INTRODUCTION

Mobile animals need to navigate for various reasons, including to locate resources, find mates, or return to their home area, while simultaneously minimizing predation risk (Noda et al. 1994; Braithwaite and Girvan 2003; Åkesson et al. 2014; Hansson et al. 2016). Animals rely on a range of spatial cognitive skills to perform these tasks; they can recognize complex cues, form long-term memories, and regain their bearings after disorientation. For example, Clark's nutcrackers (Nucifraga c. c. cristata) can memorize the locations of thousands of caches up to nine months after caching (Balda and Kamil 1992), and displaced honeybees find their hive by using spatial features learned during a single flight (Degen et al. 2016). Some fish species also have excellent spatial learning and memory abilities (Teyke 1989; Warburton 2003). Atlantic salmon (Salmo salar), goldfish (Carassius auratus), and corydoras (Corydoras affinis) can locate a food reward using visual landmarks (Braithwaite et al. 1996; Salas et al. 1996; López et al. 1999; Hughes and Blight 2000), even when released in an unfamiliar spot (Rodriguez et al. 1994). There is also evidence that some fishes (e.g. Mexican cave fish (Astyanax mexicanus), goldfish (Carassius auratus), and butterflyfishes (family Chaetodontidae) use cognitive maps to navigate their surroundings (Reese 1989; Rodriguez et al. 1994; Book De Perera 2004). Cognitive maps are internal map-like representations of relationships between different landmarks in their environment, created through spatial learning (Tolman 1948; Toates 1980; Gould 1986). Such an internal representation of the environment allows animals to adopt novel routes from previously unvisited points, removing the requirement of learning specific routes (O’Keefe and Conway 1978; O’Keefe and Conway 1978; Suzuki et al. 1990; Morris 1981; Mazmanian and Roberts 1983).

To further understand mechanisms of spatial orientation, researchers have taken advantage of aerial jumping behavior in fishes because it presents a clear directional choice of movement (Braithwaite et al. 1996). Aronson (1951, 1971) and White and Brown (2014) used this behavior to demonstrate that gobies have a cognitive map.
of their habitat as they can leap from one tidal pool to another even when they have no visual contact before leaving the water. Guppies (*Poecilia reticulata*) also show aerial jumping (Soares and Bierman 2013) and may therefore possess similar spatial abilities. In Trinidadian rivers, the guppies’ native range, seasonal changes, and weather events connect and disconnect pools; connecting them at high water and isolating them from the main river as the water recedes. By being able to jump out of such pools, guppies should be able to return to the main river, escaping isolation, and potential death as the pools desiccate. Soares and Bierman (2013) documented guppies generally starting a jump with a slow and preparatory backwards movement, followed by a forward thrust, propelling the fish into the air. These small fish are able to jump approximately 3.5 times their body length in height, with a positive correlation between jump height and back-up distance (Soares and Bierman 2013). This suggests that guppies can actively alter jump height and likely also distance. Additionally, the preparatory phase suggests jumping is not purely reflexive, but involves a clear motive. However, whether guppies are able to direct their jump towards a specific location, and what information they base their jumping direction on, remains untested.

As guppies are capable of using spatial information in maze-experiments (Chapman et al. 2008; Burns and Rodd 2008a; Miletto Petrazzini et al. 2017; Lucon-Xiccato and Bisazza 2017a, 2017b), we tested if and how guppies base their jumping directions on spatial information in two experiments. In the laboratory, we tested whether guppies use the memory of specific landmarks (cognitive maps) to jump out of “trouble” in a known small water body. We used water level changes in combination with entrapment in desiccating pools to test if guppies remember which areas are safe to jump to. In this relatively small arena, the shallow areas become dry land and the deep areas remain water-filled pools. We predicted that if guppies memorize their environment and incorporate that spatial information, they should aim their jump towards the pools.

