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Behavioral constraints for the spread of the eastern mosquitofish, *Gambusia holbrooki* (Poeciliidae)

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Abstract Eastern mosquitofish (*Gambusia holbrooki*) are native to the southeastern United States but notoriously invasive elsewhere, and are aggressive predators in ecosystems they inhabit. Information on dispersal behavior is needed to better understand mosquitofish spread upon introduction and potential means to mitigate that spread. We experimentally tested the effects of shallow water depths (3–24 mm) and obstacles (leaf litter) on mosquitofish dispersal behavior, plus a range of conditions relevant to field situations. Mosquitofish dispersed significantly faster in deeper water ($p < 0.001$) but some dispersed in only 3 mm water depth (i.e., one-half average body depth). Wetland and upland leaf litter at natural densities strongly interfered with mosquitofish dispersal behavior. Based on our results, introduced mosquitofish spread rapidly given unimpeded dispersal corridors (e.g., mowed ditches), and may do so at rates >800 m/day. Also, consistent lack of sexual dimorphism in dispersal behavior indicates that mosquitofish spread is not strongly dependent on female poeciliid reproductive biology. Our results support designation of mosquitofish as highly invasive and suggest that barriers to mosquitofish spread must obstruct dispersal pathways as shallow as 3 mm depth.

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Introduction

Many invasive species are introduced to novel regions by human actions (Rahel 2002), and spread thereafter by species' actions. Dispersal behavior is critical to the spread of many actively-dispersing species after introduction (Ehrlich 1986; Holway and Suarez 1999; Sakai et al. 2001; Rehage and Sih 2004). Therefore, dispersal behavior may also be critical to the prevention or control of an invader's spread.

The eastern mosquitofish (*Gambusia holbrooki*, Poeciliidae) is native to the Southeastern United States but has been widely introduced elsewhere; its congener, the western mosquitofish (*Gambusia affinis*) is listed among the 100 worst invasive species in the world (Lowe et al. 2000). Mosquitofish apparently disperse well following introduction to a new region (Arthington and Lloyd 1989) and have been introduced to many wetlands outside their native range for the purpose of mosquito control, though their efficacy for mosquito control has been questioned (Lloyd et al. 1986, Leyse et al. 2004, Courtenay and Meffe 1989). Mosquitofish have relatively brief generation times and live-bearing females can store sperm from multiple males; one fertilized female may start a new population with

little or no damaging founder effects (Chesser et al. 1984; Zane et al. 1999). Thus, mosquitofish potentially establish large populations after dispersing into a new habitat, where they act as major predators that affect entire food webs (Meffe et al. 1983; Meffe 1985; Courtenay and Meffe 1989; Gamradt and Kats 1996; Goodsell and Kats 1999; Pyke 2005).

Despite the central role of dispersal behavior to the understanding and control of invasive spread, too few studies have examined dispersal ability alone (Rehage and Sih 2004) and relatively little is known of mosquitofish dispersal behavior. For example, a recent and comprehensive (26 pages, 261 citations) review of *Gambusia* biology (Pyke 2005) discussed the subjects of dispersal, movement patterns and orientation in only 2 paragraphs and 12 citations. Short-term behavioral experiments can help predict long-term population-level responses in natural systems (Gilliam and Fraser 1987; Abrahams and Dill 1989). For example, Rehage and Sih (2004) observed interspecific differences in schooling behavior and risk and dispersal behavior in four *Gambusia* species using experimental arenas.

We experimentally tested the effects of seven variables on individual *G. holbrooki* dispersal behavior: sex, hunger state, light, acclimation time, source habitat, water depth (3–24 mm), and the interaction of depth × leaf litter type (wetland or upland). The first four variables were tested in preliminary experiments and then standardized for more powerful subsequent experiments of the latter three variables. Female mosquitofish are larger than males: we predicted *a priori* that females would disperse faster than males. In addition, we expected that hungry fish would disperse faster than satiated fish, and that fish would disperse faster in lighted conditions than in dim light. We expected that fish collected from a shallow pond without other fish species would disperse faster than those from a permanent lake, because mosquitofish habituated to predatory fish may be more risk-averse (Rehage et al. 2005). We also expected that net dispersal rate would be inversely proportional to water depth, because fish would seek greater depth. Finally, we expected that leaf litter would slow dispersal, but fish would disperse faster through wetland litter than upland litter, related to litter density and/or chemical cues.

