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EFFECTS OF CHANGING DENSITY AND FOOD LEVEL ON METAMORPHOSIS OF A DESERT AMPHIBIAN, *SCAPHIOPUS COUCHII*¹

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Abstract. Amphibians that breed in temporary ponds provide a good opportunity to study the ecological and evolutionary consequences of environmental variability. Ephemeral aquatic habitats provide larval amphibians a transient and highly variable opportunity for growth. In the desert ponds used by Couch's spadefoot toad (*Scaphiopus couchii*), tadpole density varies considerably among ponds and often increases within a pond as it dries. Models of optimal size and timing of metamorphosis predict that, relative to constant high resource environments, metamorphosis should occur at a smaller size in constant low resource environments, and smaller and earlier in declining resource environments, assuming all else is equal. Considerable evidence supports the first prediction, but few studies have examined the effect of decreasing resource availability. I conducted an experiment to examine the effects of increasing density and decreasing food level on metamorphosis in Couch's spadefoot toads. Tadpoles at constant high per capita food metamorphosed at the largest sizes. At low or decreasing per capita food, tadpoles metamorphosed at a uniformly small size, but varied in the time required to reach that size. Tadpoles from both increasing density and decreasing food treatments metamorphosed earlier than tadpoles from constant density, constant food treatments. These results support the idea that tadpoles can respond adaptively to resource variation.

Key words: amphibian; Couch's spadefoot toad; Chihuahuan desert; density; development; environmental variation; food level; growth; metamorphosis; phenotypic plasticity; tadpole.

INTRODUCTION

Environmental variability affects processes at all levels and scales of ecological organization. Local variation, for example, probably accounts for much within-population variation in birth and death rates. Incorporating environmental variation into theories of life histories, population dynamics, and community organization requires a detailed understanding of how environmental factors influence physiology, development, behavior, and the resulting life histories of individuals (Dunham et al. 1989). Environmental variability also has evolutionary implications (Levins 1968), both because the direction of selection may vary and alter the genetic composition of populations (Hedrick et al. 1976) and because natural selection can modify the way in which environmental factors influence organismal structure and function (e.g., Huey et al. 1991). To some extent, therefore, the phenotypic responses of a genotype to the environment (its norm of reaction) may represent an adaptation to environmental variability (Bradshaw 1965, Schlichting 1986, Via 1987, Stearns 1989, Newman 1992). Investigations of organismal responses to environmental factors are crucial for understanding both immediate ecological consequences as well as long-term evolutionary effects of

environmental variation. In this paper I present an experimental study of the responses of larvae of a desert amphibian, Couch's spadefoot toad (*Scaphiopus couchii*, Anura: Pelobatidae), to variation in density and food level.

The effects of resource level have been a major focus in empirical and theoretical studies of amphibian ecology, particularly for the larval stage (reviewed in Wilbur 1980, see also Semlitsch and Caldwell 1982, Smith 1983, Travis 1984, Travis and Trexler 1986, Werner 1986, Newman 1987, Alford and Harris 1988, Berven and Chandra 1988, Ludwig and Rowe 1990, Pfennig et al. 1991, Rowe and Ludwig 1991, and see Reznick 1990 for similar studies in guppies). Resource availability may be especially critical in ephemeral desert ponds, such as those used by spadefoot toads, where larvae must acquire sufficient energy to grow and develop before the pond dries. In these ponds, low food level or high density in combination with short pond duration may be a major cause of mortality, because tadpoles may be unable to metamorphose before a pond dries (Richmond 1947, Newman 1987, 1989, Wilbur 1987, Pfennig et al. 1991). Variation among ponds in density, food level, and duration may generate considerable variation in larval growth and development and consequently in larval survival and size at metamorphosis (e.g., Wilbur 1976, 1977a, c, Collins 1979, Smith 1983, Newman 1989, Pfennig et al. 1991). Size at metamorphosis may affect juvenile physiology or performance (Pough and Kamel 1984, Taigen and Pough

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1985, John-Alder and Morin 1990, Newman and Dunham 1994), survivorship (Martof 1956, Pfennig et al. 1991), and size, age, and reproductive success at maturity (Turner 1962, Clarke 1974, Berven 1982, Smith 1987, Semlitsch et al. 1988, Berven 1990). Variation in the larval environment, therefore, may be a major contributor to variation in individual fitness and population dynamics (Wilbur 1980, Travis 1983, Newman 1988, Berven 1990).

Theoretical investigations have attempted to evaluate optimal size at metamorphosis by weighing the relative risk of mortality due to predation or desiccation vs. the relative opportunity for growth in the aquatic and terrestrial habitats (Wilbur and Collins 1973, Werner 1986, Ludwig and Rowe 1990, Rowe and Ludwig 1991). These models predict certain patterns of metamorphosis with respect to gradients of environmental conditions. For example, when all else is equal, all of the models predict a smaller size at metamorphosis in a low resource aquatic habitat, relative to a high resource habitat (as opposed to remaining in a poor quality aquatic environment long enough to achieve a larger size). These models also suggest how tadpoles should respond to temporal changes in the environment. If resource availability is initially high, but then declines, metamorphosis should be initiated earlier, as well as at a smaller size, relative to tadpoles in a sustained high resource environment (assuming all else is equal). Both of these predictions assume that resources are adequate to allow sufficient growth to achieve metamorphosis, and that timing of metamorphosis is conditional on growth rate or size. The second prediction assumes that tadpoles are capable of responding to changes in resource level. There is considerable evidence supporting the first prediction (see *Discussion*).