In a second experiment in the wild, we tested whether guppies show directed jumping behavior when entrapped in unknown small water bodies. Such a situation may occur during flash floods when a fish gets washed ashore and finds itself in a desiccating body of water that lies outside its known area. We hypothesized that, in the scenario where the fish has no previous information about the specific environment, they should use general landmarks like visual and/or auditory cues. Hence, this scenario excludes the possibility of basing jumping direction on cognitive maps, and requires them to rely on external, general landmarks. For instance, the open canopy may function as a general landmark as it can indicate the middle of the river. Sunlight and gap size in the tropical forest determine different light environments, with canopy openness decreasing from the center of the stream to the riverbanks (Endler 1992). The canopy structure has various visual aspects that the guppies could use for orientation, including the increased light level in the middle of the river. There is evidence that several fish species show the ability to orient themselves towards or away from light sources (phototaxis) (Goodyear and Ferguson 1969; Forward Jr et al. 1972; Barki et al. 2014; Pec et al. 2017). In addition to phototaxis, the trees at either side of the river can function as a general visual landmark on which fish orient to find the middle of the stream. Although the canopy is distant, fishes have been shown to use external, general cues outside of the water to orient themselves (Rodriguez et al. 1994). Hence, the various visual aspects of the canopy structure can function as a general visual landmark on which fish orient to find the middle of the stream. Another general landmark may be the sound of flowing water as a loud local riffle may indicate flowing water and therefore a safe jumping direction. Sound can be important for orientation in aquatic animals because of its highly directional nature (Hawkins and Popper 2018). For example, sound is a meaningful orientation and attraction cue for larvae of reef fishes (Tolimieri et al. 2000; Simpson et al. 2005; Montgomery et al. 2006). Since the sound of a riffle indicates a “safe” direction towards water, it may trigger the guppies to jump towards that direction. We investigated their jump direction in a cue-conflict/cue-matching experiment, where we exposed guppies to different spatial combinations of riffle sounds and canopy openness. This experiment tested which of two general landmarks, sound or canopy openness, guppies base their jumping decision on. We hypothesized that both cues are important and predicted that guppies will show the highest directional preference when both cues match.

**MATERIALS AND METHODS**

We aimed to test the hypotheses that guppies can 1) use a cognitive map based on learned spatial information, and 2) can incorporate external environmental cues (visual and auditory) to determine where to safely jump. To do so, we ran two experiments.

**Experiment I – testing for a cognitive map in the laboratory**

In a laboratory experiment, we aimed to understand whether guppies use cognitive maps to direct their jumps. The study was carried out in the animal facilities at Wageningen University and Research in April 2020. Guppies used in the experiment were 20 adult females; laboratory-reared descendants of fish collected from a high-predation population from the Aripo river in Trinidad. Prior to experiments, fish were housed in same-sex groups of six in 4-liter flow-through tanks at Wageningen University. Temperature was kept at 24 °C with a 12:12h dark/light cycle. Fish were fed twice daily on seven days a week with flake food and freshly hatched *Artemia salina* nauplii.

Two identical experimental tanks (70 × 35 × 40 cm) were filled with gravel and shaped into four quadrants of different depths (two shallow areas, two deep areas; Figure 1). Two-centimeter ridges separated the quadrants from each other. Additionally, four markers, consisting of wooden sticks of two different colors (black to mark horizontally and brown to mark vertically), were used to mark the division between the shallow and deep areas and could serve as a visual landmark for the fish. The water level in the experimental tank could be altered by siphoning out water or adding water through two identical tubes attached to the sides of the tank. The shallow areas were approximately 5 cm deep at high-water. At low water level, the shallow areas fell dry. The deeper areas consisted of a slope, starting its decline at the border with the shallow areas. During high water the deep area ranged from 5 to 17 cm in depth. During low water, the deepest area was 12 cm deep. In the middle of the tank there was a circular testing arena with a diameter of 9 cm that was surrounded by a 1.5 cm high ring of gravel so that the water level of the rest of the tank was not visible from the inside the testing arena during low water levels. The circular testing arena had a depth of approximately 3 cm at low levels, imitating an isolated tidal pool. A camera was mounted above the experimental tank. Both deep areas were equipped with a filter during the habituation period of the test, and stones were used in the corners of
the shallow areas to limit access to the tubes used to alter the water level (Figure S1).

