

Tradeoffs Between Somatic and Gonadal Investments During Development in the African Clawed Frog (*Xenopus laevis*)

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ABSTRACT Tradeoffs between time to and size at metamorphosis occur in many organisms with complex life histories. The ability to accelerate metamorphosis can increase survival to the next life stage, but the resulting smaller size at metamorphosis is often associated with lower post-metamorphic survival or reduced fecundity of adults. Reduced fecundity is thought to be because of reduced energy reserves, longer time to maturity, or reduced capacity to carry eggs or compete for mates. This pattern could *also* be explained by a shift in allocation to somatic growth that further retards the growth or development of reproductive tissues. The main goal of this study was to determine if the relationship between growth and development of somatic and gonadal tissues depends on environmental conditions. We address this question through two experiments in which we quantify the development and growth of the body and gonads of *Xenopus laevis* reared in different resource environments. First, tadpoles were reared communally and development and growth were evaluated over time. Restricted food reduced somatic and gonadal growth rate, but did not affect the developmental rate of either tissue type. Second, tadpoles were reared individually and evaluated at metamorphosis. Restricted food reduced somatic development and growth, but only influenced size, and not developmental stage of testes at metamorphosis. This work demonstrates that environmental conditions influence tradeoffs between growth and development of somatic and gonadal tissues, apparently in a sex-specific manner. These tradeoffs may contribute to phenotypic correlations between small size and reduced fitness *J. Exp. Zool.* 307A:637-646, 2007. © 2007 Wiley-Liss, Inc.

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Life history tradeoffs occur when a beneficial change in one trait leads to a change in a second trait that is correlated with a reduction in lifetime fitness (Stearns, '89). Such tradeoffs are common in (but not limited to) environments where organisms face a high probability of mortality (Reznick, '85; Stearns, '89). One well-studied example of the cost of diverting limited resources toward increasing survival at the expense of reproduction involves the tradeoff between size at and time to metamorphosis observed in organisms that have complex life histories (Rowe and Ludwig, '91; Alford, '99; Benard, 2004). The ability to metamorphose early and at a small size can increase the probability of survival to the adult phase, especially in ephemeral habitats. However, in a variety of taxa, small size at

metamorphosis is known to be negatively correlated with adult survival and fecundity, and thus lifetime fitness (Moeur and Istock, '80; Blakley, '81; Smith, '87; Flecker et al., '88; Semlitsch et al., '88; Berven, '90; Scott, '94). For example, in milkweed bugs (*Oncopeltus* spp.) mass at metamorphosis is strongly positively correlated with adult survival and ability to tolerate periods

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of starvation, which facilitates dispersal and host-finding by reproductive females (Blakley, '81).

The tradeoffs between size at and time to metamorphosis and their fitness consequences have been extensively studied in amphibians from both theoretical and empirical perspectives (Wilbur and Collins, '73; Travis, '84; Hensley, '93; Leips and Travis, '93; Twombly, '96). Empirically, the relationship between metamorph size or age and adult fecundity has been studied by tracking individuals from metamorphosis through reproductive maturity. For example, chorus frogs (*Pseudacris triseriata*) that were small at metamorphosis experienced delayed maturity, whereas those that metamorphosed at larger sizes were more likely to reach maturity and reproduce in their first year (Smith, '87). In a 7-year study, wood frogs (*Rana sylvatica*) that metamorphosed earlier and at larger sizes experienced higher survival rates to adulthood, and were larger as adults (Berven, '90). Similarly, in another 7-year study on adult demographic traits of marbled salamanders (*Ambystoma opacum*), Scott ('94) showed that animals in low-density treatments metamorphosed larger, had higher lipid stores at metamorphosis, arrived at breeding ponds at younger ages, and had larger clutches than those animals raised as larvae in high density environments. These studies showed that conditions experienced in the larval environment affected size at and time to metamorphosis. Animals that were small at metamorphosis had lower survival and reproductive success and were smaller as adults.

Reduced fitness in organisms that metamorphose small could be due to differences in size (lower capacity to carry eggs for females or reduced mate access in males), reduced energy reserves (lipids), or increased time to maturation (Moeur and Istock, '80; Blakley, '81; Scott, '94). This pattern could also be induced by a shift in the allocation of resources to growth and development of somatic versus reproductive tissues. Larvae in suboptimal environments could allocate more energy to development of somatic structures necessary for metamorphosis and survival (e.g. limbs and carnivorous gut) at the expense of growth or development of gonads (because they are not immediately required for survival; e.g. Kaitala, '91). As a result, additional gonadal growth or development would have to occur during post-metamorphic life, which could increase age at first reproduction, alter clutch size and fecundity, and reduce post-metamorphic

somatic growth. The existence of tradeoffs between larval somatic and gonadal development could provide an underlying mechanism for phenotypic correlations between growth and reproduction (Reznick, '83); nonetheless these tradeoffs remain relatively unstudied.

