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Matrotrophy limits a female's ability to adaptively adjust offspring size and fecundity in fluctuating environments

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Summary

1. The ability to adjust the allocation of energy to maintenance, growth and reproduction in response to fluctuations in resource availability, in a way that enhances fitness, is thought to depend on the mode of maternal provisioning.

2. We manipulated food availability in the matrotrophic, livebearing fish *Phalloptychus januarius* (Poeciliidae) to examine patterns of allocation under fluctuating resource conditions.

3. We observed an asynchrony in the adjustment of offspring traits in response to changes in food availability. A reduction in food availability caused an immediate reduction in allocation of energy to offspring size and lipid content at birth, but a delayed reduction in offspring number (fecundity). Similarly, an increase in food availability caused an immediate increase in offspring size and lipid content and a delayed increase in fecundity. This asynchrony is thought to be inherent to matrotrophy, limiting a female's ability to attain an optimal fitness in fluctuating resource environments, regardless of whether food availability changes from high to low, or low to high.

4. We found no evidence for embryo abortion under low food conditions. All developing offspring were retained, yet were smaller at birth. Furthermore, although females carried large fat reserves, these were rapidly depleted during low food conditions and were not sufficient to fully buffer gestating females or their developing offspring against the detrimental effects of reduced food availability.

5. Our study shows that matrotrophy is likely to be a maladaptive strategy in environments that are characterized by fluctuations in resource availability. It further suggests that matrotrophy is most likely to evolve in high and stable resource environments.

Key-words: capital breeding, income breeding, lecithotrophy, livebearing, placenta, Poeciliidae, Trexler–DeAngelis, viviparity

Introduction

Life-history theory is concerned with the way individuals allocate resources to metabolic maintenance, somatic growth and reproduction. Finite resources constrain the amount of energy directed to each of these three functions, resulting in at least two energy allocation trade-offs related to reproduction (Heino & Kaitala 1999). First, organisms characterized by indeterminate growth, whose fecundity increases with body size, must balance the fitness benefits of allocating resources to current reproduction versus investing in future reproductive potential by increasing female body size. Secondly, for any fixed amount of energy allocated to reproduction, organisms face a trade-off between the number of offspring they can produce and the amount of energy they can invest in each of their offspring (Lack 1947; Smith & Fretwell 1974; Lloyd 1987; Roff 1992, 2002; Stearns 1992).

In variable environments females may evolve plasticity in resource allocation to enable them to respond to short-term fluctuations in environmental conditions by adjusting investment in maternal growth, fecundity and offspring size, quality and number in a way that enhances fitness (Mousseau & Dingle 1991; Mousseau & Fox 1998). For instance, short-term adverse resource conditions often elicit a reduction of maternal growth, fat reserves and fecundity, yet at the same time an increased investment in offspring size. This ability to increase offspring size under low food conditions is likely to carry an adaptive advantage if: (i) there is a positive relationship between offspring size and offspring fitness, and (ii) the

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*Correspondence author. E-mail: b.pollux@gmail.com maternal environment is an accurate predictor of the resource environment the offspring will experience (e.g. Brody & Lawlor 1984; Hutchings 1991; Gliwicz & Guizande 1992; Kamler 1992; Reznick & Yang 1993; Ebert 1994; Bashey 2006; Taborsky 2006; Allen, Buckley & Marshall 2008; Bashey 2008; Donelson, McCormick & Munday 2008). However, this link between offspring size and maternal resource environment remains somewhat tenuous and is not always observed. While many species do display an increase in offspring size and quality in response to sudden adverse resource conditions (Brody & Lawlor 1984; Hutchings 1991; Gliwicz & Guizande 1992; Reznick & Yang 1993; Ebert 1994; Bashey 2006; Taborsky 2006; Allen, Buckley & Marshall 2008; Bashey 2008; Donelson, McCormick & Munday 2008), others tend to produce smaller offspring, a presumably maladaptive response (Henrich 1988; Reznick, Callahan & Llauredo 1996; Trexler 1997; Shine & Downes 1999; Pires, McBride & Reznick 2007).

It has been argued that the ability of females to adjust allocation of energy to maintenance, growth and reproduction in response to short-term fluctuations in resource availability, in a way that enhances offspring fitness, might be contingent on the mode of maternal provisioning. A study by Reznick, Callahan & Llauredo (1996) showed that the livebearing fishes *Poecilia reticulata* and *Priapichthys festae*, which allocate all resources necessary for embryo development prior to fertilization (a strategy referred to as lecithotrophy) responded to low food by producing larger offspring, while *Heterandria formosa*, who provisions offspring after fertilization throughout embryonic development (a strategy referred to as matrotrophy) responded by producing smaller offspring. They argued that this might be a general pattern of species with a lecithotrophic and matrotrophic life history; however, because they included only one matrotrophic and two lecithotrophic species in their study they could not discriminate between the potentially confounding effects of the mode of maternal provisioning and other interspecific differences that were independent of maternal provisioning (Reznick, Callahan & Llauredo 1996). Since then several independent origins of extensive matrotrophy have been discovered in the family Poeciliidae (Reznick, Mateos & Springer 2002; Reznick *et al.* 2007; Pollux *et al.* 2009; Pires, Arendt & Reznick 2010). Here, we take advantage of one such discovery to test the generality of our earlier hypotheses.

