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Life-history phenotypes in a live-bearing fish *Brachyrhaphis episcopi* living under different predator regimes: seasonal effects?

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Abstract Several key life-history attributes in a tropical live-bearing fish, *Brachyrhaphis episcopi*, have previously been shown to differ between populations that co-occur with large predatory fish (Characin sites) and those that do not (Rivulus sites). Here we show that differences between Characin and Rivulus localities are also repeatable over time; patterns observed in the wet season also persisted during the dry. Both sexes reached maturity at a smaller size at Characin sites. Although there was no difference in fecundity between larger females living in different predator communities, smaller females at Characin sites produced more offspring. Females also produced smaller offspring at Characin localities. These differences are remarkably similar to those reported in two other species of live-bearing fish, *B. rhabdophora* and *Poecilia reticulata* suggesting possible convergent adaptation in life-history strategies due to predator-mediated effects or correlates thereof. We also found seasonal changes in life-history traits that were independent of predator community. In the wet season, mature males were larger, females allocated more to reproduction, and offspring mass was also greater. The results of our study generate testable predictions using *B. episcopi* to further our understanding of life-history evolution.

Keywords Convergent evolution · Guppy · Life-history strategy · Predation · Reproduction · Seasonality

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Introduction

An individual's lifetime reproductive success is determined by a myriad of ontogenetic and reproductive traits that make up its life-history strategy. Trait combinations are, however, typically constrained by trade-offs among traits (Roff 2002). In many taxa, for example, fecundity increases with body size, while reproduction reduces somatic growth (Roff 1992). It is within this context of trade-offs that selection operates to produce an optimal life-history strategy by influencing variables such as the timing of sexual maturation and/or subsequent reproductive effort (Fischer and Fiedler 2002; Czesak and Fox 2003). The strategy that optimises fitness will, however, vary depending on the selective environment (Johnson and Belk 2001; Jennions and Telford 2002; Messina and Fry 2003). Specifically, within species, life-history strategies are predicted to diverge among populations that occur in different selective environments, especially where traits are heritable and gene flow is restricted (Reznick 1982a, b; Johnson 2001; Räsänen et al. 2005).

Predator-mediated mortality has been touted as an especially potent selective force shaping prey life-history strategies (Reznick and Endler 1982; Johnson and Belk 1999, 2001; Hilton et al. 2002). Although numerous laboratory studies report an association between rates of extrinsic mortality and life-history evolution (e.g. Polak and Stammer 1998; Baer and Lynch 2003), natural examples showing a strong association between predation environment and life-history phenotypes are far fewer. Among the latter, some of the most compelling work comes from field studies on fish (Reznick and Endler 1982; Reznick 1989; Johnson and Belk 1999, 2001; Jennions and Telford 2002). In particular, classic work on the Trinidadian guppy, *Poecilia reticulata*, has shown that individuals mature sooner, expend greater effort on reproduction, and produce more but smaller offspring at sites with larger predators and greater extrinsic mortality (Reznick 1982a, 1989; Reznick and Endler 1982; Reznick et al. 1996). More recently, studies on two other species of live-bearing fish have yielded similar findings (Johnson and Belk 2001; Jennions and Telford 2002). Life-history traits, however, do not only shift with predation environment and/or environmental correlates of predator presence. Temporal effects can also be important.