The goals of this study were to determine (1) whether tadpoles exhibit plasticity in the development and growth of their gonads; (2) if under stressful environmental conditions (food limitation) somatic development and growth is favored while gonadal development and growth is sacrificed (i.e. there is an apparent tradeoff between investment in somatic versus gonadal growth and development); (3) if in food-restricted treatments development of the gonad is favored while gonadal growth is limited (i.e. are there tradeoffs between growth and development within the gonad); and (4) whether metamorphs fed a restricted diet through their larval period have smaller, less well-developed gonads than those fed large quantities of food. We address these questions in two experiments that manipulated larval rearing conditions (e.g. low vs. high food). In the first, we examined developmental and growth rates of the body and gonads of *Xenopus laevis* larvae; in the second, we examined gonadal developmental stage and size at metamorphosis as well as time to, and (body) size at metamorphosis.

METHODS

Experiment 1: larval traits

To test the hypotheses that in food restricted environments tadpoles (1) develop and grow gonads more slowly than those raised in less restricted food conditions (occurrence of plasticity); (2) favor growth and development of somatic tissue rather than reproductive tissue; and (3) favor gonadal development rather than gonadal growth, we raised *X. laevis* tadpoles in low- and high-food treatments.

In each of ten aquaria (five high and five low food) we raised five *X. laevis* tadpoles in 10 L of reconstituted reverse osmosis (RO) filtered water (one tadpole/2 L; rearing details below). At each sampling (approximately every 2 weeks) all the individuals from one randomly chosen high- and low-food treatment tank were weighed, somatically staged according to Nieuwkoop and Faber (Nieuwkoop and Faber, '56), and fixed in 10% buffered formalin. The size (width) and developmental stage (degree of differentiation)

of fixed gonads were evaluated histologically (described below). This design allowed us to determine the relationship between somatic and gonadal growth and development (through time) for each food treatment.

Experiment 2: metamorphic traits

To test the hypothesis that frogs reared on a restricted diet would have less developed or smaller gonads at metamorphosis than those fed larger quantities, we reared 30 tadpoles (ten per treatment—housed individually) on one of three different diets (low, medium, or high—described below) in a randomized block design. A block corresponded to a position on the shelving unit. Each individual was killed (over anesthetized in 0.1% MS222) at metamorphosis and weighed. Mass and time to metamorphosis was quantified for individuals from each of the three food treatments. Gonadal size and developmental stage were quantified via histological analysis (described below) for only the high- and low-food treatment individuals.

Rearing conditions

Tadpoles were purchased from Xenopus Express (<http://www.xenopus.com/products.htm>), and were three days old at arrival. They were allowed to acclimate to laboratory conditions for 24 hr. Because tadpoles were very small and delicate, we could not stage and weigh each individual before treatment assignments, so a subset of five animals was sampled destructively. We were able to stage each individual, but the animals were too small to accurately weigh individually (Mean Nieuwkoop and Faber stage = 46.2; Total weight of 5 = 0.0578).

In both experiments, tadpoles were kept on a 12:12 light dark cycle, and housed at the same density (one tadpole/2 L) in continuously aerated RO filtered water that was reconstituted with 0.25 g/L of Meersalz salt (Tropic Marin, Steina-cher, Wartenberg, Germany). Water was completely exchanged, and containers were cleaned three times per week. In experiment 1, animals were housed communally (five individuals per aquarium) in 10 L of water; animals in the second experiment were housed at the same density (one tadpole/2 L), but individually in 2 L of water. Throughout the experiment, dissolved oxygen concentrations remained high, averaging 95.34% saturation (SD = 3.10) in the first experiment and 92.96% (SD = 4.12) in the second experiment. In

addition, tadpoles in both experiments were kept at similar temperature (experiment 1: mean = 22°C, SD = 0.5; experiment 2: mean = 21°C, SD = 0.4) and pH (mean = 6.9, SD = 0.22 for both experiments). The experiments were conducted simultaneously in the same room. The procedures of this study were approved by IACUC permit #D699 and follow the “Guidelines for use of live amphibians and reptiles in research” compiled by American Society of Ichthyologists and Herpetologists (ASIH), The Herpetologists’ League (HL), and Society for the Study of Amphibians and Reptiles (SSAR) (<http://www.asih.org/files/hacc-final.pdf>).

