ORIGINAL PAPER

Sex differences in compensatory and catch-up growth in the mosquitofish *Gambusia holbrooki*

Julianne D. Livingston · Andrew T. Kahn · Michael D. Jennions

Abstract In many taxa, temporary nutritional shortage early in development can favour compensatory strategies that include elevated growth ('compensatory growth') and/or extension of the usual period of development ('catch-up growth') once conditions improve. The net gains from each strategy depend on the extent to which larger body size increases fitness relative to associated costs (e.g. long-term effects on adult performance, or a greater risk of juvenile mortality). These costs and benefits are likely to differ between the sexes due to sex-specific selection. We documented the responses of male and female mosquitofish (*Gambusia holbrooki*) to 3 weeks of low food availability (7–28 days old) that restricted subsequent growth and morphology compared to control fish continuously reared on a high food diet (N = 635 fish total). Neither sex elevated their growth rate immediately after being returned to a normal diet compared to control fish. When measured over the entire period until maturation, however, females showed compensatory growth. Males did not. Both sexes also exhibited catch-up growth but the delay until maturation was significantly longer for males. Despite early growth restriction, both sexes eventually matured at almost the same size as control fish, although males had a significantly smaller gonopodium (a sexually selected trait) than that of control males. Reasons for these sex differences are discussed.

Introduction

Compensatory growth is accelerated growth following a period of reduced growth early in development, usually caused by a temporary dietary restriction (reviews: Metcalfe and

J. D. Livingston · A. T. Kahn · M. D. Jennions (✉)
Evolution, Ecology and Genetics, Research School of Biology, The Australian National University,
Canberra, ACT 0200, Australia
e-mail: michael.jennions@anu.edu.au

Monaghan 2001; Monaghan 2008; Dmitriew 2011). It occurs in many taxa (meta-analysis: Hector and Nakawaga 2012) including humans (e.g. Barrenäs et al. 2005), other mammals (e.g. Therkildsen et al. 2002), fish (e.g. Ali et al. 2003), amphibians (e.g. Squires et al. 2010; Hector et al. 2012), and insects (e.g. Stoks et al. 2006). Compensatory growth enables individuals to reach adulthood at a similar size to animals that experience consistently favourable growing conditions, while minimising any delay to maturation (Ali et al. 2003).

Additionally, growth-deprived individuals sometimes delay maturation until they reach the adult size of normal individuals. Although this phenomenon is often referred to as 'compensatory growth', we follow the recommendation of Hector and Nakawaga (2012) and use the term 'catch-up growth' to differentiate it from true, elevated compensatory growth. Catch-up growth can involve partial compensatory growth if an individual undergoes accelerated growth *and* delays maturity until they reach the same size as normal individuals. Catch-up growth can be adaptive if there are fitness benefits to larger adult size (e.g. predation risk, resource acquisition and defence are often size-dependent; review: Blanckenhorn 2005). There is, however, a cost as delayed maturation increases the risk of juvenile mortality (review: Roff 2002), especially given seasonal increases in the risk of mortality (e.g. Dahl et al. 2012). Compensatory growth, on the other hand, allows individuals to reach optimal adult size without delaying maturation.

Experimental studies of compensatory growth have shown that accelerated growth can incur short- and/or long-term costs (reviews: Monaghan 2008; Dmitriew 2011; see also references in Helle et al. 2012). If there were no costs, there would be no selection for animals to grow at a rate well below the physiological maximum. For example, elevated juvenile growth seems to increase developmental errors and structural instability, and reduce the lipid and energy content of somatic and reproductive tissues (review: Ali et al. 2003). Compensatory growth can still be adaptive, however, if it increases lifetime reproductive success compared to individuals that continue to grow at the normal rate after a period of restricted growth (review: Metcalfe and Monaghan 2001). Similarly, catch-up growth can be adaptive if it increases lifetime reproductive success compared to individuals who mature at the same age as normal individuals (and are hence smaller).

Recent studies have started to investigate sex differences in life history responses to dietary manipulations (e.g. schedules of reproductive effort and lifespan; meta-analyses: Jones et al. 2009; Hector and Nakawaga 2012). To date, fairly few studies have tested for sex differences in compensatory and/or catch-up growth following food deprivation (e.g. Festa-Bianchet et al. 1994; Toigo et al. 1999; Barreto et al. 2003; Arnold et al. 2007; for bird studies see references in Chin et al. 2013). Nor have many studies attempted to account for sex differences based on variation among species in key life history traits or population parameters (e.g. the adult sex ratio). We suggest that the following three factors probably create sex differences in the optimal level of compensatory and/or catch-up growth:

1. *Sex differences in net selection (natural and sexual) on adult body size* All else being equal, we expect compensatory and/or catch-up growth to be stronger in the sex whose fitness more strongly depends on greater adult size. For example, for males a key benefit is probably the ability to still acquire mates. Male mating success typically depends on relative competitiveness in a zero-sum-game (Shuster 2010). The cost of below average size can be very high if sexual selection skews mating success towards large males (Blanckenhorn 2005). In contrast, female reproductive output often depends on a weakly positive, asymptotic, relationship between body size and fecundity (Blanckenhorn 2005). For example, in polygynous mammals male size is

often under intense directional selection due to mating competition, but there is little increase in fecundity with maternal body size (Clutton-Brock 1988). Here we expect males to show more pronounced compensatory and/or catch-up growth than females. In many ectotherms, however, body size only has a modest effect on male mating success, but a marked effect on female fecundity (Roff 2002). Here we might expect stronger compensatory and/or catch-up growth by females (although, in some insects selection for protandry might strongly favour male compensatory growth (Bulmer 1983). There is, as yet, no comparative test of whether sex differences in selection on adult size are correlated with differences in the extent of compensatory and/or catch-up growth.

2. *The sexes differ in the extent of adult growth* In extreme cases, such as Poeciliid fish, males show minimal growth after maturation (i.e. determinate growth), while females continue to grow (i.e. indeterminate growth) so that fecundity increases with age (e.g. Zulian et al. 1993). All else being equal, the benefits of compensatory and/or catch-up growth might be greater with determinate growth, as there is no subsequent opportunity to compensate for small adult body size. This might explain why compensatory growth is stronger in endotherms than ectotherms (determinate versus indeterminate growth: Hector and Nakawaga 2012).

3. *Sex differences in the 'hidden' long-term fitness costs of compensatory and/or catch-up growth* Male reproductive success usually depends on relative competitiveness, while females often have ready access to mates (Kokko et al. 2012). A reduction in sexually competitive performance could therefore have a much greater effect on male than female fitness. To date, few studies have rigorously tested how compensatory and/or catch-up growth affects sexual traits. Two studies of zebra finches (*Taeniopygia guttata*) found that males experimentally subjected to a period of poor nutrition as juveniles fully compensated in terms of their adult morphology and expression of sexually selected traits. Consequently, there was no detectable effect on their ability to acquire a mate (Blount et al. 2003; Honarmand et al. 2010). In the mosquitofish (*Gambusia holbrooki*), however, males that were deprived of food early in life appeared to be less attractive (Kahn et al. 2012; in that paper we incorrectly concluded that these males underwent compensatory growth, see "Results"). More generally, selection for plasticity in male growth rates and delayed maturation might be strongly dependent on the relative importance of body size in determining mating success compared to other sexual traits, such as weapons and ornaments, that are also negatively affected by compensatory and/or catch-up growth (e.g. Fairbairn 2005; Fernández-Montraveta and Moya-Laraño 2007; model: Lindström et al. 2005). There is evidence, however, that compensatory growth can sometimes have unexpectedly negative effects on female fecundity (e.g. Auer et al. 2010). Sex differences in the severity of 'long-term' costs are unclear.