Materials and methods

Fish were collected from Lake Claire and its neighboring pond ∼50 m to the west (hereafter Shireen's Pond) on the University of Central Florida (UCF) Orlando campus. Lake Claire is a permanent sinkhole lake with a diverse fish assemblage, whereas Shireen's Pond is shallow and may dry completely in drought years; no other fish species were observed during the primary study year. Fish were collected with minnow traps (Aquatic Eco-Systems, Inc., Apopka, FL) set overnight, or by umbrella nets or dip nets, and were transferred in pond water to the laboratory. Fish were then transferred to 45.5 l aquaria (Nanotanks; Transworld Aquatic Enterprises, Inc., Los Angeles, CA) containing dechlorinated tap water with standard filtration and fish were fed Tetramin fish flakes ad libitum at least 24 h before experiments. This protocol acclimated fish to laboratory conditions and standardized hunger levels.

Experimental trials were conducted in twelve arenas (3 m long × 0.08 m wide × 0.10 m high), also filled with dechlorinated tap water. A fish was transferred by aquarium net into a holding zone (0.12 m × 0.08 m × 0.10 m), which was partitioned from the rest of the arena by a Plexiglas door. All doors had ten 4-mm drilled flow holes and hinged up and away from fish to open simultaneously during dispersal trials. Each arena was drained after each trial and refilled with dechlorinated tap water to remove any residual chemical cues left by previous fish. Arenas were curtained to ensure that any human movement around them did not affect fish behavior.

Fish were timed with a stopwatch to the nearest 1/100 s, beginning when doors were opened until fish reached a finish line 2.58 m away from the door. Fish were observed in a mirror attached above the arenas to avoid behavioral responses to observer activity. Fish were observed for 30 min; all fish that reached the finish line were recorded for total time elapsed. Body height (mm), standard length (mm), and sex of each fish was recorded after a trial. Each fish was observed only one time, so that individual fish constituted individual replicates in all experiments.

Because each fish was free to meander within the arena and because fish varied in size, data were expressed as both absolute net dispersal rate (m s^{-1}) and relative net dispersal rate (body lengths s^{-1}) for fish that completed a trial (i.e., reached the finish line

within 30 min). Differences among treatments in net dispersal rates were analyzed by analysis of variance (ANOVA) when log_{10}-transformed values met parametric assumptions, or by nonparametric methods (Mann–Whitney or Kruskal–Wallis tests) when parametric assumptions could not be met. Some fish did not cross the finish line within 30 min, and the number of those fish was compared among treatments by χ^2 analysis of contingency tables. All data were analyzed data using SPSS V. 11.5 (SPSS Inc., Chicago, IL, USA). Power analysis was conducted with JMP 6.0 (SAS Institute, Cary, NC).

Preliminary experiments

Results of preliminary experiments were used to set parameters for subsequent experiments. In all preliminary experiments, water depth was standardized to 6 cm (10 × average body height), and arenas were free of any obstacles while fish were allowed to disperse in the arenas as described above. The first preliminary experiment tested for the effects of pretrial conditions on experimental outcomes. Fish were held in aquaria for >24 h pretrial and were either fed (ad libitum) or not within the 24 h preceding dispersal trials, and then randomly placed in arenas and permitted to acclimate within arena holding zones for 0, 2, or 10 min immediately prior to timed dispersal trials. The second preliminary experiment exposed fish to either dim (<250 lux) or bright light (990 lux; Philips Cool White Plus fluorescent bulbs). All fish in both experiments were measured and sexed after each trial, and sex was examined as a second treatment in each preliminary experiment. Power analysis of data from preliminary experiments was used to determine needed replication in subsequent experiments. Based on results of these two experiments, fish were thereafter held 24 h prior to the experiment without food, acclimated for 5 min in arenas, and trials were conducted with bright light (for easier observation).

