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Morphological convergence during pregnancy among predator and nonpredator populations of the livebearing fish *Brachyrhaphis rhabdophora* (Teleostei: Poeciliidae)

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Predation can drive morphological divergence in prey populations, although examples of divergent selection are typically limited to nonreproductive individuals. In livebearing females, shape often changes drastically during pregnancy, reducing speed and mobility and enhancing susceptibility to predation. In the present study, we document morphological divergence among populations of nonreproductive female livebearing fish (*Brachyrhaphis rhabdophora*) in predator and nonpredator environments. We then test the hypothesis that shape differences among nonreproductive females are maintained among reproductive females between predator and nonpredator environments. Nonreproductive females in predator environments had larger caudal regions and more fusiform bodies than females in nonpredator environments; traits that are associated with burst speed in fish. Shape differences were maintained in reproductive females, although the magnitude of this difference declined relative to nonreproductive females, suggesting morphological convergence during pregnancy. Phenotypic change vector analysis revealed that females in predator environments became more similar to females in nonpredator environments in the transition from nonreproductive to reproductive. Furthermore, the level of reproductive allocation affected shape similarly between predator environments. These results suggest a life-history constraint on morphology, in which predator-driven morphological divergence among nonreproductive *B. rhabdophora* is not maintained at the same level during pregnancy. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 104, 386–392.

ADDITIONAL KEYWORDS: geometric morphometrics – life history – morphology – predation – trade-off.

INTRODUCTION

Reproduction incurs a cost through reduced future fecundity and reduced survival (Williams, 1966). The latter is especially important in females, which typically undergo dramatic morphological shifts during pregnancy that reduce their ability to evade predators (Magnhagen, 1991). Predator driven morphological divergence has been demonstrated across diverse taxonomic groups (crustaceans: Dodson, 1989; fishes:

Endler, 1995; Langerhans *et al.*, 2004; insects: Mikolajewski *et al.*, 2010; amphibians: Relyea, 2002; mammals: Korpimaki, Norrdahl & Valkama, 1994), although few studies have examined whether such morphological divergence is maintained during pregnancy, despite the importance of this stage in determining female survival (Magnhagen, 1991).

Life-history shifts in response to predation are a key prediction of life-history theory (Roff, 1992). Comparisons of life-history phenotypes between wild populations in predator and nonpredator environments reveal predictable responses among prey populations, including earlier age at maturity, increased reproductive output, and smaller offspring size in predator environments (Reznick & Endler, 1982; Stibor, 1992; Johnson & Belk, 2001). However,

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adaptive life-history differences between predator environments may cause morphological changes during pregnancy that incur a fitness cost (Langerhans & Makowicz, 2009). For example, morphological changes during pregnancy reduce locomotor performance and burst speed in fence lizards (*Sceloporus occidentalis*; Sinervo *et al.*, 1991), Trinidadian guppies (*Poecilia reticulata*; Ghalambor, Reznick & Walker, 2004), and western mosquitofish (*Gambusia affinis*; Belk & Tuckfield, 2010). Alternatively, morphological adaptations associated with predator evasion (fusiform bodies, enlarged caudal peduncles) may also constrain reproductive output by reducing the space available for brood development, representing a morphologically-based life-history trade-off, *sensu* Congdon & Gibbons (1987).

Livebearing fishes (Poeciliidae) are ideal models for testing the hypothesis that there is a trade-off between predator-induced morphological divergence and predator-induced life-history divergence in reproductive females. We compared shape change during pregnancy between populations of the Costa Rican livebearing fish *Brachyrhaphis rhabdophora* Regan from environments with and without piscivorous fishes (hereafter referred to as predator and nonpredator environments). In accordance with life-history theory, previous studies demonstrated life-history adaptations of *B. rhabdophora* in response to predator environment (Johnson & Belk, 2001; Johnson & Zuñiga-Vega, 2009). Female *B. rhabdophora* exposed to predators exhibit earlier size at maturity, increased clutch size, and smaller embryo size relative to females in predator-free environments (Johnson, 2001; Johnson & Belk, 2001). Furthermore, populations in predator environments have higher mortality rates than populations in nonpredator environments in Costa Rican streams (Johnson & Zuñiga-Vega, 2009), suggesting that predation is a strong selective agent in this system. We hypothesized that the observed divergence in life history between predator and nonpredator environments might constrain morphological divergence in reproductive *B. rhabdophora* females between predator environments.

