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DIVERGENT SELECTION, NOT LIFE-HISTORY PLASTICITY VIA FOOD LIMITATION, DRIVES MORPHOLOGICAL DIVERGENCE BETWEEN PREDATOR REGIMES IN *GAMBUSIA HUBBSI*

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We recently tested the hypothesis of ecological speciation in a post-Pleistocene radiation of Bahamas mosquitofish (*Gambusia hubbsi*) inhabiting inland blue holes (vertical, water-filled caves) on Andros Island, the Bahamas (Langerhans et al. 2007). Combining morphological, molecular, and behavioral data, our results suggested that enhanced premating isolation evolved as a byproduct of differences in body shape between predator regimes, due to assortative mating for body shape. Our results strongly supported the hypothesis of ecological speciation, and parallel results were observed across species within the genus, suggesting a past history of such ecological speciation within the *Gambusia* lineage. Downhower et al. (in press) question the morphological results described for *G. hubbsi* in our paper, contending that prior work on life-history variation in *G. hubbsi* (primarily Downhower et al. 2000, 2002) invalidates our conclusions. Here we show that this contention is based on a mischaracterization of our study, inaccurate quotation of our paper, and misinterpretation of the relevance of their life-history data for morphological results observed in our study.

Downhower et al. (in press) suggest—without providing any direct evidence—that differences in body shape between predator regimes in *G. hubbsi* reflect correlative effects of phenotypic plasticity in life-history traits in response to variation in food availability. To make such a conclusion, we would have to set aside the following facts: (1) morphological differences were observed in adult males, who do not exhibit the life-history traits in question (e.g., number and size of offspring), (2) results matched well-supported a priori predictions of body shape variation based on divergent selection on locomotor performance, (3) results matched empirical results observed in other fish presumably experiencing similar forms of divergent selection between predator regimes, (4) the observed morphological differences are known to influence swimming performance in *Gambusia* fish and consequently influence endurance and survival with predators, (5) consistent results were observed for males both within and between *Gambusia* species, (6) any differences in food availability among blue holes are unknown, and (7) available evidence to date indicates that differences in body shape partly reflect genetic divergence, and not solely phenotypic plasticity. The criticisms in Downhower et al. (in press) can be summarized as three arguments: (1) incorrect attribution of evidence for divergent selection between predator regimes in *G. hubbsi* to several previous studies within one particular sentence of our paper, (2) invalid claim, in our paper, that observed morphological differences between predator regimes were due to genetic differences when they actually reflect plasticity in life-history traits, and (3) an assertion that food availability, rather than predation, is the primary factor responsible for phenotypic differences between predator regimes, as well as the presence of particular fish species in blue holes. Below we address these three arguments and conclude that all lack convincing support, and have no impact on any results or conclusions of Langerhans et al. (2007).

Prior Evidence of Divergent Selection between Predator Regimes in Gambusia hubbsi

Downhower et al. (in press) suggest that prior studies do not support our claim of existing evidence for divergent selection between predator regimes in *G. hubbsi*. Contrary to assertions in Downhower et al. (in press), this argument, even if true, would not invalidate any results of our study. Instead, the argument comprises an accusation of poor scholarship regarding our literature citations within a single sentence of the paper. We address this accusation below, describing the context of the relevant sentence, and our interpretations of previous work cited within that sentence.

The sentence referenced by Downhower et al. (in press) was in the first paragraph of the Discussion section of Langerhans et al. (2007). The full sentence is, "First, marked morphological differences between ecologically divergent blue holes match predictions based on divergent natural selection, supporting previous evidence for strong divergent selection between predator regimes in *G. hubbsi* (Krumholz 1963; Sohn 1977; Downhower et al. 2000; Langerhans et al. 2005; Langerhans 2006)." Later in the Discussion section of our paper, we evaluated these findings in more detail, and described how the nature of morphological differences observed in the study matched recent empirical findings and a priori predictions based on the hypothesis of divergent natural selection on locomotor performance between predator regimes: "The present study adds to the growing evidence that the observed pattern of morphological divergence (i.e., larger caudal region, smaller anterior body/head region in high-predation environments) represents a general ecomorphological paradigm (see Langerhans and DeWitt 2004; Langerhans et al. 2004)..." Thus, morphological results described in Langerhans et al. (2007) are (1) consistent with a priori predictions of divergent selection, (2) consistent with empirical findings in other fish (e.g., Walker 1997; Langerhans and DeWitt 2004; Langerhans et al. 2004; Domenici et al. 2008; Langerhans and Reznick 2009), and (3) consistent with prior evidence for the general role of predation as a source of diversifying selection in *G. hubbsi*. Downhower et al. (in press) only question the third form of consistency, contending that previous studies invalidate our claim that prior work identifies predation as a major agent of diversifying selection in *G. hubbsi*. We cited five studies in support of this statement, and here we briefly examine each study in turn to assess this contention.

