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## Life-history phenotypes in populations of *Brachyrhaphis episcopi* (Poeciliidae) with different predator communities

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**Abstract** Variation among populations in extrinsic mortality schedules selects for different patterns of investment in key life-history traits. We compared life-history phenotypes among 12 populations of the live-bearing fish *Brachyrhaphis episcopi*. Five populations co-occurred with predatory fish large enough to prey upon adults, while the other seven populations lacked these predators. At sites with large predatory fish, both sexes reached maturity at a smaller size. Females of small to average length that co-occurred with predators had higher fecundity and greater reproductive allotment than those from populations that lacked predators, but the fecundity and reproductive allotment of females one standard deviation larger than mean body length did not differ among sites. In populations with large predatory fish, offspring mass was significantly reduced. In each population, fecundity, offspring size and reproductive allotment increased with female body size. When controlling for maternal size, offspring mass and number were significantly negatively correlated, indicating a phenotypic trade-off. This trade-off was non-linear, however, because reproductive allotment still increased with brood size after controlling for maternal size. Similar differences in life-history phenotypes among populations with and without large aquatic predators have been reported for *Brachyrhaphis rhabdophora* in Costa Rica and *Poecilia reticulata* (a guppy) in Trinidad. This may represent a convergent adaptation in life-history strategies attributable to predator-mediated effects or environmental correlates of predator presence.

**Keywords** Guppy · Life-history variation · Offspring size · *Poecilia reticulata* · Population differences

### Introduction

Life-history traits are under strong selection because they determine lifetime reproductive success, so within-species differences among populations are predicted whenever selective environments vary, traits are heritable and gene flow is limited. In many taxa, fecundity increases with body size while reproduction reduces somatic growth (Roff 1992). This trade-off creates selection on the timing of sexual maturation and subsequent reproductive effort, and extrinsic mortality schedules largely determine the optimal strategy (Roff 1992; Stearns 1992). Reproductive-effort models that maximise the intrinsic rate of population growth ( $r$ ) for a given schedule of age-specific mortality and fecundity (Charlesworth 1980) predict that an increase in extrinsic mortality in one age-class increases reproductive effort prior to this age and decreases it thereafter. An increase in adult mortality compared to juvenile mortality therefore selects for earlier sexual maturation and greater reproductive effort (Gadgil and Bossert 1970; Charlesworth and Leon 1976; Law 1979; Michod 1979). Models that optimise the lifetime production of offspring ( $R$ ; Roff 1992) show that a uniform increase in extrinsic mortality can also influence life-history traits (Kozłowski and Uchmanski 1987; Kozłowski 1992; Abrams and Rowe 1996).

Numerous laboratory studies report an association between rates of extrinsic mortality and life-history evolution (Polak and Stammer 1998), but natural examples of strong associations between predatory fauna and prey life histories are rarer (Reznick and Endler 1982; Trexler et al. 1994; Reznick et al. 1996b; Johnson and Belk 2001). Even when associations occur, determining the selective mechanisms responsible is challenging. Data on age-based mortality schedules are usually only available for a few populations (Wellborn 1994; Bertschy and

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Fox 1999) and, when classifying populations, it is necessary to distinguish between extrinsic mortality and mortality attributable to reproductive investment (Partridge and Harvey 1988). Finally, predators may alter resource availability and prey density (Benton and Grant 1999) or induce “trophic cascades”. Mortality schedules alone cannot reveal these indirect effects, and attempts to measure or manipulate these effects in the field are rare (Rodd and Reznick 1997; Rodd et al. 1997; review: Reznick et al. 2001).

The most comprehensive evidence for an effect of predators on prey life histories comes from the guppy *Poecilia reticulata* (review: Reznick et al. 2001). At sites with larger predators and greater extrinsic mortality, guppies mature sooner, show greater fecundity and reproductive effort, but produce smaller offspring. Guppies are, however, unusual because they show considerable population divergence for almost every trait examined (Magurran 1999). Repeatable life-history shifts may be less prevalent in other freshwater fish (but see Bertschy and Fox 1999; Johnson and Belk 2001). Here we test whether life-history phenotypes of another poeciliid, *Brachyrhaphis episcopi*, differed between populations that did or did not co-occur with larger predatory fish. Our findings are broadly in agreement with those from guppies and recent work on *B. rhabdophora* (Johnson and Belk 2001), which increases confidence that direct or indirect predator effects generate population variation in poeciliid life histories.