Food treatments

In both experiments, tadpoles were fed Sera micron[®] (powdered food) suspended in reconstituted RO filtered water once per day. Medium (experiment 2 only) food quantities were based on those determined to be the minimum amount necessary for unhindered growth (beginning at 0.667 mg/L) in previous studies (Opitz et al., 2005; O. Tooi personal communication). At the start of the experiment, high-food treatments received two times the medium (1.3 mg/L/tadpole), and low received one-half the medium (0.333 mg/L/tadpole). These amounts were then adjusted each week to account for tadpole growth following the procedures of Opitz et al. (2005) and O. Tooi (personal communication) while maintaining high-food treatments at double the concentration of the medium, and four times the concentration of low-food treatments. Per capita food supply was identical for both experiments.

Histological preparations

Gonadal growth and developmental stage were evaluated from histological sections using an Olympus BX50 microscope (Olympus America, Center Valley, PA). Whole tadpoles were over anesthetized in 0.1% MS222 (pH~7) until completely unresponsive, their body cavities were opened, and they were fixed in 10% buffered formalin. Fixed specimens were trimmed, decalcified with RDO decalcifying solution (Apex Engineering, Aurora, IL) (using manufacturer’s recommendations), and embedded in paraffin (anterior down). Specimens were serially cross-sectioned at 10–15 µm, and stained using modified Masson’s trichrome technique (Presnell and Schreiber, ’97). Every slide that contained gonadal tissue was evaluated for size (see below)

and developmental stage throughout the entire length of the serial sectioned gonad.

Gonadal size was determined from digital pictures (CDC Vision Video Camera) using Image-Pro Plus image analysis software (Media Cybernetics, Bethesda, MA) by measuring the longest width, perpendicular to the kidney, for each gonad cross-section evaluated. This width was measured for the left and right gonads of approximately one section every 60 μm ; therefore, the number of sections evaluated varied with the size of the animals and sampling date, but on average about 30 sections per individual were measured. The mean of all measurements (across sections and right and left sides) was calculated for each individual.

Developmental stages of the gonads were classified according to Iwasawa and Yamaguchi ('84). In brief, gonadal development began at genital ridge formation (stage I1), and proceeded through migration of the genital ridge, appearance of medullary cells (stage I2), and formation of the cortico-medullary structure (stage I3). At this point, sexual differentiation began. In males, testicular formation was indicated by germ cell migration from cortical into medullary tissue (T1), whereas in females the medullary tissue became excavated as the ovarian cavity formed (O1). Testicular development continued as germ cells became further embedded in the medullary cells, and seminiferous tubule formation progressed (T2); further ovarian development was identified by formation of oogonia masses that became enveloped by follicle cells (O2). For analysis, we quantified developmental stage from 1 to 5 (corresponding to I1, I2, I3, T1/O1, T2/O2).

Statistical analyses

All statistical analyses were performed in the R statistical programming environment (R Development Core Team, 2006). For each analysis, data distributions were assessed for normality and homogeneity of variances and natural log transformed where necessary to improve linearity in pair wise relationships. Data presented in figures are means $\pm 95\%$ confidence intervals (calculated as $\bar{x} \pm 1.96 \cdot \text{SE}$) (Gotelli and Ellison, 2004).

In experiment 1, differences between treatments through time were analyzed via linear mixed effects models with time treated as a covariate and tank treated as a random effect. All other

analyses in experiment 1 were performed via linear mixed effects models with food treatment specified as a fixed effect, either developmental stage or tadpole mass as a covariate, and tank, treated as a random effect. Analyses of tadpole size and development through time were performed in two separate parts based on results from piecewise regressions. Specifically, the first three dates were examined independently of the final three dates (breakpoints determined by piecewise regression), so that we could test for an effect of food treatment on tadpole growth rates during the period when they were exhibiting positive allometry, and during the period when they approached metamorphosis and began to exhibit negative allometry (typical of metamorphosis). The final two dates were excluded from the analysis of developmental stages through time because some individuals had undergone metamorphosis and thus reached the final stage in the developmental staging system that we used. For gonadal end points, we tested for treatment effects on gonad size while controlling for body size by treating body mass as a covariate (McCoy et al., 2006). To test for a relationship between gonad size and gonad stage, we corrected for body size in our gonad size measures using the empirically derived scaling relationship between gonad size and body mass.

For experiment 2, we took a simpler analytic approach because tadpoles were housed individually and there was no repeated sampling through time. First, we tested for an effect of sex via independent *t*-tests for males and females from high- and low-food treatments, and found no significant differences between males and females for any of the somatic endpoints ($P > 0.2$ in all cases). As a result, sex was not included in our statistical model for these measures, and we evaluated differences among treatments for all somatic variables at metamorphosis (whole body mass, and time to metamorphosis) using one-way analysis of variance (comparing high-, medium-, and low-food treatments).