First, Krumholz (1963) investigated the importance of predation on demographic parameters in *G. hubbsi* (e.g., male size at maturity, sex ratio, litter size of females). It is true that the study lacked replication (one low-predation, one high-predation population); however, results were consistent with the hypothesis that predator regimes exert divergent selection pressures on *G. hubbsi*. Thus, results of Krumholz (1963) do not provide particularly strong evidence for divergent selection on their own, but are nevertheless consistent with the hypothesis. In support of this proposition, Downhower et al. (2000) also discussed the findings of Krumholz (1963) as being consistent with the influence of predator regime on life histories, comparing Krumholz's results to David Reznick's classic findings in the Trinidadian guppy system (see p. 424, Downhower et al. 2000).

Second, Sohn (1977) extended the work of Krumholz (1963) by experimentally evaluating a possible mechanism by which predator regime might have driven the differences in male size at maturity observed in Krumholz (1963). Sohn (1977) agreed with Krumholz (1963) regarding the importance of predation in driving divergent selection on demographic variables of *G. hubbsi*, and suggested that males attained a larger size at maturity in low-predation environments because of the proximate mechanism of delayed maturity in the presence of other males. That is, more males are present in low-predation environments due to reduced mortality rates compared to those at high-predation sites, and thus juvenile males delay maturity to a greater extent in low-predation sites. This delay in maturity results in a larger body size at maturity, which is presumably favored by selection via resource and mate competition (agents of selection that are more important in low-predation environments than high-predation ones). Thus, Sohn (1977) provided results consistent with the hypothesis of divergent selection between predator regimes in *G. hubbsi*.

Third, Downhower et al. (2000) examined differences in female life-history traits between predator regimes in *G. hubbsi* on Andros Island, the Bahamas. The study evaluated four types of habitats: blue holes without piscivorous fish, blue holes with piscivorous fish, shallow water sites of undescribed predator status, and freshwater well fields of undescribed predator status. For blue holes, predator regime is unambiguous for sites with and without *Gobiomorus dormitor*, a highly piscivorous fish (incorrectly identified as *Eleotris pisonis* in Downhower et al. 2000, 2002). For shallow water sites, Downhower et al. (in press) suggest that "*Gambusia* populations occupying these sites are potentially subject to more intense predation ... than *Gambusia* populations found in any other habitat we sampled (see Downhower et al.

2000).” Although it is true that Downhower et al. (2000) assumed that shallow water sites represented high-predation localities, they offered no supporting evidence for this assumption. We have surveyed most of these shallow water sites, and piscivorous fish are notably absent in some of them. Because of this ambiguity regarding predator regime status, we do not believe that shallow water sites can be meaningfully included in comparative analyses examining effects of predator regime in this study. For well fields, Downhower et al. (2000) assumed these sites represented low-predation localities without providing supporting evidence. We have surveyed many of these sites, and they certainly lack piscivorous fish; thus we agree that well fields represent low-predation localities. Well fields, however, also differ from both low-predation and high-predation blue holes in many other ways, such as their narrower width (∼0.5 m), shallower depth (∼2 m), and presence of water flow, representing a unique habitat type. These confounding variables reduce the utility of well fields in tests of the effects of predation. Thus, we believe that only blue holes that vary in the presence of *G. dormitor* provide unambiguous tests of the influence of predator regime on phenotypic variation in *G. hubbsi*. This exclusive focus on blue holes for the evaluation of the effects of piscivorous fish on phenotypic variation in *G. hubbsi* does not reflect a myopic view as suggested by Downhower et al. (in press), but simply reflects good science.