Habitat experiment

Based on results of preliminary experiments (above), fish were not fed for 24 h before the trial to standardize hunger state and all arenas were filled to 6 cm depth and lighted. Twenty-four fish were tested from each of the habitats (Shireen's Pond and Lake Claire). Trials were run in 1 day to eliminate temporal variation, fish were randomized among arenas, and sex and fish dimensions were recorded as above. In addition, we repeated the habitat experiment approximately 1 year later; predatory fish (warmouth; *Lepomis gulosus*) were collected in minnow traps in Shireen's Pond in the second study year (but not the first), whereas Lake Claire is known to support multiple fish species, including warmouth (*L. gulosus*) and largemouth bass (*Micropterus salmoides*). Because fish may have responded to slightly different experimental conditions (and a different mix of investigators) between years, we analyzed years as an additional experimental variable. We hypothesized that the apparent colonization of predatory fish may alter behavior in Shireen's Pond. Log-transformed absolute and relative net dispersal rates were analyzed by analysis of variance for habitat, sex, and year as treatments.

Water depth experiment

Based on prior results, fish were collected from Shireen's Pond for this experiment, fish were not fed for 24 h before the trial, and all arenas were lighted. Water depths in the arenas were based on ratios of water depth to mean body height from fish of prior experiments (6 ± 1.9 mm SD). Individual fish were randomly exposed to one of four depths: 3, 6, 12, or 24 mm. Depth treatments were randomly assigned to one of two sets of arenas (six arenas per set) because sets were plumbed together, which affected water depth. All trials were run on one day to eliminate temporal variation.

Water depth × litter experiment

Fish from Shireen's Pond were exposed to one of four depths (3, 6, 12, or 24 mm) crossed with two litter types (upland or wetland), plus the water depth experiment (above) was analyzed as controls for litter to yield a completely-randomized factorial (4 × 3) design. The amount of litter in each lane was calculated from leaf-litter densities in wetland and upland habitats on the UCF campus. Ten randomly-placed 0.1 m² quadrats were sampled for leaf litter, which was dried for 24 h at 105°C and weighed. Mean litter mass was 295 g/m² in wetland and 1265 g/m² in upland sites. Wetland litter was

composed of pond cypress (*Taxodium distichum*) needles with some maidencane (*Panicum hemitomum*), while upland litter was composed of long leaf pine (*Pinus palustris*) needles, and live oak (*Quercus virginiana*), myrtle oak (*Quercus myrtifolia*), and Chapman oak (*Quercus chapmanii*) leaves. Leaf litter from three 9 m^2 plots in each of wetland and upland sites was identically collected, dried and weighed to dispense appropriate quantities into arenas in experiments.

Leaf litter was soaked in dechlorinated water for 24 h to rehydrate, and then added to arenas containing the appropriate depth of water. Each arena then "aged" for 24 h so litter could hydrate and settle, as it would in nature following a flooding event. Six trials were conducted with each litter type each day, and the placement of treatments was randomized among days. Arenas were drained between trials and cleaned of leaf litter.

Results

Preliminary experiments

All fish completed trials within 30 min. Pretrial conditions (combinations of feeding and acclimation period; Kruskal–Wallis test) and lighting (Mann–Whitney test) did not significantly affect net dispersal rates ($p = 0.645$ and 0.379, respectively). However sexes significantly differed in relative net dispersal rate (Mann–Whitney, $p = 0.041$), with males swimming slightly faster than females per unit body length. Because males are typically smaller than females, this effect did not translate to absolute net dispersal rate (Mann–Whitney, $p = 0.364$). Based on this outcome, we analyzed both relative and absolute net dispersal rates for subsequent experiments, but for brevity reported (below) only statistical results for absolute rates unless there is disparity.