Here we test for sex differences in compensatory and catch-up growth, and for possible hidden costs of compensatory growth in the mosquitofish, *G. holbrooki*

Study species

The mosquitofish, *Gambusia holbrooki*, is a small Poeciliid fish endemic to North America. It was introduced into Australia in the 1920s, and is a pest species (Pyke 2005). Fertilization is internal and males transfer sperm via a modified anal fin (gonopodium). Mating does not involve courtship. Instead, males pursue females and attempt to insert

their gonopodium into the female's reproductive opening (gonopodial thrusting). Despite this, females prefer to associate with larger males (Dadda et al. 2005, 2008; Agrillo et al. 2006), and those with longer gonopodia (Kahn et al. 2010; also Langerhans et al. 2005). Greater time in proximity to females should increase the opportunities a male has to make insemination attempts (Bisazza et al. 2001).

As with most Poeciliids, mosquitofish exhibits extreme reversed sexual size dimorphism (Evans et al. 2011). Females undergo indeterminate growth and can be four times the length of equivalent aged males. Males grow little after sexual maturity (Zulian et al. 1993). Despite determinate growth there is, however, considerable variation in male size (and age) at maturity. This is partly attributable to effects of population density on juvenile growth (Hughes 1985a).

How sexual selection acts on male size at maturity in mosquitofish is poorly understood. Reversed sexual dimorphism suggests that smaller males have an advantage (Bisazza and Pilastro 1997). Indeed, there is evidence that they are better at approaching females, and have greater manoeuvrability that increases their success at gonopodial thrusting (Bisazza and Marin 1995; Pilastro et al. 1997). Larger males are, however, socially dominant and better able to gain access to females when males compete (Bisazza and Marin 1995). Females also prefer to associate with larger males (Langerhans et al. 2005; Dadda et al. 2005, Kahn et al. 2010; but see Bisazza and Marin 1991). The benefit of larger body size for males could therefore partly depend on whether the population density is high enough that it pays to defend females from rivals (Bisazza and Marin 1995). It remains unclear whether the apparent plasticity in male size at maturity is adaptive. Given the enormous variation in male size, however, it is, probably reasonable to conclude that there is weak stabilising sexual selection on male body size.

Female size at maturity is likely to be under stronger directional selection because it is positively correlated with fecundity (e.g. Callander et al. 2012; Kahn et al. 2013). There is, however, a life history trade-off between size and age at maturity (Roff 1984; Stearns and Koella 1986; Auer et al. 2010). Life history theory suggests that earlier maturation is favoured when the extrinsic rate of mortality is high (e.g. due to predation; Roff 2002). Indeed, female mosquitofish appear to reach maturity at an age/size that is strongly influenced by food levels and water conditions (e.g. Hughes 1985b; Vondracek et al. 1988; Meffe 1992; Alcaraz and García-Berthou 2007).

Aims and predictions

In *G. holbrooki*, males and females differ in their growth as adults (determinate versus indeterminate). In addition, we have argued that body size at maturation will have a greater effect on female than male fitness. These observations suggest that there will be a sex difference in compensatory and/or catch-up growth. Specifically, we predicted that following a period of food deprivation as a juvenile:

1. Males will show a *weaker* compensatory growth response as any longer-term costs of elevated growth will not be matched by equivalent benefits. Females have more to gain.
2. Males are *less* likely than females to delay maturation (i.e. exhibit catch-up growth) to ensure that they reach the same adult body size as fish reared under standard food conditions.
3. If predictions 1 and 2 are correct, then males are *less* likely than females to attain the same adult body size as fish reared under standard food conditions.

We also made two predictions about longer-term costs of low food availability on adult performance. Specifically, that following food deprivation:

4. Males developed relatively *smaller* gonopodia than those of males reared under standard conditions. This is a test for a sexually selected cost.
5. Post-maturation growth of food deprived females is *lower* than that of females reared under standard conditions. This is a test for a naturally selected cost of female compensatory growth (i.e. assuming fecundity increases with body size; but see Auer et al. 2010).

Methods

Compensatory and/or catch-up growth

We tested whether *G. holbrooki* undergo compensatory and/or catch-up growth by comparing juveniles that were raised under normal conditions ('control') or on a restricted diet ('low food') for: (1) juvenile growth rate; (2) size at maturity; (3) age at maturity. We then tested for longer term reproductive costs of a restricted early diet by comparing control and low food treatment fish for: (4) male gonopodium length and (5) female adult growth.

Experimental fish and food treatment

We mated 20 males to 80 females (4 dams/sire) in a full-sibling/half sibling experimental design as part of a quantitative genetics study (J. Livingston, in prep). These parents were unrelated because they were each offspring of different wild-caught females collected from large, feral populations in Canberra, Australia in March–April 2010. We reared offspring from the 69 that gave birth. At birth, up to 10 fry were taken from each brood and housed individually in 1 l tanks ($N = 635$ tanks) at 28 °C on a 14L:10D photoperiod. Fish from the same brood were evenly distributed across ten levels of shelving to account for any relationship between shelf height and temperature/light levels that might affect growth.

We divided the fry in each brood as evenly as possible between a control ($N = 324$) and 'low food' treatment ($N = 311$; ideally 5 fry/group). Sickly offspring and those with obvious spinal curvature were subsequently excluded prior to the low food treatment commencing (<3 %, $N = 19$). Offspring in the control group were fed brine shrimp *ad libitum* twice daily from birth until the end of the experiment. Offspring in the treatment group were initially fed at the control level for 7 days to prevent early starvation (Chen et al. 2008). Their feeding regime was then reduced to 2.89 ± 0.2 mg of brine shrimp once a day every second day for 21 days. This amount of food was found to be adequate for maintenance and minimal growth in pilot studies (unpublished data, J. Livingston). Thereafter treatment fish were returned to the same dietary regime as the control fish. There was minimal death of juveniles and no difference in mortality between the two groups during the period of food deprivation.

Size measurements

We measured the standard length (SL: snout to base of the caudal fin) of all offspring at birth to ensure that there was no initial difference between treatment and control fish. All

offspring were then remeasured at the end of the low food treatment period (i.e. at 28 days of age) to test whether the food treatment significantly reduced the juvenile growth rate, hence body size, of treatment fish relative to control fish. We confirmed that our food treatment reduced juvenile growth (see "Results"). We then measured fish every 3 weeks until 16 weeks of age for females (who grow post-adulthood) or until sexual maturity for males. Size measurements of females post-maturation allowed us to test for treatment effects on adult growth.

The SL of each fish was measured from photographs of fish immobilised in cold water (<90 s, with no post-photography elevation in mortality detected). Fish were placed in a Petri dish filled with water, aligned alongside a microscopic ruler (0.1 mm gradations), and photographed using a digital camera attached to a dissecting microscope. We used *ImageJ* software (Abramoff et al. 2004) to measure their SL. We remeasured 200 randomly selected photos to confirm that our length measurements were repeatable ($r > 0.95$, $P < 0.0001$). We also measured the body length and gonopodium length (apical tip to base) of all males that were alive after 150 days ($N = 136$ treatment, 133 control males).

Age at sexual maturation

From day 28 onwards, fish were visually checked every second day for sexual maturation. We defined males as sexually mature when we detected a clear apical hook at the gonopodium tip (Zulian et al. 1993). We defined females as sexually mature by the presence of yellow colouration in their egg sacs, which are visible through the body wall. Yellowing indicates that a female is reproductively mature with yolked eggs (Pyke 2005; Stearns 1983).