For gonadal endpoints, there was no overlap in body sizes among the treatment groups and we lacked sufficient ranges in body sizes in either treatment group to estimate within group scaling relationships between body size and gonad size, so we could not treat body size as a covariate (Huitema, '80; McCoy et al., 2006). Therefore, we tested for effects of food treatment and sex on metamorph gonadal stage, gonadal width, and body size (so that gonadal and body sizes could be

compared qualitatively) in separate two-way analyses of variance (comparing food treatment, sex, and their interaction).

RESULTS

Experiment 1: larval traits

Somatic endpoints

Tadpoles changed in size at different rates during the first and final three dates of the experiment. During the first three dates tadpoles in the high-food treatment grew 0.04 g/day faster than those in the low-food treatment (i.e. significant interaction, $P = 0.024$; Fig. 1a). After the tadpoles transitioned into negative allometry,

tadpoles in the high-food treatment remained significantly larger than tadpoles in the low-food treatment ($P = 0.004$). However, there were no significant differences in the rate at which size changed ($P = 0.68$). In contrast, somatic developmental stage significantly increased through time ($P = 0.0002$), but there was no significant effect of food treatment on the rate of that change (interaction, $P = 0.857$; Fig. 1b).

In addition, during the first three samplings, there was no tradeoff between body growth and developmental rates of tadpoles in the two food treatments (i.e. homogeneous slopes, $P = 0.885$; Fig. 1c). Similarly, on the final three sampling dates there was no difference in the relative growth and developmental rates (no “tradeoff”) for the two food treatments. However, tadpoles were larger in the high-food treatment when they began to undergo negative allometry, and this difference in size remained through metamorphosis ($P = 0.036$; Fig. 1c).

Gonadal endpoints

Gonadal width was significantly positively correlated with tadpole mass for both food treatments (slope = 0.183, SE = 0.07, $P = 0.007$). On average, however, tadpoles in the high-food treatment had 58% larger (i.e. wider) gonads than did tadpoles in the low-food treatment ($P = 0.0259$, Fig. 2a). In contrast, there was no significant effect of the food treatment ($P = 0.413$) or of the food treatment by time interaction ($P = 0.813$) on gonadal development rate (Fig 2b). Additionally, there was a significant positive relationship between gonadal stage and somatic stage ($P < 0.001$); however, neither the food treatment ($P = 0.227$), nor the food by somatic stage interaction ($P = 0.754$) influenced the relationship between gonadal and somatic development.

To test for a relationship (correlation) between gonadal size (width) and gonadal stage, we corrected gonadal size for the effects of tadpole size (mass) by dividing gonadal size by tadpole mass^{0.183} (determined from the slope in Fig. 2a). However, size-corrected gonadal width was independent of gonadal stage ($P = 0.422$).

Experiment 2: metamorphic traits

Somatic endpoints

Metamorphosed frogs in the low-food treatment were significantly smaller ($F_{2,26} = 143.41$, $P < 0.001$; Fig. 3a) and metamorphosed significantly later ($F_{2,26} = 49.87$, $P < 0.001$, Fig. 3b) than

