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## ONTOGENETIC LOSS OF PHENOTYPIC PLASTICITY OF AGE AT METAMORPHOSIS IN TADPOLES<sup>1</sup>

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**Abstract.** Amphibian larvae exhibit phenotypic plasticity in size at metamorphosis and duration of the larval period. I used *Pseudacris crucifer* tadpoles to test two models for predicting tadpole age and size at metamorphosis under changing environmental conditions. The Wilbur–Collins model states that metamorphosis is initiated as a function of a tadpole's size and relative growth rate, and predicts that changes in growth rate throughout the larval period affect age and size at metamorphosis. An alternative model, the fixed-rate model, states that age at metamorphosis is fixed early in larval life, and subsequent changes in growth rate will have no effect on the length of the larval period. My results confirm that food supplies affect both age and size at metamorphosis, but developmental rates became fixed at approximately Gosner (1960) stages 35–37. Neither model completely predicted these results. I suggest that the generally accepted Wilbur–Collins model is improved by incorporating a point of fixed developmental timing. Growth trajectories predicted from this modified model fit the results of this study better than trajectories based on either of the original models. The results of this study suggest a constraint that limits the simultaneous optimization of age and size at metamorphosis.

**Key words:** *Amphibia*; *Anura*; complex life cycle; developmental constraint; larval ecology; metamorphosis; optimal body size; phenotypic plasticity; *Pseudacris crucifer*; Wilbur–Collins model.

### INTRODUCTION

A complex life cycle is characterized by an abrupt morphological metamorphosis and usually includes a change in habitat (Wilbur 1980). Animals that have complex life cycles, such as amphibians and insects, are of particular interest in the study of life history evolution. The timing of developmental events such as metamorphosis, diapause, and sexual maturity can influence life histories directly by determining age at first reproduction or indirectly by affecting age-specific fecundity. Therefore, understanding factors that influence age and size at metamorphosis is an important step in understanding the evolution of life histories.

Amphibian larvae are phenotypically plastic in size at metamorphosis and length of the larval period. Changes in environmental factors, such as temperature and food supply, can affect rates of growth and development, and thus affect size at metamorphosis and duration of the larval period (Wilbur and Collins 1973, Smith-Gill and Berven 1979, Travis 1984, Pandian and Marian 1985, Alford and Harris 1988). To predict accurately how an environmental change will affect age and size at metamorphosis and ultimately influence life history, it is essential to understand how an animal's sensitivity to its environment changes during ontogeny.

Developmental rates that are initially influenced by

changes in food supply but later become fixed have been reported for metamorphosis in barking treefrog (*Hyla gratiosa*) tadpoles (Travis 1984) and for sexual maturation in male guppies, *Poecilia reticulata* (Reznick 1990). Whether such developmental transitions are general phenomena, and the extent of variation in the point of fixation within and among species, are unknown. Further, models that predict optimal age and size at metamorphosis or maturity (Stearns and Koella 1986, Werner 1986, Rowe and Ludwig 1992) do not consider developmental rates that are initially variable but become fixed. Simultaneous optimization of age and size may not be possible if developmental rate becomes fixed while growth rate continues to vary.

In this study I use tadpoles of the winter-breeding treefrog *Pseudacris crucifer* (Hylidae) to test whether the timing of tadpole metamorphosis becomes fixed at a specific developmental stage. I then consider how fixation of developmental rate relates to existing models for predicting amphibian metamorphosis, with particular attention to two alternative models.