Ten females were simultaneously transferred into one of the experimental tanks at high water and allowed to habituate for one hour. This and all subsequent procedures were done in parallel in the two experimental tanks. The fish were exposed to the experimental tanks for a total of three consecutive days. During these days, they experienced three 2-hour periodical flood cycles per day. Within one cycle, the water receded for approximately 25 min. After a 10 min rest period, the water started rising for 25 min. This was repeated twice per cycle. After finishing the third cycle of the day, the fish were fed. The same procedure was repeated on the second day. On day 3, after one full cycle, the water level was lowered once more, and the guppies were caught and moved to temporary holding tanks. Guppies were caught individually with a net, then transferred into the circular testing arena (3 cm depth) with a cup, and observed for their jumping behavior during the low water phase (maximum depth of 12 cm). Latency to jump and landing location were determined from video footage. Note that before the testing phase the shallow areas fell completely dry at low water, yet, during the testing phase, a depth of 1 cm was maintained to avoid fish jumping on dry land and possibly injuring themselves. Thus, even when they jumped towards the shallow areas, they landed in shallow water. The water level was well below the visible threshold from within the testing arena.

Experiment II – testing for general spatial cues in the wild

In a field experiment, we aimed to understand whether guppies use auditory cues of moving water and/or visual cues of the open canopy to orient themselves when jumping. To do so, we conducted an experiment in the lower Aripo river in Trinidad (Lat.: 10.6667; Long.: −61.2285) in March 2020. This site was chosen due to its steady guppy population, its pronounced network of riffles and pools, and a relatively high canopy openness in the middle of the river. A riffle was defined as a small waterfall or a localized fast-flowing current generated by numerous boulders within the river (Figure S3). Apart from the sound of the riffles, the site was calm and the riffles were spaced apart, limiting the sound interference between different riffles.

We selected three locations towards the left bank and two locations towards the right bank so as to vary the direction to the open canopy. At each of these locations, two different spatial arrangements (treatments) relative to two cues were created on either side of the riffle (Figure 2). The riffle was either spatially matching – at the same side of the open canopy – or contrasting – at the opposite side of the open canopy (Figure 2). Water depth ranged from a few centimeters close to a riffle to 1 m in the deeper areas. Note that all locations were within the stream for ethical reasons. Thus, all jumping directions led back to water.

Nine trials were done at two locations, and eight trials were done at the other eight locations. Female, male, and juvenile guppies (N = 492) used in this experiment were collected with dip and butterfly nets within a range of 20 m around the test site in pools and the main stream. We chose to assay females, males, and juveniles to obtain a more representative sample of jumping behavior in the
species, but made no specific predictions on how females, males, and juveniles should differ in their jumping behavior.

During jumping trials, guppies were placed in opaque white Styrofoam cups (5.5 cm diameter, 3.5 cm height) that were filled with 30 ml of fresh stream water so that the height difference between the water surface and cup edge was roughly 1 cm. At the start of a trial, six cups were placed near the edge of a boulder at the riffle side and guppies were individually placed into the cups. Trials were filmed for 10 min using an overhead stationary GoPro camera, mounted on a PVC tube structure (Figure S3). Observers kept a distance of at least one meter.

For each trial, individual fish were scored for whether or not they jumped within 10-minutes and the jump latency was recorded. Subsequently, for the fish that jumped ($n = 275$), still frames were isolated from the video footage and analyzed to estimate the jumping angle (Fig S2). A first frame was selected when the fish started to protrude above the water surface. In this frame, a line was drawn from the fish's center to the riffle center. This line was used as a reference and was set at 0 degrees using modular arithmetic. Thus, all subsequent calculated angles were relative to this line. A second frame was then selected where the fish crossed the edge of the cup. In this frame, a line was drawn from the fish's center when starting the protrude to the fish's center when crossing the edge of the cup. The angle between the two drawn lines was calculated by measuring the shortest clockwise path using the Protractor feature in the PicPick software (version 5.0.7; 2020). This angle is referred to as the jumping angle. Three jumps were excluded from the analysis because the angle was impossible to measure due to low quality footage. The jumping angle was calculated in 272 individual guppies by a single researcher to avoid observer differences.

### Statistical analysis

#### Experiment I

To test whether the jumping rate towards the pools was significantly different than random chance we used a two-sided binomial exact test. We chose against running circular statistics on this experiment due to the sample size. Subsequently, to test whether the latency to jump varied between the fish jumping towards deep areas or the fish jumping towards the shallow areas we used a Wilcoxon rank sum test.