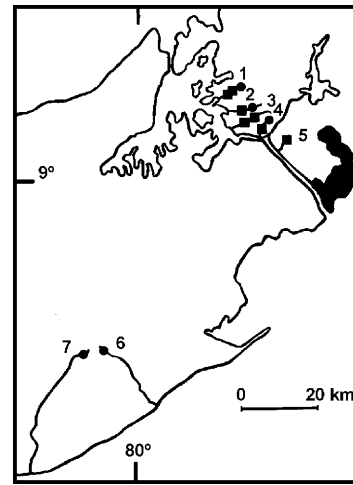
## Materials and methods

### Study species and sites

*Brachyrhaphis episcopi* (Steindachner) (Poeciliidae) is a live-bearing fish endemic to Panama (Loften 1965). Although male poeciliids generally cease growth upon maturation (Rodd and Reznick 1997; Johnson and Belk 2001), male *B. episcopi* within a single population can range from 15 to 36 mm in length (Turner 1938). Adult males are smaller than females (range 14.3–30.6 mm versus 19.2–51.7 mm standard length; this study). As with *B. rhabdophora* (Turner 1938; Reznick et al. 1993), there is no post-fertilisation transfer of nutrients to offspring, whose mass decreases 21.8% (range 4.3–35.2%,  $n=12$  sites) during development (this study). Females develop one brood at a time.

At some sites the only piscine predator we observed was the small killifish *Rivulus brunneus* (Cyprinodontidae). It is mainly insectivorous, small-gaped and incapable of eating adult *B. episcopi* (Angermeier and Karr 1983). The congeneric *R. harti* consumes primarily immature size-classes when offered *P. reticulata* guppies (Mattingly and Butler 1994). Other sites contained *R. brunneus* and several, larger piscine predators (e.g. *Aequidens coeruleopunctatus*; *Piabucina panamensis*, *Brycon* spp., *Hoplias microlepis*, *Roeboides guatemalensis* and *Rhamdia wagneri*). Stomach-content analysis shows that these species all include fish in their diet (Angermeier and Karr 1983; Kramer and Bryant 1995). We classified sites as “Rivulus” localities if the only predatory fish seen was *R. brunneus*. Sites with larger predatory fish were classified as “Characin” localities, since Characiformes species (of the families Lebiasinidae or Characidae) were present.

We collected *B. episcopi* from 12 sites, 10 along streams in the Parque Nacional Soberanía during the 1998 dry season. Streams drain into Gatun Lake, the Panama Canal or intermediate lakes, and this open water represents a barrier to downstream movement.



**Fig. 1** Location of the 12 study sites. The rivers are: (1) Río Macho, (2) Río Mendoza, (3) Río Frijolito, (4) Quebrada Juan Grande, (5) Quebrada Sardinilla, (6) Río Mato Ahogado and (7) Río Antón. Circles represent Rivulus sites, squares Characin sites. The dark area is Panama City

*B. episcopi* is primarily an upstream species, replaced downstream by the congener *B. cascajalensis* (personal observation; Mojica et al. 1997). We therefore consider different streams to represent different populations. In the streams waterfalls prevent upstream, and limit downstream, movement. As with other studies, each of our 12 collection sites is considered an independent data point (see Reznick and Endler 1982). We collected from two sites each on the Quebrada Juan Grande, Río Frijolito and Río Mendoza; three sites on the Río Macho and one on Quebrada Sardinilla (for site details see Angermeier and Karr 1983). We also collected from one site each on the Río Antón and Río Mato Ahogado. The position of sites is given in Jennions and Kelly (2002) (Fig. 1). Five Characin sites were below waterfalls; Frijolito 1 was above a waterfall, and Sardinilla was at the stream’s headwaters. Four Rivulus sites were above waterfalls, while Mato Ahogado was near the stream’s headwaters, above a long series of small rapids.

### Field and laboratory procedures

At least 150 fish/site were collected using hand nets repeatedly run along the shoreline. The fish were anaesthetised with MS-222 and preserved in 5% formalin. Sexually mature males have a translucent, sharply pointed gonopodium (anal fin modified for sperm transfer). Fish standard length was measured to a precision of  $\pm 0.1$  mm using dial callipers.