### The models

Wilbur and Collins (1973) proposed that both the duration of the larval period, and the size at metamorphosis are products of larval growth history. Their model postulates a minimum body size ( $b$ ) at which initiation of metamorphosis is possible, and a maximum body size ( $b + c$ ) at which initiation of metamorphosis is obligatory. Between these two sizes, metamorphosis is initiated when a tadpole's mass-specific

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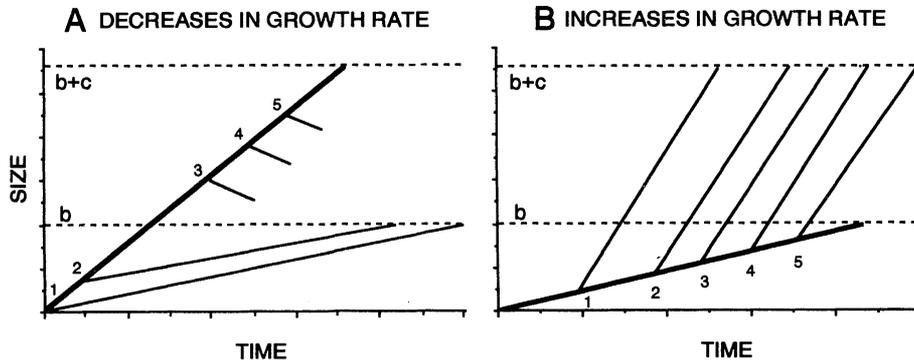


FIG. 1. Hypothetical growth trajectories based on the Wilbur-Collins model (after Alford and Harris 1988). ---- indicates minimum ( $b$ ) and maximum ( $b + c$ ) size for metamorphosis. Slopes indicate growth rates; lines terminate at metamorphosis. Boldface line represents a constant growth rate, and numbered branches off this line represent predicted effects of changes in growth rate at various times during development. (A) Decreases in growth rate before minimum size is reached (1, 2) lead to later metamorphosis and smaller size at metamorphosis as compared to tadpoles with the constant growth rate. Later decreases (3-5) lead to earlier metamorphosis. (B) Increases in growth rate result in larger size at metamorphosis and generally accelerate development (1-4), but may delay metamorphosis (5) relative to tadpoles with constant growth rate.

growth rate drops below a certain level ( $g$ ) (Wilbur and Collins 1973, Collins 1979). According to this model, environmental factors influence size and age at metamorphosis by changing individual growth rates. Growth trajectories, size at metamorphosis, and age at metamorphosis predicted on the basis of the Wilbur-Collins model are presented in Fig. 1, as modified from Alford and Harris (1988).

Based on this model, Collins (1979) predicted that if food is limiting, the variation in individual growth rates will lead to a positive correlation between size at metamorphosis and duration of the larval period. When competition is intense, the first tadpoles to reach the minimum body size for metamorphosis will have low mass-specific growth rates and will transform early. Tadpoles that reach the minimum body size later will have less competition for food and can grow to a larger size before initiating metamorphosis.

Travis (1984) tested this prediction using *H. gratiosa* tadpoles raised individually with initially fixed per-capita food levels. When tadpoles in the cohort transformed, he divided their abandoned food equally among the remaining larvae, thus simulating the increase in food availability associated with reduced competition. The combination of low initial food level and release from competition produced the predicted correlation between size and age at metamorphosis, supporting the Wilbur-Collins model. Although the increased food supply had a significant effect on the size at which tadpoles transformed, it had no effect on the duration of the larval period compared to tadpoles that received unchanging per-capita food supplies. This result is not consistent with the Wilbur-Collins model. Travis (1984) concluded that the developmental rate in *H. gratiosa* is programmed early in the larval period and is insensitive to later changes in growth rates.

Smith-Gill and Berven (1979) proposed that the timing of metamorphosis is determined by a tadpole's

differentiation rate, defined as the rate of passage through stages of larval development. They argued that growth rates are dependent on differentiation rates and that the correlation of growth rate with the length of the larval period is spurious. The Smith-Gill and Berven model states that in a constant environment, developmental stage and differentiation rate are the only variables necessary for prediction of metamorphosis. In a variable environment the interaction of growth and differentiation rates changes, and thus accurate prediction of metamorphosis requires knowledge of both rates (Smith-Gill and Berven 1979).