Statistical analysis

Food treatment effects

We ran separate generalised linear mixed models (GLMM) to test for fixed effects of food treatment and sex on each measured trait (initial size, growth rates, size at maturity, age at maturity). We also tested for a food treatment by sex interaction. Models were fitted using restricted maximum likelihood (REML) estimation in *R* (v2.12.2) with *lme4* (v0.999375-39). Sire and dam were included as random factors to account for offspring relatedness. Shelf height (10 levels) was also included as a fixed factor. To test for an effect of food treatment on gonopodium length we ran a GLMM with the same random effects, but with food treatment, body size and their interaction as fixed effects. Body size was centred (mean = 0) so that the effect of treatment was readily interpretable (Schielzeth 2010). The significance of fixed terms was taken from the estimated parameter mean divided by its SE, and assuming it follows a *Z*-distribution (Crawley 2007).

Compensatory growth

We confirmed that the low food treatment stunted the growth of treatment fish by first ensuring there was no initial size difference at birth between control and treatment fish. We then tested for an effect of the treatment on juvenile growth between birth and 28 days of age (termination of the low food treatment), estimated as the instantaneous rate of growth, $G = \ln (L_{t1}/L_{t0})/t$, where L is length at subscript t_n age and t is time (days) between

measurements. We also formally tested for a size difference between treatment and control fish at 28 days of age.

To test for compensatory growth after the low food treatment ended it is important to recall that growth rate is generally negatively correlated with body size in fish (Elliot et al. 1995; Elliot and Hurley 1995). We therefore expected a higher growth rate in 'low food' treatment fish that returned to the control diet, simply because of their smaller body size at day 28 (see "Results"). To test for compensatory growth we must estimate growth rates of fish from the same initial size (e.g. Nicieza and Alvarez 2009; Auer et al. 2010; for a full review of methodological issues see Hector and Nakawaga 2012). In other words, the growth trajectories of treatment fish have to be compared to those of control fish of the same size (i.e. when controls were younger). To do this, we compared the mean size of the treatment fish at 28 days to the estimated mean size of control fish at all ages between 7 and 14 days of age. The size of each control fish at each age was estimated by calculating the daily growth rate until 28 days of age [$(L_{28\ days} - L_{birth})/28)$] for each fish and then adding the appropriate daily size increment (multiplied by the relevant number of days) to its birth size. This assumes linear growth, which is appropriate when estimating body size over a short period (21 days) with too few data points to fit an informative growth curve (Auer et al. 2010).

We calculated that 11 day old control fish were equivalent in size to treatment fish at 28 days of age (mean $\pm$ SE: females 11.36 ± 0.071 and 11.26 ± 0.071 mm, respectively; $F_{1,270} = 1.6$, $P = 0.21$: males 11.30 ± 0.063 and 11.24 ± 0.065 mm, respectively; $F_{1,260} = 0.81$, $P = 0.30$). The growth trajectories of treatment fish from 28 to 49 days of age were thus 'slid back' and compared to those of control fish from 11 to 28 days of age (i.e. both groups were statistically the same size at the start of the growth period). The instantaneous rates of growth, G, of females were then analysed for four growth periods (Table 1). Male growth was only analysed for the three periods, as most males matured during the fourth period.

In addition, we tested for a difference in the instantaneous rate of growth, G, for each fish from an age giving a comparable initial body size (treatment: day 28; control: day 11) to maturation. The duration of this period varied among individuals in the same treatment group due to differences in development time.

Adult female growth

We compared the growth of treatment and control fish from sexual maturity to 112 days of age. Daily growth rates were estimated as ln $(L_{112\ days}/L_{maturity})/(112 - A_{maturity})$, where L is length at subscript age and A is age (days).

Unless otherwise stated all summary statistics are presented as mean $\pm$ SE. All tests are two-tailed, with alpha set at 0.05, and all analyses were run using R (v2.12.2).

Results

All test statistics and parameter estimates from the linear mixed models for the effects of treatment and sex are in Table 2. Descriptive statistics based on raw data are in Table 3.

Compensatory growth

There was no size difference at birth between fish assigned to the control and low food treatment for either sex (Tables 2, 3A). As expected, the low food treatment strongly

Table 1 Age of control and treatment fish (in days) at the start and end of each growth period

Growth period	GP1	GP2	GP3	GP4
Control fish	1–28	11–28	28–49	49–70
Treatment fish	1–28	28–49	49–70	70–90

GP1 can be used to test for a direct effect of food deprivation on growth. GP2, 3 and 4 can be used to test for compensatory growth correcting for initial body size (given that control fish at day 11 were equivalent in size to treatment fish at day 28; see "Methods" for details)

suppressed growth (Tables 2, 3B): treatment fish of both sexes were significantly smaller than control fish after 28 days (Tables 2, 3C). There was no evidence for initial compensatory growth after being returned to the standard diet (i.e. faster growth in GP2) for fish of either sex. In fact, the growth rate of treatment fish was slightly, but significantly, slower in GP2. There was no significant interaction between sex and treatment, with treatment fish having a slower growth rate relative to control fish for both males and females (82.1 and 85.4 % of the control rate). There was therefore no support for our prediction that females will initially exhibit significantly *stronger* compensatory growth response than males (Tables 2, 3D; Fig. 1; *contra* Prediction 1, but see below). Subsequently, treatment fish of both sexes grew at the same rate as control fish until maturity (i.e. during GP3 and GP4). Females, however, grew faster than males during GP3 (Tables 2 and 3E–F).

For growth from the end of the low food period to sexual maturation (after correcting for size at the start of the measured period; see "Methods") there was a significant interaction between sex and treatment (Table 2G). There was no increase in growth rate for males, but females grew significantly faster than controls of the same size (Table 3G). Thus, while there was no evidence for compensatory female growth in any of the three growth periods after treatment fish returned to the standard diet, across the entire period of juvenile development there was evidence for compensatory growth by treatment females who grew 16.6 % faster than control females (*supporting* Prediction 1).

Catch-up growth: size and age at maturity

Both sexes showed catch-up growth through a significant delay in the time to maturation by treatment fish. There was, however, a significant sex difference in the effect of early food deprivation on age at maturity. Treatment females matured on average only 4 days later than control females, while treatment males took 15 days longer than control males (Tables 2, 3H; *contra* Prediction 2). This sex difference in the effect of food deprivation on delayed maturation did not result in females maturing at a relatively smaller size than controls compared to males. Although there was a weakly significant interaction between sex and treatment ($P < 0.05$) treatment females were, on average, only 0.8 mm smaller than control females at maturity, while treatment males were 0.3 mm smaller than control males at maturity. This is equivalent to maturing at 98.7 and 96.9 % of the size of the average control fish for males and females respectively (Tables 2, 3I; Fig. 2). So there was no trend for treatment males to mature at a smaller size relative to control males than was the case for the same comparison for females (*contra* Prediction 3). This is due to partial compensatory growth by females, but not males, leading to a more severe trade-off between size and age at maturity for males (with size more important than age in determining sexual maturity).