Wilbur and Collins' (1973) model of facultative metamorphosis explicitly considered the idea that individual tadpoles may respond optimally to changes in their immediate resource environment. They suggested that a sufficiently large decrease in growth rate induced by deterioration in the resource environment may alter the timing of metamorphosis, assuming that a tadpole can acquire sufficient energy to develop and reach the minimal size required for metamorphosis to be physically possible. Alford and Harris (1988) experimentally demonstrated that changing food levels during the larval period can alter timing of metamorphosis in Fowler's toad, *Bufo woodhousei fowleri*, as predicted by Wilbur and Collins (1973). Other studies have demonstrated that tadpoles can also respond to other aspects of the aquatic environment, including pond duration (Wilbur 1987, Newman 1988, 1989, Semlitsch et al. 1990) and predation risk (Skelly and Werner 1990, Wilbur and Fauth 1990).

Changes in growth rate resulting from changes in resource level may also be found in drying ponds. Newman (1988, 1989) found that *S. couchii* tadpoles metamorphosed earlier from shorter duration natural and

experimental ponds than from long duration ponds. Newman (1989) noted that unless there is substantial mortality during the larval period, tadpoles will experience higher density as a pond dries. In ephemeral ponds, therefore, there may be two factors favoring earlier metamorphosis: high risk of desiccation and a diminishing opportunity for growth as a pond shrinks and tadpole density increases. Lower growth rate may result from a diminishing supply of food per tadpole or greater interference competition (or both). Regardless of the mechanism, it is not known if tadpoles can respond to increasing density.

The experiment reported in the present paper was designed to test the hypothesis that temporal changes in density alter timing of metamorphosis. Because this is a laboratory investigation, any connection between effects of increased density and earlier metamorphosis in drying ponds will remain speculative, but the laboratory setting allows the effects of changing density to be evaluated in the absence of other correlates of pond drying. In addition, because effects of increased density may result from decreased per capita food availability, a second hypothesis was tested: does decreased food level, with density held constant, affect timing of metamorphosis, and specifically, does the effect mimic that of increased density when the change in per capita food level is the same? This addresses the issue of whether behavioral or chemically mediated interactions (positive or negative) among individuals that might be associated with density have the same impact on larval performance (and recruitment) as resource level per se (Wilbur 1977a, b, Steinwascher 1978, Murray 1990), and whether changes in food or density might be a more likely candidate for explaining earlier metamorphosis in drying ponds.

METHODS

Density changes in natural ponds

Although density (tadpoles per unit water volume) often increases visibly as ponds dry, it is necessary to estimate the pattern of density increase in order to design an appropriate experimental protocol. This is difficult because of a lack of good quantitative estimates of tadpole number and water volume. In an earlier study (Newman 1987) I categorized ponds according to a rough visual approximation of tadpole number. Ponds could be reasonably well categorized as having small populations (<300 tadpoles) or large populations (>1000 tadpoles), because most ponds were either extremely crowded or sparsely populated (Newman 1987). Ponds were also categorized according to the fate of the tadpole population. For example, ponds that started with large populations either retained large populations, or had populations substantially reduced by predation. The majority of ponds had large populations and retained large populations, which subsequently died when the pond dried (Newman 1987).

TABLE 1. Rate of drying and dimensions of natural breeding ponds on Tornillo Flat, Big Bend National Park, Texas.* Data in this table are based on breeding events when the pond was filled and then dried without refilling.

Pond	Depth (cm)	Width (m)	Length (m)	Drying rate (cm/d)		N	n	R ²
				Mean	SE			
3	24.4	1.9	10.7	-2.69	0.18	4	28	0.90
4	30.5	2.1	10.5	-2.99	0.31	3	18	0.85
4A	55.9	2.2	6.6	-2.61	0.18	4	37	0.85
5	38.1	2.0	4.5	-3.37	0.21	5	42	0.86
5A	53.3	2.5	4.5	-4.42	0.21	4	34	0.93
6	61.0	1.3	13.8	-5.17	0.31	4	32	0.90
8	33.0	2.0	15.6	-3.64	0.30	6	37	0.80
9	30.5	1.0	15.6	-5.61	0.79	4	14	0.81
10E	45.7	1.6	9.3	-5.61	0.38	5	27	0.90
10W	35.6	1.2	10.0	-5.31	0.58	5	18	0.84
11	35.6	2.0	12.3	-2.43	0.13	4	37	0.91
15	24.1	2.8	23.0	-2.40	0.26	5	20	0.83
16	19.0	2.3	9.0	-2.33	0.24	5	21	0.83
18	33.0	1.5	6.2	-4.85	0.52	5	22	0.81

* Depth, width, and length refer to the maximal first measurements taken after a pond was filled. Drying rate was estimated by the slope of a linear regression of depth vs. time (days since pond filled), pooling several (N) rounds of filling and complete drying for each pond. n = the total number of depth measurements on which the regression was based.

Generally only ponds with relatively small tadpole populations produced metamorphs, unless they were refilled by a second rain (Newman 1989), and there is some indication that the failure to grow in crowded ponds was the result of low food level (Newman 1987). Even in sparsely populated ponds, however, density increases as volume decreases.

As a pond dries volume decreases in a way that depends on the shape of the pond. Most spadefoot toad breeding ponds on Tornillo Flat, in Big Bend National Park, Texas, form in depressions in natural run-off channels, and are consequently long and thin, with roughly elliptical surfaces and a semicircular cross section (Table 1, and see Newman 1987 for site description). I recorded depth every 1–3 d after ponds were filled and found that depth decreased at a nearly constant rate (Table 1, linear regressions for depth vs. time for 14 ponds that were filled by run-off and then dried without being refilled had R² between 0.80 and 0.93). Volume changes can be estimated for each pond based on measured rates of drying, measurements of initial maximum length and width, and assuming a geometric shape for which volume can be calculated from these measured dimensions. The basins were shaped roughly like an ellipse rotated about its long axis and truncated lengthwise. The volume of such an object is

$$V(x) = \int \pi \cdot a \cdot c \cdot \left[1 - \left(\frac{b-d}{b} \right)^2 \right] dx,$$

where $a = 1/2$ initial length, $b =$ initial depth, $c = 1/2$ initial width, $d =$ current depth, and the integral is evaluated from $x = 0$ to d (Stein 1977). This represents a summation of the areas of progressively smaller, horizontally stacked ellipses (Beyer 1981). The integral was evaluated using Mathcad (Mathsoft 1992). The reduction in volume with time for each pond was derived according to the observed time required for a

pond to reach a particular depth (based on the regression) and the estimated volume of that pond at that depth. I also examined other pond shapes (e.g., a longitudinally truncated cylinder) to see if the pattern was sensitive to shape, but these shapes differed somewhat in the height of the curves, but not the pattern of decreasing volume. These estimates of volume are necessarily rough, but the general pattern that emerged is probably robust.

