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Parallel evolution of the sexes? Effects of predation and habitat features on the size and shape of wild guppies

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Abstract

Environmental gradients often lead to the parallel evolution of populations and species. To what extent do such gradients also lead to parallel evolution of the sexes? We used guppies (*Poecilia reticulata*) to examine the parallel and independent (sex-specific) aspects of population divergence in response to predation and habitat features. Geometric morphometrics was used to analyse size and shape variation for 1335 guppies from 27 to 31 sites sampled in each of 2 years. Body size showed strong parallel population divergence; both sexes were larger at sites with a more open canopy and with higher flow. Body shape showed a mixture of parallel and independent population divergence. The strongest and most consistent effects were (1) high-predation sites had males with smaller heads and deeper caudal peduncles, (2) open-canopy sites had females with smaller heads and more distended abdomens and (3) high-flow sites had males and females with smaller heads and deeper caudal peduncles.

Introduction

When different populations experience different selective environments, they often diverge in traits that influence survival and reproductive success (Schluter, 2000). This adaptive population divergence often occurs in parallel for different lineages (e.g. species) arrayed across the same range of selective environments. That is, different lineages settle on similar adaptive solutions to the same spatial patterns of variation in selection. This parallel (or convergent) evolution in response to environmental gradients may be a general evolutionary principle given its prevalence at a variety of taxonomic scales (Harvey & Pagel, 1991; Jones *et al.*, 1992; Schluter, 2000; Langerhans & DeWitt, 2004; Schluter *et al.*, 2004). But to what extent does this principle also hold for males and females of the same species? The present paper outlines issues relevant to parallel evolution of the sexes, and then tests for its importance within a natural system.

Environmental gradients may impose divergent selection among populations in a manner that is broadly parallel for males and females. If so, the sexes might show similar patterns of population divergence, given that they also share the majority of their genome (Lande, 1980). All else being equal, the sexes might therefore exhibit parallel patterns of population divergence along environmental gradients. But all else is not equal. For example, males often exhibit exaggerated displays that enhance their competitive ability or attractiveness to mates (Andersson, 1994), whereas females often develop specialized morphologies for egg storage, egg laying or offspring provisioning. The sexes can also differ in behaviour, even outside of a reproductive context (Magurran & Maciás Garcia, 2000). For example, males and females can be spatially segregated, prefer different microhabitats, and use different food resources (Shine, 1989; Magurran, 1998; Temeles *et al.*, 2000; Butler & Losos, 2002; Reimchen & Nosil, 2004). Critically from the perspective of parallel evolution, these differences in sexual selection, reproductive morphology, and behaviour may interact with environmental gradients. As one example, the more conspicuous mating displays of males than females may make males more susceptible to predation than are females (Magnhagen, 1991; Kotiaho

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et al., 1998; Quinn & Buck, 2001). In the case of such interactions, males and females may be subject to different spatial patterns of variation in selection along the same environmental gradients. If so, they may settle on different adaptive solutions: i.e. 'nonparallel', 'sex-specific', 'independent' or 'unique' population divergence.

Sex-specific aspects of population divergence may thus be the result of sex-specific divergent selection. They may also be the result of sex-biased dispersal, sex-specific plasticity or sexual niche partitioning. First, sex-biased dispersal might weaken population divergence for the sex with higher dispersal. For example, Moore & Hendry (2005) suggested that this phenomenon might explain sex-specific morphological clines in threespine stickleback, *Gasterosteus aculeatus*. Second, sex-specific plasticity (e.g. Robinson & Wilson, 1995) might enhance phenotypic divergence for the sex that matches the environment more precisely. This greater plasticity, however, might weaken divergent selection and therefore decrease genetically based phenotypic divergence along the same gradient (Price *et al.*, 2003). Third, sexual niche partitioning may contribute to deviations from parallelism if competition between the sexes favours different forms of partitioning in different environments (Butler & Losos, 2002).

Few studies have explicitly examined parallel evolution of the sexes, but some have presented relevant data. As one example, *Drosophila subobscura* are distributed along broad latitudinal gradients in Europe, South America and North America (the latter two because of introductions). Gilchrist *et al.* (2004) found that both sexes show increases in body size with latitude on all continents, but that the trend in South America is weaker for males than for females. Weaker latitudinal clines in males than females have also been noted for houseflies, *Musca domestica* (Alves & Bélo, 2002). As another example, among-population variation in the body depth of breeding sockeye salmon (*Oncorhynchus nerka*) is negatively correlated with the intensity of bear predation, but the trend is stronger for males than for females (Quinn *et al.*, 2001). As these examples illustrate (see also Brinsmead & Fox, 2002; Butler & Losos, 2002; Stuart-Fox *et al.*, 2004), some aspects of population divergence can be shared between the sexes (parallelism) and some can be unique to each sex (independence). We here quantify the parallel and independent components of population divergence for male and female guppies (*Poecilia reticulata*) arrayed across environmental gradients.

Guppies

Guppies are a live-bearing poeciliid fish native to Trinidad and parts of northern South America. Populations of this species are distributed across a well-studied predation gradient (reviews: Endler, 1995; Reznick & Travis, 1996; Houde, 1997; Magurran, 1998). Guppies at low elevations are typically exposed to strong predation from several fish species ('high predation'), whereas guppies at high elevations are typically exposed to weak predation from few fish species ('low predation'). Guppy populations in high- vs. low-predation environments have diverged in many traits, as illustrated by the following examples. High-predation guppies spend more time in shoals, inspect predators more carefully, swim faster, and are better at escaping predators (e.g. Magurran & Seghers, 1994a; O'Steen *et al.*, 2002; Kelley & Magurran, 2003; Ghalambor *et al.*, 2004). High-predation females mature earlier, have greater reproductive effort, and produce more but smaller offspring (e.g. Reznick & Endler, 1982; Reznick *et al.*, 1996b). High-predation males are less colourful (Haskins *et al.*, 1961; Endler, 1980; Millar *et al.*, in press). All of these differences have a genetic basis and are adaptive, as revealed by common-garden experiments, laboratory predation experiments, and introductions in nature (see above citations).

In contrast to the above traits, population divergence in guppy body shape has received comparatively little attention. And yet, size and shape present excellent opportunities to test for parallel population divergence of the sexes. First, body size and shape influence swimming ability and therefore predation risk in fishes (e.g. Walker, 1997; Ghalambor *et al.*, 2004; Langerhans *et al.*, 2004). Second, guppies are sexually dimorphic for size and shape. For body size, females have indeterminate growth whereas males have largely determinant growth, leading to a larger size at maturity for females than males (Reznick, 1983). For body shape, females have increasingly distended abdomens as their young develop (Ghalambor *et al.*, 2004). Third, males and females differ critically in behaviours that may influence selection on size and shape. For example, females spend most of their time feeding, whereas males spend most of their time courting and attempting to copulate with females (Magurran & Seghers, 1994b; Houde, 1997; Magurran, 1998). Also, males forage less on the benthos and are generally more mobile than females (Magurran, 1998; Croft *et al.*, 2003).

