29], acoustic communication in *Pomatoschistus pictus* [30], and *Trichopsis vittata* [31]).

Male Siamese fighting fish (Betta splendens) are well known for being highly territorial and aggressive towards intruder conspecifics [32]. Additionally, this fish is increasing in popularity as a model species for behavioral ecology studies (e.g. [33,34]). Specifically, it is reported that both male and female fighting fish would be consistent in their responses within and across the different types of boldness assays [35-37]. The primary aim of this study was to determine the behaviors involved in boldness of male Siamese fighting fish as a function of temperature fluctuations which may occur in laboratory studies using different complementary behavioral assays. This may be important because studies continue to ignore small temperatures fluctuations of a few degrees or less, even though it can have substantial effects on physiology and behavior [18,23,27,29,38]. For example, in studies of fish, temperature differences of 3° [39], 4° [40], and 5 °C [41] exist during experiments but were not accounted for in analysis; however, differences in temperature of 2° [38], 2.5° [23], and 3 °C [27,29] had significant effects on physiology and/or behavior endpoints.

Here, we studied the responses of male Siamese fighting fish to a modest temperature manipulation to test for individual and meanlevel effects on behavioral traits related to boldness. Importantly, we show substantial effects of temperature that are independent of any time-related changes in behavior that could potentially confound results and interpretations. As predicted, boldness related behaviors increased with temperature in the manipulation treatment (even after 10 days of acclimation), but remained constant across trials in the control.

2. Materials and methods

2.1. Study species

Forty sexually mature male Siamese fighting fish of the veil tail strain were purchased from a local distributor. Fish were transported to the laboratory and kept individually in opaque 0.5 L plastic containers to prevent visual contact between them. Temperature of the room used for fish keeping and experimental trials was maintained continuously at 20–24 °C. To establish conditions with higher and constant temperatures, fish containers were placed into a larger water-bath; a wide, short-wall rectangular plastic container filled with water to a depth of 7–8 cm that was heated using aquarium heaters to adjust the desired temperature on the fish container. The container water temperature during acclimatization was 26 °C. In the wild, *Betta* fish prefer water that is 25° to 31.5 °C [42,43]. However, a wide range of temperature, 21–30 °C, have been used to keep this fish in laboratory [41,44–46]. The daily photoperiod in the lab was set as 14 h light to 10 h dark with lights on at 0800. Fish were fed ad libitum once daily with formulated pellet diet (0.9 mm) and frozen blood worms. The water in the individual holding containers was completely changed every three days. The fish were kept in these conditions to acclimatize for two weeks prior to the temperature manipulation.

2.2. Experimental design

Prior to temperature manipulation, thirty size-matched fish from the stock population were randomly allocated into one of two groups of 15 fish, and their behaviors were observed to obtain the baseline boldness (described below). After completion of the baseline behavioral observations, one group was randomly designated as the control $(1.57 \pm 0.24 \text{ g})$ and maintained at the normal temperature (26 °C), and the second group was assigned to the high temperature treatment $(1.60 \pm 0.11 \text{ g})$ in which the subjects were kept at 30 °C. The high temperature of 30 °C was used to simulate the mean temperature during the breeding season (April and May) in the natural habitat of Siamese fighting fish [42], and this temperature has also been used in previous laboratory studies on this species [46]. Fish containers were transferred to the wide short-wall rectangular water-baths, and heated to desired temperatures as stated above. Daily feeding rhythm, physiochemical properties of water, and light regime were maintained the same as during the acclimation period. The duration of the temperature manipulation for behavioral observations was 10 days. This time duration was selected because (i) it is within the acclimation time period needed for Siamese fighting fish employed in previous studies [33,36], and (ii) many experiments which quantified behavioral responses of Siamese fighting fish were conducted in a timeline of one- to two-weeks [35,47].

2.3. Boldness assessment

We used two identical glass rectangular tanks ($60 \times 25 \times 40$ cm) as the experimental apparatus. The back and side walls were covered by white opaque sheets to eliminate any external disturbances on fish behavior. The front of the tanks was left uncovered and a video camera was set at 1 m distance to record fish behavior. The experimental apparatus was filled to depth of 20 cm with treated tap water (30 L) and the bottom was left empty. Tanks were lit from above by a 30 W fluorescent lamp. Water temperature in the test tanks was 26 °C for the control and 30 °C for the high temperature treatment. Following the protocol of Hebert et al. [36] and Forsatkar et al. [37], test tanks were divided into three equal sections by drawing lines on the outside of the tank and designated as areas I (where individual was initially placed), II (middle), and III (opposite end). In half of the trials fish were initially placed on the left side of the tank and in the other half of the trials they were placed on the right side of the tank.

Boldness-related behaviors were assessed over three days, using three different assays (novel environment, open field, and novel object test) always conducted in this fixed order. The repeatability and reliability of these assays have been previously demonstrated for testing boldness in male Siamese fighting fish [35]. These assays have all been employed with a wide range of fish species [48–50].

After the 10 day acclimation period, all individuals were tested over three subsequent days. The temperature was then manipulated (treatment group only) and all fish were tested again after 10 days exposure to different water temperature. The order of the test assays were fixed and subjects were observed in the novel environment assay, open field assay, and novel object assay on days 1, 2, and 3 before, and days 14, 15, and 16 after temperature manipulation, respectively (i.e. fish were tested twice: pre and post control temperature or temperature increase). To evaluate the boldness traits of the subjects, a male was netted from its home tank and placed into the area I of the test arena in an open-bottom opaque chamber. The subject was allowed to acclimate for Download English Version:

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