Tropical environments have traditionally been perceived as providing relatively constant conditions year round (Wikelski et al. 2000). Despite this, reproduction in many tropical animals is marked seasonally, especially in areas that experience pronounced wet and dry seasons (Reznick 1989; Winemiller 1989, 1993; Morris and Ryan 1992; Wikelski et al. 2000). Even in species that breed year round, temporal shifts may occur in life-history traits such as reproductive effort. Such shifts have been attributed to factors such as conspecific mating densities, availability of resources, and synchronization of reproductive effort with optimal conditions for juvenile growth (Winemiller 1989, 1993). In *Brachyrhaphis rhabdophora*, for example, divergence in life-history traits was reported between populations living in different predator communities (Johnson and Belk 2001). Although the patterns observed persisted over three years and between wet and dry seasons, Johnson and Belk (2001) found that brood mass increased during the wet season relative to the dry, presumably due to an increase in resource availability. Such results, showing possible temporal shifts in life-history traits, underscore the need to test whether patterns observed among populations are repeatable over time (see also Reznick 1989). Here we investigate life-history phenotypes in populations of a related live-bearing fish, *Brachyrhaphis episcopi*, living with different predator communities, with particular emphasis on comparing samples collected during the wet and the dry seasons.

Material and methods

Study species and sites

Brachyrhaphis episcopi is a predominantly upstream-dwelling species of live-bearing fish endemic to Panama (Loften 1965). Like many poeciliids (Bisazza 1993; Bisazza and Pilastro 1997) males greatly reduce growth upon maturation and, as adults, are smaller than females (Jennions and Telford 2002). Sexually mature males can easily be distinguished by the presence of a translucent, sharply pointed gonopodium (modified anal fin) which is used to transfer sperm to the female. Females develop one brood at a time (Turner 1938). As there is no post-fertilisation transfer of nutrients from mother to offspring (Turner 1938), offspring mass in this species decreases during development (Jennions and Telford 2002) in common with its congener, *B. rhabdophora* (Johnson and Belk 2001).

Jennions and Telford (2002) compared life-history phenotypes among populations of *B. episcopi* collected at the end of the 1998 dry season from 12 sites near Panama City. In each population, fecundity, offspring size and reproductive allocation increased with female body size. When controlled for maternal size, Jennions and Telford (2002) found that offspring mass was correlated negatively with offspring number consistent with a phenotypic trade-off between the two variables. Divergent life-history phenotypes were also found between *B. episcopi* populations living in different predator communities. Individuals of both sexes reached sexual maturity at a smaller size at sites with large fish predators. Small to average sized females at these sites also had higher fecundity and reproductive allocation compared to those from populations that lacked large fish predators. Interestingly, no population difference in fecundity or reproductive allocation was detected among larger females. It was suggested that this could be due to weaker selection operating on larger (compared with smaller) females at Characin sites because so few females actually attain a large size at those localities (Jennions and Telford 2002). Offspring mass was, however, reduced at sites with large predatory fish. More recently, population differences in *B. episcopi* have also been reported with respect to the morphology, behaviour, physiology and cognitive abilities of fish living with and without predators (Jennions and Kelly 2002; Brown and Braithwaite 2004, 2005; Brown et al. 2004, 2005a, b; Simcox et al. 2005). In the current study we analysed data from a wet season survey of key life-history traits from the same 12 populations as those sampled by Jennions and Telford (2002) during the dry season. This was done to (1) examine whether life-history phenotype differences observed between Characin and Rivulus sites in *B. episcopi* are repeatable between seasons, and (2) investigate whether life-history patterns also shift seasonally independent of predator community.

Fish from the wet season samples were collected in December 1997 (i.e. end of wet season). The position of the 12 surveyed sites, and detailed description of the streams, is provided elsewhere (Angermeier and Karr 1983; Jennions and Kelly 2002; Jennions and Telford 2002). In brief, fish were collected along streams that drain into areas of open water which, for this primarily upstream species, represent an important barrier to movement between streams. Hence different streams were considered to represent different populations (Jennions and Telford 2002). Within streams, waterfalls prevent upstream, and limit downstream, movement. As with other studies, each of the 12 collecting sites was regarded as an independent data point. Jennions and Telford (2002) previously categorised these sites based on predator community as either 'Rivulus' or 'Characin' localities. The only piscine predator observed at Rivulus localities was a small killifish, *Rivulus brunneus*. This relatively innocuous species is primarily insectivorous, has a small gape, and is incapable of consuming adult *B. episcopi* (Angermeier and Karr 1983). Characin localities were categorised by the additional presence of Characiformes and were inhabited by several large piscine predators (e.g. *Aequedens coeruleopunctatus*; *Piabucina panamensis*, *Brycon* spp., *Hoplias microlepsis*, *Roeboides guatemalensis* and *Rhamdia wagneri*), all of which are known to include fish in their diets (Angermeier and Karr 1983; Kramer and Bryant 1995). In total, there were five Rivulus sites and seven Characin sites (Jennions and Kelly 2002).