A total of 22 breeding events (heavy summer rain storms) occurred between 1984 and 1991 on Tornillo Flat (although not all ponds were used every time), and the number of tadpoles found in a pond varied from one event to another (e.g., see Newman 1987, 1989). To evaluate the pattern of density change that would be experienced by tadpoles in drying Tornillo Flat ponds, I used the estimated changes in volume for 14 ponds and assumed a population size of 1000 tadpoles. Different densities simply alter the scale of the y axis (e.g., to estimate densities in the same ponds with 500 tadpoles, divide the y axis scale by 2). The general pattern that emerged was an initially slow and gradual, but accelerating increase in density, with initial densities generally < 1 tadpole per litre, and final densities several orders of magnitude higher (Fig. 1).

Experimental design

Experimental investigations of multiple factors, such as food and density, often call for factorial experimental designs. However, this was not possible in the present experiment because of the logistical requirements of an increasing density treatment. To make the results of increased density and decreased food treatments comparable, though, requires at least a minimal degree of overlap in the treatment levels employed. Treatments were divided into two subsets (Fig. 2): (1) different densities at constant high food to test the effects

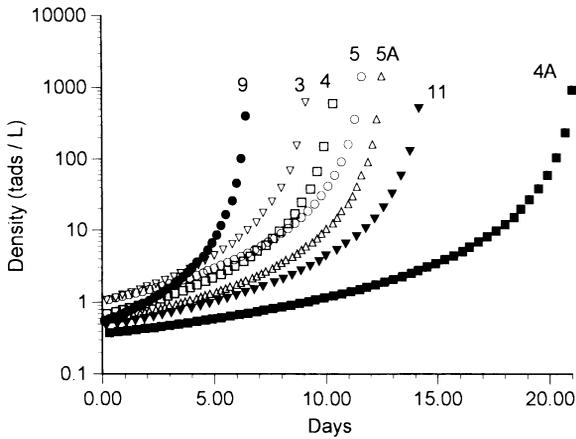


FIG. 1. Estimated changes in density in some natural breeding ponds for spadefoot toads on Tornillo Flat, Big Bend National Park, Texas. Day is day since breeding (= day since pond filled). Only ponds that were not refilled before drying are included. The number over each curve refers to the pond numbers in Table 1. Not all ponds are illustrated, for clarity. Density was estimated based on observed drying rates and assuming no larval mortality.

of varying density, and (2) different food levels at constant low density to test the effects of varying food. Constant density treatments included 1, 2, and 4 tadpoles per container (1.4, 2.9, 5.7 tadpoles per litre, respectively), and constant food treatments included low (one-quarter ration), medium (one-half ration), and high (one ration) per container. The high food level, determined by previous experience, was approximately the maximum a single tadpole would consume in the interval between feedings and that would not foul the water. Because the maximum quantity that a single tadpole could consume increased as it got larger, the baseline food ration was increased as the experiment progressed. In this sense, the high food ration remained approximately constant relative to the foraging demands of the tadpoles. Medium and low food rations

were changed proportionally on the same schedule as the high food ration.

The combination of high food and low density created a high per capita food level, and all other treatment combinations in both subsets were a fraction of this. Because the ratios of treatment levels were 1:2:4 for both food and density, different food and density combinations gave the same per capita food level. For example, low food and low density, medium food and medium density, and high food and high density were all identical (low) per capita food treatments (Fig. 2).

The first subset of treatments involved the high food level and compared tadpoles raised at low, medium, high, and increasing (low to high) densities (Fig. 2). The increasing density treatment was achieved by combining tadpoles in such a way that all tadpoles within each container at every point in time had experienced the same sequence of density changes (Fig. 3). To obtain nine replicates of containers with tadpoles that experienced a gradual increase in density (one at a time) from one per container to four per container required 36 tadpoles that were initially isolated. The combining sequence for one "block" of containers is illustrated in Fig. 3. There were three such combining blocks. The exact timing of density increases was somewhat arbitrary, but increases were timed to mimic the gradual way in which density increases in a drying pond (Fig. 1). Although drying ponds vary in the rate at which density increases, this treatment provided a reasonably natural pattern for testing the effects of density change.

The second subset of treatments was designed to compare food levels at constant low density. Food treatments included three constant food levels (low, medium, and high), and a decreasing food treatment (high ration to low ration). Food level was changed in the decreasing food treatment on the same time schedule as density increases in the increasing density treatment, so the treatments produced the same pattern of change from high to low per capita food.