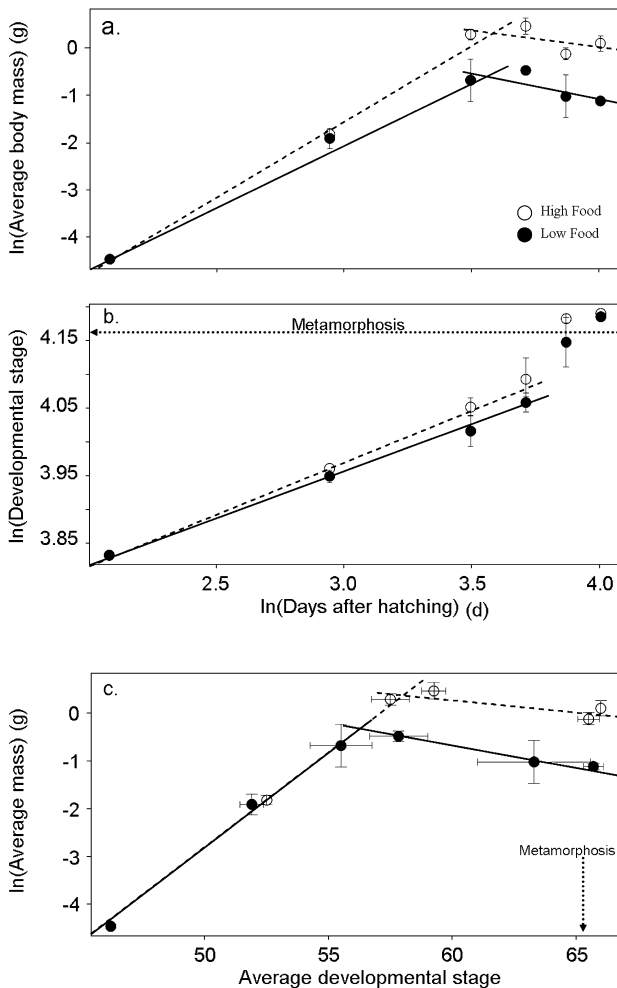


Fig. 1. Growth and development of *Xenopus laevis* tadpoles reared in different resource environments. (a) Tadpole growth rate (ln grams), (b) tadpole somatic developmental rate, (c) tadpole mass (ln grams) as a function of somatic development. Breaks in the data for each graph were determined via piece-wise regression. Error bars are 95% confidence intervals.

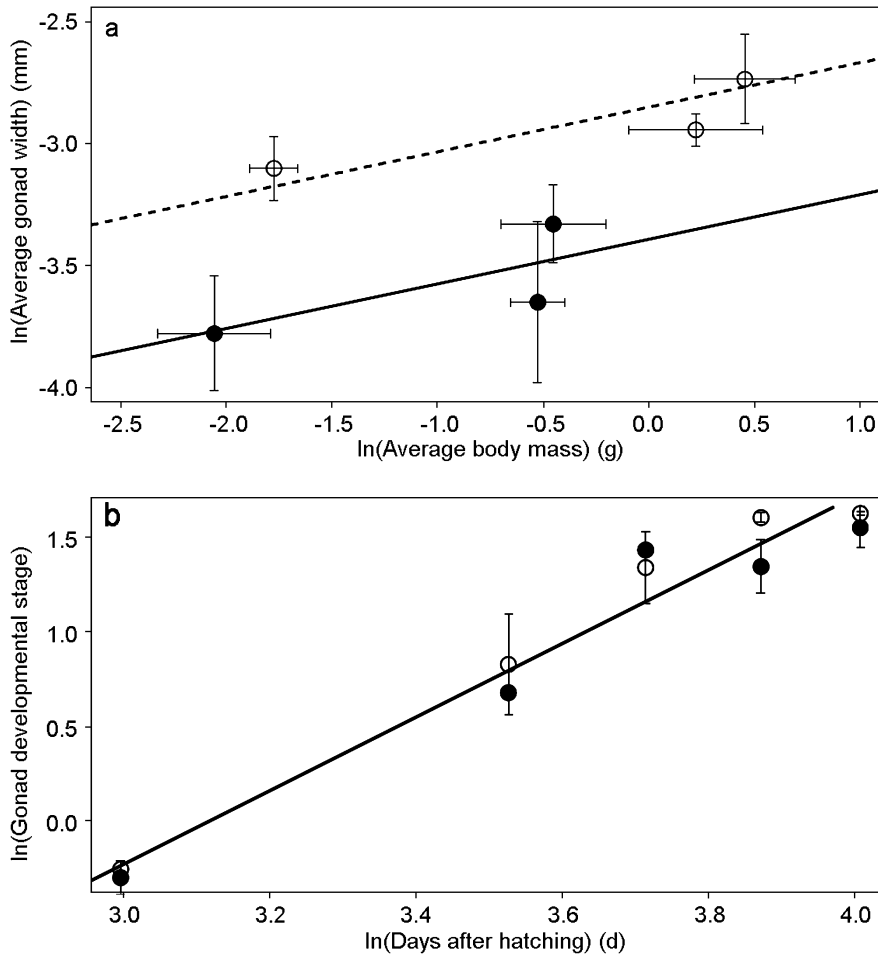


Fig. 2. Growth and development of gonads of *Xenopus laevis* tadpoles reared in different resource environments. (a) The relationship between gonad width and tadpole mass (slope = 0.183) for each food treatment, (b) tadpole gonadal developmental rate. Error bars are 95% confidence intervals.

those in either the medium- or high-food treatments. Metamorphs from the low-food treatment were on average 0.15 g lighter and metamorphosed 4 days later than those in the medium-food treatment, and were 0.45 g lighter and metamorphosed 7.5 days later than animals from the high-food treatment (Fig. 3).