#### Experiment II

To test for differences in the Likelihood to Jump, we used a linear mixed model (binomial distribution, $1 = \text{jump}; 0 = \text{no jump}$) with Treatment (opposite or matching cues), Life-stage (male, female, juvenile), and the interaction of Treatment $\times$ Life-stage as predictor variables, as well as a random factor for Location using again the “lme4” package. Model terms were tested for significance using the ANOVA function in the car package (Fox and Weisberg 2018), specifying Type III Wald chi-square tests. The interaction between Life-stage and Treatment in this model was removed from the model as it was non-significant and uninformative for our research question ($P = 0.403$). If Life-stage was a significant predictor in the model, we assessed Tukey corrected multiple comparisons between Life-stage levels using the “lsmeans” function in the “emmeans” package (Lenth et al. 2019). To meet the homogeneity and normality assumptions, we performed a log (10) transformation on Jump latency.

To investigate the role of sound and/or canopy cover for jumping orientation, we used circular statistics techniques. The Rayleigh test was used to assess the uniformity of the jumping direction. If no clear direction is preferred, then all directions would be approximately equally covered on the circumference of a circle, visible in a circular uniform distribution. Any deviation from a circular uniform distribution would be indicative of a preferred direction. The Rayleigh test assumes that the data follow a unimodal and symmetrical von Mises distribution (Landler et al. 2019). To rule out multimodal departures and unknown symmetry, the Herrmans-Rasson test was performed. All statistical analysis was performed in R-3.6.2 (R Development Core Team 2012).

### RESULTS

#### Experiment I

In the laboratory experiment testing if guppies direct their jumps using a cognitive map, all female guppies jumped out of the testing arena. Of the twenty tested animals, 16 jumped towards a deep area and 4 jumped towards a shallow area (Figure 3A). Thus, fish were more likely to jump towards the deeper pools than expected at random with a 50:50 chance ($N = 20; \bar{Z} = 16; P = 0.006$).

We found no difference in the latency to jump between the guppies jumping towards the deep areas compared with the guppies jumping towards the shallow areas (Wilcoxon rank sum test; $N = 20; W = 45; P = 0.237$; Figure 3B). Note that there were only 4 fish in the group jumping towards the shallow areas, thus, there is little power to assess differences in the latency to jump towards these different areas.

#### Experiment II

In the field experiment testing for general spatial cues, 55.9% (275/492) individuals jumped out of the testing cup, whereas 44.1% (217/492) did not jump within the 10-minute experimental time. We found no differences in the likelihood to jump between the treatment groups ($\chi^2_{1,270} = 0.019; P = 0.892$), but the likelihood to jump differed between juveniles, females and males ($\chi^2_{2,270} = 23.392; P < 0.0001$). Pairwise comparisons showed that juveniles jumped significantly less than males and females (Juvenile - Male: $P = 0.019$ and Female - Juvenile: $P < 0.0001$).

When filtering the data to only fish that jumped, we found no differences in the latency to jump of fish from the matching cues treatment compared with those from the contrasting cues treatment ($F_{1,270} = 3.626; P = 0.057$; Figure 4A). Yet, we found that juveniles, females, and males differed in jump latency ($F_{2,270} = 23.229; P < 0.0001$; Figure 4B). Pairwise comparisons indicated that females jumped approximately 26 s faster than juveniles and 19 s faster.
than males (Female – Juvenile: $P < 0.0001$ and Female – Male: $P = 0.012$).

When exposed to matching cues, the jumping direction for all fish showed a significant deviation from a uniform distribution ($R = 0.253$; $Z_{135} = 8.659$; $P = 0.0002$; Figure 5A), which indicates that fish preferentially jump towards a specific direction. We found that the mean direction of the jump was 18.75 degrees relative to the middle of the riffle, pointing towards the riffle and canopy openness.

In contrast, fish exposed to contrasting cues showed a randomly distributed jumping orientation, with no clear preferred jump direction ($R = 0.058$; $Z_{137} = 0.463$; $P = 0.630$; Figure 5B).

When investigating the jump direction of males, females, and juveniles separately, only females in the matching cues treatment showed a preferred direction towards the two cues, departing from a uniform direction (Rayleigh test; $R = 0.342$; $Z_{60} = 7.037$; $P < 0.0009$; Figure 6A). Although the mean jumping direction for the
males and juveniles appeared qualitatively similar (Figure 6A), the jumping direction did not differ from uniformity. When exposed to contrasting cues, neither of the sexes nor juveniles showed a preferred jumping direction (Figure 6B).