Each treatment was replicated 8 times (eight con-

FOOD	DENSITY			
	LOW	MEDIUM	HIGH	LOW-to-HIGH
LOW	8 low (5)			
MEDIUM	7 med (8)	9 low (5)		
HIGH	1 high (6)	2 med (3)	3 low (3)	0 decr (6)
HIGH-to-LOW	4 decr (7)			

FIG. 2. Treatment numbers, number of replicates (in parentheses) and corresponding per capita food levels (low, medium, high, and decreasing [high-to-low]). The treatments inside — — — test the effect of density at constant high food (subset 1). The treatments inside - - - - test the effect of food level at constant low density (subset 2).

tainers), except the increasing density treatment, which was intended to have nine replicates (it had to be a multiple of three; see Fig. 3). However, mortality resulted in fewer replicates, ranging from three to eight (Fig. 2). Any container in which one or more tadpoles died was excluded from the experiment, because mortality resulted in altered density and per capita food levels. Mortality was statistically random across treatments ($G_{adj.} = 7.83$, $df = 7$, $P > .3$). There was also a potential problem with nonindependence of replicates in the increasing density treatment. This is discussed in the section on statistical analysis.

Tadpole care

Larvae ≈ 30 h old (just prior to breaking free from jelly, stage 20, Gosner 1960) were collected from eight egg clusters from a single natural pond in Big Bend National Park, Texas (see Newman 1987, 1989 for site descriptions) and returned to the laboratory, where they were placed in a large (20 L) bucket of charcoal-filtered tap water. Larvae were drawn haphazardly for assignment to treatments, and placed in $10.6 \times 10.6 \times 8.6$ cm plastic containers with 0.7 L of charcoal-filtered tap water. Containers were arranged in a randomized array to homogenize background environmental variation (i.e., temperature). Water was changed every 3rd d for the 1st wk and every 2nd d thereafter. Rations of finely ground rabbit chow were weighed to 0.001 g on a Sartorius A210P balance and added after each water change. Snout-vent length was measured for one tadpole per box on day 4 of the larval period, and for all tadpoles on days 7 and 10, and every 2nd d thereafter until metamorphosis. Measurements were taken to the nearest 0.1 mm using an ocular micrometer and a dissecting microscope. Development stage was scored following Gosner (1960). Metamorphs (stage 42, Gosner) were removed and measured as they appeared, and the food ration was adjusted for the remaining tadpoles in a box (for medium and high density treatments) to preserve a constant per capita ration. Temperature was not controlled, but remained near the lower end of the range for natural ponds that were not close to drying (mean daily low = 21.2°C, mean daily high = 26.2°C, see Newman 1989 for natural pond temperatures as a function of depth).

Statistical analyses

Analyses were generally performed on container means using the general linear models procedure of SAS (1988). Analyses of metamorph traits that included the increasing density treatment were also analyzed using combining block means for the increasing density treatment. Size and age at metamorphosis were \log_{10} transformed prior to analysis to meet the assumptions of analysis of variance (Sokal and Rohlf 1981). Growth and development trajectories were analyzed as vectors of size (on days 4, 7, 10, 12, and 14) and development stage (on days 7, 10, 12, and 14) using separate MAN-

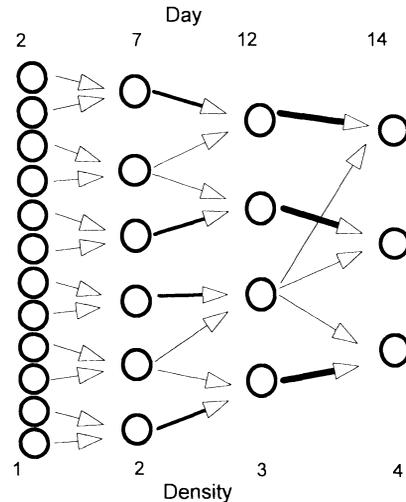


FIG. 3. Protocol for increased density treatment. Tadpoles were started separately (density = 1), and then combined in the indicated pattern. Thick arrows indicate transfer of three tadpoles (third transfer), medium arrows indicate two tadpoles (second transfer), and thin arrows indicate a single tadpole (first, second, and third transfer). In this way, all tadpoles experienced the same increase in density. The design called for nine replicates of the treatment, which required 36 tadpoles started separately. This figure illustrates one-third of the containers (one of three combining blocks).

OVAs. This tests the hypothesis that the overall heights of the mean growth and development curves did not differ significantly among treatments. Measurements after day 14 were not included in this analysis, because metamorphs began appearing after day 14. If the MANOVA indicated significant overall differences in the trajectories, then univariate analyses were performed on the treatment means on each day to determine when treatments were significantly different (Morrison 1976). Metamorph traits (size and age) were analyzed using separate ANOVAs.

Treatment subsets 1 and 2 were analyzed as separate one-way designs, rather than as a single two-way (food, density) analysis with no interactions (see Searle (1987) for a discussion of separate subset analyses vs. a single analysis of missing-cell designs), because tests of the effects of each changing factor required all other factors to be constant. In a two-way analysis, a high food treatment mean would have included the increasing density treatment, and a low density treatment mean would have included the decreasing food treatment.

The first subset was intended to test the specific hypothesis that increasing density (deteriorating growth environment) alters timing of metamorphosis relative to a constant low density (continuing high growth environment); accordingly, a planned pairwise contrast of average age at metamorphosis in treatment 0 vs. 1 was estimated. A pairwise contrast of age at metamorphosis in decreasing food vs. constant high food was made for treatment subset two. A third one-way

TABLE 2. Analyses of growth and development trajectories for treatment subset 1 (constant high food, varying density), treatment subset 2 (constant low density, varying food), and by per capita food level (Treatments 0 and 4 were both considered decreasing per capita food).