As noted above, sex-specific divergent selection should arise from interactions between environmental gradients and sex-specific morphology or behaviour. These interactions appear likely for guppy size and shape in relation to predation. As one example, increasing abdomen distension in females decreases swimming performance (Ghalambor *et al.*, 2004), which should increase mortality at high-predation sites. As another, males from high-predation, but not low-predation, sites prefer shallower water than do females when both are exposed to predation risk (Croft *et al.*, 2004), which may then influence selection on shape imposed by hydrodynamics. The sexes also differ in overall predator-induced mortality rates, which may then alter the nature of selection on size and shape. Specifically, mortality in high-predation sites is greater for males than for females (Reznick *et al.*, 1996a), perhaps because males spend less time in anti-predator behaviour and are more conspicuous than females (Endler, 1980; Magurran & Seghers, 1994b). Environmental gradients other than predation may also influence the evolution of guppy size and shape. Foremost among these gradients are canopy openness (Grether *et al.*, 2001; Reznick *et al.*, 2001), water flow (Nicoletto & Kodric-Brown, 1999) and stream size (Grether *et al.*, 2001; Reznick *et al.*, 2001). Like predation, these habitat features impose selection on size and shape that may differ between the sexes.

Our study

We studied 31 different sites across two Trinidadian watersheds. For each site, we characterized the predation regime ('high' vs. 'low') and quantified habitat features: canopy openness, water flow, water depth and stream width. We then used geometric morphometrics (Rohlf & Marcus, 1993) to quantify the size and shape of 715 females and 620 males from these sites. The parallel and independent aspects of population divergence were then assessed based on two complementary approaches. On the one hand, we used path models to determine the significance of factors influencing among-site variation in size and shape. On the other hand, we partitioned the total variation in size and shape (e.g. Langerhans & DeWitt, 2004) into (1) the effects of sex that are shared across environmental gradients, (2) the effects of environmental gradients that are shared between the sexes (parallel population divergence) and (3) the effects of environmental gradients that are unique to each sex (independent population divergence).

Materials and methods

Sampling sites

Sampling took place in the Marianne and Paria watersheds, both located on the north slope of the Northern Range Mountains of Trinidad (Fig. 1). These rivers are similar in many respects, which we confirmed by comparing site means for canopy openness, water flow, water depth and stream width (two-sample *t*-tests $P > 0.130$ for all). The only substantial difference between the watersheds is that major predatory fishes are absent from the entire Paria – because of a large barrier waterfall near the ocean. In the Marianne, major predatory fishes are present in the lower reaches, but are excluded from the upper reaches owing to barrier waterfalls on the tributaries (Fig. 1). Low-predation sites in both watersheds contain killifish, *Rivulus hartii*, and freshwater prawns, *Macrobrachium faustinum* and *Macrobrachium crenulatum* (Endler, 1983; Reznick *et al.*, 1996b; Millar *et al.*, in press). High-predation sites in the Marianne contain killifish, prawns, up to three species of gobies (*Eleotris pisonis*, *Gobiomorus dormitor*, *Dormitator maculatus*), and the mountain mullet (*Agonostomus monticola*) (Endler, 1983; Reznick *et al.*, 1996b).

Guppies were sampled near the end of the dry season (March) from discrete sites in each watershed (Fig. 1). At each site in 2002 and 2003, hand-held butterfly nets were used to capture 20 males and 20 females across multiple locations in multiple pools. The fish were killed with an overdose of tricaine methanesulphonate (MS-222), placed on a standard background, and photographed with a digital camera (Fig. 2). All photographs were screened for high image quality, which retained a

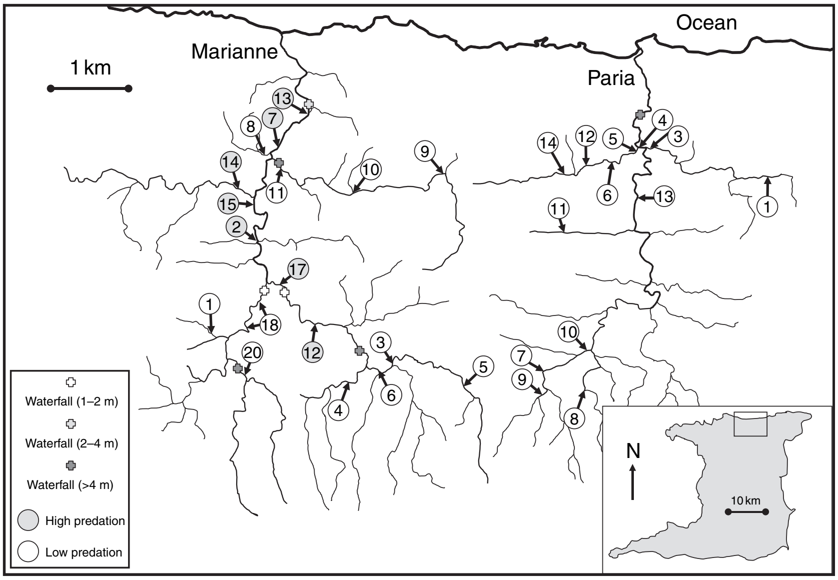

Fig. 1 Map of the Marianne and Paria watersheds, representing an area corresponding to the box in the inset map of Trinidad. Site numbers reflect the chronological order of sampling within each watershed, and match those in related publications (Millar *et al.*, in press; Crispo *et al.*, in press). Missing site numbers (16 and 19 in the Marianne and 2 in the Paria) reflect sites that could not be included in the present analysis because guppies were sampled in only 1 year. Males were not analysed for sites 9 and 20 in the Marianne, and sites 11 and 13 in the Paria (see text). Site 18 in the Marianne was sampled in slightly different locations in the two years, as indicated with arrows. Additional waterfalls are present on tributaries but are not shown because they are not between any of our sampling sites.

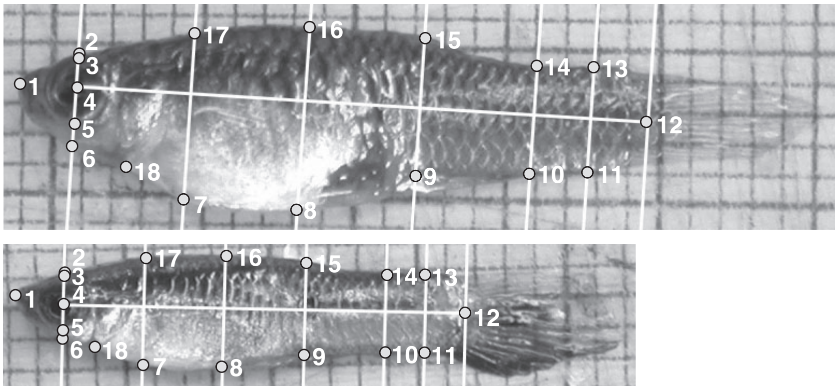

Fig. 2 Typical female (top) and male (bottom) guppies used in our analysis. The background (small squares are 1 mm^2) was used to standardize landmark distances to the same absolute scale across all images. The overlaid grid and points illustrate landmarks used for geometric morphometrics (see text for details).

total of 715 females (368 in 2002, 347 in 2003) and 620 males (319 in 2002, 301 in 2003). The females were from 18 sites in the Marianne and 13 sites in the Paria, and the males were from 16 sites in the Marianne and 11 sites in the Paria (Fig. 1). This difference in site numbers arose because males were smaller and therefore required higher image quality. Note that we have also analysed these same fish for male colour in both watersheds (Millar *et al.*, 2006) and gene flow in the Marianne (Crispo *et al.*, 2006).

