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In-stream analysis of predator-prey interactions in Hawaiian stream fishes

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Predator-prey encounters are among the most critical interactions that animals face. However, studying these interactions in natural environments is challenging due to their unpredictable and transient nature. Furthermore, habitat features may give predators an advantage by inhibiting the ability of prey to detect or evade predation attempts. In fishes, one habitat feature that can impede predator detection is water flow. Previous laboratory studies of juvenile Hawaiian stream gobies, *Sicyopterus stimpsoni*, found that prey fish respond less frequently to simulated attacks occurring in the same direction as the dominant flow of water (i.e. the predator attacking from upstream). Additionally, predators with higher perch angles from the stream bed may be able to detect oncoming prey from a greater distance and, hence, be better able to take advantage of this hydrodynamic “blind spot”. We tested these possibilities by collecting in situ high-speed video of instream attacks on juvenile gobies by an ambush predator, the sleeper *Eleotris sandwicensis*, in a natural Hawaiian stream setting. We specifically tested whether (1) predators take advantage of the prey hydrodynamic “blind spot” shown in laboratory trials during in situ encounters, and (2) if the angle that predators perched their body above the stream bed before an attack influenced their success. In contrast to laboratory results, our data showed no preferential association of attacks with a particular pre-strike angle, suggesting that predators do not target the “blind spot” of their prey during attacks. However, the only successful strikes were performed by predators attacking from higher perch angles, suggesting a predator’s orientation before initiating an attack may be more important than the angle at which they attack prey. This study underscores how field-based tests of laboratory generated hypotheses have the potential to improve insight into the diversity of animal performance in nature.

Introduction

Predators must be able to detect, attack, and consume prey in order to gain essential nutrients for survival. In natural habitats, both abiotic and

biotic ecological factors (e.g. water clarity, species abundance) can aid or hinder the ability of predators to capture prey (Abrahams & Kattenfeld, 1997; Morice et al., 2013). These ecological factors can create more favorable prey-capture conditions

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or alter escape opportunities for prey (Higham et al., 2015). When environmental factors prevent prey from detecting predators, or impact prey escape performance, there is an opportunity for predators to improve their chance of successfully capturing prey. For example, in turbid aquatic habitats, visual predator detection is impeded, allowing predators to swim closer to prey before initiating an attack (Higham et al., 2015). However, predators may fail to initiate attacks if they cannot detect prey before they themselves are detected by their prey. In this context, it is also possible that some environmental conditions impose selection on prey performance. The strength of this selection depends on whether the predators take advantage of environmentally induced performance detriments. Few studies have succeeded in overcoming the combination of technical challenges and the unpredictable nature of predator-prey interactions to generate sufficient in situ observations to draw conclusions about how different environmental factors contribute to the outcomes of predator-prey encounters (Domenici et al., 2014; Freymiller et al., 2019).

Laboratory-based studies of interspecific interactions aim to measure aspects of performance and assume that animals in nature would perform similarly to those in lab studies in order to capture prey or escape predators (Dill, 1987). However, the best way to understand how the environment impacts predator-prey interactions is to observe these encounters in a natural setting. Recent advances in filming and analytical techniques are addressing historic challenges to field studies of performance, enabling tests of laboratory-based theories in natural settings. In aquatic settings, studies that have used underwater cameras to collect data on fish behavior include examinations of herbivory (Gill & Hein, 2017), interspecific interactions (Turesson & Brönmark, 2007), and group swimming (Holubová et al., 2020), but fewer studies have attempted to examine predator-prey interactions in situ. One recent example of such a study in a terrestrial environment used high speed video cameras and infrared lights to capture the attack kinematics of rattlesnakes (Higham et al., 2017) as well as the escape kinematics of their kangaroo rat prey (Freymiller et al., 2019) in natural settings. Likewise, marine predator-prey interactions have been recorded in open water habitats (Domenici et al., 2014). However, to our knowledge, predator attacks on an aquatic vertebrate species in an

unmodified stream environment have not yet been recorded or analyzed.