Field and laboratory procedures

We collected at least 150 fish/site by running hand nets repeatedly along the shore. After collection, fish were anaesthetized with MS-222 and then preserved in 5% formalin before being transported back to the laboratory for analyses.

We were interested in measuring five life-history traits per population (1) male size at maturity; (2) female size at maturity; (3) reproductive allocation; (4) number of offspring; (5) size of offspring. Our methods are described in detail by Jennions and Telford (2002). Briefly, male size at maturity was estimated from the average standard length of adults, identified by the presence of a completely developed gonopodium. Females were divided into 2-mm size classes. The minimum size class at maturity was defined as the smallest size class for which there were at least as many females with full sized ova or embryos as females with non-vitellogenic eggs. Reproductive allocation was defined as: RA = dry weight of embryos/(somatic dry weight + dry weight of embryos) (Reznick and Endler 1982). Dry weights were obtained after 24-h in a 55°C desiccating oven. Somatic dry weight refers to the total dry weight of a female minus the reproductive tissue and hind gut and stomach content. The number of offspring was calculated from the number of developing individuals per yolked ova. Offspring size comprised the average dry weight of embryos. Offspring eye diameter was measured to control for the effect of developmental stage on offspring mass.

Statistical analysis

Linear mixed models run in S-Plus 6.4 were used to assess the effect of predator community on each trait. Jennions and Telford (2002) reported that life-history variables were sensitive to whether site was treated as a 'fixed' or 'random' factor. In the current study, predator community (i.e. Rivulus versus Characin) and season were treated as fixed effects, and site was treated as a random effect. These analyses reflect the fact that the 'treatment' (i.e. predation) occurs at the site level.

Reproductive allocation and offspring mass are both affected by female body size and stage of development. Consequently, both terms were included in our initial models as fixed effects. For fecundity, only female mass was included in the initial model. Initial models included all two-way interactions between fixed terms.

The model assumptions were checked for each analysis, including assumptions of consistent model variance in each season, community and site. Response and dependent variables were log transformed when necessary to ensure residuals were normally distributed.

Model simplification proceeded by sequentially removing non-significant terms, starting with the highest-order interactions until the final model only contained significant terms (Crawley 2002). The significance of fixed effect terms was determined by conditional *t*-tests of their parameter estimates in the final model. This method is considered preferable to likelihood ratio tests of nested models with and without the fixed term of interest (see Pinheiro and Bates 2000, pp 87–92).

In Table 1 we present summary statistics for each site in each season. Most of the data used for the dry season has previously been presented by Jennions and Telford (2002) (Table 1). However, here we adjust the values for RA, offspring mass and fecundity to those for the mean ± 1.0 s.d. female size and mean developmental stage calculated across the pooled data set for both seasons. This makes it easier to directly compare the two seasons.

Results

Adult size

The effect of season on male size was the same in both predator communities ($t_{1077} = 0.81$, $P = 0.42$) with sexually mature males being larger in the wet season than in the dry season ($t_{1078} = 4.26$, $P < 0.001$). In both seasons, males were also smaller at Characin sites than at Rivulus sites ($t_{10} = 2.52$, $P = 0.030$; Table 1).