To analyse reproduction, we divided females into 2-mm size-classes. If possible, we sampled five or more females per size-class with embryos or, for non-reproductive size-classes, four or more females with non-vitellogenic ova ( $n=40-99$  females/site). We recorded: (1) standard length (SL); (2) somatic dry weight; (3) mean offspring dry weight; (4) number of developing offspring/yolked ova; (5) stage of offspring/ova development. For dry weights, we placed specimens overnight in a desiccating oven at 55°C, then weighed them with a Sartorius balance (to a precision of  $\pm 0.1$  mg).

Somatic dry weight was the total weight following removal of reproductive tissue, the hind gut and stomach contents. Fat associated with the gut was, however, included in the estimate of somatic weight. Ova were defined as fully developed if the diameter was  $\geq 2.4$  mm. All ova with early-stage embryos were slightly larger than 2.4 mm in diameter. To stage embryonic development we used the continuous variable “median eye diameter/brood” (range 0.26–1.24 mm). Reproductive allotment (RA) was defined

as: RA = dry weight of embryos/(somatic dry weight + dry weight of embryos) (Reznick and Endler 1982). To calculate minimum female size at sexual maturity, female reproductive state was defined as: (1) embryos visible; (2) full-sized, yoked ova present ( $\geq 2.4$  mm), but no embryo visible; (3) yolked ova present, but  $< 2.4$  mm; (4) only non-vitellogenic ova present. The minimum size-class for sexual maturity was defined when there were at least as many females with full-sized ova or embryos as females with non-vitellogenic eggs. Most females in smaller size-classes lacked developing embryos.

### Statistical analysis

We measured five life-history traits per population: female and male size at maturity; reproductive allotment; and number and size of offspring. To compare traits between predator community types we performed univariate, nested ANCOVA using the GLM procedure of SYSTAT 8.0, with predator community (Rivulus or Characin) as the main effect, and site nested therein. We treated "site" as a fixed effect because community type was known a priori and each site was chosen for its predator assemblage (Bennington and Thayne 1994; see Reznick 1989; Leips and Travis 1999). If the effect of the covariate "female somatic mass" on the dependent variable differed among sites (i.e. slopes differed), we calculated three "adjusted" values: those for a female at, and one standard deviation above or below, the grand mean for body weight. To generate "adjusted" values, the dependent variable was regressed on female body weight at each site after removing 0–2 outliers per site (their inclusion did not change results, however). The site-specific regression slope was used to project the observed value of the variable for each female to that expected at the appropriate mass (see also Reznick and Endler 1982), keeping developmental stage (i.e. eye diameter) fixed at the grand mean (see Results). These values were then analysed in separate nested ANOVA.

Although we argue that "site" is a fixed effect, we re-analysed the data, treating sites as a random effect in mixed models using the restricted maximum-likelihood (REML) procedure in Genstat 4.5.1 (Genstat 1997). Significance was estimated by dropping a term from the full model and examining the change in deviance, which approximates a  $\chi^2$  distribution. Final models contained on-

ly significant terms ( $P < 0.05$ ). Aside from main terms, we also tested the significance of the two-way interactions between predator type and female size or developmental stage.

To test the consistency of certain relationships across sites, we performed meta-analyses (Cooper and Hedges 1994). At each site, the effect size was calculated as Fisher's Z-transformation of Pearson's  $r$ . We calculated the mean weighted effect size using MetaWin 2.0 (Rosenberg et al. 2000). Heterogeneity in effect sizes among sites or between predator-locality types was tested using  $Q$  which has a  $\chi^2$  distribution ( $df = n - 1$ ). Unless otherwise stated, all tests are two-tailed. Data are presented as mean  $\pm$  SD.