Based on these results, fish in subsequent experiments were held without food for 24 h pretrial to standardize hunger, and acclimation periods in holding zones were 5 min. Also, all subsequent experiments were conducted with full lighting (for easier timing) and a mixture of sexes (which were recorded for analysis). Finally, power analysis of preliminary experiment results indicated that 24 replicate fish per treatment in subsequent experiments would exceed levels needed to observe significant effects.

Habitat experiment

There was no significant difference between habitats for the number of fish that completed trials in each of the 2 years that this experiment was conducted (χ^2, $p = 0.122$, 0.873, respectively). In addition, neither habitat of origin ($p = 0.26$) or sex ($p = 0.38$) significantly affected absolute (and relative) net dispersal rates, though mosquitofish dispersed significantly faster in the second year's experiment than in the first ($p = 0.026$). This effect was apparently related to minor differences between years in experimental conditions (vibrations from an air pump), but was not critical to the main questions of the study. Based on the Year 1 results for habitats (and borne out by Year 2 results), subsequent experiments in Year 1 were conducted with mosquitofish from one habitat (Shireen's Pond) only.

Water depth experiment

Water depth significantly affected dispersal behavior: dispersal was primarily inhibited when water depth approximated one-half body height, or immersion of approximately one-half of the gill. The number of fish that completed dispersal trials was significantly reduced in shallower depth (χ^2, $p = 0.004$) and this effect was due to the 3 mm depth (Fig. 1a), as evidenced by the lack of significant difference (χ^2, $p = 0.58$) between depths of 6, 12, and 24 mm. We note that a fish may have meandered within the arena, but if it did not reach the "finish line" it did not complete the trial. Also, it should be noted that one-half of tested mosquitofish completed trials in only 3 mm water depth. Of the fish that completed trials, water depth significantly affected absolute (and relative) net dispersal rate ($p = 0.001$). Again, there was no significant difference in net dispersal rate between sexes ($p = 0.64$) or a sex × depth interaction ($p = 0.15$). Mosquitofish dispersed progressively slower as depth decreased from 24 to 6 mm, but increased rates again in 3 mm water (Fig. 1b). Thus, significantly fewer fish dispersed successfully in 3 mm water, but those that dispersed did so at rates comparable to fish in deeper water.

Water depth × litter experiment

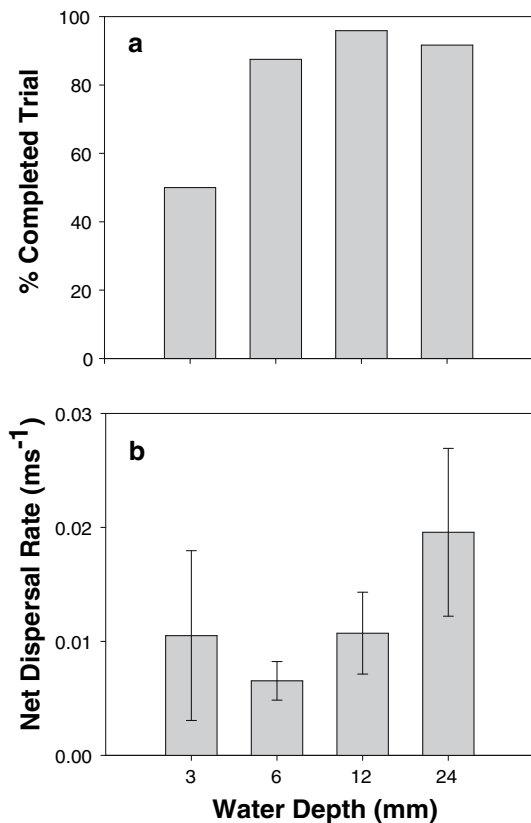Leaf litter strongly inhibited mosquitofish dispersal behavior (χ^2, $p < 0.001$) and the effect differed with