Examining these blue holes, Downhower et al. (2000) found that females from low-predation populations exhibited smaller litters, larger egg diameters, smaller regression coefficients for litter size on total length, and lower reproductive investment (both initial investment and subsequent investment) than those from high-predation populations. All of these differences match predictions of divergent selection between predator regimes based on life-history theory (e.g., Roff 1992; Stearns 1992; Charlesworth 1994), and also match empirical findings regarding the effects of predators on life histories of other poeciliid fish (e.g., Reznick and Endler 1982; Reznick et al. 1990; Reznick et al. 1997; Johnson and Belk 2001; Jennions and Telford 2002; Jennions et al. 2006). Yet apparently contradicting these findings, Downhower et al. (in press) claim that this study did not find results consistent with a role of predation in driving differences in female life histories. Downhower et al. (in press) suggest that we could have reanalyzed data presented in their previous study if we wished to refute their claim, however this was not necessary as their own conclusions in that paper actually refute this claim. That is, based on results from blue holes, shallow-water sites, and well fields, Downhower et al. (2000) concluded that “predation plays a role in life history variation among mosquitofish populations on Andros,” although they also contended that “it alone is insufficient to account for the observed variation among populations”—the latter being a reference to the possible roles of food availability and temperature variation, neither of which were measured in the study. Thus, Downhower et al. (2000) did indeed conclude that predation is important in determining life-history traits of *G. hubbsi*, with the caveat that it is unlikely the full story. We have no argument with this conclusion, and agree with Downhower et al. (2000) that their results are consistent with the hypothesis of divergent selection between predator regimes in *G. hubbsi*.

Fourth, Langerhans et al. (2005) investigated differences in the size of male genitalia (the gonopodium, a modified anal fin serving as an intromitttent organ) between predator regimes in *Gambusia affinis* in Texas, USA and *G. hubbsi* on Andros Island, the Bahamas. They found that gonopodia were larger in low-predation localities in both species, and experimental results in *G. affinis* suggested that larger gonopodia attract female mates, but reduce burst speeds during escape responses. Thus, the study suggested that divergent selection between predator regimes was responsible for divergence in male genital size: premating sexual selection favored larger gonopodia in the absence of predators, but natural selection for increased escape speed favored smaller gonopodia in the presence of predators.

Finally, Langerhans (2006) reviewed and synthesized the evolutionary consequences of predation in diverse organisms. Regarding *G. hubbsi*, the study demonstrated that low-predation populations tend to exhibit greater intensity of orange on the unpaired fins of males compared to high-predation localities on Andros Island, the Bahamas. These results are consistent with the hypothesis of divergent selection on coloration between predator regimes in *G. hubbsi*, with sexual selection favoring brighter coloration in the absence of predators and natural selection favoring less conspicuous coloration in the presence of predators. These findings also match patterns observed between predator regimes in other poeciliid fish (e.g., Endler 1982, 1995; Houde 1997; Millar et al. 2006).

After evaluating each study cited in the sentence questioned by Downhower et al. (in press), we feel that prior support for divergent selection between predator regimes in *G. hubbsi* is unequivocal, as all cited studies described results consistent with the hypothesis.

Phenotypic Plasticity and Life Histories

Downhower et al. (in press) suggest that we claimed in Langerhans et al. (2007) that observed morphological differences between predator regimes in *G. hubbsi* reflected “genetically constrained phenotypes,” and that rather than derived from genetic differences, previous results regarding phenotypic plasticity of female life-history traits suggest that body shape differences likely reflect plasticity. We argue that we made no such claims in our paper, describe how all existing evidence runs contrary to the assertion of phenotypic plasticity in body shape, maintain that this question can only be answered with future experimental work as we originally stated in our paper, and suggest that plasticity in female life-history traits has little relevance to plasticity in the morphological features on which we focused in our study (particularly for males).

