Morphology, performance, fitness: functional insight into a post-Pleistocene radiation of mosquitofish

R. Brian Langerhans*

Biological Station and Department of Zoology, University of Oklahoma, Norman, OK 73019, USA

*landerhan@ou.edu

Bahamas mosquitofish (Gambusia hubbsi) colonized blue holes during the past approximately 15,000 years and exhibit relatively larger caudal regions in blue holes that contain piscivorous fish. It is hypothesized that larger caudal regions enhance fast-start escape performance and thus reflect an adaptation for avoiding predation. Here I test this hypothesis using a three-pronged, experimental approach. First, G. hubbsi from blue holes with predators were found to possess both greater fast-start performance and greater survivorship in the presence of predatory fish. Second, using individual-level data to investigate the morphology–performance–fitness pathway, I found that (i) fish with larger caudal regions produced higher fast-start performance and (ii) fish with higher fast-start performance enjoyed greater survivorship in the presence of fish predators—trends consistently observed across both predator regimes. Finally, I found that morphological divergence between predator regimes at least partially reflects genetic differentiation, as differences were retained in fish raised in a common laboratory environment. These results suggest that natural selection favours increased fast-start performance in the presence of piscivorous fish, consequently driving the evolution of larger caudal regions. Combined with previous work, this provides functional insight into body shape divergence and ecological speciation among Bahamian blue holes.

Keywords: adaptation; biomechanics; locomotion; morphology; population differentiation; predation

2. MATERIAL AND METHODS

Fish from four blue holes (2 L, 2 H) were photographed alive for morphometric analysis following Langerhans et al. (2007). Body size was estimated as centroid size; body shape was calculated by assigning each fish a score on a canonical axis describing lateral body shape variation. This axis ranges from shapes characteristic of L blue holes (small caudal region) to those characteristic of H blue holes (large caudal region) (electronic supplementary material, figure S1).

Fast-start performance trials were recorded with a high-speed digital video camera (electronic supplementary material). For each fast-start video sequence (40 ms), I measured four performance variables: $d_{\text{max}}$, $v_{\text{max}}$, $\phi_{\text{max}}$, and $q_{\text{max}}$. $d_{\text{max}}$ is the net distance travelled by the centre of mass. $v_{\text{max}}$ is the average rotational velocity of the head during stage 1 of the fast start (stage 1 rotation angle divided by stage 1 duration). $\phi_{\text{max}}$ and $q_{\text{max}}$ are the maximum velocity and acceleration, computed using the mean-squared error quintic spline to smooth the centre-of-mass displacement data. All four variables have been previously implicated as important in evading predatory strikes (Wallier et al. 2005). Differences between predator regimes in fast-start performance were tested using nested multivariate analysis of covariance, followed by mixed-model nested analysis of covariance with each performance variable. Predator regime and population
3. RESULTS

Gambusia hubbsi from H blue holes exhibited greater fast-start performance (18% higher $\omega S_1$, 42% higher $\omega_{\text{max}}$ on average) and higher survivorship in the presence of predatory fish (50% higher survival) than conspecifics from L blue holes (figure 1). No differences were observed for the other two fast-start performance variables (electronic supplementary material, table S1).

Analysis of the M–P–F pathway indicates that body shape differences between predator regimes, consequently facilitating locomotor differences, are largely responsible for differences in survivorship (figure 2; electronic supplementary material, tables S2 and S3). Three M–P relationships were strong and highly significant (all one-tailed $p < 0.0001$): smaller fish produced greater average rotational velocity, and fish with larger caudal regions had both greater average rotational velocity and maximum acceleration. One M–P relationship approached significance: fish with larger caudal regions tended to generate greater maximum velocity (one-tailed $p = 0.09$). One M–P relationship was not significant, but suggestive based on AIC: smaller fish tended to generate greater maximum acceleration ($p = 0.18$). Two P–F relationships were strong and highly significant: fish with greater average rotational velocity and maximum acceleration exhibited higher survivorship (both one-tailed $p < 0.005$).

All relationships were consistently observed within predator regimes, indicating that correlated traits that merely covary with the predator regime cannot explain these findings (electronic supplementary material).

The total selection gradient on body shape—selection resulting exclusively from its influence on survival as mediated by its effects on fast-start performance—was $\beta = 0.28$, meaning that a positive change in one standard deviation of the body shape axis is predicted to result in 28 per cent greater survival probability. Because H fish exhibit a body shape axis score 1.63 standard deviations greater, on average, than L fish, they are predicted to enjoy an approximately 46 per cent greater survival probability. Results from predation trials are remarkably close to this prediction, as H fish exhibited 50 per cent greater survivorship than L fish.

After rearing in a common laboratory environment, 80 per cent of the laboratory-born fish were correctly assigned to their predator regime of origin using a discriminant function derived from wild fish ($p < 0.0001$;
Predation is a major force of phenotypic evolution and speciation. This study suggests that natural selection via predation by piscivorous fish has driven the evolution of larger caudal regions, greater fast-start performance and higher survivorship in *G. hubbsi* inhabiting blue holes with predatory fish. Based on theory and recent empirical work in a congener (e.g. Langerhans in press), enlarged caudal regions are predicted to suffer endurance costs during steady swimming, and perhaps explain why fish in L blue holes—where cruising for food and mates, not bursting from predators, is commonplace—exhibit smaller caudal regions. Future work should test this ‘flip-side’ to the M–P–F pathway examined here. In any case, morphological divergence between blue holes has apparently played an important role in the process of ecological speciation. First, fish inhabiting divergent predator regimes exhibit divergent body shapes and consequently have reduced mating probabilities owing to assortative mating for body shape (Langerhans et al. 2007). Second, if L fish were to colonize H blue holes, they would probably suffer increased mortality relative to resident fish (this study). Both processes increase reproductive isolation between fish from different predator regimes relative to fish from the same predator regime (i.e. ecological speciation).

Experiments were approved by the Washington University Animal Studies Committee and the Bahamas Department of Fisheries.

I thank the Bahamas Government for permission to conduct this work, M. Blackwell, E. Joseph and Bahamas Environmental Research Center for logistical support and two anonymous reviewers for improving the manuscript. The study was funded by US EPA STAR fellowship, NSF grants DEB-0344488 and DEB-0722480, Explorers Club Exploration Fund and Society of Wetland Scientists Student Research Grant.