The mechanisms that would underlie differences in offspring size/number trade-offs between lecithotrophic and matrotrophic females remain poorly understood. The timing of offspring provisioning (pre- vs. post-fertilization provisioning) and the source of energy that supports reproduction ('Capital vs. Income breeding') are potential mediating variables that determine the response time between the change in maternal resource environment and the change to somatic growth and reproduction. Lecithotrophic females are thought to finance reproduction by female reserves, drawing down their lipid storage during oogenesis and then restore these reserves between litters ('Capital breeding strategy'), while matrotrophic females immediately divert a fraction of their energetic income to nourish their developing embryos each time they ingest food ('Income breeding strategy') (Trexler & DeAngelis 2003). Consequently, in lecithotrophic species fecundity and offspring size are determined prior to fertilization based on prior food availability. In matrotrophic species the timing at which fecundity and offspring size is determined is likely to be decoupled, with fecundity determined prior to fertilization based on current resource availability and offspring size after fertilization perhaps depending on future resource availability rather than maternal reserves, thus a decline in food availability should, in theory, have an immediate effect on offspring size (Reznick, Callahan & Llauredo 1996).

Trexler & DeAngelis (2003) proposed, based on simulation models, that gestating females of matrotrophic species would be better buffered against the effects of short-term fluctuations in resource availability if they had the ability to abort part of a developing litter when energetic resources are limited and re-allocate maternal resources to the remaining offspring and/or the ability to store large quantities of fat reserves. Both abilities would convey fitness benefits, both to the mother as well as her surviving offspring at birth, in unpredictable environments (McClure 1981; Bronson 1985; Bronson & Marsteller 1985; Schneider & Wade 1989), yet the available data on two species in the genus Poeciliopsis suggest that females cannot abort developing young (Banet & Reznick 2008; Banet, Au & Reznick 2010).

In this study, we examine the effects of fluctuations in maternal resources on energetic investment in somatic growth, maintenance and reproduction, as well as possible effects on physiological performance, in the highly matrotrophic fish species *Phalloptychus januarius* Hensel 1868 (Poeciliidae, Cyprinodontiformes). We adopt the experimental design used by Reznick & Yang (1993) for the closely related lecithotrophic guppy *Poecilia reticulata*, in which gestating females are subjected to food-manipulation treatments that simulate fluctuating resource conditions. Specifically, we address the following questions: (i) what are the effects of fluctuations in resource availability on maternal growth, somatic maintenance and locomotory performance; (ii) what are the effects and response times of fluctuating resources on phenotypic changes in offspring number, offspring size and offspring quality; and (iii) do *P. januarius* females have life-history traits, as predicted by the Trexler & DeAngelis model, that help buffer them against fluctuating resource availability? The implications of our findings will be discussed in light of the evolution of the animal placenta.

Materials and methods

STUDY ORGANISMS

The genus *Phalloptychus* occupies one of the basal branches of the Poeciliid phylogeny (Hrbek *et al.* 2007). The species used in our study, *Phalloptychus januarius*, Hensel 1868 (Poeciliidae, Cyprinodontiformes) is found in coastal drainages in Rio de Janeiro, São Paulo and Paraná States of Brazil (Lucinda & Reis 2005). *P. januarius* has a high degree of post-fertilization maternal provisioning (matrotrophy), displaying a 20- to 30-fold increase in embryo dry mass between fertilization and birth (M.N. Pires, unpublished data). In Poeciliid fishes, the post-fertilization transfer of nutrients from the mother to the offspring occurs via a placenta (Pollux *et al.* 2009). Gestation time is estimated to be *c.* 30 days based on data from closely related species (M.N. Pires, unpublished data). This species further has superfetation, or the ability to carry multiple litters in different stages of development, as well as the ability to store sperm for an indeterminate amount of time allowing us to keep females in isolation for the course of the experiment (M.N. Pires, unpublished data). The *P. januarius* used in the experiment were second and third generation laboratory-born individuals derived from laboratory stocks originally collected in the Rodrigo de Freitas Lagoon, Rio de Janeiro (Brazil) in November 2006 and held at the Fish Research Facility at the University of California Riverside.

STUDY DESIGN

Experimental subjects were reared from birth to sexual maturity in 18·9-L community tanks at a density of 15 fish of equal age per tank. As soon as the fish reached maturity they were isolated in 8-L aquaria, one male and one female per tank, and kept on an *ad libitum* diet of liver paste and brine shrimp until the start of the experiment, at which time the males were removed. To ensure a sufficient supply of viable sperm during the experiment females were remated (overnight) every 2 weeks.

To evaluate the effect of fluctuating food availability on life-history traits we performed a 12-week experiment, in which females were assigned to either a 'low-food' or a 'high-food' ration for the first 6 weeks then randomly reassigned to a low or high food ration for the next 6 weeks, generating four experimental food treatments: high-high (HH), high-low (HL), low-high (LH) and low-low (LL). There was a fourfold difference in food quantity between the low and high food treatments, consisting of either 30 μL (low food) or 120 μL (high food) liver paste in the morning and 30 μL or 120 μL of newly hatched brine shrimp (*Artemia* nauplii; M & M Suppliers, Bothell, Washington, USA) in the afternoon. Preliminary experiments indicated that the low food rations were sufficient to sustain reproduction while the high food rations were close to *ad libitum* feeding. We used 500-μL Hamilton micropipettes to dispense volumetric food quantities to each tank. The experiment followed a randomized complete blocks (RCB) design (Sokal & Rohlf 2001) with 15 blocks of four females (of similar age and size) randomly assigned to the four treatments.

Female length (to the nearest mm) and wet mass (to the nearest mg) were measured at the start of the first and second food periods as well as at the end of the 12-week experiment. Experimental tanks were checked daily for the presence of newborn young and all litters were immediately euthanized in an overdose MS-222 (Sigma-Aldrich Co., St. Louis, Missouri, USA) and preserved in 5% formaldehyde (Fisher Scientific, Fair Lawn, New Jersey, USA) until further analysis (Reznick 1983; Reznick & Yang 1993). The offspring dry weight was determined by air-drying the offspring overnight at 60 °C in a drying oven, then weighing them to the nearest 0·01 mg on a Mettler® AE 163 Microbalance (Mettler Instruments Corp., Hightstown, New Jersey, USA). Lean dry weights were measured by extracting the fat twice with anhydrous ethyl ether (Fisher Scientific) to remove triglycerides, and subsequently air-drying and re-weighting the offspring (as above). The fat content, expressed as the offspring lipid percentage, was calculated by dividing the difference between the dry (DW) and lean weights (LW) of the offspring by their dry weights, then multiplying these values by a hundred.