Migrating amphidromous fishes provide systems that present outstanding opportunities to study aquatic predator-prey interactions in nature. Many species in stream ecosystems of oceanic islands exhibit such life cycles, in which fry that have hatched upstream are swept to the ocean for a period of development and dispersal, but later return to streams and swim against the current to migrate back to adult habitats (Fitzsimons et al., 1997; McDowall, 2004; Moody et al., 2015). As these species migrate upstream, they face strong currents and attacks from predators that live in these fast-flowing waters (Fitzsimons et al., 1997; McDowall, 2004; Blob et al., 2010; Diamond et al., 2016). Thus, as part of their life cycles, many amphidromous fishes undertake a unidirectional, upstream migration that allows piscivorous predators in these systems to anticipate the direction in which prey are moving and, potentially, take advantage of this pattern to capture prey. In streams of the Hawaiian Islands, such migrations are performed by gobiid fishes, which pass through the ranges of piscivorous predatory fish, including the Hawaiian sleeper *Eleotris sandwicensis* (Corkum, 2002; Schoenfuss & Blob, 2007; Maie et al., 2014). *Eleotris sandwicensis* is a benthic ambush predator that lies camouflaged on the substrate before attacking prey which swim higher in the water column (Tate, 1997; Corkum, 2002; Schoenfuss & Blob, 2007; Maie et al., 2014). These stream beds provide ideal conditions for studying in situ predator-prey interactions, due to the density of predators in a single location and reliability of prey that travel past during migrations.

Previous laboratory-based measurements of the escape performance of juvenile gobies in flowing water provide a context for evaluating whether environmental impacts on performance ultimately prove detrimental to the survival of prey species (Diamond et al., 2016). In that study, a water-jet stimulus in a flow tank arena was used to simulate predatory attacks on juvenile *Sicyopterus stimpsoni* from several directions (Diamond et al., 2016). Juvenile *S. stimpsoni* did not respond as frequently when stimulated in the same direction as water flow (i.e. head on) compared to stimuli oriented in other directions (Diamond et al., 2016). Because this direction of flow is the same direction that juvenile gobies would face during upstream migrations, it is possible that

flowing water might produce a hydrodynamic “blind spot” in the ability of these fish to detect predator strikes. Investigations of a spider-cricket predator-prey system demonstrated that upstream disturbances to air flow caused by the movement of the predator alert the downstream prey and narrow the window of opportunity for a successful strike (Casas & Steinmann, 2014). Conversely, the motion of flowing water may mask the disturbance caused by the attacking predator or may physically obstruct visual cues of the approaching predator from this direction.

The impact of flowing water on the ability to detect and escape from predatory attacks could strongly influence prey survival, if predatory sleepers take advantage of the hydrodynamic “blind spot” indicated for juvenile gobies by attacking migrating individuals from an upstream direction. If *Eleotris sandwicensis* have adapted to attacking prey from orientations aligned with stream flow, it could lead to increased prey capture success if prey are less likely to evade attacks from this direction. However, in other piscivorous species, predators tend to orient themselves perpendicular to their prey, which may maximize the surface of the prey that can be seen and attacked during a strike (Webb, 1980). In addition, observations of *E. sandwicensis* during field collections have indicated that, prior to striking, stream topography allows these predators to orient themselves with varying levels of perch angles (defined as facing towards the surface at an angle above zero degrees relative to the horizontal). Predators at higher angles may have higher success rates because they are already facing upward towards prey swimming above them, allowing them a better visual field to detect and attack prey (Arnold, 1974; Combes et al., 2013).

In this study, we tested for the first time in situ whether predatory *Eleotris sandwicensis* take advantage of the potential hydrodynamic “blind spot” of their goby prey, or otherwise adjust orientation towards prey, during attacks in flowing water. We collected in situ video of *E. sandwicensis* attacks on juvenile Hawaiian stream gobies to test the following specific predictions: (1) predators will take advantage of the hydrodynamic “blind spot” of prey by attacking in the direction of flow more often than in other directions; (2) attacks that take advantage of the hydrodynamic “blind spot” will successfully capture prey more frequently than attacks from other directions; and (3) predators using higher perch angles will

successfully capture prey more frequently than predators that attack from a less perched position. These observations will allow us to evaluate whether performance detriments observed in laboratory trials are likely to impact the survival of individuals in nature.

Methods

Video collection and analysis. In March 2017, we collected underwater, in-stream high speed video (120 frames/s) at the base of the first waterfall in Hakalau Stream (19°53'55" N 155°07'52" W) over six recording days, using an array of two GoPro Hero 4 cameras. Cameras were mounted 35 cm apart on an aluminum frame and anchored on the stream bed in an area known to have frequent predator and prey activity (Fig. 1). The onset of instream migrations of juvenile *Sicyopterus stimpsoni* are usually preceded by flash flooding several days prior, resulting in daily waves of juveniles. Due to their strong rheotactic behavior, juvenile *S. stimpsoni* move swiftly upstream and encounter predatory *Eleotris sandwicensis* along their migration route. We filmed between 10.00 and 15.00 h on each day to ensure that recordings were taken when the fish were active (Keith, 2003) and that there was ample sunlight for filming. The six-day observation period represented a single migratory event, assuring consistency in the predator population as *E. sandwicensis* is an ambush predator that relies on remaining still to capture unsuspecting migrating prey (Maie et al., 2014). Indeed, migration events can be somewhat predicted by increased density and territoriality of *E. sandwicensis* (Schoenfuss, pers. observation).