Fig. 1 (a) Percent of mosquitofish that successfully completed dispersal trials, and (b) net dispersal rate (mean ± 95% CI) of mosquitofish in relation to water depth (mm)

Fig. 2 (a) Percent of mosquitofish that successfully completed dispersal trials, and (b) net dispersal rate (mean ± 95% CI) of mosquitofish in relation to combined treatments of water depth and leaf litter (from upland and wetland sources). Compare with Figure 1 to evaluate the effect of leaf litter on mosquitofish dispersal behavior

the leaf litter source (upland or wetland). Most mosquitofish (81%) completed dispersal trials in the absence of leaf litter (and at all tested depths), but in the presence of wetland or upland leaf litter these proportions were reduced to 7% and 1%, respectively (Fig. 2a). In addition, water depth continued to significantly affect the number of mosquitofish that completed dispersal trials (χ^2, $p = 0.017$, Fig. 2a). In the presence of leaf litter, dispersal was essentially stopped at shallow depths: no mosquitofish completed trials with leaf litter present in 3 or 6 mm water, only 1 of 48 mosquitofish (2%) did so in 12 mm water depth, and 7 of 48 (14%) were successful in 24 mm. Leaf litter created a complex 3-dimensional matrix for the mosquitofish to navigate and greatly reduced dispersal. In the presence of leaf litter, many mosquitofish did not exit from the holding zone, whereas in the absence of leaf litter most would at least meander if not complete the trial.
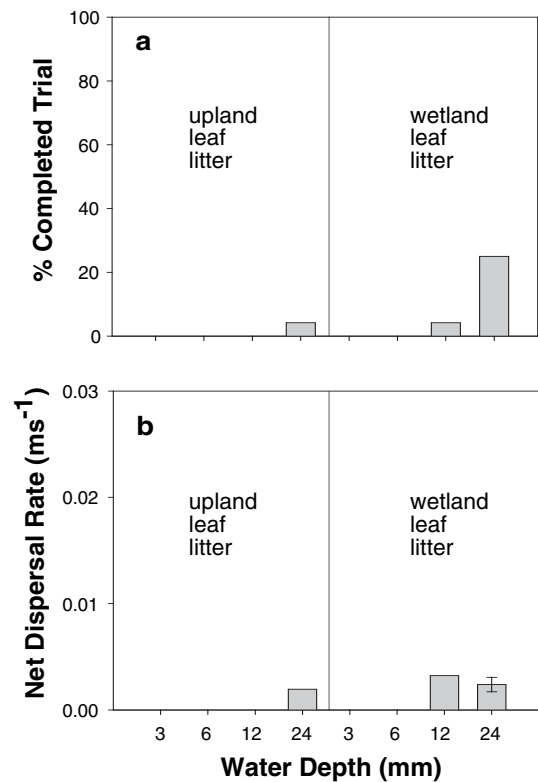
Of the few mosquitofish that completed trials in the presence of leaf litter, absolute (and relative) net dispersal rate was strongly reduced by the presence of leaf litter ($p < 0.001$), water depth remained significant ($p = 0.022$), and there was no significant leaf litter × depth interaction ($p = 0.37$; Fig. 2b).

Discussion

Our results provide insight to mosquitofish dispersal dynamics, including clues to better manage mosquitofish spread. Mosquitofish dispersed more slowly in shallower water (down to 3 mm water depth), but sex, hunger status, lighting, and habitat of origin did not affect their net dispersal rate. However, physical complexity in their dispersal corridor that was calibrated to natural levels strongly inhibited

mosquitofish dispersal at these very shallow depths, and dispersal still occurred in only 12 mm water.