## Results

### Do adults mature sooner at Characin sites?

Sexually mature males from Characin sites were smaller than those from Rivulus sites ( $F_{1,501} = 106.56$ ,  $P < 0.001$ ; least-squares mean  $\pm$  s.e. Rivulus  $22.48 \pm 0.16$  mm,  $n = 229$  and Characin  $20.22 \pm 0.15$  mm,  $n = 284$ ; Table 1). The minimum size-class for sexually mature females was also significantly smaller for Characin than for Rivulus sites (Mann–Whitney test,  $U = 29.5$ ,  $n = 5,7$ ,  $P = 0.042$ ; Table 1). In all populations, mature-male size varied considerably (Table 1) and was unimodal, such that  $\log_{10}$  male size was normally distributed at 11 of 12 sites (Lilliefors's test, all  $P > 0.05$ ). Across sites, females with developing embryos ranged from 19.2 to 51.7 mm SL (grand mean 30.8 mm). Mean somatic mass for gravid females was  $163 \pm 101$  mg ( $n = 431$ ). When "adjusting" dependent variables, we therefore calculated values for females weighing 62, 163 and 264 mg. Embryo mean eye diameter was 0.73 mm ( $n = 342$  broods).

**Table 1** Mean site values for reproductive allotment (RA), offspring mass and fecundity adjusted to female somatic mass of 62, 163 and 264 mg (see text). For females, the larger sample size is for fecundity, the smaller, for RA and offspring mass

	Females									Males			
	Minimum size (n) mm	Fecundity (brood size)			Reproductive allotment %			Offspring mass mg			Mean size (range) mm	CV %	n
		62	163	264	62	163	264	62	163	264			
<b>Rivulus sites</b>													
Juan Grande 1	29 (36/27)	0.56	3.37	6.82	4.61	5.96	6.69	2.64	2.83	2.93	22.0 (17.1–26.8)	13.3	40
Mendoza 1	25 (43/32)	1.05	3.97	6.13	4.94	5.98	6.53	2.79	2.92	2.99	19.5 (16.4–24.8)	9.3	58
Macho 1	23 (72/50)	2.55	8.42	12.62	8.59	10.53	11.57	1.80	2.33	2.66	23.9 (18.6–30.1)	11.2	63
Antón	31 (17/12)	0.00	2.95	6.57	0.68	4.35	7.37	2.29	3.07	3.54	23.9 (20.2–30.6)	9.1	36
Mato Ahogado	31 (21/16)	0.54	4.55	8.00	6.68	9.58	11.22	2.52	3.40	3.94	23.1 (20.1–26.5)	6.8	32
Mean	27.8	0.94	4.77	8.03	5.10	7.28	8.68	2.41	2.91	3.22	22.6 (18.5–27.8)	9.9	
<b>Characin sites</b>													
Juan Grande 2	23 (34/28)	2.01	6.81	9.44	6.22	10.06	12.32	1.94	2.42	2.71	19.1 (15.8–23.6)	11.0	44
Frijolito 1	21 (38/35)	1.65	4.32	6.13	6.08	6.23	6.30	2.44	2.66	2.77	17.9 (14.3–23.2)	10.5	52
Frijolito 2	27 (38/35)	0.40	4.44	8.06	4.01	7.05	8.87	2.58	2.67	2.72	18.8 (15.2–25.6)	12.8	39
Mendoza 2	23 (48/36)	3.06	5.91	7.68	10.13	8.69	8.02	2.22	2.42	2.53	20.3 (15.2–27.6)	15.4	33
Macho 2	23 (41/33)	3.39	8.10	11.21	10.55	10.45	10.39	1.96	2.46	2.76	22.9 (18.0–28.8)	11.1	39
Macho 3	23 (22/19)	2.65	5.70	7.66	9.61	10.33	10.69	2.28	2.78	3.07	21.8 (16.4–28.5)	12.5	49
Sardinilla	25 (20/19)	0.81	4.50	7.46	3.72	5.83	7.06	2.23	2.55	2.73	20.7 (17.0–26.2)	11.9	28
Mean	23.6	2.00	5.68	8.23	7.19	8.38	9.09	2.24	2.57	2.76	20.1 (16.0–26.2)	12.2	

### Is reproductive allotment greater at Characin sites?

Female body mass ( $F_{1,311}=25.55$ ,  $P<0.001$ ) and developmental stage ( $F_{1,311}=24.24$ ,  $P<0.001$ ) both predicted reproductive allotment of females with eyed embryos. There was no interaction between developmental stage and site ( $F_{11,300}=1.01$ ,  $P=0.44$ ), but there was one between female body mass and site ( $F_{11,311}=2.27$ ,  $P=0.011$ ). Partial regression coefficients for female body mass were positive for 10 of 12 sites, and significantly so for 5 ( $P<0.05$ ); those for developmental stage were negative for 11 of 12 sites, and significantly so for 5 ( $P<0.05$ ). We therefore compared reproductive allotment “adjusted” to the three reference female weights, while holding developmental stage constant.