Geometric morphometrics

A standardized grid was superimposed onto the digital image of each fish (e.g. Langerhans *et al.*, 2003). This grid was formed by a horizontal line from the centre of the eye to the end of the caudal peduncle, with perpendicular vertical lines dividing the fish into five sections of equal length (Fig. 2). The caudal section was further subdivided into two sections of equal length (e.g. Alexander & Breden, 2004). TPSDIG (Rohlf, 2003) was then used to place landmarks on each digital image. Six of the landmarks were clearly defined homologous points (Fig. 2): tip of snout (landmark 1), top of eye orbit (3), middle of eye orbit (4), bottom of eye orbit (5), end of caudal peduncle (12) and an inflection point on the fish outline (18). Fin insertions were not used for landmarks because this would have required pinning out individual fins, which would have drastically reduced sample sizes. Instead, the remaining landmarks (2, 6–11 and 13–17) were placed where the vertical lines of the standardized grid intersected the outline of the fish. This grid method captures aspects of body shape that would be missed by widely spaced homologous points, but is relatively insensitive to fin positions.

The fish were analysed in random order by one of the authors (MLK) who did not know the site of origin. The background in each photograph (Fig. 2) was used to standardized landmark distances to the same absolute scale across all images. Repeatability was determined by placing landmarks onto the same 10 females on four separate occassions . Distances were measured between a subset of these landmarks and compared among occassions (Pearson's correlation coefficients). These correlations ($r^2 = 0.808$–0.999) were high, indicating good repeatability.

The following analyses were performed separately for three different data sets: males only, females only and males and females combined. TPSREGR (Rohlf, 2003) was used to rotate, translate and scale landmark coordinates using generalized least squares superimposition (Bookstein *et al.*, 1985; Bookstein, 1991; Marcus *et al.*, 1996). TPSREGR outputs scores for each fish that represent two general types of shape variation: affine (two 'uniform components' that describe common covariation in the x- or y-planes) and nonaffine (a series of 'partial warps' that describe local shape deformations). In addition, we used TPSRELW (Rohlf, 2003) to extract scores for each fish on a series of relative warp (RW) functions, which are equivalent to principal component axes derived from the partial warps and uniform components.

Partial warps and RWs do not include any isometric effects of body size, but may include allometric effects (evident as correlations between RW scores and body size). We estimated the body size of each fish as its centroid size (Bookstein, 1986; Monteiro *et al.*, 2002) which is the square root of the sum of the squared distances from each landmark to the location on the fish that minimizes that sum (i.e. the fish's centroid). Centroid size was then included as a covariate in body shape analyses, thus ensuring both isometric and allometric effects of body size were absent from analyses.

Environmental gradients

Each site was characterized as 'high predation' or 'low predation' based on the presence/absence of predatory fishes, as well as the size of down-stream barrier waterfalls (personal observations in 2002–2005; Endler, 1983; Reznick *et al.*, 1996b). These sources of information were always consistent with each other. Although this simple 'high' vs. 'low' predation dichotomy is coarse, it would be prohibitively difficult to obtain quantitative estimates of predation intensity for a large number of sites. Fortunately, the simple high- vs. low-predation dichotomy has effectively revealed adaptation in many other studies (reviews: Endler, 1995; Reznick & Travis, 1996; Houde, 1997; Magurran, 1998).

Habitat features were measured in March 2003 (for details see Millar *et al.*, 2006). At each site, we established 6–11 evenly spaced transects along the area from which guppies were collected: 100–200 m at 25 sites, 50 m at 5 sites and 25 m at 1 site. At each transect, the wetted width of the channel was measured. At each of three equidistant points across the channel at each transect (18–33 points per site), water depth and flow were measured, the latter with a Swoffer model 2100 flow meter (impeller positioned 60% of the distance from the substrate to the surface). Canopy openness was measured with a concave spherical densiometer (Lemmon, 1957). Four readings, one facing in each cardinal direction, were taken in the middle of the stream at five equidistant locations between the first and last transect at each site. Site means were calculated for each habitat feature and used in subsequent analyses.

Statistical analyses

Analyses were conducted in SPSS VERSION 11.0.1, unless otherwise noted. A watershed effect was ignored in all analyses (1) to increase degrees of freedom, (2) because habitat features did not differ between watersheds (see 'Sampling sites') and (3) because both predation and watershed could not be include in the same analysis (the Paria was entirely low predation). Three complementary analyses were performed as summarized here and detailed later. First (*Effects of sex, year and site*), we used data for individuals to determine whether size or shape differed (1) between the sexes, which would precipitate sex-specific analyses; (2) between the years, which would precipitate year-specific analyses or (3) among the sites, which would justify analyses of environmental gradients. Second (*Effects of environmental gradients*), we used site means to statistically infer how predation and habitat features influenced spatial variation in size and shape. Third (*Partitioning shape variation*), we used data for all individuals to partition the total variance in size and shape into that explained by various predictor variables (sex, year and environmental gradients), as well as by interactions between sex and each predictor variable. Each analysis used scores extracted only for the fish in that analysis: i.e. all fish combined, females only, or males only.

Effects of sex, year and site

Body (centroid) size was first analysed in a three-way ANOVA that included effects of sex (fixed), year (random) and site (fixed; all 27 sites with data for both sexes), as well as all possible interactions. Sex often interacted with site and year (see Results), which precipitated sex-specific two-way ANOVAS (all available sites; 27 for males, 31 for females). For body shape, analyses were identical to the above, except that (1) centroid size was included as a covariate (i.e. ANCOVA) and (2) separate ANCOVAS were performed for each RW. Only the first three RWs were examined because these could be readily interpreted (see Results), and because they explained most of the variation (32.7, 18.6 and 14.9% for females; 30.4, 26.8 and 12.1% for males).

Effects of environmental gradients

We first examined the extent to which among-site variation in mean body (centroid) size and shape (RW1–3) was consistent between years (2002 vs. 2003 values in Pearson's correlations). We next used sex/year-specific path models (AMOS, VERSION 5.0.1) to test for the direct effects of predation and each habitat feature on variation in site means. Nonsignificant correlations among predictor variables (Fig. 3) were excluded, which reduced the number of parameters to be estimated. The models for RW1–3 included centroid size as a covariate, while excluding interactions between centroid size and the other predictor variables.

Partitioning shape variation

The relative contribution of each factor or interaction to the total variation in size and shape was compared based on effect sizes (partial η^2). Partial η^2 values represent components of partial variance [$SS_{effect}/(SS_{effect} + SS_{error})$], and so will not sum to unity (see Langerhans & DeWitt, 2004). In these analyses (JMP, VERSION 4.0.3), response variables were centroid size (for the body size ANCOVA) or all principle warps and uniform components (for the body shape MANCOVA).