The minimum size of sexually mature females did not differ between seasons (paired *t*-test: $t_{11} = 1.74$, $P = 0.111$; Table 1). During the wet season, however, females bred at a smaller size at Characin sites compared with those at Rivulus sites ($t_{10} = 3.05$, $P = 0.019$; Table 1). In the wet season the mean minimum size for Rivulus sites was 26.6 mm compared to 22.4 mm for Characin sites. A similar, albeit weaker, trend was also observed for the dry season ($t_{10} = 2.38$, $P = 0.058$; Table 1).

Reproductive allocation

There was no significant interaction between the effects of season and predator community on reproductive allocation ($t_{721} = 0.071$, $P = 0.94$). Reproductive allocation increased with female somatic mass, with allocaton being greater in the wet season than in the dry season (predicted mean reproductive allocation of females in wet season = 9.18%, dry = 8.83%, $t_{722} = 1.99$, $P = 0.046$; Fig. 1). As expected, reproductive allocation also

Table 1 Site values for life-history traits measured in *Brachyrhaphis episcopi*. Averaged across all sites, log somatic mass of females (mean ± s.d.) was 2.169 ± 0.251 (n = 898). When 'adjusting' dependent variables, values were therefore calculated for females with log somatic mass of 1.92, 2.17 and 2.42. These correspond to an actual mass of 83, 148 and 263 mg, respectively

	Female mass (mg)														Males		
	Minimum size (mm)	Fecundity (brood size)				Reproductive allocation (%)				Offspring mass (mg)				Mean size (range) (mm)	CV %	*n*
		83	148	263	*n*	83	148	263	*n*	83	148	263	*n*			
Dry season																
Rivulus sites																
Juan Grande 1	29	1.25	3.47	6.80	36	4.99	5.75	6.51	27	2.66	2.78	2.91	26	22.0 (17.1–26.8)	13.3	40
Mendoza 1	25	1.73	3.58	6.11	43	5.58	6.10	6.63	32	2.88	2.98	3.09	32	19.5 (16.4-24.8)	9.3	58
Macho 1	23	3.95	7.66	12.59	72	8.73	10.00	11.27	50	1.97	2.30	2.69	50	23.9 (18.6-30.1)	11.2	63
Anton	31	0.28	2.38	6.53	17	0.00	3.70	7.68	12	2.57	3.04	3.59	12	23.9 (20.2-30.6)	9.1	36
Mato Ahogado	31	1.66	4.31	8.19	21	7.94	9.66	11.38	16	2.86	3.43	4.11	16	23.1 (20.1-26.5)	6.8	32
Mean	27.8	1.77	4.28	8.04		5.45	7.04	8.69		2.59	2.91	3.28		22.6 (18.5-27.8)	9.9	