Gonadal endpoints

There were no significant effects of food treatment ($F_{1,15} = 0.54$, $P = 0.47$) or the food treatment by sex interaction on gonad stage ($F_{1,15} = 0.81$, $P = 0.38$), but males had significantly more developed gonads ($\bar{x} = 0.66$ stages) at metamorphosis than females ($F_{1,15} = 13.32$, $P = 0.002$) (Fig 4a). The food treatment by sex interaction significantly affected gonad size ($F_{1,15} = 4.76$, $P = 0.045$). Male gonads were on average 49% (0.057 mm) smaller

in low- versus high-food treatment individuals. However, female gonads were only 17% (0.014 mm) smaller in low versus high food (Fig. 4b). Neither metamorph sex ($F_{1,15} = 1.04$, $P = 0.32$) or the food treatment by sex interaction significantly affected metamorph body mass ($F_{1,15} = 0.005$, $P = 0.94$). However, metamorphs from the high-food treatment were 34% larger on average than those from low food ($F_{1,15} = 160.79$, $P < 0.0001$) (Fig. 4c).

DISCUSSION

Our findings support predictions of classical life history theory that in the absence of environmental stressors, in this case food limitation, resources are allocated toward reproduction (gonadal growth) as well as somatic growth through development. This work also clearly

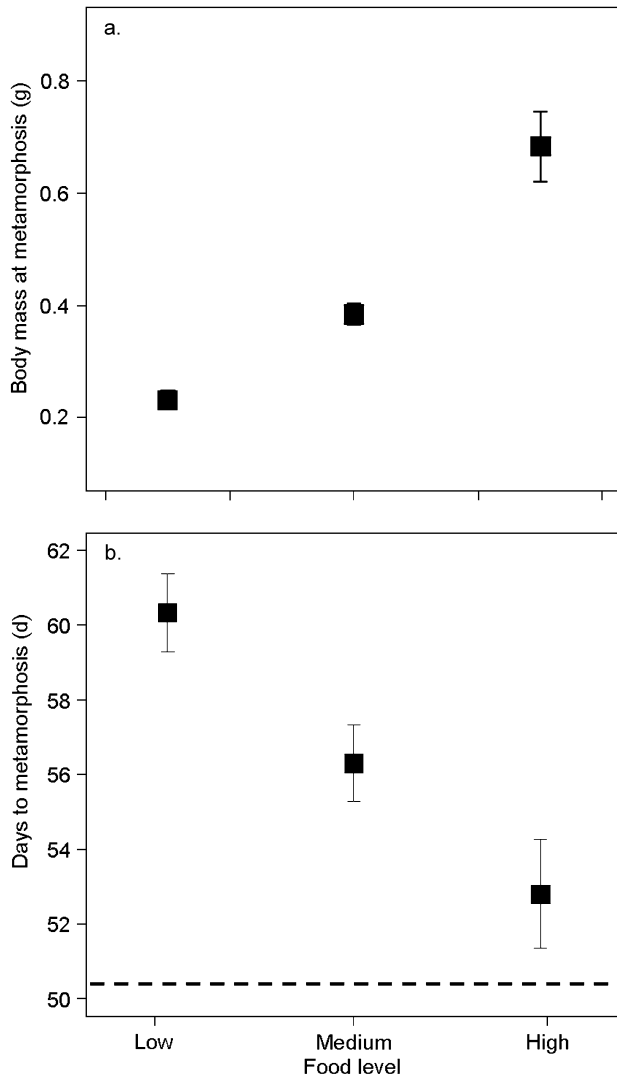


Fig. 3. Growth and development of *Xenopus laevis* reared in different (larval) resource environments. (a) Size at metamorphosis, (b) time to metamorphosis (developmental rate). Dashed line denotes approximately when animals in experiment 1 underwent metamorphosis. Error bars are 95% confidence intervals.

demonstrates that environmental conditions influence tradeoffs between growth, development, and reproductive potential. Furthermore, our research provides a mechanism for phenotypic correlations between growth and reproduction—like body growth, gonadal growth is altered in different environments, and thus resource levels during the larval period could influence lifetime fitness.

Numerous studies have suggested that both size at and time to metamorphosis have important implications on the lifetime fitness of organisms