On the last day of the 12-week food-manipulation experiment, each female was subjected to a swimming performance test (modified after Beamish 1978; Plaut 2001). Critical swimming speed (U_{crit}) trials were conducted using a 55-L, re-circulating swim tunnel modified after Brett (1964, 1967). The tunnel system consisted of a vertically standing loop of polyvinyl chloride (PVC) pipes, with a clear acrylic swim chamber on top (dimensions L × W × H: 119·5 × 15·3 × 18·3 cm). The fish swam in a 12 × 15·3 × 11·5 cm section of the acrylic chamber, with plastic flow filters at both ends. These flow filters reduced turbulence and promoted a consistent rectilinear flow profile along the swim chamber over the range of velocities used in the trials. A submersible propeller motor (Bodine® Series 600 Type NSH-55; Chicago, IL, USA) was used to generate water flow. Flow velocity was regulated with a Minarik® Electric drive (Model SLF61; Los Angeles, CA, USA), which controlled the frequency of rotation of the propeller motor. Females were transferred from the experimental tanks to the swim chamber where they remained for 10 min at a low flow velocity of 8·89 cm s^{-1}. During this acclimation period the females recovered quickly from handling and oriented themselves against the water current. Following the acclimation period, the flow velocity was increased by 4·5 cm s^{-1} every 3 min until the fish was fatigued (defined as the inability to escape from the downstream grid after three consecutive taps on the side of the tunnel). Once a fish was fatigued, it was removed from the swim tunnel. Critical swimming speeds were calculated using an equation described by Brett (1964): $U_{crit} = U_i + [U_{ii}(T_i/T_{ii})]$, where U_i is the highest velocity maintained during the swim trial, U_{ii} is the speed increment by which the velocity is increased, T_i is the time elapsed at the final velocity, and T_{ii} is the interval time. No solid blocking correction was applied since the fish in this study occupied < 10% of the cross-sectional area of the swimming chamber (Webb 1971). To exclude any effect of feeding status on swimming performance, fish were food-deprived for 24 h prior to the swimming trials. Water temperature was recorded throughout each swimming trial (mean ± SD over all trials: 22·4 ± 0·4 °C) and used as a potential covariate in the statistical analyses.

Immediately after the swimming test, females were sacrificed in an overdose MS-222 and preserved in 5% formaldehyde. The females were dissected as described in Reznick (1983). Reproductive tissues, which included yolking ova as well as multiple developing litters in different developmental stages, were separated from somatic tissues. The tissues were dried overnight at 60 °C and the somatic and reproductive dry masses were measured to the nearest 0·01 mg. The reproductive allotment (RA) was calculated by dividing the dry mass of the reproductive tissues by the total dry mass of the female. The fat content of the females was estimated by repeatedly extracting the dried reproductive and somatic tissues with anhydrous ethyl ether following the same protocol used for the offspring.

STATISTICAL ANALYSES

Unless otherwise specified, the effects of food availability during food period 1 (FP1; weeks 1–6) and food period 2 (FP2; weeks 7–12) on the dependent variables of interest were analysed by means of General Linear Mixed Models, using the MIXED procedure (SAS version 9.2; SAS Institute Inc., Cary, North Carolina, USA. 2007).

Changes in female length and female wet mass throughout the experiment were assessed using mixed model repeated measures analyses of variance (RMANOVA), with food availability (four levels: HH, HL, LH, LL), time (three levels: 0, 6, 12 weeks) and their interaction effect included as a fixed effects, block as a random effect (15 levels) and female as the subject effect (Littell, Henry & Ammerman 1998).

Female lipid content, lean somatic dry mass and reproductive allotment at the end of the experiment were analysed using mixed model analyses of variance (ANOVA) with food availability during FP1 (two levels: high and low) and FP2 (two levels: high and low) and their interaction effect (FP1 × FP2) included as fixed effects, block as a random effect (15 levels) and the respective female trait variables at the end of the second food period as dependent response variables. Critical swimming velocity at the end of the experiment was analysed using a mixed model analysis of covariance (ANCOVA), in which female length, female wet mass, reproductive allocation and water temperature were included as potential covariates. The most complicated models, which included all four covariates, were fitted first and then simplified by back-fitting (the sequential step-wise removal of the single non-significant covariate that explains the least variance) until a model containing only significant covariates was identified. Back-fitting releases degrees of freedom, thereby increasing power for testing main effects (McCulloch & Searle 2001).

The dependent variables that characterize the offspring (i.e. fecundity, offspring dry mass and fat content) were analysed using mixed model analyses of covariance (ANCOVA). We defined fecundity as the total number of young produced by each female over each 5-day period of the experiment, and is therefore the product of both litter size (the number of offspring per litter) and the frequency of litter production. The effect of food availability on the dependent variables was assessed both at the end of the first and at the end of the second food period. The first analysis included food availability during FP1 (two levels: high and low) as a fixed effect, block as a random effect (15 levels) and female wet mass at the end of FP1 as a covariate. The second analysis included food availability during FP1 and FP2 (two levels: high and low), as well as their interaction effect (FP1 × FP2), as fixed effects, block as a random effect and female wet mass at the end of FP2 as a covariate. Since the data on offspring production were count data (non-negative integer values) that were not normally distributed, they were analysed by fitting Generalized Linear Mixed Models to the data, using the GLIMMIX procedure in SAS 9.2 with a Poisson error distribution and log link function (Littell *et al.* 2006). Goodness-of-fit of the Poisson models was assessed by checking the overdispersion parameter, Φ (generalized χ^2/df). Ideally, Φ should be equal to 1 and large departures from this value indicate that the data are overdispersed. Examination of the overdispersion parameter indicated strong model fits, with Φ falling between 1·18 and 1·33 for all Poisson regression analyses in our study (Littell *et al.* 2006).