Before each recording session and after battery changes, we filmed a calibration object (Fig. 1) built following the guidelines of Neuswanger et al. (2016). One side of the calibration object had a black and white checker 1 × 1 cm grid to correct for distortion. The other side of the object provided a calibration frame using black and white disks of known dimensions that were drawn on both a clear sheet of Plexiglas that was closer to the cameras, and on an opaque sheet further from the cameras (Neuswanger et al., 2016). We collected video images of this combination of two sheets of disks before each trial to allow us to calibrate our measurements in 3D space, using freely available VidSync software (Neuswanger et al., 2016).

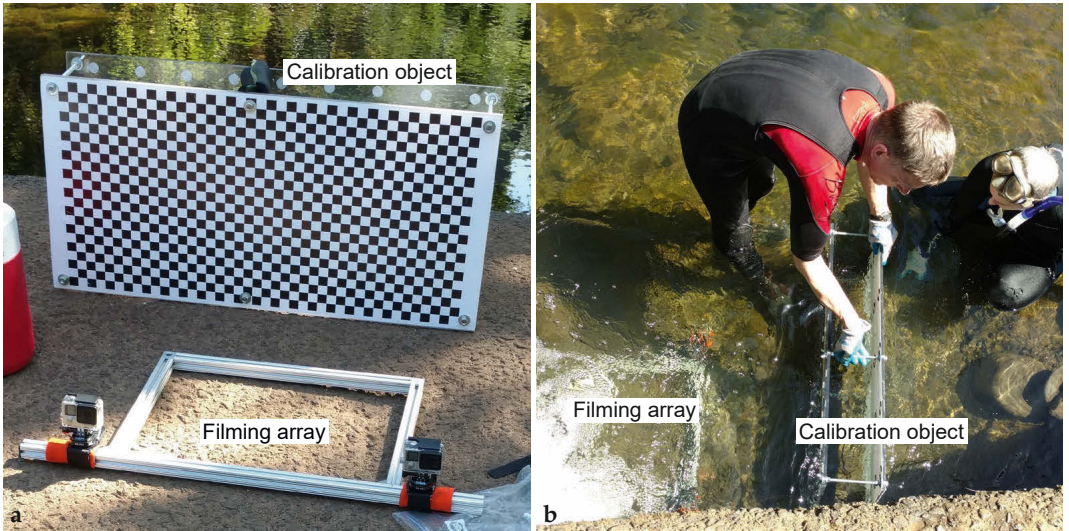


Fig. 1. Instream filming array and calibration object: a, out of the water, b, during calibration of a filming trial in Hakalau Stream.