Alford and Harris (1988) formalized the results of Travis (1984) and Smith-Gill and Berven (1979) into a model for predicting the timing of metamorphosis. This model includes both a fixation of developmental rates early in the larval period and continually variable growth rates. Growth trajectories predicted on the basis of this fixed-rate model are presented in Fig. 2, as modified from Alford and Harris (1988).

Alford and Harris (1988) empirically compared the fixed-rate and Wilbur-Collins models. They raised Fowler's toad (*Bufo woodhousei fowleri*) tadpoles individually and induced changes in growth rates by changing the per-capita food availability. Alford and Harris found that timing of metamorphosis in five of six treatments was consistent with the Wilbur-Collins model; the fixed-rate model was supported by one treatment. They concluded that their results generally supported the Wilbur-Collins model and that developmental rates are influenced by changes in growth rate at any time during the larval period.

The different methods and results of Alford and Harris (1988) and Travis (1984) leave unresolved the question of which model is most appropriate. If there is a stage at which developmental timing becomes fixed, then the effect of food manipulation on tadpole development will depend on whether this critical stage

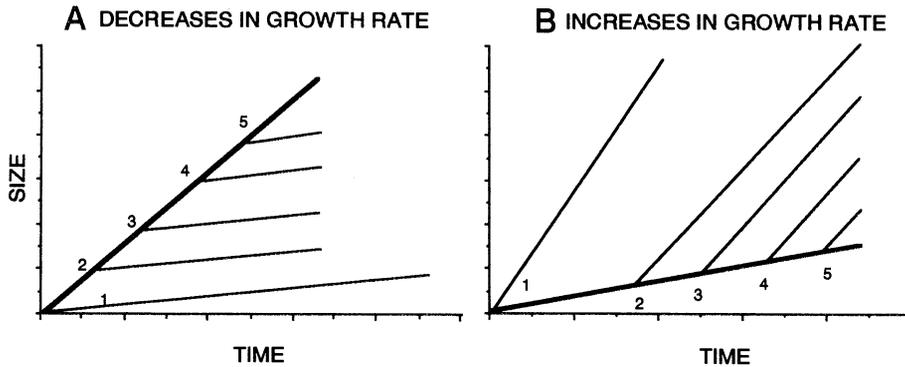


FIG. 2. Predictions of the fixed-rate model (after Alford and Harris 1988), in which development rate becomes fixed early in the larval period. (A) Low early growth rate (1) delays metamorphosis as compared to tadpoles with high growth rate (bold line). Development rate is fixed early, and subsequent decreases in growth affect size, but not age at metamorphosis (2–5). (B) High early growth (1) accelerates metamorphosis. Developmental timing is fixed early and subsequent increases in growth rate (2–5) affect only size at metamorphosis.

has been reached. Prior to this critical stage, changes in food supply will affect age and size at metamorphosis, but manipulations after the critical stage will affect only size. I designed the experiments in this study to test the effects of changes in food supply at various developmental stages. Treatments were spread across a wide range of developmental stages in an attempt to include all phases of larval development that were examined by Travis (1984) and Alford and Harris (1988). The goals of my experiments were to estimate the developmental stage, if any, at which the timing of metamorphosis becomes fixed, and to compare the results to the fixed-rate and Wilbur–Collins models (Figs. 1 and 2).

## METHODS

### Experiment 1

Experiment 1 tested the effects of increases in food availability at various stages of development on size and age at metamorphosis. Because changes in food availability cause changes in tadpole growth rates (Wilbur and Collins 1973, Travis 1984, Alford and Harris 1988), the effects of food availability on age and size at metamorphosis can be compared to predictions from the models. I raised tadpoles individually and controlled food availability to each individual. The experiment included a control treatment (L) raised on a constant, low level of food, and four experimental treatments (I1–I4) that experienced increased food availability on four different days during development.