MATERIAL AND METHODS

STUDY SITES

We collected *B. rhabdophora* with a handheld seine from six streams in the Guanacaste region of Costa Rica between 5 and 13 May 2006. The streams are characterized by a pool-riffle-pool structure and represent a subset of well-studied streams in this area for which the primary environmental determinate of *B. rhabdophora* life history and survival is the presence of predators (Johnson, 2001; Johnson & Belk,

2001; Johnson & Zuñiga-Vega, 2009). *Brachyrhaphis rhabdophora* typically occur in pools and other low-velocity habitats. Three streams contain piscivorous fish (*Parachromis dovii* and *Rhamdia guatemalensis*; Quebrada Quesara: 10°27.248 N, 84°59.258 W; Rio Machuca tributary 9°57.792 N, 84°29.468 W; Quebrada Grande: 10°26.489 N, 84°59.260 W), and three do not (upper Rio Cañas: 10°25.151 N, 84°59.311 W; Rio Piedras: 10°31.780 N, 85°16.852 W; Rio San Rafael: 9°59.064 N, 84°37.511 W) (Fig. 1). Nonpiscivorous predators may also provide predation pressure on *B. rhabdophora* (e.g. birds: Riesch *et al.*, 2010; reptiles: Colston, Costa & Vitt, 2010; arthropods: Abraham, 1923)], although we considered piscivores to be the primary predatory selective agent in these streams based on the documented importance of piscivores to *B. rhabdophora* life history in previous studies (Johnson, 2001; Johnson & Belk, 2001; Johnson & Zuñiga-Vega, 2009).

FISH

A total of 309 female fish were included in the analysis; 145 from predator sites and 164 from nonpredator sites. The number of females per collection location ranged from 37 to 68. For each fish, we measured standard length (mm), wet mass (g), number of embryos, developmental stage of embryos, and wet mass of embryos (g). Embryo development stage was classified on an 11-point scale where 1 = least developed and 11 = most developed, *sensu* Haynes (1995). Fish were classified as reproductive when embryos were above developmental stage 3. Reproductive allocation was defined as the wet mass of embryos relative to fish wet mass. Wet mass was used to represent the volumetric effect of reproductive allocation because we expected the volumetric change to be more important to potential shape variation than the energetic differences as measured by dry mass.

Twelve biologically homologous landmarks were digitized on a lateral image of each fish for morphometric analysis (Fig. 2) (tpsDig; Rohlf, 2005). Landmarks were located as: (1) anterior tip of the snout; (2), anterior origin of the dorsal fin; (3) posterior extent of head on dorsal outline; (4) dorsal origin of the caudal fin; (5) ventral origin of the caudal fin; (6) semi-landmark midway between landmarks 2 and 4; (7) anterior origin of anal fin; (8) semi-landmark midway between landmarks 5 and 7; (9) anterior origin of the pelvic fin; (10) intersection of the operculum with the ventral outline of the body; (11) semi-landmark midway between landmarks 9 and 10; and (12) anterior extent of the eye (Fig. 2). Three additional points placed along the lateral midline allowed digital unbending of the specimens (tpsUtil; Rohlf, 2004), although they were not used in the final