Table 2 Results from mixed models (see text) with Wald's Z tests for estimated parameters for low food treatment effects

Response	N	Predictor	β	se	Z	p
(A) Length at birth (mm)	M: 312	Intercept	7.618	0.050	152.60	<0.001
	F: 323	Treatment	0.041	0.032	1.30	0.194
		Sex (male)	0.011	0.032	0.35	0.726
		Interaction	-0.020	0.046	-0.43	0.667
(B) Growth period 1 (during diet restriction) (ln [mm]/day)	M: 312	Intercept	3.92×10^{-2}	5.74×10^{-4}	68.34	<0.001
	F: 323	Treatment	-2.02×10^{-2}	3.34×10^{-4}	-60.43	<0.001
		Sex (male)	-2.30×10^{-4}	3.43×10^{-4}	-0.88	0.379
		Interaction	3.41×10^{-4}	4.88×10^{-4}	0.70	0.484
(C) Length at day 28 (mm)	M: 312	Intercept	17.353	0.143	121.50	<0.001
	F: 323	Treatment	-5.839	0.086	-67.88	<0.001
		Sex (male)	-0.090	0.088	-1.02	0.308
		Interaction	0.082	0.126	0.65	0.516
(D) Growth period 2 (ln [mm]/day)	M: 302	Intercept	2.48×10^{-2}	3.42×10^{-4}	72.75	<0.001
	F: 318	Treatment	-3.69×10^{-3}	2.51×10^{-4}	-14.71	<0.001
		Sex (male)	-1.11×10^{-4}	2.53×10^{-4}	-0.45	0.653
		Interaction	-6.54×10^{-4}	3.65×10^{-4}	-1.79	0.073
(E) Growth period 3 (ln [mm]/day)	M: 285	Intercept	9.75×10^{-3}	3.12×10^{-4}	31.30	<0.001
	F: 308	Treatment	1.24×10^{-4}	2.14×10^{-4}	0.58	0.563
		Sex (male)	-7.51×10^{-4}	2.18×10^{-4}	-3.45	<0.001
		Interaction	3.33×10^{-4}	3.17×10^{-4}	1.05	0.293
(F) Growth period 4 (ln [mm]/day)	M: 107	Intercept	5.67×10^{-3}	2.52×10^{-4}	22.48	<0.001
	F: 309	Treatment	-1.06×10^{-4}	1.46×10^{-4}	-0.73	0.467
(G) Growth from 11 (control) or 28 (treatment) days to sexual maturity (ln [mm]/day)	M: 303	Intercept	1.06×10^{-2}	3.53×10^{-4}	30.17	<0.001
	F: 297	Treatment	1.49×10^{-3}	2.26×10^{-4}	6.59	<0.001
		Sex (male)	2.35×10^{-3}	2.29×10^{-4}	10.29	<0.001
		Interaction	-1.32×10^{-3}	3.25×10^{-4}	-4.062	<0.001

Table 2 continued

Response	N	Predictor	β	se	Z	p
(H) Age at sexual maturity (days)	M: 303	Intercept	91.251	2.944	30.99	<0.001
	F: 297	Treatment	4.241	1.881	2.26	<0.05
		Sex (male)	−25.063	1.900	−13.19	<0.001
		Interaction	11.360	2.701	4.21	<0.001
(I) Length at sexual maturity (mm)	M: 303	Intercept	25.466	0.226	112.72	<0.001
	F: 297	Treatment	−0.795	0.151	−5.27	<0.001
		Sex (male)	−2.522	0.153	−16.53	<0.001
		Interaction	0.508	0.217	2.34	<0.05
(J) Female adult growth (ln [mm]/day)	F: 268	Intercept	2.97×10^{-3}	5.31×10^{-4}	5.59	<0.001
		Treatment	1.10×10^{-3}	3.15×10^{-4}	3.50	<0.001
(K) Gonopodium length (ln [mm])	M: 269	Intercept	1.878	0.009	205.83	<0.001
		Body length	0.052	0.004	13.53	<0.001
		Treatment	−0.020	0.004	−4.42	<0.001
		Interaction	0.017	0.005	3.73	<0.001

Growth periods are defined in Table 1. For models A–H, the intercept is the model estimate of the mean for control females

F females, M males

Table 3 Means and SE from raw data from all fish (i.e. not model estimates)

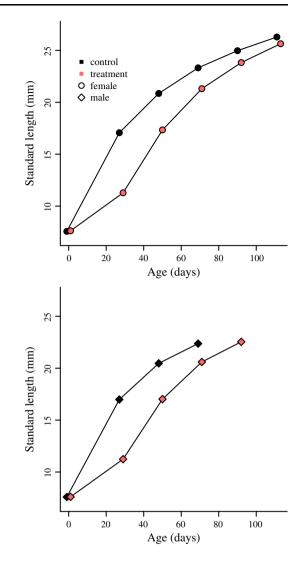|	Female		Male	
	Control	Treatment	Control	Treatment
(A) Length at birth (mm)	7.568 (0.028)	7.623 (0.026)	7.593 (0.026)	7.610 (0.027)
(B) Growth period 1 (diet restriction) (mm/day)	3.87×10^{-2} (2.86×10^{-4})	1.86×10^{-2} (3.38×10^{-4})	3.83×10^{-2} (1.85×10^{-4})	1.85×10^{-2} (3.08×10^{-4})
(C) Length at day 28 (mm)	17.067 (0.085)	11.280 (0.072)	16.984 (0.075	11.239 (0.067)
(D) Growth period 2 (ln [mm]/day)	2.42×10^{-2} (1.46×10^{-4})	2.05×10^{-2} (2.29×10^{-4})	2.40×10^{-2} (1.04×10^{-4})	1.97×10^{-2} (2.37×10^{-4})
(E) Growth period 3 (ln [mm]/day)	0.0097 (0.0002)	0.0098 (0.0001)	0.0090 (0.0002)	0.0093 (0.0001)
(F) Growth period 4 (ln [mm]/day)	5.34×10^{-3} (9.83×10^{-5})	5.29×10^{-3} (1.09×10^{-4})	–	–
(G) Growth from 11 (control) or 28 (treatment) days to sexual maturity (ln [mm]/day)	9.78×10^{-3} (1.50×10^{-4})	1.14×10^{-2} (2.00×10^{-4})	1.22×10^{-2} (1.50×10^{-4})	1.23×10^{-2} (2.00×10^{-4})
(H) Age at sexual maturity (days)	96.231 (1.464)	99.307 (1.590)	70.133 (1.276)	86.808 (1.437)
(I) Length at sexual maturity (mm)	25.199 (0.112)	24.366 (0.129)	22.604 (0.098)	22.394 (0.121)
(J) Female adult growth (ln [mm]/day)	2.75×10^{-3} (1.54×10^{-4})	3.86×10^{-3} (2.34×10^{-4})	–	–
(K) Gonopodium length (mm)	–	–	6.409 (0.035)	6.18 (0.045)

Effects of treatment on adults

As predicted, the allometric relationship between gonopodium length and body size was significantly steeper for treatment than control fish (Tables 2, 3K). Across the range of observed body sizes, however, most treatment males had a shorter gonopodium than did equivalent sized control males (Fig. 3). For an average sized male, gonopodium length was significantly shorter for treatment males (Tables 2, 3K; *supporting* Prediction 4). Unexpectedly, treatment females had a significantly *higher* adult growth rate than control females (Tables 2, 3J; *contra* Prediction 5).