To evaluate differences among treatments, pairwise *post hoc* analyses were performed with a Bonferroni significance level adjustment. The data of female and offspring fat content and female reproductive allotment were transformed (arc-sine square-root proportions) prior to the analyses to conform to the assumptions of the analysis of variance. There were initially 15 individuals for each of the four treatment groups, however, some individuals got sick or died from jumping out of their tanks over the course of the experiment and were subsequently omitted from the statistical analyses. In addition, three females refused to swim at the end of the experiment and were excluded from the statistical analysis on critical swimming velocity (U_{crit}). Consequently, the degrees of freedom may vary among analyses and tend to decline over the course of the experiment.

Results

FEMALE LENGTH AND WET MASS

Female length and wet mass were affected by both food treatment (length: $F_{3,134} = 2{\cdot}61$, $P = 0{\cdot}036$; wet mass: $F_{3,134} = 9{\cdot}44$, $P < 0{\cdot}001$) and time (length: $F_{2,134} = 108{\cdot}57$, $P < 0{\cdot}001$; wet mass: $F_{2,134} = 2{\cdot}94$, $P = 0{\cdot}056$). High food conditions typically allowed the female to grow (leading to an increase in length and wet mass), whereas low food conditions inhibited female growth, causing a cessation of length increase and a decline in wet mass, respectively (Fig. 1a,b). Significant treatment-by-time interaction effects (length: $F_{6,134} = 36{\cdot}59$, $P < 0{\cdot}001$; wet mass: $F_{6,134} = 49{\cdot}88$, $P < 0{\cdot}001$), revealed an effect of the order in which females were subjected to different food levels. Females receiving first high and then low food were significantly smaller and lighter at the end of the experiment than females receiving first low and then high food (HL vs. LH: length, $P = 0{\cdot}018$; wet mass, $P < 0{\cdot}001$; Fig. 1a,b), despite receiving an equal amount of food over the course of the experiment. This difference was due to a striking 'catch-up' growth of low-high females during the second period, at the end of which females attained a

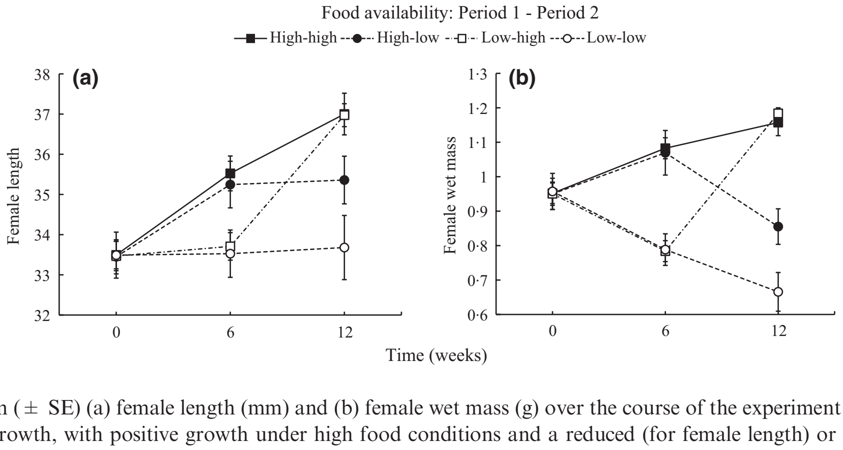

Fig. 1. Changes in mean (± SE) (a) female length (mm) and (b) female wet mass (g) over the course of the experiment reveal an effect of food availability on female growth, with positive growth under high food conditions and a reduced (for female length) or negative (for wet mass) growth under low food conditions. Black and white markers represent females that received high and low food, respectively, during food period 1; squares and circles signify females that received high and low food during food period 2.

length and wet mass that was not significantly different from high-high females (LH vs. HH: length, $P = 0{\cdot}844$; wet mass, $P = 0{\cdot}566$; Fig. 1a,b).

FEMALE SOMATIC LEAN DRY MASS

Female somatic lean dry mass was significantly affected by food availability during the second ($F_{1,31} = 73{\cdot}23$, $P < 0{\cdot}001$) but not the first food period ($F_{1,31} = 2{\cdot}39$, $P = 0{\cdot}133$), with females receiving high food during the second period having a higher somatic lean dry mass at the end of the experiments than females that received low food during period 2 (Fig. 2a). A significant interaction term (FP1 × FP2: $F_{1,31} = 6{\cdot}56$, $P = 0{\cdot}015$) indicated a significant effect of the order in which females were subjected to different food levels. Again, females receiving first high and then low food had a significantly lower somatic lean dry mass at the end of the experiment than females receiving first low and then high food (HL vs. LH: $P < 0.001$; Fig. 2a), despite receiving an equal amount of food over the course of the experiment. At the end of the second period low-high females had attained a somatic lean dry mass that was not significantly different from high-high females (LH vs. HH: $P = 0{\cdot}474$; Fig. 2a).

FEMALE LIPID CONTENT

The quantity of fat stored in the females was significantly affected by food availability during the second ($F_{1,31} = 32{\cdot}65$, $P < 0{\cdot}0001$), but not the first food period ($F_{1,31} = 0{\cdot}98$, $P = 0{\cdot}330$) nor by a period 1 by period 2 interaction effect (FP1 × FP2: $F_{1,31} = 0{\cdot}48$, $P < 0{\cdot}496$). Females that received high food during the second period had more fat reserves at the end of the experiment than females that received low food (Fig. 2b).