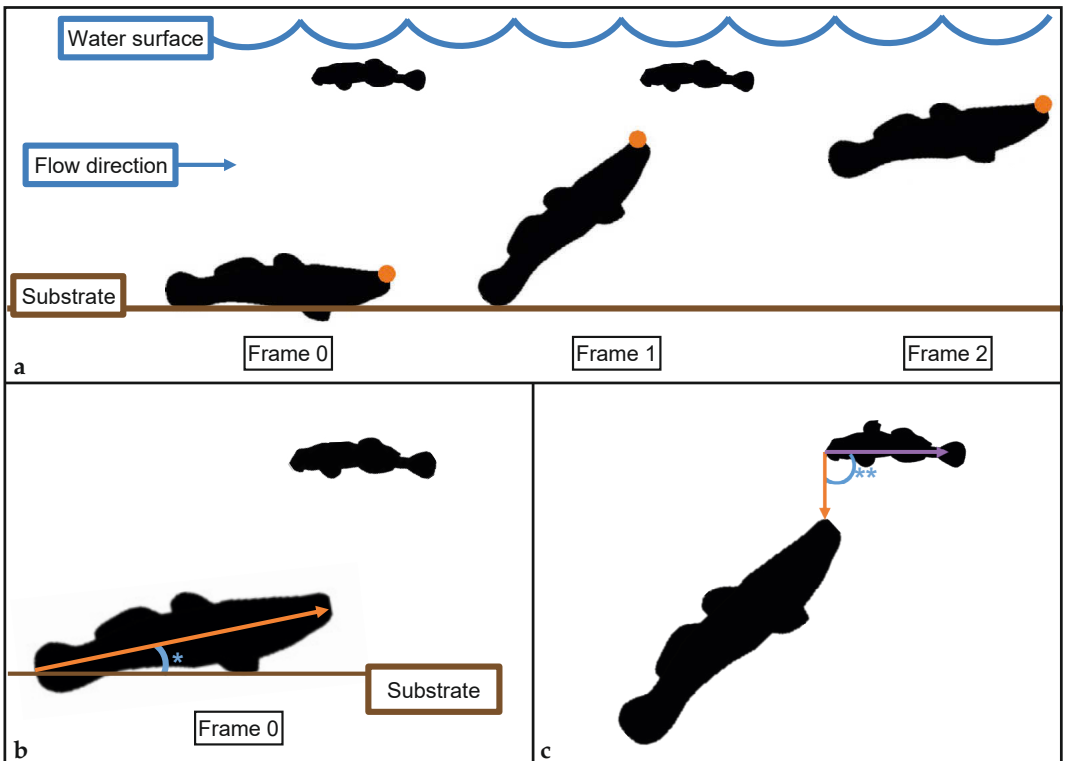


Fig. 2. Measurements collected: a, predator path during attack sequence recorded as a 3D-coordinate of the predator rostrum in each frame of the predator attack; b, perch angle (*) between a predator length vector (orange) and a vector representing the substrate at frame 0; c, prestrike angle (**) between the predator vector (orange) and prey vector (purple) on the frame immediately before predator attack.

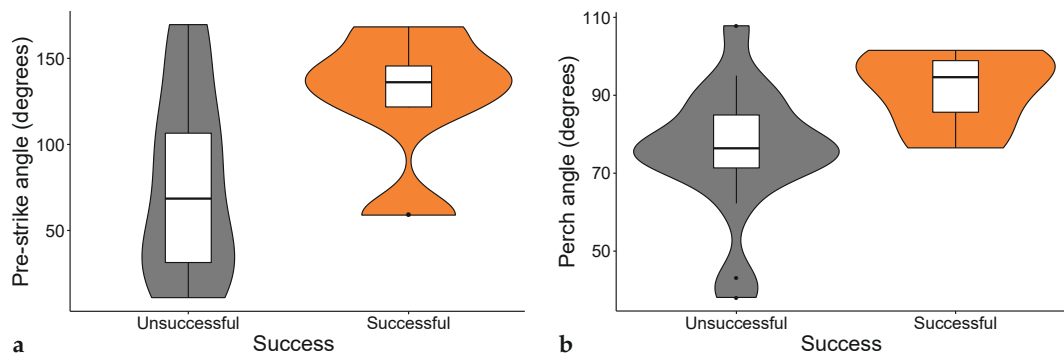


Fig. 3. Violin plots of unsuccessful (grey) ($n=19$) and successful (orange) ($n=5$) attacks for **a**, pre-strike angles and **b**, perch angles. Boxplots overlaid within each violin plot show median values, the lower and upper hinges correspond to the first and third quartiles, whiskers show median \pm (1.5 \times inter quartile range), and outliers are noted as separate points.

We surveyed 20 hours of video data collected over six days to identify predator attacks on migrating goby prey. Following calibration and distortion correction, we used VidSync (Neuswanger et al., 2016) to digitize the 3D coordinates of the predator and prey throughout in situ attacks (Fig. 2). From the digitized positions, we calculated the prestrike angle (product between predator and prey vectors) and perch orientation (angle above the substrate) of each predator attack using a custom R script (v 3.5.1; R Core Team, 2018) and determined if the predator was successful or unsuccessful at capturing the prey. We defined the prestrike angle as the angle between the predator vector and the prey vector on the frame before the predator either ate the prey fish, or the prey fish performed a successful escape response (Fig. 2c). On the video frame immediately before the prey is consumed or evades attack, a predator vector was drawn from the rostrum of the prey to the rostrum of the predator. A prey vector was also created on the same frame, originating at the caudal peduncle and directed through the rostrum. We defined zero degrees as an attack angle for which a predator attacked the prey in line with its rostrum, and 180 degrees as an attack angle for which the predator attacked directly in line with the prey's caudal fin. Perch angle was determined by comparing a vector of the predator (running from the rostrum to the caudal peduncle of the predator) relative to the substrate, which was defined as 0 degrees (Fig. 2b) in the frame immediately before the predator started moving for the attack (Frame 0). Strikes were termed successful if the predator caught

the prey and it was no longer seen on screen, or unsuccessful if the prey was seen in the field of view after the end of the attack strike. Data on the distance between predator and prey before the start of an attack, and the path the predator followed during the interaction, were collected and evaluated. However, we found no significant difference between either of these variables and success rate, and excluded these factors from further analysis.