DISCUSSION

In two complementary experiments, we found evidence that guppies direct their jumps towards a specific direction and use both a cognitive map and general landmarks to orient themselves. When guppies were confined in a small and shallow pool in a familiar environment, they swiftly jumped out to land in deeper water bodies. In contrast, when they found themselves in unknown confined water bodies, they were less likely to jump, but when they did, they oriented themselves using general landmarks such as the sound of moving water and canopy openness.

The first aim of this study was to test whether guppies have the capacity to memorize their surroundings and use this information to determine their jumping direction. We found that all animals jumped out of the test arena within minutes and most of the animals jumped towards areas with deeper water, supporting our prediction that guppies can use cognitive maps to direct their jumps. Spatial cognition has been well studied in guppies (Burns and Rodd 2008b; Kotrschal et al. 2015; Lucon-Xiccato and Bisazza 2017a). For example, they can learn to navigate a complex maze consisting of up to six consecutive T-junctions (Lucon-Xiccato and Bisazza 2017b). Our data add cognitive maps to this portfolio of spatial abilities because, similar to fishes such as the amphibious spotted rock skipper and some gobies (Aronson 1971; White and Brown 2014; Buo et al. 2020b), they reliably jump to favorable areas even when the direct line of sight is blocked. Due to the way our test pool was designed, the guppies could not see the water level outside of the pool during the test and could only orient using the provided visual cues and/or internally stored information. External visual cues included the quadrant division markers, cues from the experimental room, and differences in ceiling color. While maze experiments show that guppies typically do not rely on subtle cues when navigating (Lucon-Xiccato and Bisazza 2017b), they could have done so in this study and memorized external landmarks may be part of the cognitive map of the environment. In line with our predictions, we found that guppies have the ability to create cognitive maps of their environment and retrieve those to direct their jump in order to successfully return to deeper bodies of water.

The second experiment tested how guppies react to being trapped in small water bodies that are unknown to them but lie within their known home range. In these cases, they likely had no memory of the quality of the environment they jumped towards. We hypothesized that guppies then may rely on external visual and/or auditory cues, that is the canopy structure and a local riffle,
to orient themselves when jumping out of an isolated area. In line with our predictions, we found that only when visual and auditory cues were aligned guppies showed clear directional jumping towards the middle of the stream, while under contrasting cues no clear directional choice was evident. Guppies seem to apply multimodal orientation as several cues need to align for effective re-orientation.

Most spatial task studies in fish have focused on the relevance of learned landmarks for orientation (e.g. Odling-Smee and Braithwaite 2003; Buo et al. 2020b). Guppies in the present study were predicted to orient spontaneously without training or reinforcement. Guppies live in large and highly changing habitats. Hence, the use of cognitive maps might not always be feasible or optimal. General landmarks, such as the geometry of the environment, should provide a better tool to orient than local landmarks when stranded in an unknown area. Indeed, the shape of the environment is crucial for reorientation in fishes, rats, and pigeons, showing that large-scale geometry of the environment is more relevant than local non-geometrical cues (Cheng 1986; Kelly et al. 1998; Sovrano et al. 2002).

In a guppy’s habitat, we hypothesized that canopy openness and riffle sound may be suitable general landmarks. Brighter light conditions can be indicative of the location of the middle of the stream, as the canopy is less dense there. This should provide information about where the water is likely the deepest. On top of light level, the canopy also provides other visual features that animals have been shown to use for orientation, including specific shapes in the canopy pattern or the overall contrast between the trees at both sides and the open sky. For instance, ants orient using the high contrast cues created by canopy patterns (Elmer 1999; Hölldobler 1980) and in fishes, depending on species, positive or negative phototaxis are widespread (Forward Jr et al. 1972; Barki et al. 2014). Additionally to optical features, we hypothesized that water murmur, or the disturbance caused by water flowing against rocks at riffles, might function as a general auditory landmark, as fishes can use sound as an orientation cue (Montgomery et al. 2006). We found that guppies showed only a preferential jumping direction when the two hypothesized landmarks, open canopy and riffle sound, were aligned. We conclude that both general landmarks are important for orientation and are used collectively.