REPRODUCTIVE ALLOTMENT

The reproductive allotment (expressed as the proportion of female mass allocated to reproduction) was significantly affected by food availability during the second ($F_{1,30} = 9{\cdot}00$, $P = 0{\cdot}005$), but not the first food period ($F_{1,30} = 2{\cdot}04$, $P < 0{\cdot}164$) nor by a period 1 by period 2 interaction effect ($F_{1,30} = 1{\cdot}03$, $P = 0{\cdot}318$). Females that received high food during the second period had a higher reproductive allotment at the end of the experiment than females that received low food (Fig. 2c).

FEMALE CRITICAL SWIMMING VELOCITY

Back-fitting identified a minimal model containing only female length as a significant covariate ($F_{1,25} = 6{\cdot}20$, $P = 0{\cdot}019$). When adjusting for female length, the critical swimming speed (U_{crit}) of a female was significantly influenced by the second ($F_{1,25} = 7{\cdot}09$, $P = 0{\cdot}013$) but not the first food period ($F_{1,25} = 0{\cdot}65$, $P = 0{\cdot}428$), with females receiving high food during the second period having a higher critical swimming performance at the end of the experiments than females that received low food during period 2 (Fig. 2d). A significant interaction effect (FP1 × FP2: $F_{1,25} = 6{\cdot}20$, $P < 0{\cdot}019$) indicated that the strength of this effect was dependent upon the food availability during the first food period (Fig. 2d). Specifically, the switch from low to high rations (LH treatment) was associated with an

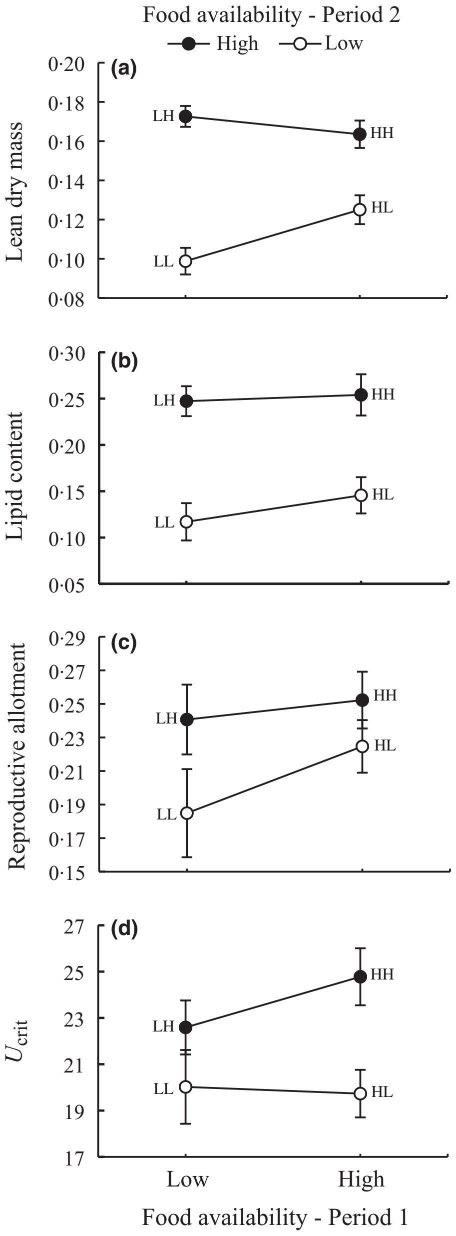

Fig. 2. Mean (± SE) trait values characterizing the females at the end of the food-manipulation experiment, as a function of food availability during the first and second periods: The *x*-axis represents food availability during the first food period (weeks 1–6) and the two different lines represent food availability during the second period (weeks 7–12; black marker = high food, white marker = low food). (a) Female lean somatic dry weight (g), (b) female lipid content (calculated as the proportional loss in somatic dry mass after repeated extraction with anhydrous ether), (c) reproductive allotment (the proportion of female mass devoted to reproductive tissues), and (d) critical swimming velocity (cm s^{-1}; means adjusted for female length).

increase in critical swimming speed, but not enough for them to equal the performance of the HH treatment group (Fig. 2d).

FECUNDITY

Fecundity at the end of the experiment was significantly affected by the first ($F_{1,28} = 15·35$, $P < 0·001$), but not the second food period ($F_{1,28} = 0·06$, $P = 0·811$) nor by a period 1 by period 2 interaction effect ($F_{1,28} = 0·57$, $P = 0·455$). Female mass was not a significant covariate predictor of fecundity ($F_{1,28} = 0·05$, $P = 0·816$). Low food during the first period caused a decline in fecundity; however, this effect did not manifest itself until the second period (i.e. 55–59 days after the start of the treatment; Fig. 3a). The effect of the first period extended to the end of the second period, with females that received low food during period 1 having a significantly lower fecundity than females that received high food (Fig. 3a).

OFFSPRING SIZE AND OFFSPRING LIPID CONTENT

Offspring size at the end of the experiment was significantly influenced by both the first ($F_{1,103} = 30·30$, $P < 0·001$) and the second food period ($F_{1,103} = 48·76$, $P < 0·001$). Low food typically resulted in an immediate decline of offspring size (Fig. 3b). Female mass was not a significant covariate predictor of offspring size ($F_{1,103} = 3·75$, $P = 0·056$). A significant period 1 by period 2 interaction term (FP1 × FP2: $F_{1,103} = 10·08$, $P = 0·002$) indicated an effect of the order in which females were subjected to different food levels. Females receiving first high and then low food gave birth to significantly smaller offspring at the end of the experiment than females receiving first low and then high food (HL vs. LH: $P < 0·001$; Fig. 3b), despite receiving an equal amount of food over the course of the experiment. This difference was because of a decrease in offspring size at birth of high-low females during the second period and, most notably, a striking and rapid increase in the size of offspring of low-high females during the same period (Fig. 3b). At the end of the experiment low-high females even produced offspring that were significantly larger than those of high-high females (LH vs. HH: $P < 0·001$; Fig. 3b).