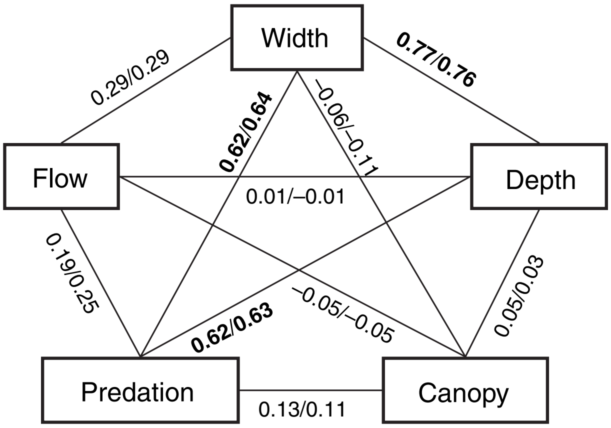

Fig. 3 Pearson's correlation coefficients among habitat features based on site means. Different numbers of sites for males and females necessitated coefficients for each (shown as female/male). Significant correlations are shown in bold. Nonsignificant correlations were excluded from the path models.

Predictor variables included (1) main effects of sex, year, predation, canopy openness, water flow, water depth and stream width; (2) two-way interactions between sex and each main effect, and between year and predation, and (3) the three-way interaction between sex, year and predation. The MANCOVA for body shape also included centroid size as a covariate, while excluding interactions with other predictor variables. Although additional interactions could have been included, the above set encompasses the hypotheses of interest with respect to parallelism of the sexes. The above analyses were then repeated for males and females separately. Finally, the body shape MANCOVAS were used to generate scores for each individual along canonical variates optimized with respect to predation and each habitat feature. Shape variation associated with these environmental gradients was then visualized by using TPSREGR to generate thin-plate spline transformations for the extremes of each canonical variate (e.g. Langerhans & DeWitt, 2004).

Results

Effects of sex, year and site

Body (centroid) size was influenced by sex (females were larger; $F_{1,1} = 146.91$, $P = 0.052$), site ($F_{26,26} = 22.55$, $P < 0.001$), the sex-by-site interaction ($F_{25,25} = 3.84$, $P = 0.001$), the sex-by-year interaction ($F_{1,25.6} = 6.15$, $P = 0.020$), and the three-way interaction ($F_{25,1107} = 1.69$, $P = 0.019$); but was not influenced by year ($F_{1,0.94} = 3.15$, $P = 0.340$) or the site-by-year interaction ($F_{26,24.8} = 0.81$, $P = 0.698$). When analysing females alone, body size was influenced by year ($F_{1,31.6} = 24.50$, $P < 0.001$), site ($F_{30,30} = 8.81$, $P < 0.001$), and the site-by-year interaction ($F_{30,653} = 1.83$, $P = 0.005$). When analysing males alone, body size was influenced by site ($F_{26,26} = 8.19$, $P < 0.001$) and the site-by-year interaction ($F_{26,566} = 2.29$, $P < 0.001$), and was marginally influenced by year ($F_{1,26.9} = 3.70$, $P = 0.066$).

Body shape variation as captured by RW1–3 is illustrated in Fig. 4 and described later. RW1 was influenced by sex ($F_{1,1.4} = 75.17$, $P = 0.032$), centroid size ($F_{1,1106} = 20.40$, $P < 0.001$), and the three-way interaction ($F_{25,1106} = 1.96$, $P = 0.003$). It was marginally influenced by site ($F_{26,26.2} = 1.83$, $P = 0.064$), the sex-by-year interaction ($F_{1,25.7} = 3.47$, $P = 0.074$), and the site-by-year interaction ($F_{26,24.8} = 1.86$, $P = 0.063$). RW1 was not influenced by year ($F_{1,1.5} = 0.10$, $P > 0.130$) or the sex-by-site interaction ($F_{25,25.1} = 1.00$, $P = 0.496$). RW2 was influenced by site ($F_{26,26.3} = 1.97$, $P = 0.044$), centroid size ($F_{1,1106} = 20.30$, $P < 0.001$), the sex-by-year interaction ($F_{1,26} = 11.13$, $P = 0.003$) and the site-by-year interaction ($F_{26,24.8} = 2.24$, $P = 0.024$). It was marginally influenced by the sex-by-site interaction ($F_{25,25.1} = 1.88$, $P = 0.060$) and the three-way interaction ($F_{25,1106} = 1.44$, $P = 0.076$). RW2 was not influenced by sex ($F_{1,1.2} = 4.42$, $P = 0.252$) or year ($F_{1,1.2} = 13.44$, $P = 0.133$). RW3 was influenced by centroid size ($F_{1,1106} = 96.28$, $P < 0.001$), the sex-by-year interaction ($F_{1,26.4} = 7.18$, $P = 0.013$) and the site-by-year interaction ($F_{26,24.7} = 4.40$, $P < 0.001$). It was not influenced by sex ($F_{1,1.4} = 0.08$, $P = 0.819$), year ($F_{1,2.1} = 1.23$, $P = 0.379$), site ($F_{26,26.2} = 1.26$, $P = 0.280$), the sex-by-site interaction ($F_{25,25.2} = 0.68$, $P = 0.832$), or the three-way interaction ($F_{25,1106} = 1.05$, $P = 0.402$). Main effects in these analyses are difficult to interpret owing to ubiquity of interactions. We therefore next analysed males and females separately.

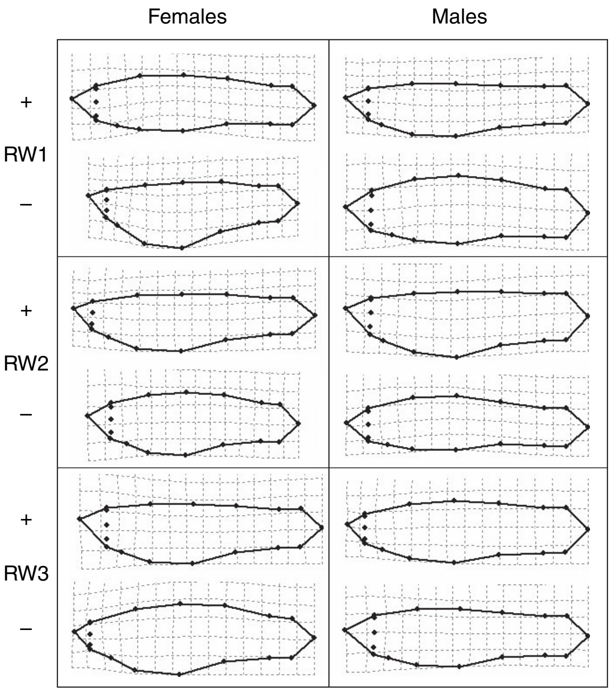

Fig. 4 Shape variation captured by the first three RWs (RW1–3) for females (left-hand panels) and males (right-hand panels). Shown are thin-plate spline transformations from TPSREGR that depict extremes of observed variation. Note that RWs were extracted separately for each sex and a particular RW is therefore not directly comparable between sexes.