Statistical Analyses. All statistical analyses were conducted using R version 3.5.1 (R Core Team, 2018). Based on predator sizes and color patterns, we were able to collect attacks from multiple predators. However, these characteristics were not sufficiently unique to identify individual predators among the population present at our study site in the video that we collected. In order to minimize human interactions, we chose not to mark or interact with fish in any way other than placing cameras in the stream. Therefore, each attack was treated as an independent event, though we acknowledge that it is possible that we may have filmed multiple attacks from some individuals. To test if predators took advantage of the hydrodynamic “blind spot” of prey we used a one sample Kolmogorov-Smirnov test to compare the distribution of prestrike angles to a normal distribution. To test if predators that do take advantage of the “blind spot” were more successful at capturing prey, we conducted an analysis of variance (ANOVA) to evaluate whether success was explained by the pre-strike angle. Finally, to assess if more highly perched predators were

more successful at capturing prey than lower perched predators, we ran an ANOVA to evaluate whether success was explained by perch angle.

Results

Our six-day observation period succeeded in capturing 24 predator attacks using high speed videography. Of these attacks, five were successes (predator consumed prey) and 19 were failures (prey evaded predator). This success rate (21 %) falls within the range of values reported for other vertebrate predators (McLaughlin et al., 2000; Thiebault et al., 2016; Wilson et al., 2018). The distribution of pre-strike angles was normal ($p < 0.01$) meaning that, in our sample, predators did not preferentially attack prey in any particular direction. Prestrike angles of successful and unsuccessful attacks showed substantial overlap ($F = 4.036$, $p = 0.058$); however, successful captures were only achieved by predators attacking prey at higher pre-strike angles ($\bar{x} = 126^\circ$; Fig. 3a).

Predators that were perched at higher angles also experienced a greater chance of success. Similar to comparisons of pre-strike angle, comparisons of perch angle for successful attacks overlapped with those that failed ($F = 3.667$, $p = 0.069$). However, only strikes from a perch angle above 80° were successful at capturing prey (Fig. 3b).

Discussion

Observing predator-prey interactions in situ can provide a wealth of information about environmental factors influencing outcomes not accessible in controlled laboratory experiments. However, capturing sufficient quantities of events that are similar enough to control for environmental conditions is challenging in any environment. In streams, swift currents further complicate the use of water-sensitive recording equipment. Yet these observations are crucial for understanding which environmental conditions could prove potentially fatal for prey, but advantageous for predators. In this study, we succeeded in recording 24 predator-prey interactions at high frame rates and with corrections for distortions. This data set, collected with homogeneous environmental conditions and predators, allowed us to test hypotheses obtained from prior laboratory experiments (Diamond et al., 2016). However, we acknowledge that the

field conditions in which we collected data may not exactly replicate the conditions of the original lab trials that formed the foundation for this study (Diamond et al., 2016), as it was not possible for us to reliably measure flow rates at the locations where in situ interactions were filmed.

While flowing water may limit the ability of migrating fish to detect predator attacks, our results suggest that Hawaiian sleepers do not actively take advantage of the hydrodynamic “blind spots” of their goby prey. In contrast to our predictions, not only did predators fail to preferentially attack from a particular direction, but predators that attacked at higher pre-strike angles (i. e. in the direction opposite to flow) were more successful at capturing prey (Fig. 3a). This success may be attributed to the differences in how prey detect predators in a more natural (vs. laboratory) setting (Caves et al., 2017), or it is possible that predators may have more difficulty attacking prey in the direction of stream flow, though further exploration would be needed to test these possibilities. Experiments that suggested the presence of the hydrodynamic “blind spot” in juvenile *S. stimpsoni* used water jets as stimuli to provoke escapes, which focused on the perception of a stimulus by the lateral line system in flow (Stewart et al., 2013, 2014; Diamond et al., 2016). However, once predator-prey interactions occur in the full context of a natural environment, it is possible that other factors, such as visual or olfactory cues, or even previous exposure to predator attacks, might contribute to both the success of predators and the anti-predator strategy of prey. For example, in situ studies of kangaroo-rat escape performance found that individuals that had been exposed to predator attacks before trials had higher escape performance (Freymler et al., 2017). Alternatively, it is possible that such hydrodynamic “blind spots” may be able to persist in gobies because predatory selection against them is not strong. Laboratory-based studies of fish performing suction feeding in flow tanks suggest that flow can impede the accuracy of predator strikes by altering the amount of water the predator is able to bring into the mouth during suction (Asaeda et al., 2005; Domenici et al., 2007; Higham et al., 2015). It is possible that predators have more difficulty accurately using suction feeding in the same direction as flow, as opposed to allowing stream flow to aid in bringing fish into the mouth when predators attack prey in the opposite direction of flow. Such factors