	MANOVA				Univariate ANOVAs				
	Wilks' λ	<i>F</i>	df	<i>P</i>	Day 4	7	10	12	14
Subset 1									
Growth	.026	5.13	15, 28	<.0001	*	*
Development	.301	1.41	12, 29	.22
Subset 2									
Growth	.121	3.84	15, 50	.0002	*	*
Development	.269	2.71	12, 51	.007	*	*
Per capita food									
Growth	.154	6.26	15, 97	<.0001	*	*	*
Development	.437	2.93	12, 96	.002	*	*

* MANOVA results are given first for each analysis; asterisks indicate measurement days on which size or development stage differed significantly among treatments ($P < 0.05$).

analysis on per capita food level was done to compare the two changing condition treatments. All eight treatment combinations (Fig. 2) were used in this analysis. Increasing density and decreasing food were entered as separate treatments even though they generated the same (high-to-low) pattern of per capita food. A planned contrast was estimated comparing the decreasing food and the increasing density treatments. In all analyses, unplanned pairwise comparisons were made with the Ryan-Einot-Gabriel-Welsch (REGWQ) multiple-range test (SAS 1988, Day and Quinn 1989) when ANOVAs were significant.

Additional analysis of the increasing density treatment

By the end of the experiment, containers within the increasing density treatment were not all independent. Some tadpoles transferred on days 7 and 12 from some source containers went to different destination containers (Fig. 3). Destination containers, therefore, might have correlated means, because they shared tadpoles from a common source. Statistically, this means the increasing density treatment was potentially pseudoreplicated within combining blocks. Conservatively, there were at least three independent replicates, because combining blocks were completely independent. In actuality, pseudoreplication was probably not a significant problem. Because of mortality, only six of the nine planned containers remained by the end of the experiment, three in the first combining block, two in the second, and one in the third. Of the two in the second block, they did not acquire a tadpole from a common source container until day 14, so they were completely independent for analysis of growth and development trajectories, and only shared a potential dependency for a few days prior to metamorphosis. Of the three containers in the first combining block, two were completely independent until day 14, and the third shared one tadpole source with each of the other

two. So only one of the six containers can be considered a potential pseudoreplicate for analyses of premetamorphic growth and development. For metamorph traits (size and age), if shared tadpole sources caused tadpoles to be less variable than truly independent replicates, the variance among containers within combining blocks should have been less than the variance among blocks within the increasing density treatment. To test for this, I analyzed the increasing density treatment using a nested analysis of variance, with containers nested in combining blocks. Block effects were tested using the among-container, within-block mean square as an error term. However, to be conservative, I also used combining block means, rather than container means, in analyses of metamorph traits that included the increasing density treatment (i.e., the analyses reported in Table 4). This eliminated the potential problem of pseudoreplication altogether.

RESULTS

Growth and development trajectories

Tadpoles raised at high food, but at different densities (treatment subset one), varied significantly in growth to day 14 (Table 2, Fig. 4A). However, the trajectories did not diverge significantly from each other until between days 10 and 12 (Table 2), by which time tadpoles at high density were significantly smaller than those at other densities (Fig. 4A). By day 14, tadpoles experiencing increasing density were also smaller than those at low and medium density, but still larger than those at high density (Fig. 4A). Tadpoles at all constant densities, including high density, continued to grow after day 14; in contrast, those experiencing increasing density metamorphosed soon after and consequently did not grow much after day 14 (Fig. 4A). Despite the effect on timing of metamorphosis, the overall developmental trajectories did not vary significantly among density treatments by day 14 (Table 2, Fig. 4B). The effect on developmental trajectories

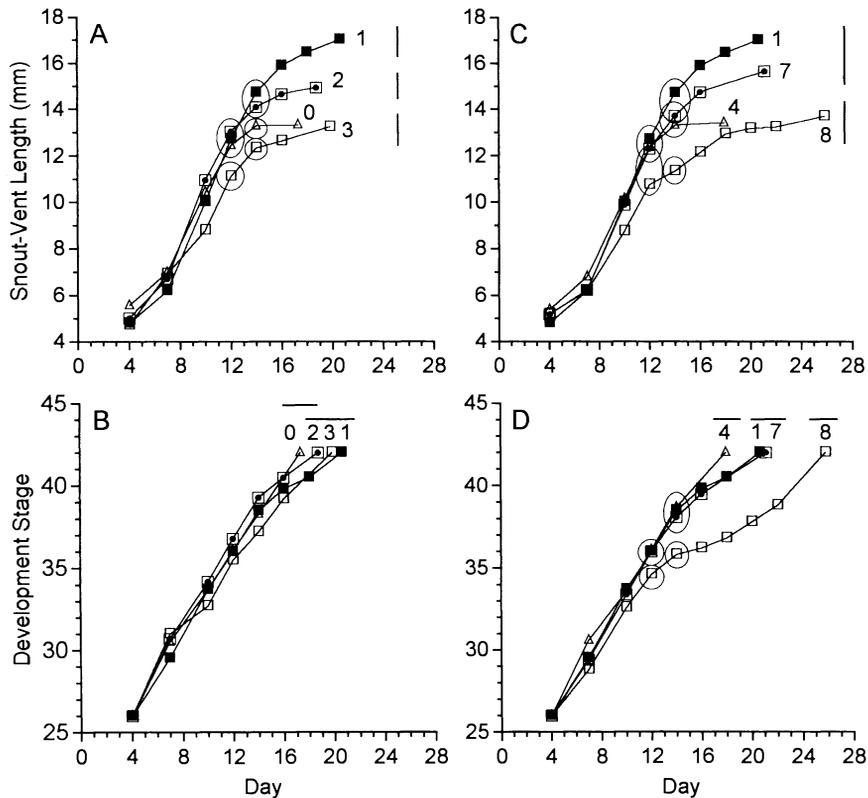


FIG. 4. Growth (A and C) and development (B and D) trajectories for each treatment. (A, B) Trajectories of high food treatments (treatment subset 1). Low density = solid squares, medium density = squares with dots, high density = open squares, increasing density = triangles. (C, D) Trajectories of low density treatments (treatment subset 2). High food = solid squares, medium food = squares with dots, low food = open squares, decreasing food = triangles. Symbols also indicate per capita food level: high = solid squares, medium = squares with dots, low = open squares, decreasing = triangles. All points except the last point on each curve represent the treatment mean (number = treatment number) on each day prior to the emergence of any metamorphs from that treatment. The last point on each growth curve is the treatment mean size at metamorphosis plotted against the treatment mean age at metamorphosis. Ovals indicate treatment means on each day (up to day 14) that were not significantly different in a REGWQ multiple pairwise comparison test. Vertical or horizontal lines indicate treatment means of size at metamorphosis (A and C) or age at metamorphosis (B and D) that were not significantly different in a REGWQ test.