When analysing females alone, RW1 was influenced by the site-by-year interaction ($F_{30,652} = 28.87$, $P < 0.001$), but not by the main effects of year ($F_{1,32.1} = 0.015$, $P = 0.903$) or site ($F_{30,30.2} = 1.10$, $P = 0.399$). RW2 was influenced by year ($F_{1,33.8} = 31.95$, $P < 0.001$), site ($F_{30,30.3} = 3.54$, $P < 0.001$) and the site-by-year interaction ($F_{30,652} = 1.84$, $P = 0.005$). RW3 was influenced by year ($F_{1,32} = 6.52$, $P = 0.016$) and the site-by-year interaction ($F_{30,652} = 3.52$, $P < 0.001$), but not by the main effect of site ($F_{30,30.2} = 1.27$, $P = 0.260$). In these ANCOVAS, females with larger centroid sizes had smaller values for RW1 ($F_{1,652} = 28.87$, $P < 0.001$) and RW3 ($F_{1,652} = 165.31$, $P < 0.001$), and larger values for RW2 ($F_{1,652} = 19.61$, $P < 0.001$).

When analysing males alone, RW1 was influenced by year ($F_{1,27} = 77.86$, $P < 0.001$) and the site-by-year interaction ($F_{26,565} = 2.57$, $P < 0.001$), but not by the main effect of site ($F_{26,26.3} = 1.62$, $P = 0.111$). RW2 was influenced by site ($F_{26,26.4} = 1.95$, $P = 0.046$) and the site-by-year interaction ($F_{26,565} = 2.39$, $P < 0.001$), but was not influenced by the main effect of year ($F_{1,27.1} = 4.40$, $P < 0.224$). RW3 was influenced by year ($F_{1,27} = 19.61$, $P < 0.001$), site ($F_{26,26.3} = 3.68$, $P = 0.001$), and the site-by-year interaction ($F_{26,565} = 2.57$, $P < 0.001$). In these ANCOVAS, males with larger centroid sizes had larger values for RW1 ($F_{1,565} = 39.81$, $P < 0.001$) and RW3 ($F_{1,565} = 31.95$, $P < 0.001$). Centroid size was not correlated with RW2 ($F_{1,565} = 1.48$, $P = 0.224$). Owing to site-by-year interactions in these sex-specific analyses, subsequent path models were both sex- and year-specific.

Effects of environmental gradients

For body (centroid) size, site means were highly correlated between years for females (Pearson's $r = 0.822$, $n = 31$, $P < 0.001$) and males ($r = 0.758$, $n = 27$, $P < 0.001$). Body size for both sexes was greater at sites with a more open canopy and sometimes greater at sites with higher flow (Table 1). No other environmental gradients had significant effects (Table 1).

For female body shape, site means ($n = 31$) were correlated between years for RW2 ($r = 0.513$, $P = 0.003$) and RW3 ($r = 0.551$, $P = 0.001$), and marginally correlated for RW1 ($r = 0.325$, $P = 0.075$) (Fig. 5). Path models explained substantial amounts of the among-site variation in mean RW scores (53–62%, except for one case at 20%), but the specific effects of a given predictor variable often differed between years (Table 1). The strongest and most consistent effects, although not always statistically significant, were that (1) sites with a more open canopy had females with smaller heads, more distended abdomens, and shorter caudal peduncles (RW1, Fig. 4); (2) sites with higher flow had females with smaller heads, shallower anterior bodies, and longer caudal peduncles (RW2, Fig. 4) and (3) high-predation sites and sites with higher flow had females with smaller heads and deeper bodies, primarily owing to the height of the back (RW3, Fig. 4).

For male body shape, site means ($n = 27$) were correlated between years for RW3 ($r = 0.665$, $P < 0.001$), marginally correlated for RW2 ($r = 0.345$, $P = 0.078$), and not correlated for RW1 ($r = 0.105$, $P = 0.603$) (Fig. 5). Path models explained low (13%) to high (85%) amounts of the among site variation in mean RW scores (Table 1). The strongest and most consistent effects, although not always statistically significant, were that (1) high-predation sites had males with deeper bodies, primarily owing to the height of the back and the depth of the caudal peduncle (RW1, Fig. 4); (2) sites with a narrower channel and higher flow had males with

Table 1 Effects of predation and habitat features on site means for body size (centroid size) and body shape (RW1–3, extracted separately for each sex).

	r^2	Predation	Width	Depth	Flow	Canopy	Centroid size
Centroid size							
Females 2002	0.41	–0.24	–0.01	–0.11	0.28**	0.49****	–
Females 2003	0.32	0.02	–0.19	–0.11	0.16	0.47***	–
Males 2002	0.38	–0.09	–0.11	–0.11	0.28*	0.47***	–
Males 2003	0.53	–0.33	0.19	–0.13	0.44***	0.49****	–
RW1							
Females 2002	0.55	–0.04	0.43**	–0.08	–0.15	–0.19	–0.61****
Females 2003	0.58	0.45***	–0.40**	0.40**	–0.02	–0.38***	–0.40****
Males 2002	0.13	–0.14	–0.08	0.11	0.15	–0.19	0.23
Males 2003	0.42	–0.62***	0.46*	–0.22	0.25*	0.09	–0.24
RW2							
Females 2002	0.53	0.28*	0.28	–0.02	0.29**	–0.1	0.44****
Females 2003	0.20	0.34	–0.12	0.06	0.29*	–0.07	–0.13
Males 2002	0.46	0.29	–0.53**	0.25	0.33**	0.12	0.46***
Males 2003	0.42	–0.15	–0.12	–0.42*	0.12	0.15	0.03
RW3							
Females 2002	0.60	–0.14	–0.03	0.05	–0.13	0.02	–0.75****
Females 2003	0.62	–0.33**	0.35*	–0.2	–0.28**	–0.19*	–0.63****
Males 2002	0.85	0.34***	–0.26**	0.26**	0.36****	–0.04	0.76****
Males 2003	0.74	0.59****	–0.57****	0.26	0.26***	0.12	0.61****

Shown are r^2 values for each year/sex-specific path model, along with standardized partial regression coefficients for each predictor variable. Samples sizes are $n = 31$ sites for females and $n = 27$ sites for males.

$^*P < 0.10$, $^{**}P < 0.05$, $^{***}P < 0.01$, $^{****}P \leq 0.001$.