Characin sites																
Juan Grande 2	23	3.05	5.80	9.42	34	7.26	9.42	11.58	28	1.99	2.27	2.59	28	19.1 (15.8-23.6)	11	44
Frijolito 1	21	2.32	3.99	6.11	41	6.21	6.34	6.47	33	2.49	2.60	2.73	33	17.9 (14.3-23.2)	10.5	52
Frijolito 2	27	1.43	3.95	7.72	22	5.30	6.87	8.43	19	2.57	2.64	2.72	19	18.8 (15.2-25.6)	12.8	39
Mendoza 2	23	3.82	5.58	7.67	38	9.64	8.80	7.96	35	2.24	2.37	2.50	35	20.3 (15.2-27.6)	15.4	33
Macho 2	23	4.65	7.30	10.55	38	10.22	10.25	10.27	35	1.91	2.24	2.64	35	22.9 (18.0-28.8)	11.1	39
Macho 3	23	3.44	5.33	7.64	48	9.47	10.36	11.24	36	2.45	2.82	3.24	36	21.8 (16.4-28.5)	12.5	49
Sardinilla	25	1.60	3.99	7.43	20	4.46	5.74	7.01	19	2.37	2.57	2.79	19	20.7 (17.0-26.2)	11.9	28
Mean	23.6	2.90	5.13	8.08		7.51	8.25	9.00		2.29	2.50	2.74		20.1 (16.0-26.2)	12.2	
Wet season																
Rivulus sites																
Juan Grande 1	25	1.67	4.01	7.37	61	6.09	7.00	7.90	43	2.82	2.94	3.06	43	22.4 (17.3-28.7)	12.5	52
Mendoza 1	27	1.71	4.00	7.27	47	6.91	7.31	7.72	43	2.85	2.97	3.09	43	21.7 (16.7-29.5)	14.1	94
Macho 1	23	3.52	6.15	9.53	33	11.48	11.48	11.48	30	2.31	2.53	2.76	30	23.9 (18.8-30.2)	13.4	59
Anton	29	2.21	6.04	11.78	39	8.85	11.32	13.80	27	2.60	3.14	3.78	27	23.7 (20.2-31.0)	10.7	19
Mato Ahogado	29	1.14	3.69	7.71	27	8.65	10.35	12.05	17	3.27	3.82	4.46	17	24.8 (21.1-30.6)	11.1	11
Mean	26.6	2.05	4.78	8.73		8.40	9.49	10.59		2.77	3.08	3.43		23.3 (18.82-30.0)	12.4	
Characin sites																
Juan Grande 2	21	3.11	5.92	9.64	34	8.22	9.12	10.01	31	2.22	2.48	2.76	31	20.3 (16.4-26.3)	14.6	40
Frijolito 1	25	2.29	4.58	7.65	35	8.90	8.22	7.55	29	2.65	2.77	2.89	29	18.4 (14.8-24.6)	10.9	115
Frijolito 2	23	2.16	4.43	7.51	32	5.83	6.81	7.78	30	2.34	2.45	2.56	30	19.3 (14.9-26.2)	14.2	43
Mendoza 2	21	3.30	6.19	9.98	42	7.72	8.84	9.97	42	2.18	2.54	2.95	42	22.1 (16.4-28.7)	16.2	32
Macho 2	21	3.45	5.02	6.88	36	8.70	8.93	9.15	30	2.35	2.59	2.86	30	21.7 (19.1-27.8)	11.1	31
Macho 3	21	3.10	4.43	6.01	41	8.45	7.92	7.38	35	2.52	2.81	3.14	35	21.5 (15.9-29.1)	15.2	39
Sardinilla	25	4.00	8.04	13.49	40	10.63	11.82	13.01	39	2.32	2.45	2.59	39	22.8 (17.3-31.2)	14.6	43
Mean	22.4	3.06	5.52	8.74		8.35	8.81	9.27		2.37	2.58	2.82		20.9 (16.4-27.7)	13.8	