I collected an amplexant pair of spring peepers (*Pseudacris crucifer*) from a temporary pond in Alachua County, Florida. The pair produced eggs that hatched in 5–6 d. Six days after hatching ended, I haphazardly assigned 16 tadpoles to each treatment. Using individually raised siblings eliminated competition and reduced genetic variation among individuals, increasing the probability that any observed differences in size

and age at metamorphosis would be due to treatment effects.

I established two feeding rates by feeding each tadpole either  $48 \pm 1$  mg (low rate) or  $100 \pm 1$  mg (high rate) of food per 12-d period. Each tadpole received approximately one-fourth of the 12-d ration every 3rd d. This regime insured that food availability to tadpoles within each treatment varied by no more than 1 mg over each 12-d period, though daily variation was not controlled precisely. The diet consisted of a 1:1 mixture by mass of finely ground Purina Rabbit Chow and TetraMin fish food. I raised tadpoles individually in polyethylene cups (9.5 cm tall  $\times$  9.2 cm maximum diameter) containing 370 mL of dechlorinated tapwater (7.7 cm deep) and changed water prior to each feeding. Tadpoles that died during the first 2 d of the experiment were replaced with siblings. I arranged equal numbers of each treatment in a stratified random pattern on each of four shelves of an incubator with a 12L:12D photoperiod at  $25 \pm 1^\circ\text{C}$ . This temperature was chosen as an estimate of the mean temperature that *P. crucifer* tadpoles experience locally.

Three of the experimental food increases were made in the later stages of larval development to increase the probability of detecting any fixation of developmental rates that might occur. Because it was difficult to determine the developmental stage of the tadpoles without injuring them, I switched food levels within each treatment on the same day rather than at the same developmental stage. To estimate the developmental stages of I1–I4 when switched, I raised 16 additional tadpoles (LS) on the control (low) food level and preserved four of them on each of the four days when treatments were switched. I determined developmental stages according to Gosner (1960) and used these developmental stages to estimate developmental stages for I1–I4.

Treatments I1–I4 were switched on days 13, 25, 28, and 31 of the experiment, respectively. These dates

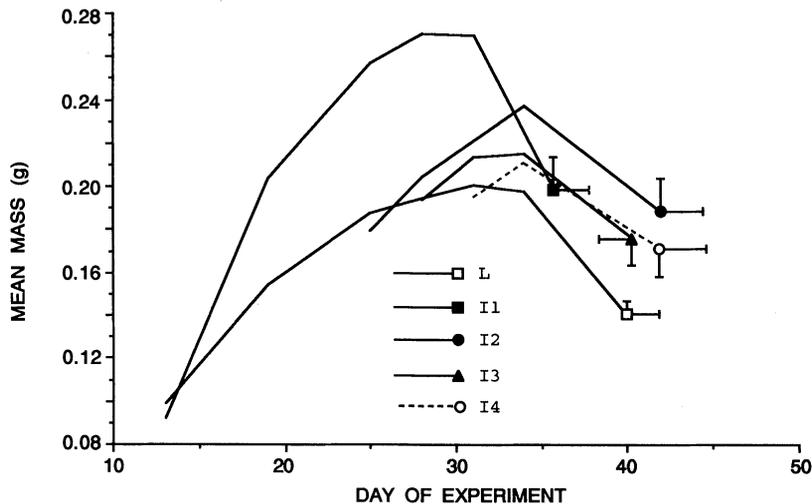


FIG. 3. Growth of tadpoles in Experiment 1. Lines represent the mean live mass of tadpoles within treatments. Endpoint of each curve is mean size and timing of metamorphosis. Bars indicate one side of the 95% confidence intervals. Treatments are explained in *Methods: Experiment 1*. Premetamorphic mass loss is primarily due to tissue dehydration.

were not chosen a priori because I did not know how rapidly tadpoles would develop; instead I switched feeding rates based on estimates of how rapidly tadpoles were developing. My goal was to have the last three food switches evenly spread over the last one-third of development (stages 37–42). Prior to each food level change I compared the mean mass of tadpoles in the treatment being switched to that of the control (L) using a two-tailed *t* test to ensure that they did not differ by chance.