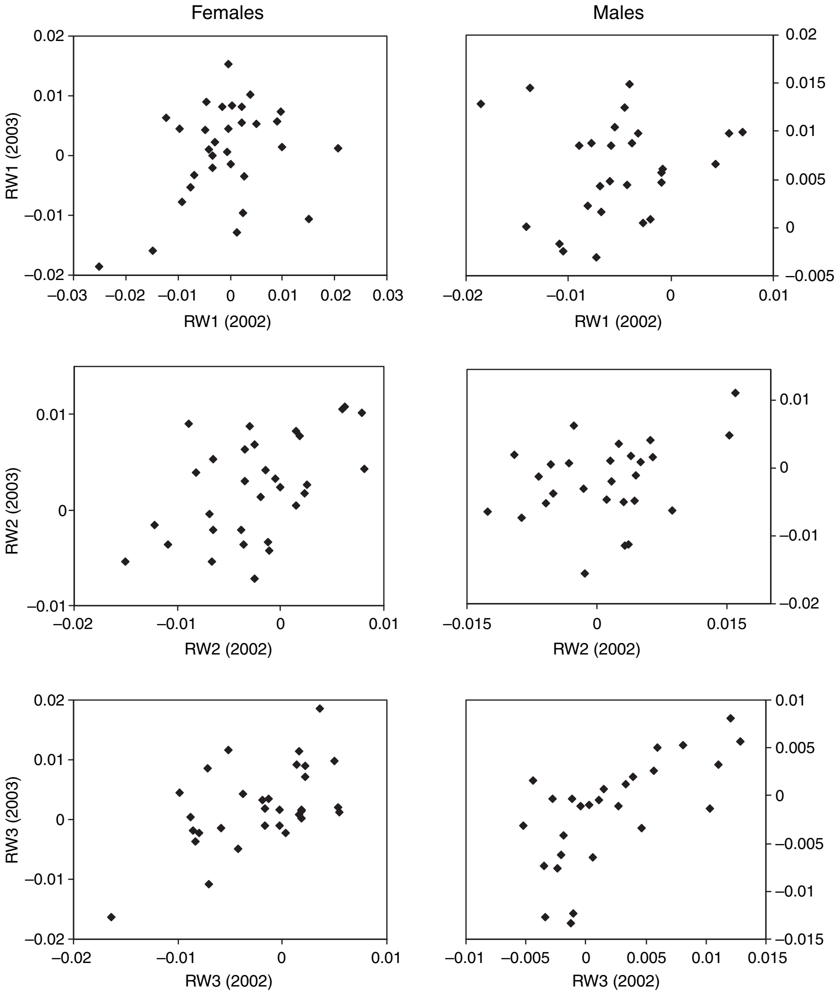

Fig. 5 Inter-annual variation in site means for RW scores for females (left-hand panels) and males (right-hand panels). Shown are correlations between site means in 2002 vs. 2003.

deeper bodies, primarily owing to the depth of the abdomen and the caudal peduncle (RW2, Fig. 4) and (3) high-predation sites and sites with a narrower channel and higher flow had males with smaller heads and deeper bodies, primarily in the caudal area (RW3, Fig. 4).

Partitioning shape variation

For body size, sex was the most important predictor variable (Table 2), followed by canopy openness and water depth, which respectively explained 29.1 and 11.2% as much of the partial variance as did the main effect of sex. Interactions between sex and environmental gradients were weak and often nonsignificant. When the sexes were analysed separately, body size for each was primarily influenced by canopy openness and, to a lesser extent, by water depth and stream width (Table 3).

For body shape, sex was the most important predictor variable (Table 2), followed by year and centroid size, which respectively explained 80.1 and 62.3% as much of the partial variance as did the main effect of sex. The most important environmental gradients in parallelism of the sexes were flow (24.3% as much as sex), canopy openness (18.2% as much as sex), and predation (17.5% as much as sex). Significant independence of the sexes was evident in interactions between sex and water depth (78.2% as much as the main effect of depth), sex and predation (58.3% as much as predation), and sex and flow (19.8% as much as flow). When the sexes were analysed separately, body shape was primarily influenced by year and centroid size, followed by lesser effects of canopy openness and flow for females, and predation and flow for males (Table 3).

Thin-plate spline visualizations based on canonical variates further illustrated both parallel and independent responses of males and females to environmental gradients. The gradient of most *a priori* interest was predation. Here, the parallel response to high predation was smaller heads, shallower anterior bodies, and deeper caudal peduncles (Fig. 6). When the sexes were analysed separately, high-predation sites had (1) males and females with smaller heads and deeper bodies owing to higher

Table 2 Statistical partitioning of the total variance in body size (centroid size) and body shape (all partial warps and uniform components).

Factor	Body size		Body shape	
	Partial variance	Relative variance	Partial variance	Relative variance
Sex	34.0****	100	58.6****	100
Year	1.4****	4.3	47.0****	80.1
Predation	0.2*	0.6	10.3****	17.5
Width	1.6****	4.6	6.2****	10.6
Depth	3.8****	11.2	4.6****	7.8
Flow	0.6***	1.7	14.2****	24.3
Canopy	9.9****	29.1	10.7****	18.2
Centroid size	–	–	36.5****	62.3
Sex × centroid size	–	–	9.6****	16.3
Sex × year	0.5**	1.5	14.5****	24.7
Sex × predation	0.0	0.0	6.0****	10.2
Sex × width	0.1	0.2	2.4	4.2
Sex × depth	0.4**	1.2	3.6**	6.1
Sex × flow	0.0	0.0	2.8	4.8
Sex × canopy	1.6****	4.8	5.4****	9.1
Predation × year	0.2	0.6	4.4****	7.5
Predation × sex × year	0.2	0.5	1.9****	3.3

'Partial variance' gives the percentage of the partial variance explained by each factor or interaction (partial η^2). 'Relative variance' scales the partial variance to that for the most important factor (sex). The degrees of freedom for all factors and interactions are 1, 1319 for body size and 32, 1286 for body shape.
$*P < 0.10$, $**P < 0.05$, $***P < 0.01$, $****P \leq 0.001$.

backs and (2) males (but not females) with shorter and deeper caudal peduncles (Fig. 6). For the other environmental gradients, we concentrate on the sex-specific analyses because these were more revealing. Sites with a more open canopy had (1) males and females with smaller heads and deeper/shorter caudal peduncles (less so for females) and (2) females (but not males) with more distended abdomens (Fig. 7). Sites with higher flow had (1) males and females with smaller heads and deeper caudal peduncles (less so for females), (2) females (but not males) with more distended abdomens and (3) males (but not females) with shorter caudal peduncles (Fig. 7). Sites with deeper water had males and females with shallower caudal peduncles, females (but not males) with smaller heads and males (but not females) with longer and shallower caudal peduncles (Fig. 7). Sites with a wider channel had males and females with larger heads (less so for males), shallower bodies along their entire length and longer caudal peduncles (Fig. 7).

Discussion

Most of the variation in guppy size and shape was the result of differences between males and females (Table 2; Fig. 2). For body size, environmental gradients led to parallel population divergence; both sexes were larger at sites with a more open canopy and with higher flow (Tables 1–3). For body shape, parallelism was much weaker. Here, the most important effects (after sex) were sampling year and body size (Tables 2 and 3). The effect of year highlights the importance of temporal replication in studies of body shape, and the effect of body size indicates allometry (which was then removed by including body size as a covariate). Body shape was influenced to a lesser degree by predation and habitat features (Tables 1–3). Males and females showed some shared (parallel) responses to these environmental gradients, but interactions with sex (independence) were nearly as important (Table 2). Indeed, separate analyses of males and females revealed substantial differences in their responses to environmental gradients (Table 1; Fig. 7). We conclude that sex has by far the greatest effect on guppy size and shape, and that sex influences shape divergence along environmental gradients. At present, the relative contributions of genetic divergence and phenotypic plasticity to this variation are unknown.

Table 3 Sex-specific partitioning of variance in body size (centroid size) and body shape (all partial warps and uniform components).