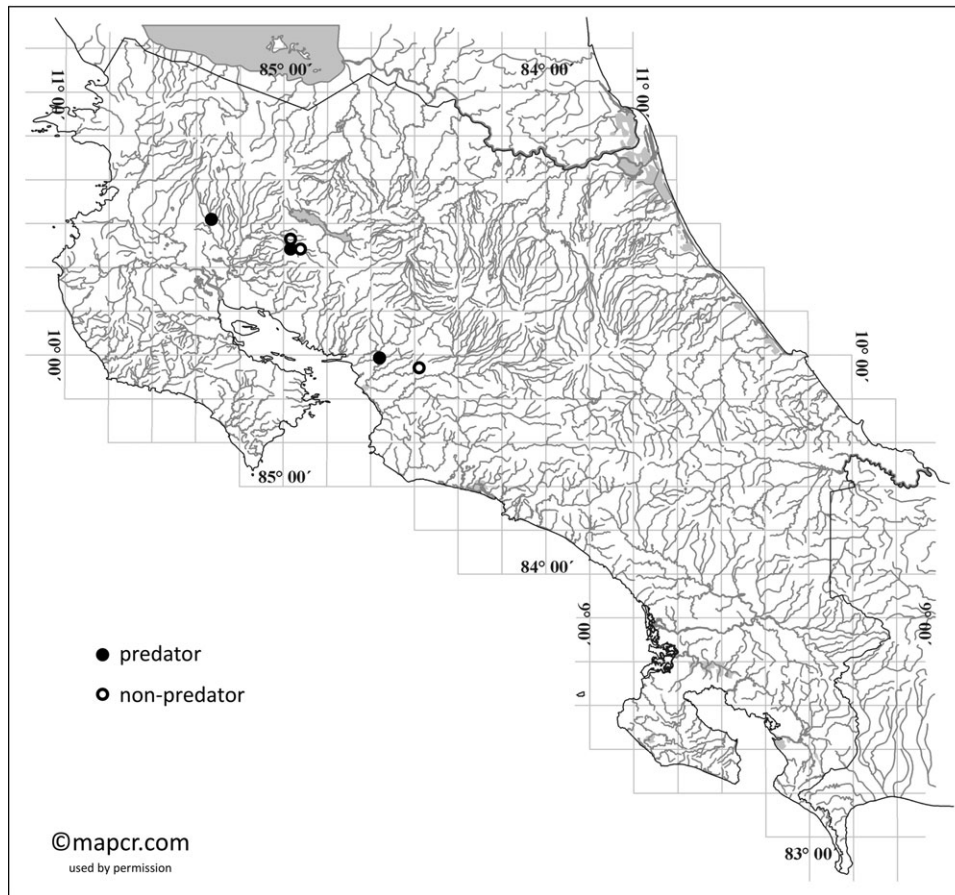


Figure 1. Map of collection sites in the Guanacaste region of Costa Rica.

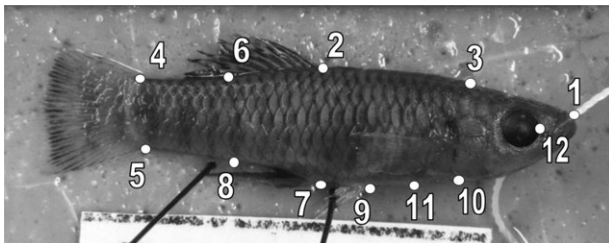


Figure 2. Location of landmarks used for geometric morphometric analysis on *Brachyrhaphis rhabdophora*.

analyses. Shape variation from digital landmarks was summarized into relative warps (i.e. principal components) using tpsRelw (Rohlf, 2003). Relative warps are linear combinations of affine and non-affine shape components. We used the first 11 relative warps, which explained more than 96% of the shape variation, to reduce the number of variables and account for the reduced dimensionality from use of sliding semi-landmarks.

Data were analyzed using mixed model multivariate analysis of variance [mixed multivariate analysis of variance (MANOVA) in SAS, version 9.2 (SAS Insti-

tute). Because relative warps are orthogonal and ordered according to the amount of variation they explain, they can be treated as repeated measures with the use of an index variable analogous to time in traditional repeated measures model. Thus, the identifying order number of the relative warps (i.e. 1–11; reflecting the order of the warps but not the value) was treated as an index variable and included in the repeated statement for mixed model analyses. We tested two hypotheses: (1) shape varies between predation environments consistently across reproductive states: nonreproductive to reproductive and (2) reproductive allocation affects female shape similarly across predation environments. To test the first hypothesis, we tested for main effects and interactions of predation environment, reproductive state, and index variable for the whole dataset (reproductive and nonreproductive individuals; $N = 309$). To test the second hypothesis, we tested for main effects and interactions of predation environment, allocation (a covariate; wet mass of clutch relative to somatic wet mass), and the index variable for reproductive females only ($N = 166$). Wet mass of embryos increases with developmental stage of embryos, so

that the developmental stage was initially included in the second model to assess its effect on female body shape. However, neither the main effect of developmental stage, nor its interaction with other predictors was a significant predictor of female body shape, and so it was dropped from the second model. The results of other predictor variables in the second model were unaffected.