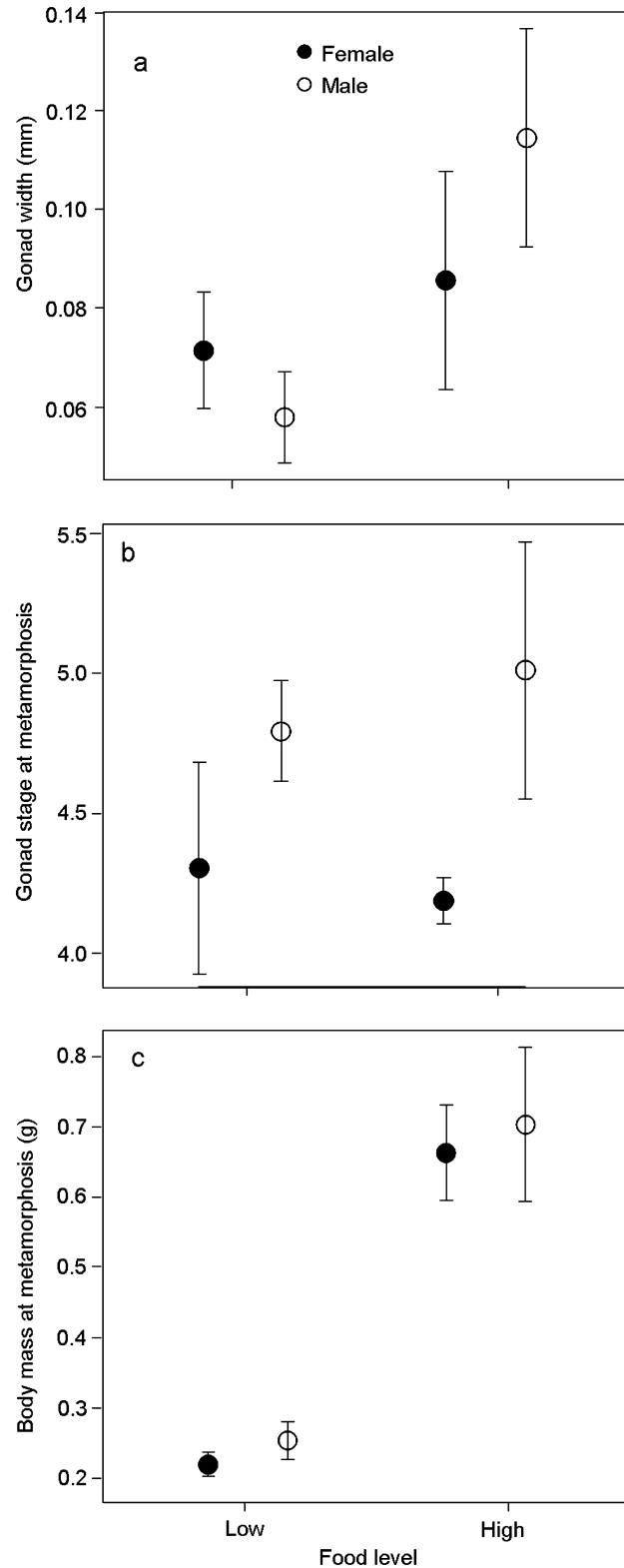


Fig. 4. Growth and development of gonads of male and female metamorphic *Xenopus laevis* reared in different (larval) resource environments. (a) Gonad size, (b) Gonad stage, and (c) body mass at metamorphosis. Error bars are 95% confidence intervals.

with complex life histories (Flecker et al., '88; Taylor et al., '98). When conditions are poor (competition, low food, decreasing water levels), one appropriate response is to metamorphose to escape certain death, but this typically leads to transitioning between life history stages at a smaller size. Although differences in size at metamorphosis can be ameliorated by compensatory growth in the terrestrial environment for some anuran species (e.g. Goater, '94; Boone, 2005), most studies have shown that post-metamorphic growth is not sufficient to compensate for differences in mass at metamorphosis (e.g. Beck and Congdon, '99; Morey and Reznick, 2001; Altwegg and Reyer, 2003; Relyea and Hoverman, 2003; Boone, 2005). Furthermore, small size at metamorphosis has been associated with small size at maturity, longer lags in time to first reproduction, and lower fecundity (Smith, '87; Semlitsch et al., '88; Berven, '90; Scott, '94). We argue that the mechanism driving the lag in time to first reproduction and smaller broods in animals that metamorphose small, at least in some species, could be related to gonadal size at metamorphosis and not solely to somatic development and growth rate during the larval period.

We demonstrate that tadpoles and metamorphs reared in low-food environments have smaller gonads than individuals reared in high-food environments (Figs. 2a and 4b). In addition, gonadal growth and development are decoupled processes that can proceed on separate trajectories depending on conditions imposed by the environment. In experiment 1, in restricted food treatments tadpole gonadal growth was sacrificed while gonadal development remained constant (Fig. 2a and b). In experiment 2, males in low food had smaller testes than those in high food, but testes from both treatments were at similar developmental stages (Fig. 4a and b). These observations suggest that gonadal growth is more plastic than gonadal development. In both experiments, gonadal growth was more strongly linked to whole organism growth than to gonadal development (Figs. 2 and 4). Therefore, metamorphosis at small size, results in smaller gonadal size (Figs. 2a, b and 4a, b), and this likely leads to reduced fecundity.