Timing of metamorphosis was measured as the number of days from the beginning of the experiment to the emergence of at least one forelimb (stage 42 of Gosner 1960). Because forelimbs emerge fully developed, this event serves as a discrete indicator of metamorphosis. I checked all tadpoles for forelimb emergence daily, at approximately the same time each day.

I weighed tadpoles at 3–6 d intervals and at metamorphosis. When weighing a tadpole I blotted excess surface moisture from it with a moist paper towel, then weighed it in a tared beaker of water to the nearest 0.001 g.

I performed two ANOVAs to test the effects of feeding treatment and incubator shelf on age and size at metamorphosis. The assumption of equality of variances among treatments was justified (Bartlett's test; Pimentel and Smith 1990). After each ANOVA I used a stepwise Dunnett's test to make a priori pairwise comparisons between each treatment and the control (Zar 1984, Day and Quinn 1989). I performed all statistical analyses using BioStat I version 2.0 software (Pimentel and Smith 1990) or methods from Zar (1984).

#### Experiment 2

Experiment 2 tested the effects of decreased food availability at different developmental stages on age

and size at metamorphosis. Experiment 2 was performed simultaneously with Experiment 1, using tadpoles from the same clutch of eggs, and conducted exactly as Experiment 1 except as follows. The control tadpoles (H) were raised on the high feeding rate, and the experimental treatments (D1–D4) were switched from high to low food rations on days 13, 22, 23, and 25, respectively. Again, these dates were not determined a priori; the schedule differs from that in Experiment 1 because tadpoles grew more rapidly in Experiment 2 due to the higher initial feeding rate. Treatment HS tadpoles were raised on the high food level and used to estimate developmental stages of D1–D4 tadpoles. I used four additional shelves in the same incubator as Experiment 1; from top to bottom, Experiment 1 occupied odd-numbered shelves and Experiment 2 was placed on even-numbered shelves.

## RESULTS

### Experiment 1

In Experiment 1 at least 14 tadpoles survived to metamorphosis in each treatment. Immediately prior to the food increases, none of the treatments I1–I4 differed in mass from the control L (I1–I4:  $P > .55$ ,  $.65$ ,  $.90$ , and  $.50$ , respectively). Developmental stages of the LS tadpoles indicate that at the time of the food increases I1 tadpoles varied from stages 29 to 34, I2 tadpoles were at stages 36–38, I3 were at stages 37–40, and I4 tadpoles were at stages 39–40. Growth curves for L and I1–I4 are plotted in Fig. 3.

The two-way ANOVA of size at metamorphosis revealed a significant treatment effect ( $F_{4,56} = 13.92$ ,  $P < .0001$ ). The shelf effect and interaction were not significant ( $P = .17$  and  $P = .57$ , respectively). Dunnett's test showed that all four treatments that expe-

TABLE 1. Means of age and size at metamorphosis in *Pseudacris crucifer* whose food level was changed (from the low to the high food level or vice versa) on the indicated day of growth. Time measures are relative to the beginning of the experiment.

	Experiment 1 Treatments				
	I1	I2	I3	I4	Low (L)*
Day switched	13	25	28	31	never
Size (g)	0.199†	0.189†	0.176†	0.171†	0.141
Age (d)	35.7†	41.9	40.2	41.8	40.0
	Experiment 2 Treatments				
	D1	D2	D3	D4	High (H)*
Day switched	13	22	23	25	never
Size (g)	0.158†	0.185†	0.208	0.203	0.215
Age (d)	31.3†	29.3	29.4	29.6	29.1

\* Control group.

† Significantly different from control ( $\alpha = .05$ , Dunnett's tests).

rienced increased food transformed at significantly larger mean sizes than the control (Table 1).