decreased significantly with developmental stage (t_{722} = 9.05, P < 0.001). Reproductive allocation did not, however, differ between Characin and Rivulus sites (t_{10} = −0.40, P = 0.70; Table 1).

Fecundity

There was no significant interaction between the effects of season and predator community on female fecundity (t_{881} = 0.33, P = 0.74). There was no seasonal difference in fecundity (t_{882} = 1.45, P = 0.15; Table 1). However, the effect of female somatic mass on fecundity differed between Characin and Rivulus sites (interaction: t_{883} = 2.23, P = 0.026; predicted brood size for a female of average mass at Characin sites = 3.90, Rivulus sites = 3.37). Although larger females showed similar fecundity, smaller individuals from Characin sites had higher fecundity than their comparable-sized counterparts from Rivulus sites (Fig. 2).

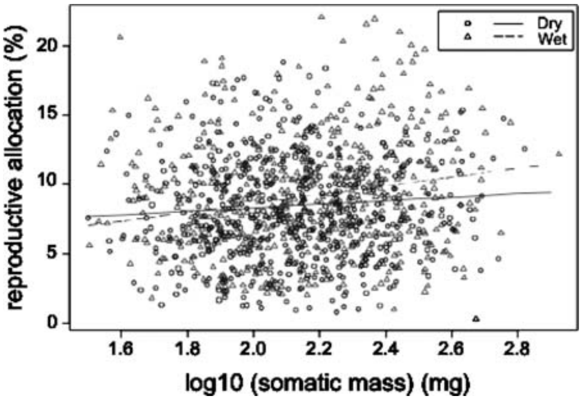

Fig. 1 The relationship between $\log_{10}$ (somatic mass) and reproductive allocation for the dry and wet seasons

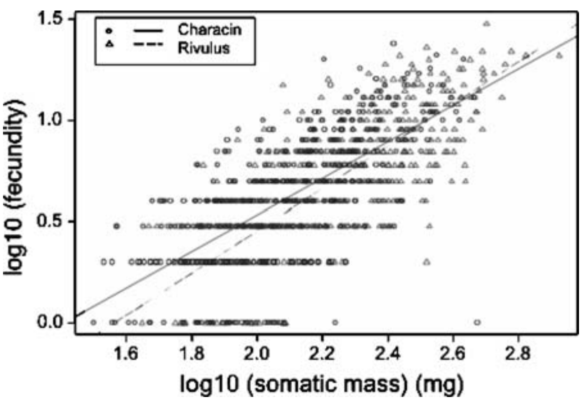

Fig. 2 The relationship between $\log_{10}$ (somatic mass) and $\log_{10}$ (fecundity) for Characin and Rivulus localities

Offspring mass

There was no significant interaction between the effects of season and predator community on offspring mass ($t_{721} = 0.239$, $P = 0.811$). Offspring mass increased with female somatic mass ($t_{722} = 14.70$, $P < 0.0001$) and decreased with developmental stage ($t_{722} = 12.86$, $P < 0.0001$). After adjusting for differences in offspring mass due to somatic mass and developmental stage, we found that there was a significant effect of season, with offspring mass being higher in the wet season than in the dry season ($t_{722} = 3.55$, $P = 0.0004$). After adjusting for all of the above effects, we also found that offspring mass was significantly lower at Characin compared to Rivulus sites ($t_{10} = 2.24$, $P = 0.049$; Table 1).

Discussion

Several key life-history attributes in *B. episcopi* differed between populations that co-occur with large predatory fish (Characin sites) and those that did not (Rivulus sites) (Jennions and Telford 2002). Here we show that differences between Characin and Rivulus localities are repeatable over time, with patterns observed in the wet season remaining unchanged during the dry. In both seasons, females matured at smaller sizes and mature males were smaller at Characin sites than those at Rivulus sites. Although reproductive allocation did not differ between predator communities, small females at Characin sites produced more offspring than their Rivulus counterparts. Females from Characin sites also produced smaller offspring. Studies on other Poeciliids have yielded comparable results (Reznick 1982, 1989; Reznick and Endler 1982; Reznick et al. 1996; Johnson 2001; Johnson and Belk 2001). Together, these patterns suggest convergent adaptation in life-history strategies with similar differences in other species being attributed largely to predator-mediated selection and/or correlates of predator presence (Johnson and Belk 2001; Jennions and Telford 2002). In the congener, *B. rhabdophora*, populations that coexisted with fish predators also matured at smaller sizes and had more, and smaller, offspring than those from predator-free environments (Johnson and Belk 2001). Classic studies on the Trinidadian guppy, *Poecilia reticulata*, showed similar life-history patterns to *Brachyrhaphis*, with the exception that female guppies living in high-predation sites also had higher reproductive allocation (Liley and Seghers 1975; Reznick and Endler 1982; Reznick et al. 1996; Reznick 1989). The results of selection experiments in the laboratory, however, suggest that reproductive allocation could be less strongly affected by predator-mediated selection pressure than other life-history traits (Reznick 1982a, b).

