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# PREDATION, FOOD LIMITATION, PHENOTYPIC PLASTICITY AND LIFE-HISTORY VARIATION IN *GAMBUSIA HUBBSI*

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Langerhans et al. (2007) present molecular data, morphological variation of both males and females, and female mate preferences as evidence that ecological speciation, mediated by differences in exposure to predation by piscivores (*Gobiomorus dormitor* as well other piscivorous fish), occurred among populations of *Gambusia hubbsi* occupying blue holes on Andros, Commonwealth of the Bahamas. Their conclusion rests on two critical assumptions, namely, that previous studies of *G. hubbsi* (Krumholz 1963; Sohn 1977; Downhower et al. 2000) provide "… evidence for strong divergent selection between predator regimes." and that "observed differences are unlikely to merely reflect environmentally induced phenotypic variation as morphological differences … between populations within species exhibit a strong genetic basis." The first assumption is essential to their claim that differences in body shape are due to differences in exposure to predation and hence predator avoidance. The second is essential if their observed mate preferences are to have evolutionary consequences. Previously published studies show these claims to be false, at least for *G. hubbsi* on Andros Island (Downhower et al. 2000, 2002), and invalidate Langerhans et al.'s conclusions regarding predation and its role in presumptive ecological speciation in this species.

With regard to "strong divergent selection between predator regimes," Krumholz collected fish from just two localities, a "tidal pool" in which piscivores were present and a man-made, brackish water pond with no predators but where phytoplankton blooms reduced visibility to "as little as one foot." As a consequence, any conclusions regarding the role of predation in shaping differences between these two populations are confounded by other edaphic and ecological factors (see Hurlbert 1984). We note that other piscivore-present, piscivore-absent comparisons cited by Langerhans et al. are similarly confounded.

Sohn's laboratory study used fish collected "…from a pond on South Bimini…" No further details are given, and no piscivores were used in his experiments. Rather, he showed that a juvenile male reared in the presence of an adult male delayed maturation until it is larger than the adult, and when juvenile males are raised together, the second male to mature is larger than the first male to mature. Because male poeciliids grow little after their gonopodium has matured (Turner 1941), Sohn's findings would be expected to apply to any poeciliid in which male size affects the outcome of competition with other males for access to females (Borowsky 1973; Hughes 1985). Hence, neither Krumholz nor Sohn provides evidence that predation shaped the differences they reported.

More seriously Langerhans et al. also claimed that our work provides "evidence for strong divergent selection between predator regimes." In fact, we rejected that hypothesis and demonstrated remarkable phenotypic plasticity in this species. Our dataset, nearly four-times larger than theirs, was published in full, discussed at length, and were available for Langerhans et al. to reanalyze, and refute if they desired to do so. However, they did not.

It may be argued that by comparing *Gambusia* populations cohabiting blue holes with piscivores with populations occupying blue holes where piscivores are absent provides a "rigorous" evaluation of the role of piscivory in shaping the morphology and behavior of these fish, but such myopia may be misleading (e.g., Grant 1972; Gould 1996), particularly when there are known, nearby populations where predation is likely to be more intense, and others that appear to be predator free. Because there is no flowing water on Andros (save for tidal creeks), shallow ponds and ditches and freshwater wells, like blue holes, are permanent bodies of water resulting from exposure, by one means or another and at different times, of the freshwater lens that underlies Andros. Hence variation in life histories and morphology of *Gambusia* from these habitats is particularly relevant to discussions of the importance of piscivory in blue hole populations.

Briefly, we sampled 14 blue hole populations lacking piscine predators of *G. hubbsi* ("low" predation), 12 blue hole populations in which *G. hubbsi* and *G. dormitor* co-occurred sometimes together with other piscivorous fish ("high" predation), 10 populations from shallow water sites, and nine populations occupying freshwater wells (know locally as well fields).

Shallow water sites vary seasonally and daily in temperature, may be occupied by piscivores, and are hunted by wading birds and kingfishers. *Gambusia* populations occupying these sites are potentially subject to more intense predation and environmental stress than *Gambusia* populations found in any other habitat we sampled (see Downhower et al. 2000).