Low food also led to an immediate decline in offspring lipid content (Fig. 3c). However, offspring lipid content at the end of the experiment was only influenced by the second ($F_{1,103} = 9·23$, $P = 0·003$) and not the first period ($F_{1,103} = 1·80$, $P = 0·183$), nor by a period 1 by period 2 interaction effect ($F_{1,103} = 0·86$, $P = 357$; Fig. 3c). Female mass was not a significant covariate predictor of offspring lipid content ($F_{1,103} = 0·02$, $P = 0·896$).

Discussion

The mode of maternal provisioning may dictate how and when a female can allocate energy to reproduction, somatic growth and maintenance of a female's physical conditioning in a fluctuating resource environment (Reznick, Callahan & Llauredo 1996). We examined patterns of allocation by the matrotrophic fish *Phalloptychus januarius* in response to changes in food availability. We show that under the experimental conditions used in our study matrotrophy is likely to be a maladaptive strategy.

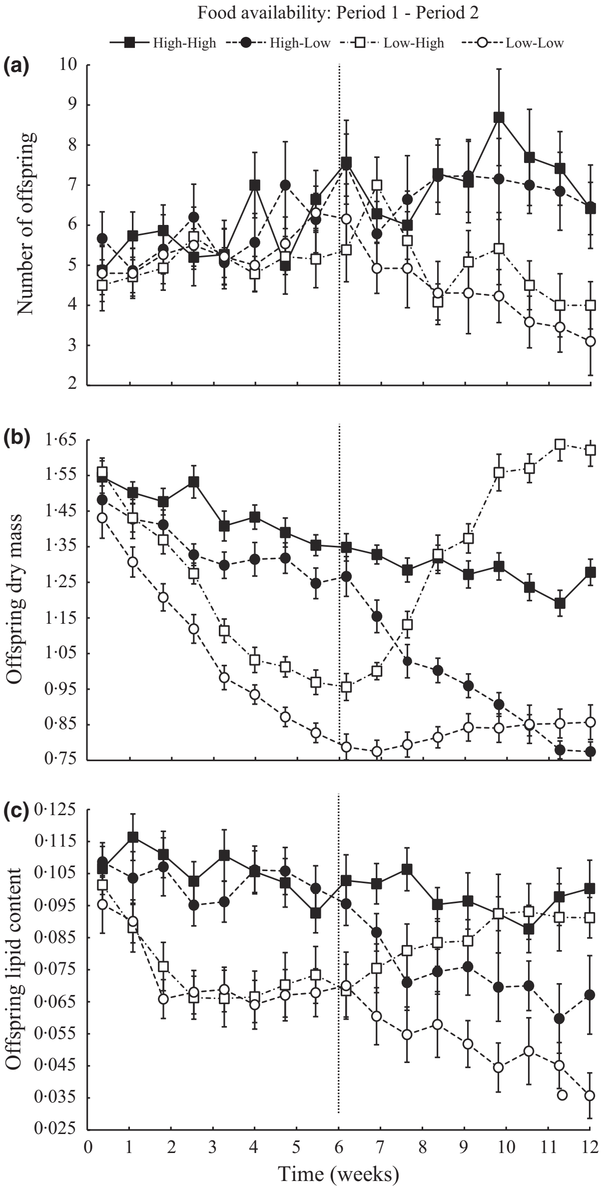

Fig. 3. Changes in mean (± SE) offspring characteristics over the course of the experiment reveal differences in response time to changes in food availability, with a delayed effect on (a) fecundity (expressed as the number of offspring produced over each 5-day interval), and an immediate effect on (b) offspring dry mass (g) and (c) offspring lipid content (expressed as the proportional loss in somatic dry mass after repeated extraction with anhydrous ether). Black and white markers represent females that received high and low food, respectively, during food period 1; squares and circles signify females that received high and low food during food period 2.

MODEL OF ALLOCATION

Fluctuations in food availability elicited phenotypic changes in resource allocation to growth, maintenance and reproduction (fecundity, offspring size and offspring quality). The response time between the change in food availability and the phenotypic adjustment, however, differed significantly among these traits. For example, the time interval between fertilization and birth in poeciliid fishes ranges from 3 to 5 weeks based on the intervals between successive broods in species that lack superfetation (Reznick & Miles 1989). A decline in offspring number in 3–5 weeks after the start of the experiment would thus indicate that a female immediately adjusts the number of fertilized eggs when encountering low food conditions, because young born around this time will have initiated development at the start of the experiment. In this study, a decline in fecundity was not evident until 55–59 days after the reduction in food availability (Fig. 2a), meaning that females continue to initiate a number of offspring commensurate with a high food ration for weeks after ration level declined. This result implies a time-lag of *c.* 20–30 days between the start of the food treatment and the actual adjustment in the number of fertilized eggs. It is conceivable that this lag reflects a bet-hedging strategy in which a female, rather than immediately lowering her fecundity, bets on the possibility that the drop in food level is short-lived and will improve before the current broods complete gestation. By contrast, the response in offspring size and offspring 'quality' (expressed as offspring lipid storage) was immediate, meaning that a reduction in food availability results in the immediate production of smaller offspring that have significantly lower fat reserves (Fig. 2b,c). These results are consistent with the earlier results for another placental species (*Heterandria formosa*; Reznick, Callahan & Llauredo 1996) and suggest that 'income breeding', or the provisioning of offspring based on the immediate availability of resources, may be a common attribute of placental species.