Factor	Body size (females)		Body size (males)		Body shape (females)		Body shape (males)	
	Partial variance	Relative variance	Partial variance	Relative variance	Partial variance	Relative variance	Partial variance	Relative variance
Year	2.2****	20.0	0.8**	6.7	45.7****	77.2	58.6****	100
Predation	0.2	1.9	0.4	3.3	10.3****	17.4	17.8****	30.4
Width	1.3***	12.0	3.2****	27.5	6.9**	11.7	12.1****	20.7
Depth	4.2****	37.0	5.2****	45.3	8.4***	14.3	7.6**	12.9
Flow	0.5*	4.2	1.2***	10.7	17.2****	29.0	14.5****	24.8
Canopy	11.3****	100	11.5****	100	19.5****	33.0	9.3***	15.9
Centroid size	–	–	–	–	59.2****	100	36.5****	62.2
Predation × year	0.4*	40	0.0	0.0	4.8	8.1	10.9****	18.6

'Partial variance' gives the percentage of the partial variance explained by each factor or interaction (i.e. partial η^2). 'Relative variance' scales the partial variance to that for the most important factor. The degrees of freedom for all factors and interactions are 1,707 for female body size, 1,612 for male body size, 32,675 for female body shape, and 32,580 for male body shape.
$*P < 0.10$, $**P < 0.05$, $***P < 0.01$, $****P \leq 0.001$.

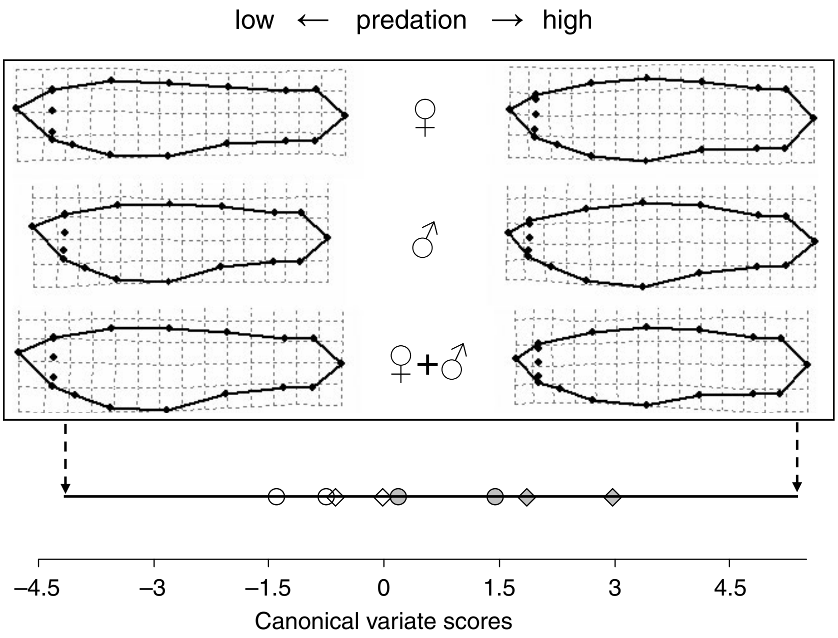

Fig. 6 Effects of predation on body shape. The axis at the bottom shows the canonical variate optimized with respect to predation from the MANCOVA with both sexes included. Points above that axis are averages for each combination of sex (open symbols for females; grey symbols for males), predation (circles for low-predation; diamonds for high-predation), and year (specific years not labelled). The ends of the line passing through these averages correspond to the score for the individual whose shape was most low predation (left terminus) or whose shape was most high predation (right terminus). Above this line, the bottom pair of images shows thin-plate spline transformations depicting body shapes at the observed extremes of the canonical variate. The top two pairs of images show the corresponding extremes when males and females are analysed separately.

Predation

Predation did not influence guppy body size (Tables 1–3). In general, growth of females is indeterminant whereas that of males is determinant. As a result, among-site variation reflects terminal size for males and a combination of age, growth and mortality for females. Adult size distributions in a given population can therefore depend on the relative strength of several opposing factors (Rodd & Reznick, 1997). Relative to guppies at low-predation sites, those at high-predation sites grow faster (Reznick *et al.*, 2001), mature younger and smaller (Reznick & Endler, 1982; Reznick *et al.*, 1996b), have higher mortality (Reznick *et al.*, 1996a), and have larger asymptotic sizes (Reznick *et al.*, 2001). Faster growth and larger asymptotic sizes should increase average adult body size, whereas earlier maturity and higher mortality should decrease average size. Our results suggest that the net outcome can be no difference in average size for either sex. Other studies have sometimes found average size differences between predation regimes, but this may be due in part to covariation between predation and productivity (Reznick *et al.*, 2001). Our study removed at least some of this covariation by accounting for habitat features, particularly canopy openness, that influence productivity.

Here we attempt a direct comparison between parallel evolution of the sexes and of related species. Specifically, the shared (parallel) and unique (independent) aspects of body shape divergence between high- and low-predation environments have been quantified for males vs. females in guppies (present study) and for males of three poeciliid species (Langerhans & DeWitt, 2004). Based on the same variance partitioning techniques, males and females within a species show as much independence in their response to predation as do males of different species. First, the shared response of the sexes to predation was weaker in relation to the overall effect of sex (17.5% as much of the partial variance) than was the shared response of the species in relation to the overall effect of species (47.9% as much of the partial variance). Second, the interaction between sex and predation in guppies was as strong in relation to their shared response (58.3% as much of the partial variance) as was the interaction between species and predation in relation to their shared response (61.0% as much of the partial variance). The equivalent or greater independence of sexes than of species is remarkable given that males and females in the present study came from the same physical locations, whereas the different species in Langerhans & DeWitt (2004) came from different locations having different predator species and (presumably) different habitat features. We conclude that sex can be at least as important as species in modifying body shape divergence in response to predation.

When considering males and females separately, predation was the most important environmental gradient for male shape, but only the third most important environmental gradient for female shape (Table 3). This result, in combination with studies showing higher predation on males than on females (Reznick *et al.*, 1996a), suggests that divergent selection between predation environments may act more strongly on male shape than on female shape. We therefore suggest that deviations from parallelism of the sexes in guppies reflect sex-specific divergent selection. Deviations from parallelism

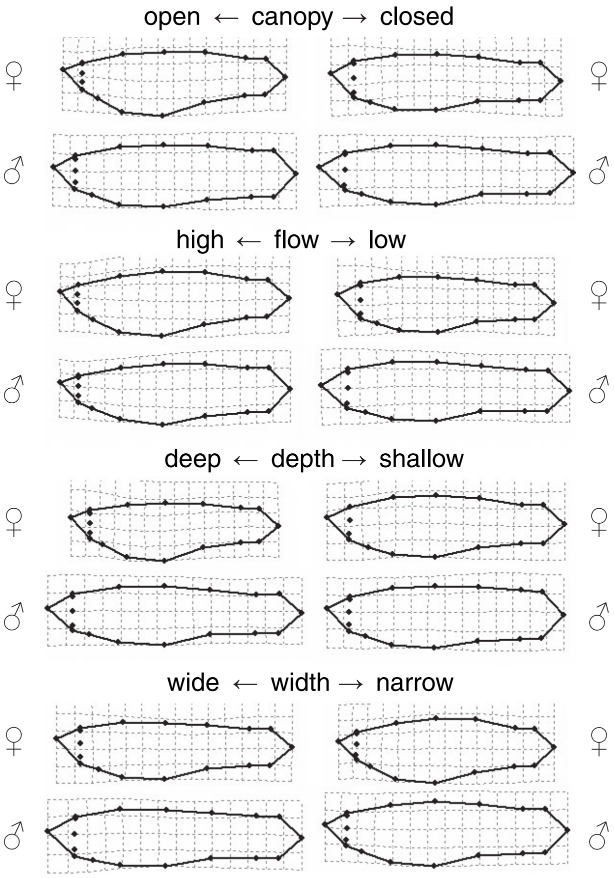

Fig. 7 Effects of habitat features on sex-specific body shape. Each pair of images shows thin-plate spline transformations depicting body shapes at the observed extremes of each canonical variate from sex-specific MANCOVAS.

might also reflect sex-biased dispersal, sex-specific plasticity and sexual niche partitioning (see introduction). Among these possibilities, sex-biased dispersal seems unlikely to cause the weaker divergence of females given that dispersal in guppies appears male-biased (Croft *et al.*, 2003). The other alternatives cannot be assessed at present.