(i.e., timing of metamorphosis) was not apparent until after day 14 (Fig. 4B).

Both overall growth and development trajectories to day 14 varied significantly among food treatments in treatment subset 2 (Table 2, Fig. 4C, D). Significant differences were apparent by day 12 as a result of slow growth and development in the low food treatment. By day 14, tadpoles in the decreasing food treatment were smaller than those in the high food treatment, but still larger than those in the low food treatment (Fig. 4C). Tadpoles in all three constant food treatments continued to grow after day 14, whereas those in the decreasing food treatment metamorphosed sooner and did not grow much after day 14 (Fig. 4C). This allowed tadpoles in the low food treatment to metamorphose at the same size as those in the decreasing food treatment. As with treatment subset 1, effects of changing conditions on the developmental trajectory were not apparent by day 14. The significant treatment effect on developmental trajectories to day 14 (Table

2) was the result of slower development at constant low food (Fig. 4D).

Differences according to per capita food level were statistically significant (Table 2). Growth trajectories followed similar paths within per capita food levels, with the high per capita food treatment lying above, and the low per capita food treatments lying below the others (Fig. 4A, C). Trajectories of the two decreasing per capita food treatments were indistinguishable (Fig. 4A, C, triangles). Interestingly, for trajectories of treatment means within the medium and low per capita food levels, the higher density, higher food combinations followed similar paths (including treatment 9, which is not illustrated in Fig. 4 because it belongs to neither subset), but terminated sooner than lower density, lower food combinations (Fig. 5). Overall developmental trajectories to day 14 were also significantly different (Table 2), but this was primarily the result of slow development of tadpoles at low food and low density (Fig. 4).

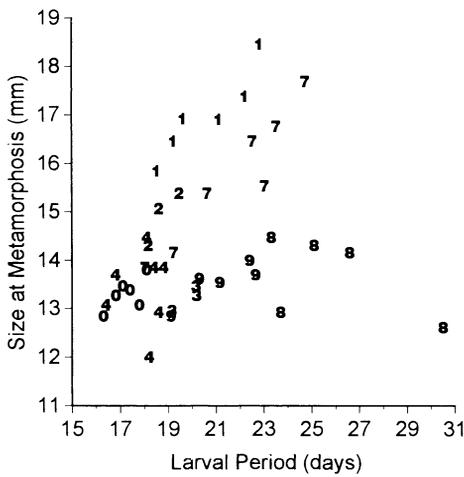


FIG. 5. Container means of size vs. age at metamorphosis, showing the range of responses within treatments and the within-treatment correlation between size and age at metamorphosis. See Fig. 2 for details of density and food levels.

Size and age at metamorphosis

There was substantial variation in size and age at metamorphosis within some treatments (Fig. 5), but means of both traits varied significantly among treatments (Tables 3 and 4, Fig. 4). An analysis of block effects (combining blocks) for the increasing density treatment (treatment 0) did not reveal any significant block effects (for size: $F_{2,3} = 0.76, P > .05$; for age: $F_{2,3} = 1.61, P > .05$), and tadpoles in all containers in the increasing density treatment (treatment 0) metamorphosed earlier than tadpoles from any other density treatment (treatments 1, 2, and 3, Fig. 5). However, to avoid any possibility of pseudoreplication of the increasing density treatment, all ANOVAs involving that treatment were done on block means for the increasing density treatment and container means for other treatments. In treatment subset 1, density level accounted for 58% of the variation in larval period and 91% of the variation in size at metamorphosis (Table 3). Tadpoles in the increasing density treatment metamorphosed earlier than tadpoles that remained at low density (planned contrast, Table 3). The larval periods of

tadpoles at constant densities and high food were statistically indistinguishable from each other (Fig. 4B). Size at metamorphosis was greatest for tadpoles raised at low density, followed by those raised at medium density and then those raised at either high or increasing density (Figs. 4A and 5, Table 3).

For tadpoles raised at low density (treatment subset 2), food level accounted for 64% of the variation in larval period and 70% of the variation in size at metamorphosis (Table 4). Tadpoles in the decreasing food treatment (treatment 4) metamorphosed significantly earlier, on average, than those in the constant food treatments, and those at low food (treatment 8) metamorphosed significantly later than those at medium or high food (Table 4, Figs. 4D and 5). Tadpoles in the medium and high food treatments metamorphosed at similar sizes, and significantly larger than those in the low and decreasing food treatments (Figs. 4C and 5, Table 4).

Analysis according to per capita food level indicated that the larval periods of tadpoles from the decreasing food and increasing density treatments were not statistically distinguishable (planned contrast, Table 5, Fig. 4A vs. C, Fig. 5). The average larval periods of the constant per capita food treatments were also not statistically distinguishable from each other (in a REGWQ multiple-range test). Inspection of Fig. 5 reveals why this was so: tadpoles at low food and low density metamorphosed, on average, substantially later than tadpoles in other low per capita food treatments (medium/medium and high/high). In the medium and low per capita food treatments, there was a tendency for tadpoles raised at higher food and higher density to metamorphose earlier than those at lower food and lower density (Fig. 5, e.g., compare treatments 2 vs. 7 and 3 vs. 9 vs. 8). Per capita food level accounted for 74% of the variation in average size at metamorphosis (Table 5), which was significantly greater in the high per capita food treatment, followed by the medium per capita food treatments, and then the decreasing and low per capita food treatments (Fig. 5). Within per capita food levels, treatment means were relatively homogeneous (Fig. 5), and not statistically distinguishable (in a REGWQ multiple-range test).