Discussion

There were sex differences in the growth response of *G. holbrooki* juveniles after a period of low food availability (hereafter 'treatment' fish). We also identified associated fitness effects, but these were not always in the predicted direction. Mosquitofish juveniles did not undergo detectable compensatory growth (i.e. accelerated growth for their size) immediately after returning to a normal diet). Across the entire period of growth, however, females, but not males, exhibited partial compensatory growth (*supporting* Prediction 1). In addition, both sexes exhibit catch-up growth because they delayed maturation to reach almost the same size as control fish. The cost paid for catching up differed between the sexes: males substantially delayed maturity compared to females, with a 23.4 versus 4.6 % increase in development period relative to control fish (*contra* Prediction 2). Due to partial compensatory growth by females, however, both sexes matured at approximately the same size as control fish (1.3 vs. 3.1 % smaller; *contra* Prediction 3). Treatment males also

Fig. 1 Mean growth trajectories of fish separated by sex and treatment. Data shown for growth periods prior to sexual maturity only (see Fig. 2). The *top graph* shows treatment females on an accelerated growth trajectory, eventually catching up to their control counterparts. The *bottom graph* shows treatment males staying on a delayed growth trajectory relative, parallel to control males
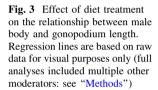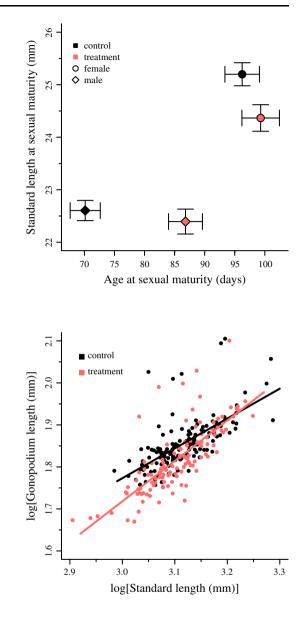

incurred a potential sexually selected cost as they developed relatively shorter gonopodia (*supporting* Prediction 4). In contrast, we did not find a cost for treatment females (*contra* Prediction 5) as their adult growth rate was higher than that of control females. It should be noted, however, that the effect of this elevated adult growth rate on fecundity and lifespan (i.e. fitness) is unknown, and that we did not measure longer-term costs for females. In general, the combined evidence suggests that males are more adversely affected than females by an early period of nutritional stress, assuming that the use of the same duration of low food availability for both sexes allows for an appropriate contrast (see below).

Is there compensatory and/or catch-up growth?

Unlike many fish species (review: Ali et al. 2003; meta-analysis: Hector and Nakawaga 2012), mosquitofish did not respond to an early period of low growth by immediately

Fig. 2 Mean age and length at sexual maturity (and 95 % confidence interval) of fish separated by sex and treatment (based on raw data). Treatment males matured much later than control males, but at roughly the same length. Treatment females, conversely, matured at about the same age as control females, but at a shorter average length

Fig. 3 Effect of diet treatment on the relationship between male body and gonopodium length. Regression lines are based on raw data for visual purposes only (full analyses included multiple other moderators: see "Methods")

elevating their growth rate following a return to a standard diet (i.e. exhibiting compensatory growth). Instead, treatment fish initially grew slightly slower than control fish after the low food treatment ended. Fish probably undergo (reversible) physiological changes that make them less efficient at converting food into body mass immediately after a period of food shortage. Alternatively, treatment juveniles might initially convert food into lipids rather than skeletal growth (De Block et al. 2008). Fish typically rely on stored fat as energy reserves when food is limited (e.g. Metcalfe and Thorpe 1992; Blake et al. 2006), which could favour the ability to build up fat stores in an unpredictable environment (Metcalfe and Monaghan 2001). This theory could be tested by comparing body condition

between treatment and control fish shortly after a low food period (e.g. Saastamoinen et al. 2010; Dahl et al. 2012).

Only females showed compensatory growth across the remainder of the developmental period after the low food treatment. In contrast, both sexes delayed sexual maturation (i.e. showed catch-up growth). Female maturation was, however, less adversely than that of males (see also Ali et al. 2003). Treatment females matured only 4 days later than the average control female (4.6 % increase in development period) at 96.9 % of her size. In contrast, treatment males matured 15 days later (23.4 % increase) than the average control male, at 98.7 % of his size. The shorter developmental period for females is presumably partly due to their compensatory growth.

Why are there sex differences in growth and developmental rate?

The observed sex differences in growth rate and age at maturity raise two closely related questions. First, why do only females show compensatory growth? Second, why do males greatly prolong their development period rather than simply maturing at a smaller size?

Sex-differences in compensatory growth could be caused by differences in food consumption (Barreto et al. 2003; Lozan 2003), efficiency of converting food into body mass (Yasuda and Dixon 2002), digestive tract physiology (Saillant et al. 2001), metabolic rate (Guinet et al. 1999) or hormonal regulation (Toguyeni et al. 1996). Under normal conditions, however, male and female mosquitofish grow at roughly the same rate (1-2 mm per week) until maturity (Schoenherr 1981; Trendall 1982; Stearns 1983; this study). This suggests that sex differences in the effects of low food on these physiological traits are unlikely to affect subsequent juvenile growth in mosquitofish. Furthermore, there were no detectable sex differences in food consumption as food was entirely consumed by each fish at every feeding (JL, personal observation). Alternatively, the difference in compensatory growth response may be due to a difference in the relative level of stress caused by the low food treatment. Male *G. holbrooki* have a shorter developmental period than females (see "Results" for control fish), which means that the 21 day low food treatment restricted male growth over a larger proportion of their standard development period. This relatively greater stress may have restricted the males' ability to undergo compensatory growth but not catch-up growth. We suggest that the sex difference might be due to higher costs of developmental errors in males, which prevent them from elevating their growth rate. Sexually selected traits are often complex and errors can reduce their effectiveness (e.g. Nowicki et al. 2002; Ohlsson et al. 2002; Byers et al. 2010). Faster growth is likely to increase errors, selecting against male compensatory growth. The traits in question could range from sex-specific morphological traits (e.g. the gonopodium; see Langerhans et al. 2005; Kahn et al. 2010) to general traits that affect male sexual performance (e.g. swimming speed and manoeuvrability are likely to affect insemination success; Pilastro et al. 1997).

The more pronounced effect of low food availability on the development period of males than females (i.e. more extensive catch-up growth) is easily explained: partial compensatory growth by females, but not males, reduces the time taken to reach a given target size. There is, however, a follow up question: why don't males simply mature at a smaller size to reduce their developmental period? There are several possible, non-mutually exclusive answers.

First, males might be subject to developmental constraints. If it takes a fixed time period to produce necessary traits then the low food period will simply extend the time taken to reach maturation. It is noteworthy that the growth of treatment males during the 21 days of

low food treatment was equivalent to 4 days of growth by control males, which is a 17 day growth deficit. The delay in maturation by treatment males of 15 days (based on the GLMM model) or 16.8 days (based on raw values) closely matches this deficit. The gonopodium is an example of a sexually selected trait that might require a set period of time to be properly developed. It is a highly complex trait with numerous fine-scale barbs and hooks that is key to males successfully inseminating females. Under high food conditions, the 4th and 5th caudal rays of the anal fin begin to elongate and differentiate into the gonopodia when males are approximately 18 days old (Busack and Gall 1983; Meffe 1992). The low food treatment usually prevented onset of gonopodia development until after the low food period ended (i.e. >28 days; JL, personal observation). A weakness of this argument is that the high natural variation in body size, hence age, at maturity suggests that a functional gonopodium can be produced faster than the time taken for a large male to mature.

Second, the additional demand on males to produce sexually selected traits might create a sex-specific difference in how low food availability affects subsequent somatic growth. For example, a growth trade-off between body size and a sexually selected trait (the sword) occurs in another Poecilid, the swordtail (*Xiphophorus helleri*). Males transferred from a high to low food diet altered their allocation strategy to preferentially invest in sword elongation over body size (Basolo 1998). In mosquitofish, when resources for growth are at a premium after a period of low food, the necessity to develop a gonopodia might constrain accelerated body size growth in males compared to that of females who lack a comparable sexual trait. This answer, however, begs a question: why don't treatment males mature at a smaller size?