For females, a point of interest was that abdomen distension did not differ appreciably between high- and low-predation environments (Fig. 6). This lack of divergence may reflect constraints on optimization. On the one hand, distended abdomens owing to pregnancy cause reduced swimming ability (Ghalambor *et al.*, 2004), which can influence predator avoidance (Walker *et al.*, 2005). Females at high-predation sites might therefore be selected for less distended abdomens. On the other hand, females from high-predation sites are selected for increased reproductive effort (Reznick & Endler, 1982; Reznick *et al.*, 1996b; Reznick & Bryga, 1996), which causes greater abdomen distension (Ghalambor *et al.*, 2004). The observed lack of divergence in abdomen distension suggests that high-predation females may have discovered some way to increase reproductive effort without appreciably compromising body shape.

For males, high-predation sites had fish with smaller heads, deeper bodies and deeper/shorter caudal peduncles (Fig. 6). Smaller heads and deeper caudal peduncles are consistent with previous work (Langerhans & DeWitt, 2004; Langerhans *et al.*, 2004) and may reflect selection for fast-start escape responses. Specifically, a deeper caudal peduncle should increase thrust and a smaller head should decrease drag (Langerhans *et al.*, 2004). Less consistent with previous work are the deeper bodies and shorter caudal peduncles in high-predation environments (Fig. 6). One reason for the difference between studies may be that we studied guppies on the North Slope of Trinidad, whereas previous work focused on the South Slope. The species of predatory fishes differ between the slopes (Endler, 1983; Reznick & Bryga, 1996; Reznick *et al.*, 1996b), and so too might their selective effects. Previous work has shown broad parallelism between the slopes in the effects of predation on life history and colour, but some differences are still apparent (Endler, 1980; Reznick & Bryga, 1996; Reznick *et al.*, 1996b; Millar *et al.*, in press). Thus, even if overall mortality rates vary in parallel on the two slopes, differences in the specific predator species might lead to different selective effects.

Other environmental gradients

Canopy openness was the most important environmental gradient for body size in both sexes; fish at sites with a more open canopy were larger (Tables 1 and 3). This trend makes sense given that open canopy sites have higher productivity, which increases guppy growth (Grether *et al.*, 2001; Reznick *et al.*, 2001). Much of this variation probably reflects plasticity (Grether *et al.*, 2001), but genetic divergence in growth rates may also occur (Arendt & Reznick, 2005). Canopy openness was also the most important gradient for female body shape (Tables 1 and 3); females at sites with a more open canopy had more distended abdomens (Fig. 7). This trend may reflect increased reproductive effort at sites with higher productivity. Several observations support this contention. First, increased feeding rates in the laboratory lead to increased reproductive effort (e.g. Reznick & Bryga, 1996). Second, the mean number of embryos is positively correlated with canopy openness among our study sites (linear regression, $n = 31$ sites, $P = 0.015$, $r^2 = 0.187$; D. Reznick, A. Hendry and M. Kinnison, unpublished data). The influence of canopy openness on female shape might therefore reflect a plastic effect of food availability on reproductive effort, or perhaps even adaptive genetic divergence in response to variation in productivity.

Water flow was the second most important environmental gradient for both sexes (Tables 1 and 3). At high flow sites, males and, to a lesser extent, females had smaller heads and deeper caudal peduncles, females (but not males) had more distended abdomens, and males (but not females) had shorter caudal peduncles (Fig. 7). Deeper caudal peduncles and smaller heads may be adaptive because these traits increase thrust and reduce drag (Walker, 1997; Langerhans *et al.*, 2004). Accordingly, guppies from sites with faster water have higher critical swimming speeds (Nicoletto & Kodric-Brown, 1999). In contrast, greater abdomen distension at high flow sites might seem counterintuitive because fast water is often associated with streamlining (e.g. Taylor & McPhail, 1985; McLaughlin & Grant, 1994; Hendry *et al.*, 2000; Brinsmead & Fox, 2002; Kinnison *et al.*, 2003; Langerhans *et al.*, 2003). And yet, some fish species manifest deeper bodies in faster water (Hendry & Taylor, 2004) whereas others show no relationship between body depth and flow (McGuigan *et al.*, 2003; Neat *et al.*, 2003). We suggest that the effects of flow on body shape depend critically on how fish forage and maintain their position (see also Walker, 1997; Pakkasma & Piironen, 2001). In guppies, for example, benthic foraging is more common for females than for males (Magurran, 1998), which may reduce the exposure of females to high flows.

Synthesis

Males and females often exhibit broadly parallel patterns of population divergence along environmental gradients (e.g. Quinn *et al.*, 2001; Alves & Bélo, 2002; Gilchrist *et al.*, 2004). And yet this is not always the case (e.g. Butler & Losos, 2002; Stuart-Fox *et al.*, 2004). As a particularly striking example, male rainbow fish (*Melanotaenia eachamensis*) are deeper bodied in lakes than in streams, but females are deeper bodied in streams than in lakes (McGuigan *et al.*, 2003). Guppies seem to present an intermediate scenario, wherein the sexes show a combination of parallel and independent responses to environmental gradients. Given this variation among species, many more studies are required before broad generalities can be drawn about parallel evolution of the sexes.

Parallel evolution of the sexes seems a profitable area for future research. In particular, more studies should distinguish among alternative hypotheses for deviations from parallelism: sex-specific divergent selection, sex-biased dispersal, sex-specific plasticity or habitat-related sexual niche partitioning (e.g. Butler & Losos, 2002). Similarly, more studies should attempt to determine if strong parallelism is the result of shared selective pressures or genetic or functional constraints. In general, we expect that increasing sexual dimorphism will increase the potential for sex-specific divergent selection and for sex-specific evolutionary responses to that selection.

To us, parallel evolution of the sexes is at least as interesting a topic as the parallel evolution of lineages. One reason is that sex-specific divergence along environmental gradients might influence speciation (Magurran, 1998). In general, adaptive divergence is thought to drive ecological speciation through the origin of assortative mating and selection against migrants or hybrids (Schluter, 2000). Sex-specific phenotypic divergence along environmental gradients might therefore facilitate or constrain the evolution of ecologically dependent reproductive isolation.

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