Reproductive allotment was significantly greater at Characin sites for females at, or one standard deviation below, mean body mass ( $F_{1,324}=13.32$  and  $70.25$ , respectively; both  $P<0.001$ ), but not one standard deviation above it ( $F_{1,324}=1.66$ ,  $P=0.198$ ). Thus small to average-sized females at Characin sites have greater reproductive allotment than their Rivulus-site counterparts, while larger females show similar reproductive allotment (Table 1).

### Is fecundity greater at Characin sites?

We compared fecundity between predator communities for all females with embryos or full-sized ova. The effect of female body mass was significantly positive at all sites, but varied among sites ( $F_{11,402}=3.35$ ,  $P<0.001$ ). We therefore compared “adjusted” fecundities. Brood size was significantly greater at Characin sites for females at, or one standard deviation below, mean body mass ( $F_{1,415}=22.49$  and  $126.15$ , respectively; both  $P<0.001$ ), but not for females one standard deviation above the mean ( $F_{1,415}=1.21$ ,  $P=0.271$ ). So small to average-sized females at Characin localities have greater fecundity than their Rivulus counterparts, while larger females showed similar fecundity (Table 1).

### Is offspring mass lower at Characin sites?

Female body mass and embryo developmental stage both predicted mean offspring mass ( $F_{1,311}=70.96$  and  $68.81$ , respectively; both  $P<0.001$ ). Partial regression coefficients for female body mass were always positive, and significantly so for eight sites. Those for developmental stage were always negative, and significantly so for seven sites. There was no interaction between developmental stage and site ( $F_{11,300}=0.66$ ,  $P=0.78$ ), but there was between female body mass and site ( $F_{11,311}=2.93$ ,  $P=0.001$ ). We therefore compared “adjusted” offspring mass, again holding developmental stage constant. Offspring were significantly smaller at Characin than at Rivulus sites, for all three female body sizes ( $F_{1,324}=71.57$ ,  $48.33$ ,  $15.43$ , respectively; all  $P<0.001$ ; Table 1).

### Treating sites as a random factor

Using mean male size per site, males were significantly larger at Rivulus sites (Mann–Whitney test,  $U=30$ ,  $n=5,7$ ,  $P=0.042$ ). The same was true for minimum female size (see above). For reproductive allotment, there were marginally significant interactions between predator community type and female body size ( $\chi^2=3.5$ ,  $df=1$ ,  $P=0.061$ ) and developmental stage ( $\chi^2=3.6$ ,  $df=1$ ,  $P=0.058$ ). These did not enter the final model, where there was no significant effect of predator community type ( $\chi^2=0$ ,  $df=1$ ,  $P=0.98$ ). For fecundity, there was no significant interaction between female body size and predator community type ( $\chi^2=0.76$ ,  $df=1$ ,  $P=0.382$ ), and no significant effect of predator community type ( $\chi^2=0.47$ ,  $df=1$ ,  $P=0.49$ ). For offspring mass there were no significant interactions between predator community type and female body size ( $\chi^2=0.12$ ,  $df=1$ ,  $P=0.73$ ) or developmental stage ( $\chi^2=0.41$ ,  $df=1$ ,  $P=0.52$ ). There was, however, a significant effect of predator community type ( $\chi^2=4.19$ ,  $df=1$ ,  $P=0.04$ ). Offspring were larger at Rivulus sites.

### Phenotypic correlations between life-history traits across populations

We first calculated fecundity, offspring mass and reproductive allotment for a 163-mg female for each population. Across sites there was a positive correlation between offspring mass and minimum female size ( $r_s=0.735$ ,  $P<0.01$ ). Adjusted mean fecundity was negatively related to minimum female size ( $r_s=-0.819$ ,  $P<0.01$ ) and adjusted offspring mass ( $r_s=-0.755$ ,  $P<0.01$ ), and positively related to adjusted reproductive allotment ( $r_s=0.811$ ,  $P<0.005$ ) ( $n=12$  for all sites). Following sequential Bonferroni correction, the latter three relationships remained significant. Given these correlations, we tested whether the five life-history traits act as a correlated suite of characters. The first two components of a principle-component analysis explained 84.4% of the variance among sites (PC1 55.9%, PC2 28.5%). A linear-discriminant-function analysis using PC1 and PC2 successfully separated the two predator–prey community types ( $F_{2,9}=4.84$ ,  $P=0.038$ ).