TABLE 3. Analyses of the influence of density level at high food on size and age at metamorphosis (Treatments 0, 1, 2, 3). Variables were \log_{10} transformed prior to analysis. Analyses were performed on combining block means of treatment 0, and on container means of other treatments. Contrasts are increasing density (Treatment 0) vs. constant low density (Treatment 1).

Source	df	ss	F	P	R ²
Larval period					
Density	3	0.0110	5.08	.0190	0.58
Treatment 0 vs. 1	1	0.0100	13.91	.0033	...
Error	11	0.0079
Snout-vent length at metamorphosis					
Density	3	0.0347	38.13	<.0001	0.91
Treatment 0 vs. 1	1	0.0227	74.89	<.0001	...
Error	11	0.0033

TABLE 4. Analyses of the effect of food level at low density on size and age at metamorphosis (Treatments 1, 4, 7, 8). Variables were \log_{10} transformed prior to analysis. Analyses were performed on container means. Contrasts are decreasing food (Treatment 4) vs. constant high food (Treatment 1).

Source	df	ss	F	P	R ²
Larval period					
Food	3	0.0730	13.23	<.0001	0.64
Treatment 1 vs. 4	1	0.0080	4.35	.0492	...
Error	22	0.0405
Snout-vent length at metamorphosis					
Food	3	0.0448	17.41	<.0001	0.70
Treatment 1 vs. 4	1	0.0345	40.27	<.0001	...
Error	22	0.0189

Correlation between size and age at metamorphosis

The correlation between size and age at metamorphosis varied among treatments. Within the high and medium per capita food levels (treatments 1, 2, and 7) a longer larval period resulted in substantially larger size at metamorphosis (Fig. 5, Table 6). Overall, in the low per capita food treatments there was no significant relationship between size and age at metamorphosis. However, the correlations in treatments 3 and 9 were both high and positive (but not statistically significant, Table 6), although the relationship (regression on container means in treatments 3 and 9: slope = 0.25, SE = 0.054, $P < .01$, $R^2 = 0.78$) did not appear as strong as in the high and medium per capita food treatments (treatments 1, 2, and 7: slope = 0.44, SE = 0.10, $P < .001$, $R^2 = 0.57$) (Fig. 5). The correlations in the increasing density and decreasing food treatments were not statistically significant (Table 6).

DISCUSSION

Response to decreasing resource level

The results of this experiment clearly demonstrate that *Scaphiopus couchii* tadpoles responded to decreasing per capita food level by metamorphosing earlier and at a smaller size than tadpoles in a constant high per capita food environment. With respect to the two decreasing per capita food treatments (treatments 0 and 4), there was no evidence for any effects of density beyond what was generated by the per capita food level. Responses to treatments where food decreased with

constant low density and where density increased with constant high food were indistinguishable. In both treatments the growth trajectories did not shift, relative to high per capita food, until after day 12, and developmental trajectories until after day 14, demonstrating that timing of metamorphosis remains flexible well into the larval period. At low per capita food, metamorphosis occurred at a fairly uniform and relatively small size compared to higher per capita food levels. Thus, the results presented here are consistent with models that predict smaller size at metamorphosis when growth opportunity in the aquatic habitat is low or diminishing and earlier metamorphosis when growth opportunity decreases during the larval period (Wilbur and Collins 1973, Werner 1986, Ludwig and Rowe 1990, Rowe and Ludwig 1991). This experiment cannot discriminate further among these models, because they all make the same prediction about the effect of lower growth rate in the aquatic environment with all else equal (Rowe and Ludwig 1991).

Across-treatment correlation between size and age at metamorphosis

Additional insight into the ecological control of metamorphosis may be gained through consideration of the varying relationships across and within treatments between size and age at metamorphosis. Frequently, metamorphosis occurs later and at a smaller size in low food environments than in high food environments. Thus, the correlation between size and age at metamorphosis across resource levels is generally

TABLE 5. ANOVAs of mean size and age at metamorphosis in per capita food (PCF) levels. Variables were \log_{10} transformed prior to analysis. Analyses were performed on combining block means of treatment 0 and on container means of other treatments. Contrasts are increasing density (Treatment 0) vs. decreasing food (Treatment 4).

Source	df	ss	F	P	R ²
Larval period					
PCF	4	0.0520	5.47	.0016	0.38
Treatment 0 vs. 4	1	0.00094	0.39	NS	...
Error	35	0.0831
Snout-vent length at metamorphosis					
PCF	4	0.0609	24.59	<.0001	0.74
Treatment 0 vs. 4	1	0.00002	0.04	NS	...
Error	35	0.0217

TABLE 6. Correlation between size and age at metamorphosis within each treatment and by per capita food level (Dh = decreasing per capita food by increasing density, Df = decreasing per capita food by decreasing food level).

	Treatment							
	0	4	1	2	7	3	9	8
Correlation	.68	.05	.92	.91	.93	.92	.86	-.54
df	4	5	4	1	6	1	3	3
P	.13	.91	.010	.27	.001	.26	.06	.34
	Per capita food							
	Dh	Df	High	Medium	Low			
Correlation	.68	.05	.92	.92	.09			
df	4	5	4	9	11			
P	.13	.91	.010	.0001	.77			

negative (Brockelman 1969, Wilbur and Collins 1973, Wilbur 1977a, b, Dash and Hota 1980, Semlitsch and Caldwell 1982, Travis 1983, 1984, Petranks and Sih 1986, Alford and Harris 1988, Berven and Chadra 1988, Newman 1989, Pfennig et al. 1991, see also Reznick 1990 for maturation time in guppies as a function of resource level). However, timing of metamorphosis in low resource environments depends on how low food is or how harsh the environment is (Hota and Dash 1981, Travis and Trexler 1986). If conditions are less severe, slowly growing tadpoles may metamorphose at a smaller size, but earlier or at the same time as tadpoles with higher growth rates, which generates a positive or no correlation across treatments.