There were significant effects of treatment ( $F_{4,56} = 6.86$ ,  $P < .001$ ) and incubator shelf ( $F_{3,56} = 6.84$ ,  $P < .001$ ) on age at metamorphosis in Experiment 1, but the interaction was not significant ( $P = .37$ ). Sporadic measurements of water temperatures throughout the experiments indicated a thermal gradient in the incubator that could account for differences among shelves. Dunnett's test showed that the first increase (I1, stages 29–34) led to earlier metamorphosis than the control (L), but later increases (I2–I4, stages 36–40) had no effect on age at metamorphosis (Table 1, Fig. 3).

#### Experiment 2

At least 14 tadpoles successfully transformed in each treatment in Experiment 2. Growth curves for H and D1–D4 are given in Fig. 4.

Prior to each decrease in food, none of the treatments

differed in mass from the control (D1–D4:  $P > .60$ ,  $.60$ ,  $.15$ ,  $.60$ , respectively). Based on the development of HS, at the time of the food decreases D1 tadpoles varied from stages 33–34, D2 and D3 from 38–41, and D4 tadpoles were at stages 39–41.

Decreases in food availability significantly affected size at metamorphosis ( $F_{4,56} = 17.86$ ,  $P < .0001$ ). The shelf effect was not significant ( $P = .36$ ), nor was the interaction ( $P = .70$ ). Dunnett's test indicates that the first two decreases in food led to significantly smaller size at metamorphosis than the control (H), but subsequent decreases did not (Table 1).

Decreased food level and incubator shelf both had a significant effect on timing of metamorphosis ( $F_{4,56} = 3.44$ ,  $P < .05$ ,  $F_{3,56} = 17.64$ ,  $P < .0001$ , respectively), but only the first decrease in food (D1, stages 33–34) caused a larval period significantly different from group H (Table 1, Fig. 4). The interaction of treatment and shelf was not significant ( $P = .76$ ).

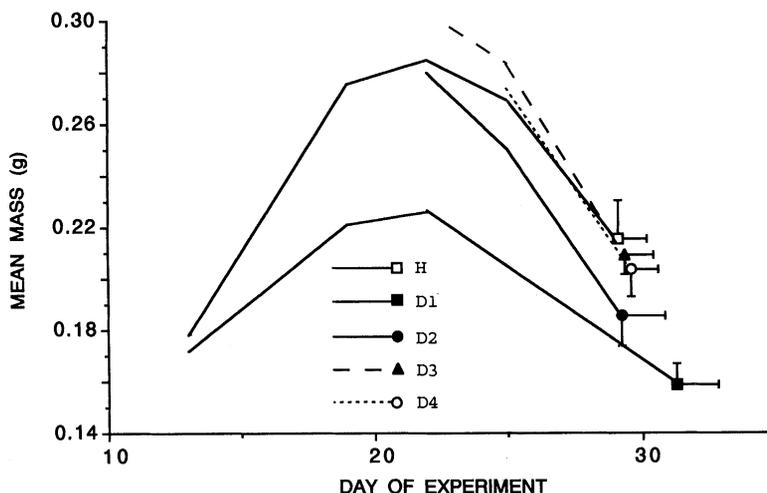


FIG. 4. Growth of tadpoles in Experiment 2. Lines represent the mean live mass of tadpoles within treatments. Endpoint of each curve is mean size and timing of metamorphosis. Bars indicate one side of the 95% confidence intervals.