There is a well-established positive relationship between body size and gonad size. For example, Gage and Freckleton (2003) demonstrated that testes mass shows a clear positive relationship with body size in 83 mammalian species. More-

over, larger testes are associated with faster spermatozoa production rates, and larger sperm reserves in many taxa (Stockley et al., '97). For example, in buffalo total number of spermatozoa were positively correlated with testes weight ($r = 0.998$), volume ($r = 0.97$), diameter ($r = 0.94$), and length ($r = 0.94$) (Soeparna, 2004). It has also been demonstrated across many taxa that greater numbers of spermatozoa enable males to gain more fertilizations (Birkhead and Moller, '98). In fact, the association between larger testes and more spermatozoa is believed to provide the least confounded and most consistent measure of the level of sperm competition across many taxa (Stockley et al., '97; Gage and Freckleton, 2003). These strong associations between body size, testis size, spermatozoa numbers, and fertilization success, suggest that animals that metamorphose small and remain small as adults will have reduced fecundity. We argue that reductions in gonad size induced by growth conditions in the larval environment could lead to reductions in reproductive success of adults that are in excess of those predicted and explained by adult size alone. However, this study did not explicitly test for such carry over effects.

Interestingly, we also found sexual dimorphism in the response of gonadal growth to the different food treatments. Males responded to increased food concentrations by increasing the size of their testes, whereas females had ovaries that were similar in size in both food treatments (Fig. 4). Growth of testes was more plastic than growth of ovaries, thus allocation of resources to somatic and reproductive tissues could be more flexible in males. In addition, females in both food treatments metamorphosed at the same time and size as males from equivalent treatments, but had less well-developed gonads (Fig. 4a and c), therefore ovaries could be more costly to develop relative to testes.

Qualitative differences in somatic and gonadal growth and development between the two experiments in this study might be due to differences in container size, the presence or absence of conspecifics, or because the two experiments focused on different life history stages (tadpoles vs. metamorphs). Regardless of the mechanism, the results from these two studies highlight that environmental conditions influence both somatic and reproductive growth and development, apparently in a sex-specific manner. In addition, our finding that animals housed together, developed and grew faster than those housed individually are

consistent with recent studies showing that tadpoles experiencing tactile, chemical, and visual stimuli from other tadpoles tend to develop and grow more rapidly than those reared in isolation (Rot-Nikcevic et al., 2005, 2006).

We found no evidence to support the hypothesis that *X. laevis* sacrifice gonadal development in favor of somatic development under food limitation. Neither developmental trajectory was affected by food treatment in experiment 1 (Figs. 1b and 2b). However, the occurrence of such tradeoffs could be species specific, so the absence of evidence for a tradeoff between somatic and reproductive development in our study might not be typical of other anurans. Ogielska and Kotusz (2004) showed that the rate of somatic development in some anurans is not strongly correlated with the rate of gonadal differentiation. The occurrence of such tradeoffs could be “stressor” specific. Limited access to food resources likely has very different implications for growth and development than a more immediate or short-term stressor such as decreasing water levels.

CONCLUSIONS

Many environmental conditions influence size at metamorphosis. Predation threat, competition, habitat duration (e.g. hydroperiod), and the presence of pollutants all influence larval development and growth, and likely influence energetic tradeoffs between these processes. We have shown that environmental conditions can influence gonadal growth and the relationship between gonadal growth and development. The implications of this phenotypic plasticity in gonadal tissues on reproductive success are unknown. Gonadal plasticity may influence population dynamics especially if animals metamorphose into environments that prohibit the ability to compensate by developing larger gonads during post-metamorphic life. In a recent study, Harper and Semlitsch (2007) maintained wood frog (*R. sylvatica*) and American toad (*Bufo americanus*) metamorphs in different density treatments and measured survival, growth, and reproductive development after 1 year. Population density had a strong negative effect on reproductive development in the terrestrial stage of both species. The degree of oviduct development in female wood frogs was a function of density such that all individuals in low-density treatments had oviducts that were maturing and becoming reproductively active, whereas oviducts in only 6% of the animals

in the highest density had any signs of reproductive activity (Harper and Semlitsch, 2007). These results indicate that population density in the terrestrial stage can modulate reproductive development. The cumulative effect of developing in an environment that induces reduced gonadal growth, and metamorphosing into an environment that reduces gonadal maturation is expected to have important implications for population regulation. Both aquatic and terrestrial habitats that are degraded owing to natural and anthropogenic disturbance will likely induce tradeoffs between growth, development, and maintenance that will influence reproductive success. The degree to which these tradeoffs occur and their importance for population regulation should be examined in more detail.

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