Third, treatment males paid the cost of delayed maturation to attain the same adult size as control males . This suggests that there are fitness consequences of smaller size. Male mating success is size-dependent in many species, and larger size is usually favoured (Shuster 2010; Blanckenhorn 2005). It is, however, still unclear if (or when) sexual selection favours larger body size in male mosquitofish, given the high variation in size at maturity in both the laboratory and field (Hughes 1985a; Pilastro et al. 1997). Variation in male adult size can, however, be partly explained by density-dependent benefit of larger size. As discussed, Mosquitofish populations often undergo significant seasonal increases in population density. When competition for females is low (e.g. low density or female-biased populations), males might mature at a small size, hence sooner, if the main reproductive benefit of larger body size is a greater ability to guard females given intense male competition (i.e. at high densities; Zulian et al. 1993; Bisazza and Marin 1995; Pilastro et al. 1997). It is possible that low food availability early in life is normally a signal of high population density, which then favours a plastic response of delaying maturation to increase body size. However, it is also probable that the raising of each fish in isolation prevented social signals from influencing male growth patterns. Without social indicators about the likely competition for mates, both treatment and control males matured at almost the identical 'average' size. This suggests that male size at maturity is actively canalized in the absence of social or environmental cues about population density or mate competition (e.g. Liefting et al. 2009; Saastamoinen et al. 2013).

Given plasticity in male size/age at maturation, it is noteworthy that the extent of compensatory growth might depend on social conditions, or environmental cues thereof (e.g. Dahl et al. 2012; Pilastro et al. 1997). For example, when competition for females is low (such as in low density or female-biased populations), male *G. holbrooki* mature at a small size, as the only mating benefit of larger body size is the ability to guard females from intense male competition (i.e. at high densities or in more male-biased populations)

(Bisazza and Marin 1995). In fact, males tend to only grow as large as the largest male in the group (Bisazza et al. 1996). Therefore, if males were released from a low food treatment into a male-biased and/or high density population, they might be more likely to exhibit compensatory growth and/or delay maturation to reach a larger adult size to increase their ability to guard females. Conversely, males released into a female-biased (or low density) population, or into individual tanks (as in the current study), might perceive little need for compensatory growth and instead mature at an average or smaller size to improve their 'sneak' mating opportunities. The sex difference observed in our current study might therefore depend on details of the study design (see Hector and Nakawaga 2012 for how other design features affect estimates of compensatory growth). Unfortunately, studies of compensatory growth by fish in the field are rare (Johnsson and Bohlin 2005). To date, none have been attempted for Poeciliids, despite high phenotypic plasticity in size at maturation (e.g. Zulian et al. 1993). This will be a profitable area for future study.

Costs of a poor start to life

Male mosquitofish who experienced a period of low food had a shorter gonopodium for their body length than control males. Mate choice trials in two species of *Gambusia* show that females prefer males with longer gonopodia (Langerhans et al. 2005; Kahn et al. 2010). In Kahn et al. (2012) we used males from the current study to show that, controlling for body size, females prefer to associate with control over treatment males. We suggested that this might be related to their relative greater gonopodium length. Even so, decreased attractiveness of mosquitofish males that underwent catch-up growth does not necessarily mean that biasing investment towards body size over gonopodia length is maladaptive.

Lindström et al. (2005) built a model to predict resource allocation into somatic tissue (body size) and sexual ornamentation after a period of low growth. The optimal strategy was highly dependent on the fitness returns from increased body size compared to sexual ornamentation. Empirical studies of several species show that males raised on consistently restricted food have different growth strategies to those with unrestricted access to food, preferentially investing in sexual traits that are presumed to yield the highest fitness returns (i.e. reproductive success; e.g. Emlen 1997; Basolo 1998; but see Cotton et al. 2004). In mosquitofish, the relative influence of gonopodium length and body size on male fitness is unknown, but body size probably has a greater effect due to its influence on the outcome of agnostic encounters between males (e.g. compare Kahn et al. 2010 with Bisazza and Marin 1995 and Pilastro et al. 1997). Thus, while treatment males might be less attractiveness due to smaller gonopodia, this is likely to be a smaller cost than that paid by reducing body size.

In addition to stronger selection on body size, a longer gonopodium may be costly to maintain in unpredictable or stressful environments. Langerhans et al. (2005) found that male *Gambusia affinis*—a close relation of *G. holbrooki*—in populations that experience more predation have shorter gonopodia than males who live in predator-free environments. A shorter gonopodium is associated with superior burst-swimming performance, which is important for escaping predators. Given that a longer gonopodium can incur fitness costs, it is possible that the low food diet in the current study provided an environmental clue that it would be more costly to maintain a longer gonopodium.

Our study, together with the associate study of Kahn et al. (2012), is one of handful of studies that report a likely or actual reduction in male attractiveness following a period of low food availability early in life. Two studies of zebra finches (*T. guttata*) found that following a period of poor nutrition, treatment males fully compensated in terms of their

morphology and the expression of sexually selected traits. Consequently, they had the same probability of acquiring a mate as did control males (Blount et al. 2003; Honarmand et al. 2010). In green swordtails (*X. helleri*), choice trials also showed no difference in female mating preferences for males that had normal access to food compared to males that had experienced early food deprivation (Walling et al. 2007). A similar finding was reported for the ladybird beetle (*Harmonia axyridis*), although this result is potentially confounded by a female preference for certain colour morphs (Ueno et al. 1998). In pheasants, however, poor nutrition in the first 3 weeks of life produced less colourful wattles, which is likely to reduce their sexual attractiveness (Ohlsson et al. 2002).

Unlike males, we did not detect a cost for females of a period of low food as juveniles, based on early adult growth. In fact, treatment females grew faster than control females (≈ 0.02 mm/day). This could lead to higher fecundity, as size and fecundity are correlated in most fish (Elgar 1990), including mosquitofish (e.g. Vondracek et al. 1988; Scalici et al. 2007). Caution is needed to make this inference, however, as the fecundity of treatment females was not measured. Juvenile compensatory growth together with a higher allocation of energy into adult growth could also lower investment into reproduction. Treatment females might even have lower fecundity than control females of equivalent size. For example, Atlantic cod (*Gadus morhua*) that underwent compensatory growth following short periods of starvation had lower fecundity that control fish. In this case, the effect was attributed to smaller body size, not a change in the relationship between body size and fecundity (Karlsen et al. 1995). In guppies (*Poecilia reticulata*), however, females that underwent compensatory growth had lower fecundity than control fish, with a 20 % decline in litter size, even after controlling for body size (Auer et al. 2010). Finally, greater adult growth in mosquitofish could also have other fitness costs such as reduced longevity, and the costs might be context-dependent (e.g. Helle et al. 2012).

Conclusion

Most studies testing for sex differences in response to poor nutritional conditions early in life have been conducted on birds, especially those with sexual dimorphism (Chin et al. 2013). Our experiment shows a sex difference in the fish *G. holbrooki* following 3 weeks of low growth due to food limitation. Only food-deprived females showed compensatory growth, while food-deprived males extended their developmental period for significantly longer than did food-deprived females. The net result was that both sexes attained almost the exact same size as control fish at sexual maturation despite their initial low growth. Additionally, we provided a rare empirical example of an early period of poor nutrition negatively affecting the expression of a sexually selected male trait. Further studies are needed to test the generality of these results, specifically to test whether the social environment affects the trade-off between size and age at maturity for males. It also remains to be tested whether or not compensatory growth had long term effects on female fecundity.