The interactions between main effects and the index variable are the most direct test of our hypothesis, as opposed to simple interactions of main effects, because the interaction with the index variable tests for differences in shape on each of the relative warps independently. If we do not consider the interaction with the index variable, we are testing the hypothesis that differences exist among treatment combinations when averaged across all relative warps. Because relative warps are independent and orthogonal, the direction (positive or negative) and magnitude of differences can vary randomly across relative warps. Thus, the interaction, which allows relative warps to vary independently, can be significant even if the main effects alone, or their interactions, are not.

Following a significant interaction between main effects and the index variable in the MANOVA, we applied phenotypic change vector analysis (PCVA; Adams & Collyer, 2007, 2009; Collyer & Adams, 2007) to determine whether the significant interaction resulted from differences in magnitude (MD) or direction (θ) of morphological change. The PCVA tests magnitude and direction across all relative warps. PCVA was conducted using ASREML-R, version 2.00 (Butler *et al.*, 2007) within R (R, version 2.8.1; R Development Core Team). To visualize differences between shape vectors, we plotted LS means on the first two relative warp axes, which accounted for approximately half of the shape variation in each analysis. In the second analysis, reproductive allocation was considered as a continuous variable. To facilitate comparative visual displays, we plotted LS means (\pm SEM) at high (allocation = 0.15) and low (allocation = 0.02) levels of the covariate reproductive allocation. We also generated thin-plate spline visualizations in tpsRelw (Rohlf, 2003) to represent the observed changes.

RESULTS

Female shape varied significantly by predation environment and by reproductive state, and there was a significant interaction between the two (Table 1). There was a significant difference in the angle of shape change between vectors in predator and nonpredator environments ($\theta = 33.4$ degrees; $P = 0.002$) but not magnitude ($MD = 0.004$; $P = 0.19$). Shape converged between predator and nonpredator environments as

Table 1. Multivariate analysis of variance of all female *Brachyrhaphis rhabdophora* (reproductive and nonreproductive)

Effect	d.f.	<i>F</i>	<i>P</i>
Predation	1, 5.56	13.84	0.0113
Index variable	10, 1310	0.11	0.9998
Predation \times Index variable	13, 1310	20.56	< 0.0001
Reproductive state	1, 1631	91.90	< 0.0001
Reproductive state \times Index variable	10, 1310	17.46	< 0.0001
Predation \times Reproductive state	1, 1631	3.42	0.0645
Predation \times Reproductive state \times Index variable	11, 1301	5.15	< 0.0001

Table 2. Multivariate analysis of variance of reproductive *Brachyrhaphis rhabdophora*

Effect	d.f.	<i>F</i>	<i>P</i>
Predation	1, 236	2.24	0.1358
Index variable	10, 694	2.84	0.0018
Predation \times Index variable	10, 694	2.20	0.0164
Allocation	1, 772	0.82	0.3646
Allocation \times Index variable	10, 694	3.76	< 0.0001
Predation \times Allocation	1, 772	1.40	0.2364
Predation \times Allocation \times Index variable	10, 694	1.59	0.1055

females became reproductive (Fig. 3A). Nonreproductive *B. rhabdophora* females in streams with predators had longer caudal regions and more shallow and elongated bodies than females in streams without predators (Fig. 3A). Pregnant females converged in shape as the abdomen became distended (Fig. 3A).

Female shape varied significantly among reproductive females between predation environments and with reproductive allocation, although there was no significant interaction between the two (Fig. 3B, Table 2). Predation environment accounted for less of the observed variation than level of allocation, and the effect of allocation was consistent in each predation environment. Females with higher levels of reproductive allocation showed more distended abdominal areas relative to females with lower levels of allocation (Fig. 3B).