The asynchrony between the determination of offspring number (delayed effect) and offspring size and quality (immediate effects) causes dramatic differences among treatments in female size and offspring size at birth. Females that received low then high food rations (LH treatment) produced extremely large offspring at the end of FP2. This is because at the end of the first food period they had initiated fewer offspring (delayed effect of low food), then experienced an increase in food availability leaving them with a surplus of resources. The surplus allowed them to allocate an excessive amount of resources to their offspring. The combination of small litters and abundant resources thus lead to fewer, but excessively large offspring in comparison to females that received continuous high food rations (HH treatment). In addition to providing extra nourishment to their offspring, these females allocated part of the surplus of resources to their own somatic growth leading to remarkable increases in female length, female wet mass, and female somatic lean dry mass (see significant interaction terms in the Results section, see also Fig. 2a–c). The rapid 'catch-up' growth of LH females (Fig. 1) at the end of the study suggests a metabolic response to food availability during the first time interval: Females appeared to have reduced their metabolic rate by the end of first (low) food period, thus making them more efficient at converting consumed food into biomass during the second (high) food period, leading to a remarkably fast growth (Miller & Wise 1976; Ali, Nicieza & Wootton 2003; Fig. 1).

By contrast, females that first received high and then low food (HL treatment) were smaller and lighter and produced significantly smaller offspring with lower fat reserves at the end of the experiment, despite receiving an overall equal amount of food as the LH fish over the course of the experiment. This is because by the end of the first food period the HL females had initiated many developing offspring, then experienced restricted food levels leaving them with scarce resources to nourish their developing offspring. Because they did not abort any developing young, the lack of sufficient resources ultimately led to the production of extremely small offspring with very few lipid reserves; notably, their offspring were only half the dry mass of the extremely large offspring produced by LH females (Fig. 3b). Offspring size in income breeders with extensive post-fertilization maternal provisioning thus depends on the interplay between delayed effects on fecundity and immediate effects of current energetic income available to reproduction.

Empirical research has revealed that the influence of offspring size on fitness can depend on resource availability. If resources are abundant, then size at birth may have little influence on fitness. If resources are scarce, however, then a larger offspring size may confer a competitive advantage to the offspring, allowing them to survive longer under low food conditions (amphibians: Parichy & Kaplan 1992; fish: Bashey 2006, 2008; insects: Fox, Thakar & Mousseau 1997; *Daphnia*: Gliwicz & Guisande 1992). Previous work on guppies *Poecilia reticulata* supports these conclusions. Guppies are lecithotrophic and respond to low food rations by producing larger offspring (Reznick & Yang 1993; Bashey 2006). Larger offspring have a significant competitive advantage when they are reared with smaller offspring on low food rations. This advantage disappears, however, when small and large offspring are reared together at high food conditions (Bashey 2006, 2008). On the basis of this prior research, the response of *P. januarius* to changes in food availability appears to be maladaptive. They respond to a reduction in food availability by producing many but small offspring, which, in a low resource environment, are likely to have a reduced fitness relative to larger offspring. Conversely, the production of a few, extremely large offspring following an increase in food availability, is also likely to be disadvantageous, because the advantage of large size at birth weakens or even disappears (i.e. the slope of the relationship approaches zero) with increasing quality of the environment experienced by the offspring at birth (Ferguson & Fox 1984; Parker & Begon 1986; Sibly & Calow 1986). Hence, in the latter case, the cost of reduced fecundity will not be compensated for by an increase in offspring fitness.

This study provides a clear mechanistic insight into the shifting patterns of resource allocation to different physiological needs in matrotrophic species that live in a fluctuating resource environment. A key finding of our study is that the asynchrony between the response in fecundity and offspring size and quality to a change in food availability causes matrotrophic species to respond 'inappropriately' to changes in food availability: i.e. matrotrophic species are unlikely to ever attain their optimal fitness in fluctuating resource environments, regardless of whether food availability changes from high to low or, conversely, from low to high. Although natural fluctuations may be shorter or longer than the 6-week interval we used in our study, our results show that a change in food availability will always elicit an immediate response in offspring size and quality. Moreover, there will be at least a transient reduction in fecundity in response to a change in resource availability that lasts longer than 3–4 weeks. Matrotrophy thus appears to be a maladaptive strategy in environments that are characterized by fluctuations in resource availability.

Reznick, Callahan & Llauredo (1996) were the first to observe that the timing at which fecundity and offspring size is determined was decoupled in the matrotrophic species *H. formosa*. However, at the time they were unable to state whether this was a common property of matrotrophic species, because the restricted sample size in their study (one matrotrophic vs. two lecithotrophic species) precluded any discrimination between the potentially confounding effects of the mode of maternal provisioning and other interspecific differences that were independent of maternal provisioning. In this study we examined a second matrotrophic species, *P. januarius*, which evolved its placenta independently from *H. formosa* (Hrbek *et al.* 2007). Because we found similar results for both matrotrophic species, we propose that the asynchronic adjustment of fecundity, offspring size and offspring quality is likely to be a general property of matrotrophic species. Our findings herewith provide direct empirical support for Trexler & DeAngelis' (2003) prediction that matrotrophy is most likely to evolve under high and stable resource conditions.

EVALUATING PREDICTIONS OF THE TREXLER & DEANGELIS MODEL

Trexler & DeAngelis (2003) postulated that the stringent environmental conditions that favour the evolution of matrotrophy might be relaxed if its evolution were preceded by, or coincided with, the ability to abort developing embryos, resorb their energy and redistribute it to growth and reproduction and/or store large energy reserves. To date, such abilities have not been established in livebearing fishes.