### Phenotypic trade-offs

The across-site correlation between offspring size and number suggests a phenotypic trade-off. Within sites, however, this relationship may go undetected because both traits are positively correlated with female size. We therefore examined residuals from the regression of each variable on female size. They were negatively correlated at ten sites, and significantly so at five sites. There was no significant heterogeneity in the relationship among sites ( $Q=18.07$ ,  $df=11$ ,  $P<0.10$ ). The weighted mean correlation was  $r=-0.234\pm 0.057$  (s.e.), which is signifi-

cantly less than zero ( $Z=4.093$ ,  $P<0.0001$ ). There is therefore a phenotypic trade-off between offspring size and number that does not differ among sites. This trade-off does not, however, result in equivalent reproductive allotment for different-sized broods. Again controlling for female body size, offspring number and reproductive allotment are significantly positively correlated at every site. The weighted mean correlation is  $r=0.867\pm 0.014$  (s.e.), which is significantly greater than zero ( $Z=60.2$ ,  $P<0.0001$ ). Again, there is no significant heterogeneity among sites ( $Q=18.7$ ,  $df=11$ ,  $P<0.10$ ). Therefore, brood size increases with greater reproductive allotment, even though offspring mass declines significantly.

## Discussion

### Comparative evidence: similar findings in other species

Populations with predators that presumably elevate adult mortality are usually associated with earlier maturation and elevated reproductive effort (Lafferty 1993; Wellborn 1994; Joekla and Lively 1995; Polak and Starmer 1998; Joekla et al. 1999). In poeciliid fish, similar patterns are seen for “predator” and “predator-free” sites in *Brachyrhaphis rhabdophora* (Johnson and Belk 2001) and “high-risk” and “low-risk” sites in *Poecilia reticulata* (Reznick 1989). Here we report significant differences in life-history traits between *Brachyrhaphis episcopi* populations co-occurring with predatory fish (Characin sites) and those without (Rivulus sites). At Characin sites, mature adults and newborn offspring were smaller, and female fecundity and reproductive allotment generally higher. Although the same trends are seen in all three species, they are far weaker in *B. episcopi* (Table 2), and, for some traits, sensitive to whether site is a “fixed” or a “random” factor. Even so, these convergent life-history phenotypes suggest either an adaptive response to predator presence or an environmental correlate thereof. The comparative approach uses the repeated occurrence of patterns of association following natural “experiments” to identify adaptations (Doughty 1996). Although causality is always uncertain, when similar trends repeatedly emerge across taxa, and plausible selective mechanisms are known, our confidence in specific adaptive scenarios increases (Harvey and Pagel 1991). Crude attempts to rank average mortality rates across species have had considerable success in predicting life-history features (Charnov 1993; Purvis and Harvey 1995; Jennings et al. 1998; Gemmill et al.

1999). Within-species comparisons of poeciliids showing convergent patterns of population differentiation provide similar supporting evidence.

### Explaining population differences

General life-history theory predicts earlier sexual maturity and greater reproductive effort if predators increase either total extrinsic mortality (Kozlowski and Uchmanski 1987) or the mortality of adults compared to juveniles (Gadgil and Bossert 1970; Charlesworth and Leon 1976; Law 1979; Michod 1979). Predictions of optimal offspring size are less clear. Smith and Fretwell (1974) do not predict that offspring size depends on maternal phenotype, although it often does (Sakai and Harada 2001). There is, however, much empirical support for a phenotypic trade-off between offspring size and fecundity (Lloyd 1987), both within and across species (Charnov 1993), and a few species-specific theoretical models exist (e.g. Hendry et al. 2001).