Several non-mutually exclusive hypotheses exist to explain aerial jumping in guppies, from predator evasion (Seghers 1973) to means of dispersal (Soares and Bierman 2013). Here we show that guppies can use aerial jumping to escape isolation. Streams in Trinidad, the guppy’s environment, are highly dynamic with rapid water level changes, and getting trapped in a desiccating pool after a flood or a dry period is likely a common event. While staying in these isolated pools would mean isolation or even death, uncertainty about the surroundings may prevent the guppy from jumping into an unknown environment. Costs of erroneous jumping decisions include landing on dry land with the risk of desiccation. Even though repeated flapping on dry land can help getting back into a water body, impact on the rocks may still cause physical injury. We found a clear difference on whether guppies jumped or not out of confinement between our two experiments. While all animals rapidly jumped from the known pools in the laboratory, almost 40% of animals did not jump out of unknown confined water bodies within the experimental time. While different circumstances make the experiments difficult to compare, we interpret this difference as evidence for a divergent cost and benefit trade-off as jumping out of an isolated pool of a known environment carries less risk than jumping in a novel environment.

We also found differences between female, male, and juvenile jumping behavior. Juveniles jumped less than adult fish, and females jumped faster than juveniles and with a stronger directional choice. While we had no clear a priori prediction about how groups may differ in jumping behavior, we speculate how this difference may be explained. Divergence in risks of jumping may be one explanation; for juveniles, the risk of jumping may be greater, because a smaller body is related to higher desiccation and injury risk in fish (Odch et al. 2002). Moreover, juveniles might lack landscape knowledge and jumping skills, which increases the chance of hitting a rock. Differences in experience may also explain the difference in latency time of jumping between males and females. Females in the wild are less predated on and live longer than males (Reznick et al. 1996; Reznick and Bryant 2007). Due to their increased lifespan, they can gather more landscape knowledge and jumping skills. In contrast, males, having a shorter lifespan, might have evolved to invest more in mating efforts than in jumping and orientation skills. This reasoning is supported by our findings that while all fish showed the same orientational pattern when exposed to matching cues, only females significantly favored one direction over another. However, this line of argument seems to oppose a previous study that found that in mazes male guppies have better spatial abilities (Lucon-Xiccato and Bisazza 2017a). The authors suggest that because males have larger home ranges and disperse further (Croft et al. 2003, 2004; Darden and Croft 2008), they have evolved better spatial cognition. Additional data are clearly needed to clarify how maze performance relates to orientational skills in the wild, focusing in particular on jumping behavior.

To conclude, this study contributes to our understanding of how fish are able to use different cues to find suitable water bodies. In a lab experiment, we found that guppies were more likely to jump towards deeper areas when they are in a familiar entrapment, hence incorporating past spatial information to jump to safety. In a matched versus mismatched spatial cue experiment in the field, we found that animals only showed directed jumping when general visual and auditory cues matched. Hence, in this study, we show that fish rely on the use of cognitive maps and a combination of general landmarks to orient themselves during aerial jumping.

SUPPLEMENTARY MATERIAL
Supplementary material can be found at Behavioral Ecology online.

AUTHOR CONTRIBUTIONS
C.V.P., R.V.-T., D.J.M., D.v.B., E.L., L.M.L., and A.K. conceived the study. C.V.P., R.V.-T., D.J.M., D.v.B., E.L., and L.M.L. collected the data. H.D.W., D.v.B., and E.L. analysed the data and wrote the first version of the manuscript. All authors provided feedback on earlier versions of the manuscript and contributed to its final version.

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Data Availability: Analyses reported in this article can be reproduced using the data provided by De Waal et al. (2022).

Ethical Considerations: The care and use of experimental animals complied with animal welfare laws, guidelines and policies as approved by the Animal Welfare Body (Instantie voor Dierenwelzijn, IvD) at Wageningen University and Research and by the Fisheries Division of the Ministry of Agriculture, Land and Fisheries of Trinidad and Tobago. Experiments involved behavioural observations, and stress to the animals was minimised as much as possible. All wild fish used in the experiments were released unharmed into the stream, and experimental females in the lab were returned as much as possible. All wild fish used in the experiments were released unharmed into the stream, and experimental females in the lab were returned as much as possible. All wild fish used in the experiments were released unharmed into the stream, and experimental females in the lab were returned as much as possible. All wild fish used in the experiments were released unharmed into the stream, and experimental females in the lab were returned as much as possible. All wild fish used in the experiments were released unharmed into the stream, and experimental females in the lab were returned as much as possible. All wild fish used in the experiments were released unharmed into the stream, and experimental females in the lab were returned as much as possible.

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