In our study, embryo abortion and resorption would have manifested itself by a decrease in offspring number within a 3–5 week period after switching from high to low food, because the gestation time of *P. januarius* is estimated to be *c.* 3–5 weeks (Reznick & Miles 1989). Such a decline was not observed, which suggests that *P. januarius* cannot abort offspring when encountering low food conditions. Our results are consistent with recent studies in two clades of the fish genus *Poeciliopsis* (Banet & Reznick 2008; Banet, Au & Reznick 2010), each clade representing an independent origin of matrotrophy (Reznick, Mateos & Springer 2002). Thus, current evidence from two different genera (*Phalloptychus* and *Poeciliopsis*), together representing three independent matrotrophic lineages, shows that in the family Poeciliidae the evolution of matrotrophy does not necessarily coincide with the evolution of embryo abortion. The absence of a facultative ability to abort and resorb offspring considerably narrows the conditions that favour the evolution of the placenta under Trexler & DeAngelis' theoretical model.

Trexler & DeAngelis (2003) further predicted that 'energy storage as fat might serve to buffer matrotrophs from fluctuation of food availability'. The idea behind this prediction is that matrotrophic species utilize these lipid reserves as a spare source of energy when energetic income from external sources becomes insufficient (an 'emergency fund'), enabling them to weather short periods of unfavourable conditions. The need for extensive fat reserves should be lower in lecithotrophic species because they furnish their offspring with all the required resources prior to fertilization (capital breeding strategy) and, thus, never carry the double burden of simultaneously having to allocate resources to reproduction and growth. A comparison of our results with those found in a similarly designed food-manipulation study for the lecithotrophic Trinidadian guppy *P. reticulata* (Reznick & Yang 1993) provides tentative evidence in support of this hypothesis. In consistently high food conditions, *P. januarius* maintained higher fat reserves than the lecithotrophic guppy (proportion lipid reserves: 0·25 vs. 0·17, respectively). More importantly, when experiencing a shift in resource conditions from high to low food availability, *P. januarius* showed a more than two times higher rate of loss of fat reserves than the guppy, with a relative loss of lipid reserves of 48% in *P. januarius* (this study) versus 22·8% in the guppy (Reznick & Yang 1993). Thus, it appears that matrotrophic species (i) maintain higher fat reserves under stable food conditions, and (ii) show a more dramatic depletion of lipid reserves under declining food conditions, compared to lecithotrophic species. We found similar differences in maintenance and employment of fat reserves between other closely related Poeciliid species that were either lecithotrophic or matrotrophic and that represent independent evolutionary origins of placentation (B.J.A. Pollux, unpublished data). Finally, Banet & Reznick (2008) and Banet, Au & Reznick (2010) also observed higher lipid stores in matrotrophs compared to lecithotrophs in two different clades within the genus *Poeciliopsis*. The generality of these results argues that a higher fat reserve has evolved in concert with the evolution of matrotrophy.

However, our study also revealed that these higher fat reserves were not sufficient to fully buffer matrotrophic females against fluctuations in resource availability. Under the conditions used in our experiment, a reduction in food availability appeared to have an unequivocally detrimental effect on both the mother and her developing offspring despite the initial presence of high fat reserves. A short period of reduced food availability led to an immediate decline in offspring size and offspring lipid content, an immediate cessation of female growth and a reduction in wet mass, dry somatic lean mass and reproductive allotment. In addition, low food negatively affected a female's swimming performance. The critical swimming velocity is a measure of a fish' physical condition in terms of sustained locomotory performance and is often measured as a correlate of fitness (Brett 1964; Taylor & McPhail 1985; Taylor & Foote 1991; Plaut 2001; Seiler & Keeley 2007). Low food females had a lower critical swimming velocity at the end of the experiment, despite being leaner and having a lower reproductive burden. This means that fluctuations in resource availability not only incur fitness costs to females through a reduction in fecundity and/or offspring size and quality, but also through a reduction of a female's sustained swimming performance. The observed detrimental effects on female growth, maintenance of somatic tissues, locomotory performance and reproductive potential clearly show that matrotrophic females allocate fewer resources to maintaining their own metabolic functions and physical fitness when resources become limited, yet that they were still not able to sustain the growth and birth weight of developing embryos. Thus, although matrotrophic species carry higher fat reserves, it appears that these reserves do not fully buffer pregnant females against detrimental effects of short-term episodes of reduced food availability.

It should be noted that the set of conditions used in our study to simulate fluctuations in food availability (i.e. a single periodicity of fluctuation characterized by a 6-week food interval and a fourfold difference in food availability) is merely one of a continuum of possible sets of fluctuating conditions that occur in nature. It is conceivable that there is a restricted range of environmental conditions where matrotrophy is not (as) maladaptive, such as under very weak and/or very short-lived reductions in food level where female lipid reserves may serve as a sufficient buffer against fluctuations in resource availability.

DIRECTIONS OF FUTURE RESEARCH

In the family Poeciliidae, matrotrophy appears to be associated with superfetation, a second reproductive strategy that refers to the ability of females to carry multiple broods at different developmental stages (Reznick & Miles 1989; Pollux *et al*. 2009; Pires, Arendt & Reznick 2010). Superfetation might impose different energetic demands on females during reproduction (Trexler & DeAngelis in press), although results reported by Reznick, Callahan & Llauredo (1996) suggest that superfetation alone is not likely to affect the pattern of maternal provisioning. To further validate the generality of our findings as well as tease apart the potentially confounding effects of matrotrophy and superfetation on energy allocation under fluctuation resources, we propose that future studies use a comparative framework that integrates both reproductive strategies; i.e. by performing food-manipulation experiments that include closely related species that differ in their degree of matrotrophy and superfetation and originate from independent matrotrophic and superfetatious lineages within the family.

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