Life-history differences among populations are often ascribed to adaptive responses to predator-mediated selection through phenotypic plasticity or genetic divergence due to different extrinsic mortality schedules (Niewiarowski 2001). This conclusion is, however, premature for *B. episcopi*, because we lack data on mortality and/or possible indirect effects of predators. Although rarely discussed, this is true for most field studies of life-history variation, even those commonly attributed to predation rates. Even if mortality rates are known, the component due to differential reproductive effort must first be removed to calculate extrinsic mortality (Partridge and Harvey 1988), since greater reproductive effort (for whatever reason) leads to increased mortality. Ironically, this direct cost of reproduction is usually removed using models that assume optimality (e.g. Bertschy and Fox 1999). Even so, it is a reasonable assumption that large predatory fish increase extrinsic mortality in *B. episcopi*, as reported for *P. reticulata* (Reznick et al. 1996a). Testing this explanation by directly measuring mortality rates in *B. episcopi* will be challenging though, since predator-rich downstream sites lack the isolated pools required for an accurate mark–recapture programme (e.g. Reznick et al. 1996a).

Even if extrinsic mortality differs among sites, other potential correlates of predator presence could also generate population differentiation. Abiotic factors are sometimes controlled for statistically (e.g. Strauss 1990), but predator-induced mortality may still be a major se-

**Table 2** Differences in mean values of traits between presumed lower and higher predation (percentage change with smaller mean as the denominator). Data from Reznick (1989), Johnson and Belk (2001) and this study

	<i>Poecilia reticulata</i>	<i>Brachyrhaphis rhabdophora</i>	<i>B. episcopi</i>
Minimum female size	23.2%	20.0%	22.9%
Minimum male size	8.1%	42.9%	12.4%
Fecundity	127.5%	32.9%	19.1%
Offspring mass	88.6%	73.9%	13.2%
Reproductive allotment	24.4%	56.3%	14.1%

lective force even when environmental factors closely covary with predator presence. In *B. episcopi*, as with *P. reticulata*, low-predation populations tend to be above waterfalls, so abiotic differences between Characin and Rivulus sites must exist (e.g. Reznick et al. 2001). Indeed, the downstream replacement of *B. episcopi* by *B. cascajalensis* is surely a biological indicator of some changes. If downstream habitats are less suitable for *B. episcopi*, this too should elevate extrinsic mortality. Ultimately, the strongest evidence for a predation effect comes from experiments: specifically, the introduction of predators to predator-free sites. A direct experimental approach is, arguably, the most compelling reason why population differentiation in guppies is directly attributed to predator presence (Reznick et al. 1990). If authorised, such experiments could easily be undertaken by introducing predators to predator-free upstream sites.

#### Phenotypic trade-offs and female body size

Female body size had positive effects on fecundity, reproductive allotment and offspring size in *B. episcopi*. Female size increases with age in fish, and most models of optimal reproductive effort predict an increase with age due to declining residual reproductive value (Gadgil and Bossert 1970; Kozlowski and Uchmanski 1987; but see Charlesworth and Leon 1976). There is generally a positive relationship between maternal size and total reproductive output in fish (Roff 1983; Hendry et al. 2001). Although larger mothers produce larger offspring in many taxa, a general explanation for this phenomenon is unavailable (review: Sakai and Harada 2001). After controlling for female size, however, we found a phenotypic trade-off between brood size and offspring mass. This trade-off could reflect a limited supply of available resources per brood, or physical constraints, such as abdominal cavity size (Olsson and Shine 1997; Doughty and Shine 1997), when female fitness increases more rapidly with offspring number than size (e.g. Oksanen et al. 2001).

In *B. episcopi*, differences in fecundity or reproductive allotment between predator community-type sites were apparent for small to medium-sized, but not for large, females. In contrast, no such trend has been reported for guppies or *B. rhabdophora* (Johnson and Belk 2001), although closer inspection may show that it exists. We compared sites using the across-site average for female size (163 mg dry weight) and values one standard deviation around the average (62 and 264 mg). At Characin sites females mature at smaller sizes. On average, only 10.0% of females at Characin sites had a dry mass above 264 mg. At Rivulus sites the corresponding proportion was 32.5%. Therefore, one explanation for our finding is that selection for increased fecundity at Characin sites (compared to Rivulus sites) for absolutely large females is weaker than that for smaller females, because so few reach large sizes. At any given age, individuals are absolutely smaller at Characin sites, and senes-

cence, expressed as a decrease in expected fecundity, may arise because deleterious genetic mutations are more often expressed in older females (Austad 1999).

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