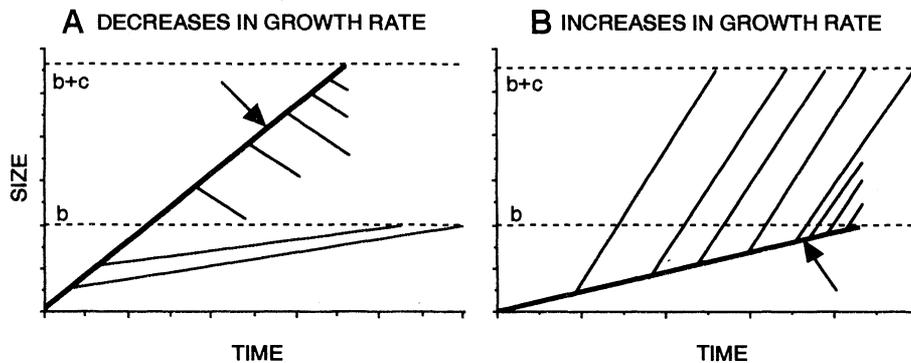


FIG. 5. Growth trajectories predicted by modification of the Wilbur-Collins model. Timing of metamorphosis becomes fixed in the latter third of the larval period (arrows) rather than early in development (Fig. 2) or not at all (Fig. 1).

#### DISCUSSION

The results support aspects of both the Wilbur-Collins model and the fixed-rate model. Changes in food supply affected growth trajectories, and the overall pattern of size and timing of metamorphosis was consistent with the Wilbur-Collins model. As predicted by the fixed-rate model, however, developmental rates became fixed and age at metamorphosis was unaffected by subsequent changes in food supply.

Based on the empirical support for both models, I suggest that modifying the Wilbur-Collins model to include a point of fixed timing makes it more accurate for predictions of age and size at metamorphosis. This modification differs from the original Wilbur-Collins model only in that at a late developmental stage the timing of metamorphosis becomes fixed, but size at metamorphosis continues to vary with growth rate. This modified model differs from the fixed-rate model in the timing of the fixation. In the fixed-rate model, the point of fixed timing occurs early in development (Travis 1984, Alford and Harris 1988). My data suggest that fixed developmental timing occurs in the latter third of the larval period. Growth trajectories predicted from this modified model are presented in Fig. 5, and are more consistent with the observed pattern of age and size at metamorphosis (Figs. 3 and 4) than trajectories from the original Wilbur-Collins model (Fig. 1) or the fixed-rate model (Fig. 2).

Using the development of surrogate sibling tadpoles, I estimate that developmental rates became fixed at approximately Gosner stages 35–37. This estimate is imprecise due to the small sample size of tadpoles staged ( $n = 16$  per experiment). I chose different feeding rates for controls in the two experiments (H and L) to maximize the effect of feeding switches on growth rates. These different initial feeding rates may have influenced the stage at which development became fixed. Nevertheless, it is clear that developmental rates were fixed by stage 38.

If developmental timing becomes fixed in other species, the contrasting results of previous studies could

be explained by differences in the timing of changes in food supply. Fixed developmental rates were observed when food availability was changed in later developmental stages (Travis 1984, Alford and Harris 1988, this study), but changes at early developmental stages affected both size and age at metamorphosis as predicted by the Wilbur-Collins model (Alford and Harris 1988, this study). Unfortunately neither Travis (1984) nor Alford and Harris (1988) estimated developmental stages when food was manipulated, so no estimates of a stage of fixed timing are possible from their data.

Data are lacking to determine if the observed point of fixation corresponds to either of the factors that trigger metamorphosis in the Wilbur-Collins model: mass-specific growth rate  $< g$ , or body size  $> b + c$ . The Wilbur-Collins model does not define initiation of metamorphosis as either a specific developmental stage or an endocrine event. Further, the Wilbur-Collins model does not address the question of whether developmental rates are environmentally sensitive after the initiation of metamorphosis. I suggest that *P. crucifer* tadpoles that showed fixed developmental timing (I2–I4, D2–D4) had already “initiated” metamorphosis (sensu Wilbur and Collins 1973) when food supplies changed. Development proceeded at a fixed rate from about stages 35–37 to 42, but growth rates varied with food availability. Further evidence that metamorphosis was “initiated” by stages 35–37 comes from endocrinology. Initiation of metamorphosis can be defined as the point at which thyroid activity rapidly increases. The transition from minimal thyroid activity to complex endocrine control generally occurs at stages X–XI of Taylor and Kollros (1946) (Dodd and Dodd 1976, Fox 1981), which are equivalent to Gosner stages 35–36 (Just et al. 1981).