References

Abramoff MD, Magelhaes PJ, Ram SJ (2004) Image processing with ImageJ. Biophotonics Int 11:36–42
Agrillo C, Dadda M, Bisazza A (2006) Sexual harassment influences group choice in female mosquitofish. Ethology 112:592–598

Alcaraz C, García-Berthou E (2007) Life history variation of an invasive fish (*Gambusia holbrooki*) along a salinity gradient. Biol Conserv 139:83–92

Ali M, Nicieza A, Wootton RJ (2003) Compensatory growth in fishes: a response to growth depression. Fish Fish 4:147–190

Arnold KE, Blount JD, Metcalfe NB, Orr KJ, Adam A, Houston D, Monaghan P (2007) Sex-specific differences in compensation for poor neonatal nutrition in the zebra finch *Taeniopygia guttata*. J Avian Biol 38:356–366

Auer SK, Arendt JD, Chandramouli R, Reznick DN (2010) Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (*Poecilia reticulata*). Ecol Lett 13:998–1007

Barrenäs ML, Jonsson B, Tuvemo T, Hellstrom PA, Lundgren M (2005) High risk of sensorineural hearing loss in men born small for gestational age with and without obesity or height catch-up growth: a prospective longitudinal register study on birth size in 245,000 Swedish conscripts. J Clin Endocrinol Metab 90:4452–4456

Barreto RE, Moreira PSA, Carvalho RF (2003) Sex-specific compensatory growth in food-deprived Nile tilapia. Braz J Med Biol Res 36:477–483

Basolo AL (1998) Shift of investment in sexually selected traits: tarnishing of the silver spoon. Anim Behav 55:665–671

Bisazza A, Marin G (1991) Male size and female mate choice in the eastern mosquitofish. Copeia 1991:730–735

Bisazza A, Marin G (1995) Sexual selection and sexual size dimorphism in the eastern mosquitofish *Gambusia holbrooki* (Pisces Poeciliidae). Ethol Ecol Evol 7:169–183

Bisazza A, Pilastro A (1997) Small male mating advantage and reversed size dimorphism in poeciliid fishes. J Fish Biol 50:397–406

Bisazza A, Pilastro A, Palazzi R, Marin G (1996) Sexual behaviour of immature male eastern mosquitofish: a way to measure intensity of intra-sexual selection? J Fish Biol 48:726–737

Bisazza A, Vaccari G, Pilastro A (2001) Female mate choice in a mating system dominated by male sexual coercion. Behav Ecol 12:59–64

Blake RW, Inglis SD, Chan KHS (2006) Growth, carcass composition and plasma growth hormone levels in cyclically fed rainbow trout. J Fish Biol 69:807–817

Blanckenhorn WU (2005) Behavioral causes and consequences of sexual size dimorphism. Ethology 111:977–1016

Blount JD, Metcalfe NB, Arnold KE, Surai PF, Monaghan P (2003) Neonatal nutrition, adult antioxidant defences and sexual attractiveness in the zebra finch. Proc R Soc Ser B 270:1691–1696

Bulmer MG (1983) Models for the evolution of protandry in insects. Theor Popul Biol 23:314–322

Busack CA, Gall GAE (1983) An initial description of the quantitative genetics of growth and reproduction in the mosquitofish, *Gambusia affinis*. Aquaculture 32:123–140

Byers J, Hebets E, Podos J (2010) Female mate choice based upon male motor performance. Anim Behav 79:771–778

Callander S, Backwell PRY, Jennions MD (2012) Context-dependent male mate choice: the effects of competitor presence and competitor size. Behav Ecol 23:355–360

Chen BN, Qin JG, Carragher JF, Clarke SM (2008) Deleterious effects of food restrictions in yellowtail kingfish *Seriola lalandi* during early development. Aquaculture 271:326–335

Chin EH, Storm-Suke AI, Kelly RJ, Burness G (2013) Catch-up growth in Japanese quail (*Coturnix japonica*): relationships with food intake, metabolic rate and sex. J Comp Physiol B 183:821–831

Clutton-Brock TH (1988) Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago, Chicago

Cotton S, Fowler K, Pomiankowski A (2004) Condition dependence of sexual ornament size and variation in the stalk-eyed fly. Evolution 58:1038–1046

Crawley M (2007) The R book. Blackwell, Oxford

Dadda M, Pilastro A, Bisazza A (2005) Male sexual harassment and female schooling behaviour in the eastern mosquitofish. Anim Behav 70:463–471

Dadda M, Pilastro A, Bisazza A (2008) Innate responses to male sexual harassment in female mosquitofish. Behav Ecol Sociobiol 63:53–62

Dahl E, Orizaola G, Nicieza A, Laurila A (2012) Time constraints and flexibility of growth strategies: geographic variation in catch-up growth responses in amphibian larvae. J Anim Ecol 81:1233–1243

De Block M, McPeek MA, Stoks R (2008) Stronger compensatory growth in a permanent-pond *Lestes* damselfly relative to temporary-pond *Lestes*. Oikos 117:245–254

Dmitriew CM (2011) The evolution of growth trajectories: what limits growth rate? Biol Rev 86:97–116

Elgar MA (1990) Evolutionary compromise between a few large and many small eggs: comparative evidence in teleost fish. Oikos 59:283–287

Elliot JM, Hurley MA (1995) The functional relationship between body size and growth rate in fish. Funct Ecol 9:625–627

Elliot JM, Hurley MA, Fryer RJ (1995) A new, improved growth model for Brown Trout *Salmo trutta*. Funct Ecol 9:290–298

Emlen DJ (1997) Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Proc R Soc Lond B 264:567–574

Evans JP, Pilastro A, Schlupp I (2011) Ecology and evolution of poeciliid fishes. University of Chicago Press, Chicago

Fairbairn DJ (2005) Allometry for sexual size dimorphism: testing two hypotheses for Rensch's rule in the water strider, *Aquarius remigis*. Am Nat 166:S69–S84

Fernández-Montraveta C, Moya-Laraño J (2007) Sex-specific plasticity of growth and maturation size in a spider: implications for sexual size dimorphism. J Evol Biol 20:1689–1699

Festa-Bianchet M, Jorgenson JT, William DW (1994) Early weaning in bighorn sheep, *Ovis Canadensis*, affects growth of males but not of females. Behav Ecol 5:21–27

Guinet C, Goldsworthy SD, Robinson S (1999) Sex differences in mass loss rate and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups at Macquarie Island. Behav Ecol Sociobiol 46:157–163

Hector KL, Nakawaga S (2012) Quantitative analysis of compensatory and catch-up growth in diverse taxa. J Anim Ecol 81:583–593

Hector KL, Bishop PJ, Nakagawa S (2012) Consequences of compensatory growth in an amphibian. J Zool 286:93–101

Helle H, Koskela E, Mappes T (2012) Life in varying environments: experimental evidence for delayed effects of juvenile environment on adult life history. J Anim Ecol 81:573–582

Honarmand M, Goymann W, Naguib M (2010) Stressful dieting: nutritional conditions but not compensatory growth elevate corticosterone levels in zebra finch nestlings and fledglings. PLoS One 5:e12930

Hughes AL (1985a) Seasonal trends in body size of adult male mosquitofish, *Gambusia affinis*, with evidence for their social control. Environ Biol Fish 14:251–258