Mosquitofish can disperse under diverse conditions (Rehage and Sih 2004) and in very shallow water, provided hydrological connections are unimpeded. The ability of an invasive species to spread depends on factors such as dispersal distances and rates (Swingland 1983; Bradford and Taylor 1997; Parker and Reichard 1998). Most mosquitofish dispersed at rates of ∼0.01 m/s given only 1–2 cm of water and an unimpaired pathway. Extrapolating from rates observed in the laboratory and assuming an open dispersal corridor and 24-h dispersal behavior (because light did not affect rates), mosquitofish could spread at rates ∼860 m/day. It is little wonder that mosquitofish can spread rapidly into a region upon introduction (Arthington and Lloyd 1989).

Mosquitofish use both natural and anthropogenic dispersal corridors (Taylor et al. 1984; Snodgrass et al. 1996; Duryea et al. 1996; Swanson et al. 1996; Taylor 1997). Road construction and associated drainage ditches can form direct corridors between aquatic habitats and potentially increase mosquitofish spread (Courtenay and Meffe 1989; Trombulak and Frissell 2000). Widespread road construction and drainage structures have changed landscape hydrology and probably promoted the spread of mosquitofish within their native range (Southeast USA) and in other regions where they are now introduced. Our results indicate that unobstructed ditches containing only a few centimeters of water will contribute to the invasive spread of mosquitofish upon deliberate introductions for mosquito control (Leyse et al. 2004), but that fine-textured physical obstructions (leaf litter in our experiments) significantly inhibit mosquitofish dispersal. A clear management application that emerges from this study is to refill unused ditches with soil and place barriers of leaf litter or mulch in otherwise unobstructed corridors (e.g., firebreaks, trails) that may occasionally flood near isolated wetlands. Leaf litter (and other vegetation?) may also be managed to provide obstacles to mosquitofish spread in drainage ditches but not substantially impede water flow for drainage purposes.

Based on our laboratory experiments, we hypothesize that naturally fishless habitats (e.g., temporary ponds) in the native range of G. holbrooki (Southeastern United States) must have no surface water connection to other aquatic habitats to remain free of mosquitofish: otherwise, mosquitofish would readily colonize from regional population sources. Likewise, in regions where mosquitofish have been introduced, we predict that mosquitofish will spread wherever there are unimpeded surface water connections (e.g., ditches). Also, our results (among an admittedly limited set of populations) suggest that G. holbrooki from different habitats will disperse at roughly similar rates. If found to hold true for more populations, this result would indicate that laboratory dispersal trials should be predictive for multiple populations, though this response may be specific to G. holbrooki, and not G. affinis (Rehage et al. 2005). Finally, our results support the use of mosquitofish as a model organism for the study of metapopulation dynamics (Gilpin and Hanski 1997) among waters, which will further inform efforts to manage mosquitofish invasive spreading.

Sex-specific dispersal is commonly observed in animals (e.g., Julliard 2000; Proctor et al. 2004). Adult female mosquitofish are typically larger and more numerous than males, and one gravid female may found a new population (Snelson 1989; Meffe and Snelson 1989). However, sex repeatedly failed to affect mosquitofish absolute ($m \ s^{-1}$) or relative (body lengths s^{-1}) dispersal rate in our experiments. Our results indicate that strong founder effects are unlikely among mosquitofish populations, given no sex difference in dispersal and the fact that smaller males may disperse in shallower water than larger females. This conclusion mitigates the presumed value of sperm storage and live-bearing reproduction as poeciliid strategies for colonization of new habitats.

In summary, mosquitofish (G. holbrooki) dispersed more readily in deeper water (<24 mm) but still dispersed in as little as 3 mm water depth. Leaf litter (especially upland) at natural densities interfered with mosquitofish dispersal behavior: introduced mosquitofish will spread most rapidly given unobstructed dispersal corridors (e.g., roadside ditches) but that spread could be inhibited by simple obstacles in dispersal corridors (leaf litter, mulch). Also, mosquitofish did not vary in dispersal behavior for several factors we expected to be important (sex, light, hunger status, habitat of origin). Our results indicate that mosquitofish are well-adapted to disperse through very shallow water and support the

extended designation of multiple *Gambusia* species as highly-invasive.

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