In the second sentence of their article, Downhower et al. (in press) misquote Langerhans et al. (2007). The misquotation implies that we claimed morphological differences observed in our study were due to genetic differences between populations. Although our study did tackle a number of questions, the roles of phenotypic plasticity and/or genetic divergence in producing morphological differences between predator regimes was not one of them. Instead, we solely discussed this question within one paragraph of the Discussion section of the paper. The full misquoted sentence is, "Observed morphological differences between *G. hubbsi* populations are unlikely to merely reflect environmentally induced phenotypic variation, as morphological differences between mosquitofish species, and between populations within species, typically exhibit a strong genetic basis (e.g., Hubbs and Springer 1957; Greenfield et al. 1982; Greenfield 1983; Greenfield and Wildrick 1984; Greenfield 1985; Langerhans et al. 2004; Langerhans et al. 2005; R. B. Langerhans, unpubl. data)." Notably, their presentation of this sentence omitted the qualifier "typically" from the sentence (producing the false appearance of certainty), as well as the numerous citations providing support for the statement, and moreover failed to place the sentence in its proper context. Seeing the full sentence reveals two important features not apparent in the misquotation: (1) no hard conclusion was made regarding this topic, but rather we asserted that phenotypic plasticity was unlikely the sole determinant of morphological differences, and (2) much prior work has previously demonstrated that differences in body shape between *Gambusia* species and populations have a genetic basis, contrary to the arguments made by Downhower et al. (in press). In fact, previous work has even demonstrated a genetic basis to body shape differences between populations inhabiting divergent predator regimes in *G. affinis* using first-generation and second-generation laboratory-reared fish (Langerhans et al. 2004; R. B. Langerhans, unpubl. ms.)—a morphological pattern highly similar to that described in Langerhans et al. (2007). To present this topic in its proper context, we now present the sentences following the misquoted sentence:

> Indeed, suggestive results were found using laboratory-born *G. hubbsi* from three populations examined in this study (one low-predation, two high-predation): individuals retained their morphological distinctiveness after eight weeks of rearing under common laboratory conditions ($n = 10$; using a discriminant function derived from wild fish, all laboratory-reared individuals were correctly assigned to their predator regime of origin, sign test $P = 0.0020$). These results are consistent with the numerous previous studies, and provide cautious support for the hypothesis that divergence in body shape between populations largely derives from genetic differentiation. A more detailed examination of the genetic basis and possible contribution of phenotypic plasticity to population differences in body morphology and swimming performance is currently underway for multiple *G. hubbsi* populations, as well as several other *Gambusia* species.

In light of the full paragraph from Langerhans et al. (2007), it is clear that the relative role of genetic divergence and phenotypic plasticity in the observed morphological differences remains unknown. However, it is also clear that all evidence to date suggests that the differences, at least partially, have a genetic basis. Furthermore, preliminary results from the common-garden experiment mentioned in the above quotation are now stronger as the sample size has increased and fish have been reared to adulthood. To date, 81% of laboratory-reared *G. hubbsi* individuals derived from wild-caught parents inhabiting the four focal blue holes examined in Langerhans et al. (2007) can be correctly assigned to their predator regime of origin using a discriminant function derived from wild fish ($n = 37$, sign test $P = 0.0002$). These fish were raised in a common water source (recirculating water system) under ad libitum feeding conditions, and females were virgin, removing any possible confoundment with life-history variation. This suggests that morphological differences described in Langerhans et al. (2007) likely reflect, in part, genetic divergence, contrary to the claim of Downhower et al. (in press). However, we note that a conclusive answer requires future work.