DISCUSSION

We found strong morphological differences among nonreproducing females in predator and nonpredator environments, although shape differences declined as females became reproductive. These results

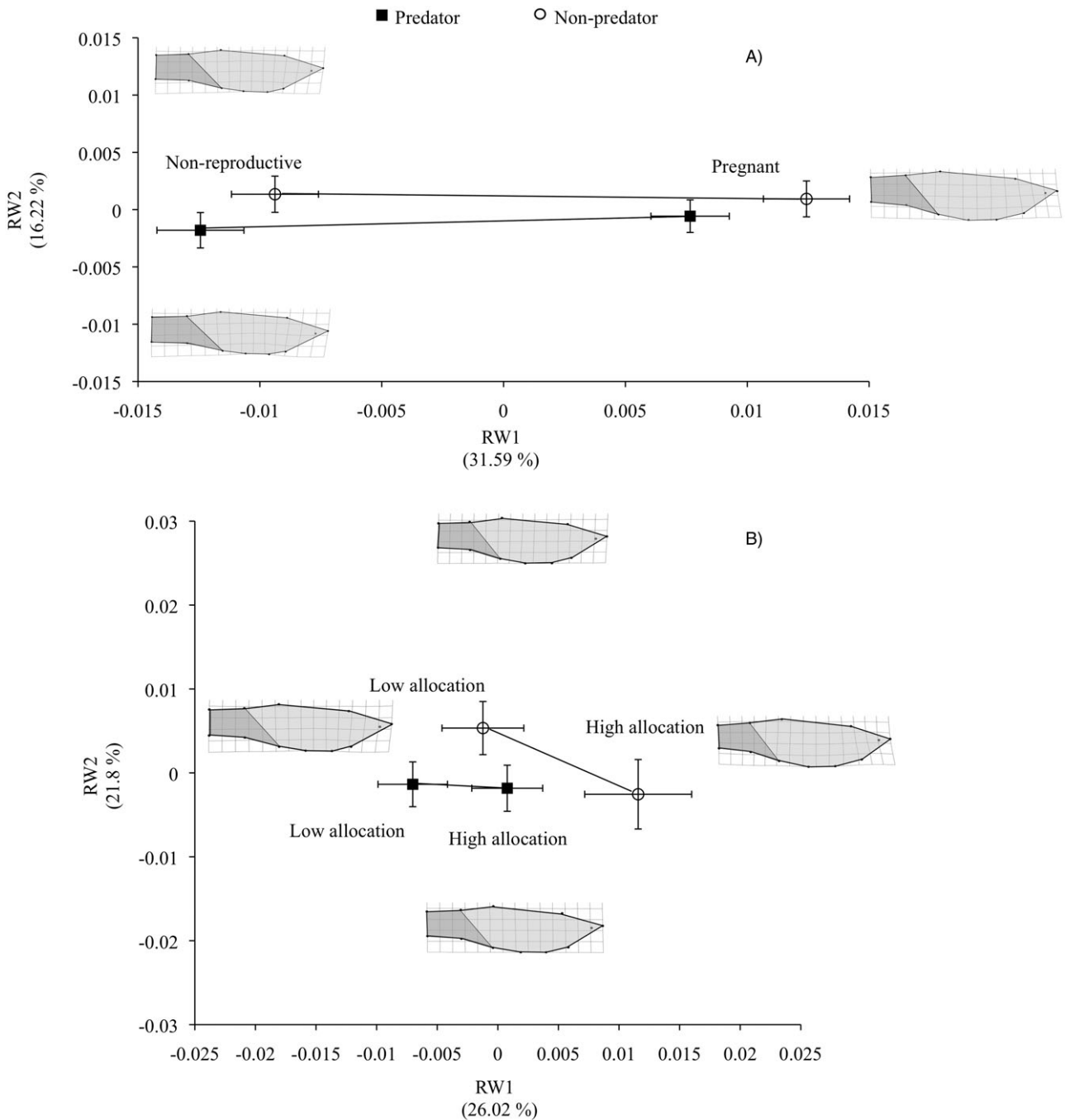


Figure 3. Least square means of relative warp (RW) scores (\pm SE). Nonreproductive and pregnant *Brachyrhaphis rhabdophora* females (A) and pregnant females with low (0.02) and high (0.15) reproductive allocation (B) in Costa Rican streams with and without predators. Fish outlines represent thin-plate spine transformations at $\times 3$ magnification. Axes are scaled according to the relative amount of variation explained by each.

complement previous studies showing that predation is a major agent of selection driving morphological and life-history divergence in livebearing fishes (Reznick & Endler, 1982; Johnson & Belk, 2001; Langerhans *et al.*, 2004; Johnson & Zuñiga-Vega, 2009). However, by demonstrating ontogenetic shape

convergence among reproductive females, we suggest that pregnancy may constrain morphological adaptation in *B. rhabdophora* females, such that evolution of divergence in nonreproducing individuals does not necessarily correlate to divergence in morphology during pregnancy.