Although fixation occurred about stages 35–37 in *P. crucifer*, there are no data to indicate whether the same would be true for tadpoles from other populations or habitats, or whether this point is common to other species. Tadpoles of *Hyla squirella* and *Osteopilus septentrionalis* showed fixed development rates late in the

larval period (Hensley 1990), as did one group of *Bufo* tadpoles (Alford and Harris 1988), but developmental stage data were not collected. Interspecific variation in the stage at which development becomes fixed might depend on habitat predictability. Species from highly unpredictable environments, such as desert spadefoots (*Scaphiopus*) might opportunistically capitalize on transient opportunities for growth by retaining developmental flexibility, while less variable environments might permit less developmental flexibility. Such facultative adjustment of developmental timing is common in temporary ponds, in response not only to changing food levels, but to risks of predation (Skelly and Werner 1990, Wilbur and Fauth 1990) and pond drying (Wilbur 1987, Newman 1988, Crump 1989, Pfennig 1992).

Fixed developmental timing has been demonstrated only with respect to changes in food availability. Other variables, particularly temperature, might continue to influence developmental rates after they are fixed relative to food supply, and might generate patterns of age and size that are not predicted by the modified Wilbur–Collins model.

The Wilbur–Collins model was developed to explain plasticity in amphibian metamorphosis, but it has been applied successfully to development in insects (Blakley 1981), plants (Willson 1981, Lacey 1986), and fish (Policansky 1983, Reznick 1990). Further evidence for a transition from flexible to fixed developmental timing comes from Reznick's (1990) study of plasticity in age and size at maturity in male guppies (*Poecilia reticulata*). Reznick tested the Wilbur–Collins model against a model that predicts that fish initiate maturation at a fixed size and require a fixed amount of time to complete maturation. Reznick's results supported the Wilbur–Collins model; guppies initiated maturity at variable sizes and ages that were related to their growth rates. Once maturation was initiated, however, there was no significant effect of food supply on the duration of the maturation process. Thus maturation in male guppies apparently follows the same pattern seen in tadpoles; developmental rates initially vary with food availability, but once the process (maturation or metamorphosis) is initiated it takes a fixed amount of time, regardless of food supply.

Stearns and Koella (1986) presented a model for predicting age and size at maturity based on growth rates and mortality. They predicted L-shaped or sigmoid reaction norms for size and age at metamorphosis in amphibians. A major assumption of the Stearns and Koella model is that age and size at maturity (or metamorphosis) are both functions of growth rate, and that in all cases reduced growth delays maturity. The results of my experiments indicate stage-specific effects of changes in growth rate; decreased growth does not necessarily delay metamorphosis and therefore the shape of the reaction norm will depend on the stage at which food supply changes.

The Wilbur–Collins model effectively predicts how metamorphosis should vary with growth rates, but it does not address the question of optimum size for metamorphosis. Werner (1986) addressed optimal age and size at metamorphosis as related to growth and predation risk. Rowe and Ludwig (1991) evaluated optimality models for predicting age and size at metamorphosis of insects and amphibians under time constraints imposed by seasonality. The applicability of such optimality models might be limited for organisms that have a period of fixed developmental rate during which age and size are decoupled. Age and size might be simultaneously optimized until the point when developmental rate becomes fixed (the initiation of metamorphosis), but optimizing size at the completion of metamorphosis might be possible only if growth rate is predictable throughout the metamorphic period, when size varies independently of the development rate.

Incorporating a point of fixed developmental timing into the Wilbur–Collins model results in predicted growth trajectories that more closely match the observations of previous workers and this study. The generality of this modification, across species and with respect to other variables such as temperature and hydroperiod, is unknown. Further research is required to complete our understanding of the interactions between ecological variables, developmental rates, and evolution of complex life cycles.

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