could contribute to why the fish we filmed were more successful when attacking in the opposite direction of stream flow. These discrepancies between prior laboratory results and our in situ observations provide rich grounds for further hypothesis testing in laboratory settings.

Predators that were perched at higher angles had greater success when compared to predators attacking from a more prone position (Fig. 3b), with no predator successfully capturing prey from an angle less than 80°. Predatory fish often attempt to maximize the surface area of the prey to be attacked by orienting themselves perpendicular to the prey (Webb, 1980). Perching in the direction of travel to the prey enables predators to detect prey from a greater distance, which could provide predators more time to assess when to attack before prey are able to detect them (Abrahams et al., 2009). Additionally, perching could minimize the distance predators must travel to produce the strike, leading to a greater chance of success (Maie et al., 2014).

Though our sample size of events was limited, particularly for successful attacks, the success rate of predators in the current study matched those reported for other vertebrate predators (McLaughlin et al., 2000; Thiebault et al., 2016; Wilson et al., 2018). The consistency of predator success across a broad range of vertebrate taxa suggests a balance in which predators achieve sufficient success to compensate for the energetic expenses of unsuccessful strikes, while prey escapes at a sufficient rate to not endanger population sustainability. Prey selection models predict that a predator needs to maximize energetic benefit either by choosing prey that offer large energetic return, or by limiting strikes to those that maximize success probability (Pyke, 1984). Since prey is uniform in size in this study (all migrating *Sicyopterus stimpsoni* are within a very narrow age and weight range [Blob et al., 2010]), maximizing strike success appears to be the critical factor for *Eleotris sandwicensis*. In the context of our results, *E. sandwicensis* should only strike from advantageous perch angles, above 70° from the horizontal. However, the abundance of prey during migratory periods may explain why predators strike from lower perches.

This study highlights the importance of testing laboratory-based findings with in situ studies to gain further insight into ecologically relevant components of predator-prey interactions. Our sample

of in situ videos indicates that predatory *Eleotris sandwicensis* do not appear to preferentially attack juvenile Hawaiian gobies in the hydrodynamic “blind spot” that had been identified in laboratory trials. Due to advances in video and analytical technology, studying predator-prey interactions in the natural environment has become more achievable (Freymiller et al., 2019). However, this is the first study to our knowledge to attempt an in situ analysis of predator-prey interactions of stream fishes in an unmodified system. Analysis of predator-prey interactions in the laboratory allows greater control of the environment and assurance of consistency between trials, and allows researchers to control which individuals are used in each experiment. However, moving an animal out of its natural environment and, thereby, imposing interactions with humans, causes intrinsic amounts of stress on the study organism, producing behavioral changes (Troxell-Smith et al., 2016). Aside from placing camera calibration objects in the stream, we did not interact with the individuals in this study. Thus, we were able to quantify completely natural predator-prey interactions. By contradicting some results of laboratory-based experiments, the current study highlights the need for field-based observations of predator-prey interactions to test laboratory findings in a natural setting. Contradictory results then provide rich grounds for further hypothesis testing in the laboratory. For example, studies of the role of prior predator exposure, impairment of the lateral line in high velocity currents, and effects of fast flow on predator suction feeding may provide further insight into factors determining success and failure of the observed in situ predator strikes in aquatic habitats.

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Supplemental Information:

A supplemental video of a failed predator attack:
<https://www.youtube.com/watch?v=SPXtA87eAXM>

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Cover photograph

Hypostomus pastinhai (Photograph by Cláudio Henrique Zawadzki)

Cláudio Henrique Zawadzki and Iago de Souza Penido

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