Because we did not test for differences in performance in the present study, it is unknown whether the shape differences we describe are large enough to produce differences in performance of reproductive females. However, the morphological convergence among reproductive individuals demonstrated in the present study is consistent with functional convergence during pregnancy in other poeciliids. For example, predation selects for faster burst speeds and longer swimming distance in nonreproductive females of Trinidadian guppies (*P. reticulata*) but not in pregnant females, suggesting a trade-off between reproductive investment and escape performance (Ghalambor *et al.*, 2004). Because morphology is correlated with swimming performance in poeciliids, our data suggest the potential for a similar trade-off in *B. rhabdophora*, in which pregnancy constrains morphological adaptation for increased escape performance. This is further supported by our phenotypic change vector analysis, which showed that most of the convergence in shape space was driven by a change in shape of females in predator environments toward females in nonpredator environments. In other words, pregnant females in predator environments looked more like pregnant females in nonpredator environments, and not vice versa.

Female body shape during pregnancy varies widely among livebearers (Poeciliidae). Some species undergo dramatic distension of the abdomen (e.g. *G. affinis*, *B. rhabdophora*), whereas others maintain a fusiform shape and show little morphological change during pregnancy (e.g. *Alpharo cultratus*; M. Belk, pers. observ.). These two extremes may represent different adaptive strategies in which females that undergo dramatic abdominal distension are able to produce larger broods but only at a cost of reduced swimming performance, whereas streamlined females enhance swimming performance at a cost to space available for brood development (Beck & Beck, 2005). The morphological strategy exhibited by a female may be determined by the type of environment they inhabit and the life-history adaptations they possess. Females of the livebearing fish *Poeciliopsis turrubarensis* in Central America exhibit a streamlined body shape in fast-flowing streams relative to females in slow-flowing coastal waters, and such adaptation is beneficial for swimming performance but constrains the volume available for brood production (Zuñiga-Vega, Reznick & Johnson, 2007). To overcome the reproductive limitations of streamlined body shape, *P. turrubarensis* in fast-flowing waters use superfetation, in which multiple broods are produced simultaneously at different developmental stages. This reduces abdominal distention during pregnancy because fewer offspring are produced per clutch (Zuñiga-Vega *et al.*, 2007). However, superfetation has

not evolved in the genus *Brachyrhaphis*. Female *B. rhabdophora* do show dramatic differences in life history between predation environments. Thus, it appears that female *B. rhabdophora* in predator environments face a trade-off between a morphology that increases predator escape (i.e. survival and future reproduction) and a life history that increases reproductive output (i.e. current reproduction). In this system, the trade-off is resolved by investing in current reproduction via life-history shifts toward earlier and greater allocation to reproduction and experiencing the consequence of convergence to a morphology similar to that of females in the nonpredator environment that potentially leads to an increased risk of mortality.

Reproductive allocation affected shape among pregnant females, although its effect did not differ between predator environments. An allocation effect could have occurred even as the mean shape of pregnant females converged in the transition from nonreproductive to reproductive because our first test of shape convergence averaged shape across pregnant females with varying levels of allocation. That we did not find an interaction between allocation and predation further supports our constraint hypothesis by suggesting that shape adaptation during pregnancy may be less flexible than shape adaptation in nonreproductive individuals of *B. rhabdophora*.

Morphology is an integrative trait that can change considerably during reproduction, yet is often measured only in nonreproducing adult individuals. To fully understand how natural selection drives morphological divergence, descriptions of body shape through different reproductive stages are needed. By demonstrating morphological convergence between predator and nonpredator populations of *B. rhabdophora* as a consequence of reproduction, we show that life history and morphological responses to predation create a trade-off that constrains simultaneous optimization of traits.

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