Freshwater wells were constructed in the 1970s and 1980s. Each well consists of four narrow trenches generally arranged in a cruciform pattern around a central pumping station (Fig. 1). *Gambusia*, most likely derived from nearby shallow water ponds, tidal creeks, or coastal populations occupied many, but not all, of the wells. There are no piscivores in the wells and their narrow configuration and vertical walls exclude other predators. In short, shallow water and well field populations of *Gambusia* bracket "low predation" and "high" predation blue hole populations with shallow water populations being subject to the highest levels of predation and well field populations being piscivore free.

In addition to field data on females from these sites, we documented changes in life histories of females from two "low" predation and two "high" predation populations that we introduced into separate, previously uncolonized, well fields. We also documented the changes in life histories of laboratory raised *Gambusia* from one "low" predation and two "high" predation populations. All of our data on these populations were published in full (Downhower et al. 2000, 2002) and bear directly on the effect of predation and food limitation on life-history variation, differences in body shape among populations, and overall phenotypic plasticity.

**Figure 1.** One of four trenches radiating from a central pump (in building in the distance) that makes up a typical freshwater well on North Andros. Note the narrowness of the trench and the vertical walls that exclude terrestrial predators. Each trench is ~2 m deep.

The documented range of phenotypic and life-history variation among *Gambusia* populations from different habitats is remarkable (Fig. 2). Females in shallow water populations have traits that are in accord with expectations when adult mortality is high or unpredictable (Stearns 1992). However, life histories of well field females confound expectations when adult survival is high. Well field females carry smaller eggs than "low" predation females, invest more in reproduction, and the increase in investment in reproduction relative to body size is significantly greater than for either "low" predation or "high" predation

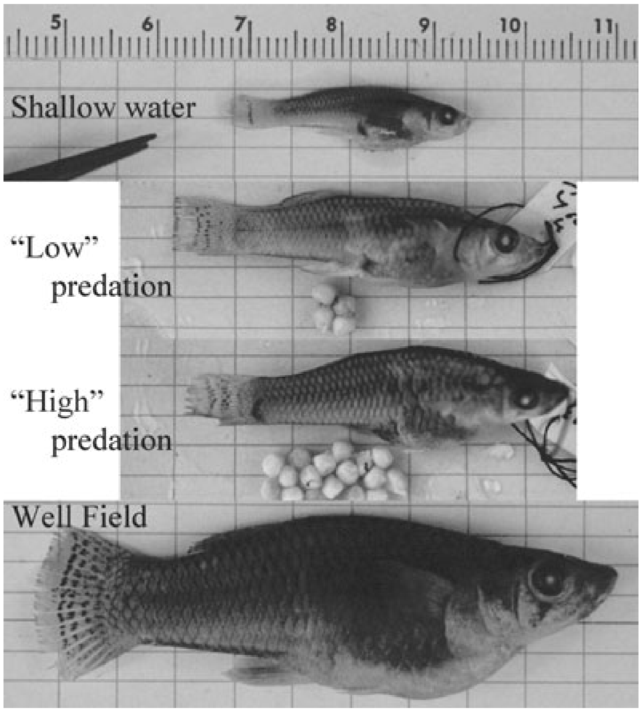

**Figure 2.** Adult female *Gambusia hubbsi* from four freshwater habitats on North Andros. Differences in egg diameter and litter size for low-predation and high-predation females are also shown.