Downhower et al. (in press) assert that their previous findings regarding female life-history differences and the role of plasticity in female life histories "bear directly on . . . differences in body shape among populations, and overall phenotypic plasticity." We do not agree that plasticity in female life histories provides much information regarding possible plasticity in body shape, and we are uncertain how female life histories might directly influence the morphological traits of interest in females, or male body shape in general. As we describe below, we believe data from Downhower et al. (2000, in press) are inconsistent with the proposition that female life-history differences between predator regimes solely reflect phenotypic plasticity in response to food availability, as suggested by Downhower et al. (in press) (see Food Limitation section below). But let us briefly give Downhower et al. (in press) the benefit of the doubt, and assume that female life-history differences do indeed purely represent plasticity. If so, there is one obvious way that this might have a correlated effect on body shape: greater investment in reproduction can lead to deeper bodies. Although Downhower et al. (in press) provide no quantitative data on this topic, we agree that the abdominal region holding the embryos can become extended to a greater degree with a

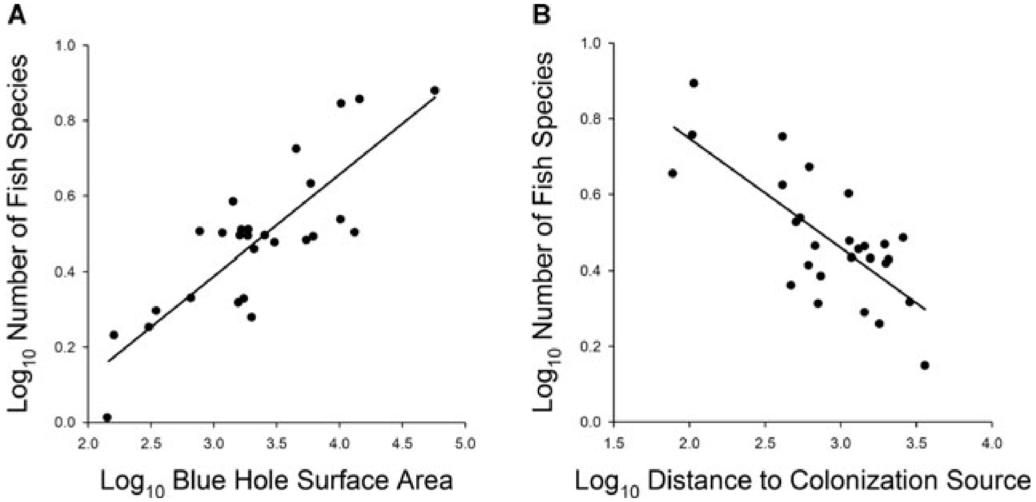

Figure 1. Island biogeography of inland blue holes on Andros Island, the Bahamas. (A) Larger blue holes ($P < 0.001$) contain more fish species. (B) Blue holes closer to potential colonization sources ($P < 0.001$) contain more fish species. These results are consistent with the theory of island biogeography, and suggest that blue holes have reached a biogeographic equilibrium (balance between colonization and extinction). Datapoints and slopes reflect back-transformed residuals and partial regression coefficients after statistically controlling for the other factor in the model.

higher investment in reproduction (e.g., see middle two images in fig. 2 of Downhower et al. in press). However, how this variation might affect the differences described in our study is unclear. First, we did not simply measure maximum body depth as implied by Downhower et al. (in press), but instead used 10 homologous landmarks to conduct geometric morphometric methods examining lateral body shape variation. Particular traits of interest were the anterior/head region and the caudal peduncle. For the females we examined in our study (four populations), it is less than clear how increased investment in reproduction might have led to the observed morphological differences. For example, depth of the insertion of the caudal fin is 9% larger in females from high-predation blue holes compared to those from low-predation populations. We have no knowledge of any link between variation in reproductive investment and such morphological variables. Second, our study focused on morphological variation in adult males (12 populations; see results in fig. 3, Langerhans et al. 2007), for which the entire topic is moot because males do not exhibit any of the relevant life-history traits. Finally, the fact that one type of trait (e.g., life history) exhibits plasticity in response to a given environmental factor does not entail that all other types of traits (e.g., morphology) will also exhibit similar levels of plasticity in response to the same factor. Indeed, it is common to observe considerable variation in the degree of plasticity for even highly similar traits (e.g., plasticity in litter size but not egg diameter in Downhower et al. 2000). Thus, the presence of life-history plasticity has little relevance for morphological differences between predator regimes, or their putative environmental or genetic basis.