The relationship between size and age at metamorphosis may depend on when slowly growing tadpoles reach some threshold size, relative to when faster growing tadpoles (that have already passed that size) metamorphose. In the experiment reported here, average size at metamorphosis was nearly the same in all low per capita food treatments, but was reached earliest in the high food, high density treatment and latest in the low food, low density treatment. Compared to the high food, low density treatment, metamorphosis occurred, on average, at a smaller size but about the same time in the high density, high food treatment (no correlation across treatments), and later and at a smaller size in the low food, low density treatment (a negative correlation across treatments). Tadpoles in the decreasing per capita food treatments metamorphosed at the same size, on average, as tadpoles in the low per capita food treatments, but even earlier (see also Alford and Harris 1988). When the decreasing per capita food treatments are considered, there was no overall correlation between size and age at metamorphosis across either food (subset 2) or density (subset 1) treatments. In all of these comparisons, variation in the across-treatment correlation is caused solely by the timing of metamorphosis in the low or decreasing per capita food treatments.

Some of the variation in timing of metamorphosis within the low per capita food level can be accounted

for by treatment. Treatments with higher density and food level tended to produce metamorphs earlier than treatments with lower density and food level (e.g., Fig. 5, treatments 3 vs. 9 vs. 8). Tadpoles at higher density/higher food, therefore, grew faster than those at lower density/lower food. This suggests that there may have been a positive effect of density at low per capita food, even though such an effect was not apparent in the decreasing per capita food treatments. Suggestions of such facilitation are also found in other studies of tadpole growth, although generally only under a limited range of experimental conditions (Wilbur 1977a, Steinwascher 1978, Breden and Kelly 1982, Travis and Trexler 1986, Berven and Chadra 1988, Murray 1990). The importance of facilitation in nature for *S. couchii* is not clear, because higher density generally means lower per capita food and slower growth and development (Newman 1987).

Within-treatment correlation between size and age at metamorphosis

Resource level and other environmental factors also influence the relationship between size and age at metamorphosis of tadpoles within treatments (Travis 1984, Newman 1989, Pfennig et al. 1991). In a previous experiment, I observed that average size and age at metamorphosis of *Scaphiopus couchii* were positively correlated within per capita food treatments for both short and long duration experimental ponds, but that the relationship was stronger among high food ponds than low food ponds (Newman 1989). In natural ponds with a high tadpole density, tadpoles that were able to metamorphose generally did so between 9 and 10 mm, even though age at metamorphosis ranged from 8 to 16 d, on average, among these ponds (R. A. Newman 1989, unpublished data). There was no correlation between size and age at metamorphosis at high density. The correlation in natural, low density ponds was 0.40 ($P = .19$, $df = 10$; R. A. Newman 1989, unpublished data).

These observations from natural and experimental ponds are consistent with the current results. Within high and medium per capita food levels the relation-

ship between size and age at metamorphosis was strongly positive (0.92), but the correlation at low per capita food was very low (0.09). Within each of the two higher density, low per capita food treatments (3 and 9), the correlations between age and size at metamorphosis were high and positive (but not statistically significant, Table 6). However, the relationship was not as steep as in the medium and high per capita food treatments (Fig. 5), so less is gained by delaying metamorphosis at low per capita food relative to higher per capita food. Overall, the low correlation at low per capita food was the result of the relatively small range of size at metamorphosis compared to the large range in age at metamorphosis. This suggests that tadpoles with low growth rates metamorphosed at a characteristic small size, whenever that size was reached. This also accounts for the variation in across-treatment correlations.

Environmental control of amphibian metamorphosis

Slowly growing *S. couchii* tadpoles do not appear to delay metamorphosis to achieve as large a size as achieved by rapidly growing tadpoles (unless they experience a sudden increase in resources, perhaps due to metamorphosis of competitors, e.g., Semlitsch and Caldwell 1982, Alford and Harris 1988). This makes sense in a highly ephemeral habitat, where minimal size gains would probably not justify the substantial risk of desiccation (Newman 1989, Ludwig and Rowe 1990). Nor do they metamorphose as small as physically possible, for they may metamorphose even smaller, if forced to by pond drying (Newman 1989). Because size at metamorphosis was relatively consistent for the low and decreasing food treatments (see also Alford and Harris 1988), there appears to be a characteristic, but not immutable size at metamorphosis for slowly growing tadpoles (possibly a "minimal" size for survival in terrestrial life, although not necessarily the developmental minimum size for metamorphosis postulated by Wilbur and Collins 1973). Perhaps, under deteriorating growth conditions, tadpoles metamorphose at this size whenever they reach it or metamorphose sooner if other factors become unfavorable (e.g., the pond is drying or predation risk increasing) and if they are able (i.e., big enough and developed enough).

Optimal timing of metamorphosis, in this view, does not depend solely on growth rate or size, but also on other environmental factors, such as pond drying and predation risk (Wilbur and Collins 1973, Werner 1986, Newman 1988, Ludwig and Rowe 1990, Rowe and Ludwig 1991). It explicitly assumes that individual tadpoles can, to some extent, respond adaptively to the varying conditions they may experience (Wilbur and Collins 1973, Harris 1987, Alford and Harris 1988, Newman 1988, 1989, 1992, Pfennig 1990, Semlitsch et al. 1990, Skelly and Werner 1990). One of the challenges now is to discover the limits to such adaptive plasticity (Newman 1992).

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