According to life-history theory (Gadgil and Bossert 1970; Charlesworth and Léon 1976; Law 1979; Michod 1979; Kozlowski and Uchmanski 1987), if predators increase total extrinsic mortality, or the mortality of adults relative to juveniles, selection might, under some circumstances, be expected to favour life-history differences similar to those observed for *B. episcopi*. Interestingly, recent comparisons of populations living in different predator communities have also revealed differences in genital morphology (Jennions and Kelly 2002), behaviour (Brown and Braithwaite 2004; Brown et al. 2005b, Simcox et al. 2005), cognitive abilities (Brown and Braithwaite 2005), cerebral lateralisation (Brown et al. 2004), and physiological response to stress (Brown et al. 2005a). Such patterns have all been credited to differences in predation pressure. Although compelling, to confidently attribute patterns of life-history traits to actual differences in predation pressure, it would also be useful to obtain actual data on rates and sources of extrinsic mortality at Rivulus and Characin localities, as well as information on which age classes are affected, and how density-dependent regulation (if present) is manifested.

Variables correlated with predator presence can also be important in shaping life-history differences. It is becoming increasingly apparent that environmental conditions may often co-vary with predator community (Grether et al. 2001; Reznick et al. 2001). Low predation localities inhabited by *B. episcopi*, for example, tend to occur above waterfalls (Jennions and Telford 2002; Brown and Braithwaite 2004, 2005). In guppies, such sites, because of lower productivity and high population densities, are also characterised by lower resource availability compared to high predation sites (Grether et al. 2001; Reznick et al. 2001). Arendt and Reznick (2005) recently showed that availability of resources may actually play a more important role than predation in shaping certain life-history traits in that species.

Life-history attributes in *B. episcopi* also varied seasonally independently of predator community. Temporal shifts in size at maturity and reproductive effort have been reported in a range of taxa, including those that live in seasonal tropical environments (Kramer 1978; Reznick 1989; Winemiller 1989, 1993; Wikelski et al. 2000). In our study, we found that sexually mature males were larger in the wet season compared to the dry season. Reproductive allocation and offspring size were also greater in the wet. Seasonal differences in life-history phenotypes often coincide with temporal changes in resource availability and competition (Kramer 1978). Wet season flooding, for instance, is believed to expand available habitat for fish and reduce the density of potential competitors and/or predators (Chapman and Kramer 1991; Winemiller 1993). For insect-eating species, like *B. episcopi*, an increase in potential food items during the wet season (e.g. surface arthropods; Levings and Windsor 1982) could also be important in explaining seasonal shifts in life-history parameters, as suggested, for example, in *Alfaro cultratus* (Winemiller 1993) and the congener, *B. rhabdophora* (Johnson and Belk 2001).

Additionally, in some poeciliids, the size of sexually mature males is affected by social environment and this, too, could help explain the differences we observed (Barowsky 1973, 1978, 1987; Snelson 1989; Kolluru and Reznick 1996). The presence of larger conspecifics, for example, delays both the timing of, and size at sexual maturity in juvenile platyfish, *X. maculatus* and *X. variatus* (Borowsky 1973, 1978, 1987). It is unknown whether the presence of dominant individuals has a similar effect on maturation in *B. episcopi*.

In conclusion, we found differences in life-history attributes among populations of *B. episcopi* living with different predator communities that persisted between dry and wet season samples. Independent of predator community, we also found seasonal differences in several life-history traits. The patterns we report here provide promising avenues for using *B. episcopi* as a model for further research. Work on other live-bearing fish suggest a myriad of potentially useful field and laboratory experiments to investigate whether life-history differences in *B. episcopi* are driven by predator-mediated selection and, if so, whether these differences are the result of phenotypic plasticity or genetic differentiation between populations (Reznick 1982a, b; Reznick et al. 1990; Johnson 2001). In this regard, researchers might wish to pay closer attention to how other environmental effects might operate, relative to predation, in shaping life-history phenotypes (Grether et al. 2001; Reznick et al. 2001; Arendt and Reznick 2005). Future studies could also test some of the ideas we proffered to explain seasonal differences in life-history traits or, indeed, test whether these seasonal differences are repeatable between years (Reznick 1989).

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