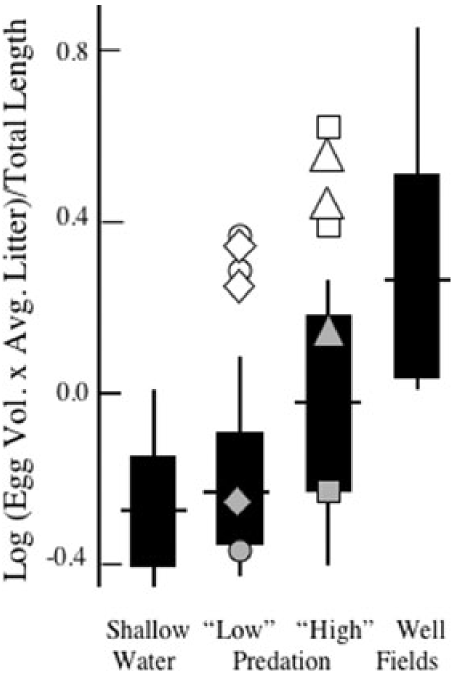

**Figure 3.** Differences in litter volume relative to body length for females from different habitats. The mean ± one standard deviation and the range are given for each habitat. Filled symbols indicate the values for females from populations that were introduced into unoccupied well fields. Filled symbols indicate the values for their well field-raised descendants. Data were calculated from those given in table 2 of Downhower et al. (2000).

females. Hence, predator-free well field females are not larger versions of “low” predation females.

In contrast to conclusions ascribed to our work by Langerhans et al., we postulated that differences in life histories of females from blue holes and well fields reflected differences in food availability in these nutrient-limited ecosystems. Food limitation results in increased egg size in other poeciliids (Reznick et al. 1996; Trexler 1997) and may account for egg size in “low” predation females being ~37% larger than those of “high” predation females. In addition, two (one “low” predation and one “high” predation) of three laboratory populations evidenced significant increases in litter size and body size when maintained and raised under ad libitum conditions.

Further we suggested that the conditions that allow the establishment of a predator population should be considered prior to invoking a primary role for predation in shaping life histories of *G. hubbsi* (sensu Brown 1971). *Gobiomorus dormitor* females produce small eggs of 0.35 mm (Winemiller and Ponwith 1998) to 0.70 mm in diameter (Bacheler et al. 2004). Average egg diameters in *G. hubbsi* populations we studied ranged from 1.5 to 2.8 mm in diameter. As a consequence the larvae of *G. dormitor* are one or two orders of magnitude smaller than those of *G. hubbsi* and necessarily feed on much smaller planktonic organisms, suggesting that there are differences in the size and abundance of plankton between “low” predation and “high” predation sites that may affect the survival and recruitment of both *G. dormitor* and *G. hubbsi* (e.g., Bremigan and Stein 1994). Further, *G. hubbsi*, cannibalize their own young under laboratory conditions hence the larvae of *G. dormitor* may be at risk of predation by *G. hubbsi*, again supporting the conclusion that the conditions that determine the presence or absence of *G. dormitor* cannot be dismissed. For example, McKaye et al. (1977) document predation on *G. dormitor* eggs and fry by cichlid species upon which *G. dormitor* adults prey.

Variation in body depth between “low“ and “high” predation blue hole populations emerges from our food limitation hypothesis when relative litter volume is considered. “Low” predation and shallow water females carry similar-sized litters relative to their body length, even though predation is more likely in shallow water sites (Fig. 3). “High” predation females carry litters that on average are ~50% larger in volume than those of either “low” predation or shallow water females and litters carried by well field females are roughly two times larger relative to their body length than those of “high” predation females. As a result, “high” predation females are necessarily deeper-bodied than either “low” predation or shallow water females and well field females even deeper bodied, independent of the presence or absence of predators (Fig. 2). Langerhans et al.’s inference that differences in body depth between “low” predation and “high” predation populations reflect enhanced predator avoidance in “high” predation populations is confounded by known differences in investment in reproduction among habitats unrelated to predation.

With regard to phenotypic plasticity, relative litter volume increased by more than fourfold for females descended from “low” predation populations and more than threefold for females descended from “high” predation populations (Fig 3). In short, females in introduced populations rapidly converged on phenotypes characteristic of well field females, phenotypes not found in the populations from which they were derived. These changes occurred in as little as nine months. Because they resulted in novel phenotypes they are most likely an expression of phenotypic plasticity rather than “a strong genetic basis.”

In light of these data and published alternative explanations for life history and morphological variation in these fish that contradict Langerhans et al.’s basic assumptions regarding predation and phenotypic plasticity in this species, their claims for ecological speciation mediated by predation acting on genetically constrained phenotypes are unwarranted.

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