Food Limitation

Downhower et al. (in press) contend that food availability is the primary determinant of female life histories, as well as body morphology of both sexes, purely via phenotypic plasticity. However, as far as we know, food availability has never been estimated in any way for any of these sites. Downhower et al. (2000, in press) use data from well field populations, and introductions into well fields from blue-hole populations, as evidence in support of these hypotheses. Apparently, this supporting evidence derives from assumptions of differences in food availability and body morphology, which in reality are both unknown. Further, we must ignore the confounding variables that differ between well fields and blue holes (see above) to make this comparison useful. Notwithstanding these inherent problems, let us assume for the sake of argument that well fields do indeed comprise relatively high food availability, and the confounding variables do not influence traits of interest. Under these assumptions, available data presented in Downhower et al. (2000, in press) regarding introductions from blue holes into well fields can indeed test the hypothesis that female life histories solely reflect phenotypic plasticity in response to food availability (although, note that their data cannot address variation in body morphology, as this was not measured). This hypothesis predicts that fish derived from either low-predation or high-predation blue hole populations will exhibit similar life histories when reared in the common high-food conditions of well fields. Although Downhower et al. (in press) claim that "females in introduced populations rapidly converged on phenotypes characteristic of well field females," their results contradict this statement. Their results indicate that life-history differences between predator regimes persisted at virtually identical magnitudes after rearing in well fields (see differences in reproductive investment between LP and HP in fig. 3, Downhower et al. in press). Moreover, more detailed results reported in Downhower et al. (2000) demonstrate that after two years of rearing in well fields (likely representing one or two generations post parental stock), fish originally derived from different predator regimes indeed maintained many life-history differences (see table 4 of Downhower et al. 2000). Thus, although all fish were reared in presumably high-food conditions in well fields, fish derived from high-predation blue holes still exhibited greater reproductive investment than fish derived from low-predation blue holes. Rather than suggesting that life-history differences derive primarily from phenotypic plasticity in response to food availability, these results suggest that the differences partially reflect genetically based differences associated with predator regime. We do not contend that food limitation plays no role in female life histories, but rather that existing evidence is inconsistent with the claims of Downhower et al. (in press).

Downhower et al. (in press) claim that phenotypic differences between predator regimes represent a coincidental effect of food availability, and also that food availability comprises a primary determinant of fish species presence in blue holes. That is, Downhower et al. (in press) assume that strong differences in food availability exist among blue holes and both the fish community and consequently fish phenotypes are determined by this level of food availability. Such a scenario can produce spurious associations between predator regime and prey phenotype because the same underlying factor was responsible for both the fish community and fish phenotype. This suggests that fish species have equal probabilities of reaching any blue hole, and the biotic parameters of the blue holes determine the success of colonization events. If true, then the theory of island biogeography would apparently not apply to inland blue holes, but rather food availability would play the dominant role as a filter for colonization success. To determine whether island biogeography might provide a more parsimonious explanation than food availability, we evaluated the effects of two key biogeographic parameters, habitat size and distance to a colonization source, on fish species richness in inland blue holes.

For 27 inland blue holes on Andros Island, the Bahamas, we determined the number of fish species present using visual surveys, and estimated the surface area of the blue hole (m^2) and the straight-line distance (km) from each blue hole to the nearest possible colonization source (major water bodies, such as lakes, tidal creeks, or the ocean). We conducted a multiple regression, and found that both habitat size and degree of isolation were significant determinants of fish species richness (Fig. 1). The number of fish species present in inland blue holes is strongly consistent with the theory of island biogeography (MacArthur and Wilson 1967): blue holes that are larger and closer to available species pools contain more species, irrespective of their possible availability of food for fish colonists (Fig. 1). These results contradict the suggestion that food availability is the primary determinant of fish communities. Biotic factors, such as food availability (planktonic and benthic invertebrate communities), might indeed serve as additional filters for colonization success of fish species, however simple biogeographic variables explain a majority of the variance in fish species richness ($R^2 = 0.69$).

In sum, we find that all arguments presented by Downhower et al. (in press) lack empirical support, and prove inconsequential for the results and conclusions described in Langerhans et al. (2007). Based on all available data, it indeed appears that adaptation to divergent predator regimes in *G. hubbsi* is driving ecological speciation as a byproduct.

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