Hughes AL (1985b) Seasonal changes in fecundity and size at first reproduction in an Indiana population of the mosquitofish *Gambusia affinis*. Am Midl Nat 114:30–36

Johnsson JI, Bohlin T (2005) Compensatory growth for free? A field experiment on brown trout (*Salmo trutta*). Oikos 111:31–38

Jones KS, Nakagawa S, Sheldon BC (2009) Environmental sensitivity in relation to size and sex in birds: meta-regression analysis. Am Nat 174:122–133

Kahn AT, Mautz B, Jennions MD (2010) Females prefer to associate with males with longer intromittent organs in mosquitofish. Biol Lett 6:55–58

Kahn AT, Livingston JD, Jennions MD (2012) Do females preferentially associate with males given a better start in life? Biol Lett 8:362–364

Kahn AT, Kokko H, Jennions MD (2013) Adaptive sex allocation in anticipation of changes in offspring mating opportunities. Nat Commun 4: Article 1603

Karlsen O, Holm JC, Kjesbu OS (1995) Effects of periodic starvation on reproductive investment in first-time spawning Atlantic cod (*Gadis morhua* L.). Aquaculture 133:159–170

Kokko H, Klug HM, Jennions MD (2012) Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient, and the scope for competitive investment. Ecol Lett 15:1340–1351

Langerhans RB, Layman CA, DeWitt TJ (2005) Male genital size reflects a trade-off between attracting mates and avoiding predators in two live-bearing fish species. Proc Natl Acad Sci USA 102:7618–7623

Liefting M, Hoffmann AA, Ellers J (2009) Plasticity versus environmental canalization: population differences in thermal responses along a latitudinal gradient in *Drosophila serrata*. Evolution 63:1954–1963

Lindström J, Metcalfe NB, Royle N (2005) How do animals with ornaments predicted to compensate for a bad start in life? A dynamic optimization model approach. Funct Ecol 19:421–428

Lozan JL (2003) Sexual differences in food intake, digestive tract, size, and growth performance of the dab, *Limanda limanda* L. Neth J Sea Res 29:223–227

Meffe GK (1992) Plasticity of life-history characters in eastern mosquitofish (*Gambusia holbrooki*: Poeciliidae) in response to thermal stress. Copeia 1992:94–102

Metcalfe NB, Monaghan P (2001) Compensation for a bad start; grow now, pay later? Trends Ecol Evol 16:254–260

Metcalfe NB, Thorpe JE (1992) Anorexia and defended energy levels in over-wintering juvenile salmon. J Anim Ecol 62:175–181

Monaghan P (2008) Early growth conditions: phenotypic development and environmental change. Philos Trans R Soc B 363:1635–1645

Nicieza AG, Alvarez D (2009) Statistical analysis of structural compensatory growth: how can we reduce the rate of false detection? Oecologia 59:27–39

Nowicki S, Searcy WA, Peters S (2002) Brain development, song learning and mate choice in birds: a review and experimental test of the "nutritional stress hypothesis. J Comp Physiol A 188:1003–1014

Ohlsson T, Smith HG, Raberg L, Hasselquist D (2002) Pheasant sexual ornaments reflect nutritional conditions during early growth. Proc R Soc Ser B 269:21–27

Pilastro A, Giacomello E, Bisazza A (1997) Sexual selection for small size in male mosquitofish (*Gambusia holbrooki*). Proc R Soc Ser B 264:1125–1129

Pyke GH (2005) A review of the biology of *Gambusia affinis* and *G. holbrooki*. Rev Fish Biol Fish 15:339–365

Roff DA (1984) The evolution of life history parameters in teleosts. Can J Fish Aquat Sci 41:989–1000

Roff DA (2002) Life history evolution. Sinauer Associates, Sunderland USA

Saastamoinen M, van der Sterren D, Vastenhout N, Zwaan BJ, Brakefield PM (2010) Predictive adaptive responses: condition-dependent impact of adult nutrition and flight in the tropical butterfly *Bicyclus anynana*. Am Nat 176:686–698

Saastamoinen M, Hirai N, van Nouhuys S (2013) Direct and trans-generational responses to food deprivation during development in the Glanville fritillary butterfly. Oecologia 171:93–104

Saillant E, Fostier A, Menu B, Haffray P, Chatain B (2001) Sexual growth dimorphism in sea bass *Dicentrarchus labrax*. Aquaculture 202:371–387

Scalici M, Aventrani P, Gibertini G (2007) Mosquitofish life history in a Mediterranean wetland. J Nat Hist 41:887–900

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficient. Methods Ecol Evol 1:103–113

Schoenherr AA (1981) The role of competition in the displacement of native fishes by introduced species. In: Naiman RJ, Soltz DL (eds) Fishes in North American deserts. Wiley Interscience, New York

Shuster SM (2010) Sexual selection and mating systems. In: Avise J, Ayala F (eds) In the light of evolution III: two centuries of Darwin. National Academy of Sciences Press, Washington

Squires ZE, Bailey PEC, Reina RD, Wong BBM (2010) Compensatory growth in tadpoles after transient salinity stress. Mar Freshw Res 61:219–222

Stearns SC (1983) The evolution of life-history traits in mosquitofish since their introduction to Hawaii in 1905: rates of evolution, heritabilities, and developmental plasticity. Am Zool 23:65–75

Stearns SC, Koella JC (1986) The evolution of phenotypic plasticity in life history: predictions of reaction norms for age and size at maturity. Evolution 40:893–913

Stoks R, De Block M, McPeek MW (2006) Physiological costs of compensatory growth in a damselfly. Ecology 87:1566–1574

Therkildsen M, Riis B, Karlsson A, Kristensen L, Ertbjerg P, Purslow PP, Aaslyng MD, Oksbjerg N (2002) Compensatory growth response in pigs, muscle protein turn-over and meat texture: effects of restriction/realimentation period. J Anim Sci 75:367–377

Toguyeni A, Baroiller JF, Fostier A, Le Bail PY, Kuhn ER, Mol KA, Fauconneau B (1996) Consequences of food restriction on short-term growth variation on plasma circulating hormones in *Oreochromis niloticus* in relation to sex. Gen Comp Endocrinol 103:167–175

Toigo C, Gaillard JM, Michallet J (1999) Cohort affects growth of males but not of females in Alpine Ibex (*Capra ibex ibex*). J Mamm 80:1021–1027

Trendall JT (1982) Covariation of life history traits in the mosquitofish, *G. affinis*. Am Nat 119:774–783

Ueno H, Sato Y, Tsuchida K (1998) Colour-associated mating success in a polymorphic ladybird Beetle, *Harmonia axyridis*. Funct Ecol 12:757–761

Vondracek B, Wurtsbaugh WA, Cech JJ (1988) Growth and reproduction of the mosquitofish, *Gambusia affinis*, in relation to temperature and ration level: consequences for life history. Environ Biol Fish 21:45–57

Walling CA, Royle NJ, Metcalfe NB, Lindström J (2007) Early nutritional conditions, growth trajectories and mate choice: does compensatory growth lead to a reduction in adult sexual attractiveness? Behav Ecol Sociobiol 61:1007–1014

Yasuda H, Dixon AFG (2002) Sexual size dimorphism in the two spot ladybird beetle *Adalia bipunctata*: developmental mechanism and its consequences for mating. Ecol Entomol 27:493–498

Zulian E, Bisazza A, Marin G (1993) Determinants of size in male eastern mosquitofish (*Gambusia holbrooki*): inheritance and plasticity of a sexual selected character. Ital J Zool 60:317–322