

Proximate and functional causes of polyphenism in an anuran tadpole

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Summary

Few systems have been explored in sufficient detail to link the proximate causes of polyphenism to the ecological factors that favour discontinuous, environmentally induced variation. I examined the developmental and physiological bases underlying polyphenism in southern spadefoot toad tadpoles (*Scaphiopus multiplicatus*). *Scaphiopus* often occurs as two discrete trophic morphs: carnivores and omnivores. Carnivores develop from omnivores if the latter are fed macroscopic prey (anostracan shrimp and tadpoles). I found that tadpoles can change to the alternative morphology if their diet was switched. Static allometric analyses indicated that morph determination results from acceleration (or retardation) of certain anatomical features. I hypothesized that morph determination is triggered by the presence of a potent accelerator of amphibian development occurring in the carnivore's prey: thyroid hormone (or its constituents). Omnivores exposed exogenously to thyroxine assumed the carnivore morphology within days. This endocrine response enables tadpoles to develop into the morph with the greater fitness since the rapidly developing carnivores are favoured in highly ephemeral ponds, which contain more shrimp. Carnivores also are more efficient predators of shrimp. This study thus links the underlying physiological causes of a polyphenism to the ecological factors that likely favour the occurrence of alternative morphs. More generally, this study illustrates how an endocrine signal may allow an individual to assess and continuously adapt to a changing environment.

Key-words: Phenotypic plasticity, *Scaphiopus multiplicatus*, trophic polyphenism, thyroxine

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Introduction

Polyphenism is the occurrence in a single population of multiple, discontinuous phenotypes produced from a single genotype in response to changing environmental stimuli (Mayr 1963). Examples include caste differentiation in social insects (Brian 1965), environmental sex determination (Bull 1983), seasonal heterophylly in plants (Lloyd 1984), many predator-induced polymorphisms (Dodson 1989), and certain trophic polymorphisms (Stearns 1989).

Despite the widespread occurrence of polyphenism (Shapiro 1976) the developmental and physiological processes mediating this phenomenon are largely unknown. Proximate causation often can be understood by studying functional significance. Theory predicts that the external cues triggering environmentally induced polymorphism should correlate with morph fitness (Levins 1968; Charnov & Bull 1977; Lively 1986a). For example, Lively

(1986b) found that certain barnacles develop either a typically shaped or a bent-shaped morphology, the latter being less susceptible to snail predation. The presence of the snail also induces the bent-shaped morphology (Lively 1986b). Polyphenism occurring in response to environmental cues that correlate with morph success also occurs in many plants (Harper 1977), bryozoans (Harvell 1984), *Daphnia* (Grant & Bayly 1981), gastropods (Crowl & Covich 1990), lepidopteran insects (Shapiro 1976; Greene 1989), fish (Meyer 1987), salamanders (Collins & Cheek 1983), many organisms with environmental sex determination (Charnov & Bull 1977), and many organisms that undergo metamorphosis (Wilbur & Collins 1973). The key point is that once the functional significance of environmentally induced polymorphism is identified the range of possible proximate causes can be narrowed.

In this paper, I examine the proximate basis of a major developmental polymorphism in a larval anuran. Larvae of at least three species of spadefoot toads (*Scaphiopus bombifrons* Cope, *S. intermontanus* Cope, and *S. multiplicatus* Cope) vary intraspeci-

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fically in morphology, development, and behaviour (Turner 1952; Bragg 1957; Orton 1954; Pomeroy 1981). Depending upon the pond, a varying percentage of tadpoles assumes one of perhaps three trophic forms (Pomeroy 1981). Carnivores are large, rapidly developing, solitary individuals that prey on fairy shrimp (anostracans) and tadpoles. Omnivores are small, more slowly developing, gregarious individuals that feed on detritus and algae. A possible third morph, intermediates, lies midway between the other two in size and developmental rate, but closer to omnivores in behaviour and feeding habits (Pomeroy 1981).

Carnivores are elicited in the laboratory by feeding young tadpoles shrimp or other tadpoles (Pomeroy 1981; Pfennig 1990). Using shrimp as a cue for morph determination is apparently adaptive. Carnivores have greater survivorship in rapidly drying ponds because they develop fast and are less likely to desiccate. Omnivores, by contrast, have greater survivorship in more slowly drying ponds probably because their more substantial lipid reserves enhance their chances of surviving the period immediately after metamorphosis (D.W. Pfennig, submitted for publication). Because shrimp density correlates negatively with pond longevity (Pfennig 1990), tadpoles can assess pond longevity indirectly by evaluating shrimp density. Carnivores are also more efficient than omnivores in preying on shrimp (Pomeroy 1981).

A more specific role of shrimp in morph determination is suggested by the observation that carnivores may be developmentally accelerated omnivores. Compared to similar-aged omnivores, carnivores have shorter guts and more concentrated melanophores (Pomeroy 1981). Both features characterize a larval amphibian approaching metamorphosis (Bagnara 1963; Carver & Frieden 1977). The developmentally accelerated nature of carnivores suggest that morph determination may involve the endocrine signal for rapid differentiation, thyroid hormone (Dodd & Dodd 1976). Tadpoles may acquire thyroid hormone or its constituent iodine through predation on tadpoles (which contain thyroxine, or tetraiodotyrosine [T_4]) and shrimp (which contain diiodotyrosine [T_2]; Ingbar 1981).

This study had two goals. First, are carnivores developmentally accelerated omnivores? I addressed this question by analysing the allometric relationships of features characterizing the variation. Second, does the presence of thyroxine, a potent accelerator of amphibian development, trigger morph determination? I addressed this question by experimentally manipulating an animal's exposure to thyroxine and noting its effects on morph determination.

My results are consistent with the notion that carnivores are more developmentally advanced than omnivores. Moreover, exposure of omnivores to

exogenous thyroxine can produce a carnivore. This response indicates a link between the functional and physiological bases of polyphenism in spadefoot tadpoles.

Materials and methods

MORPHOLOGY AND ALLOMETRY

S. multiplicatus from natural ponds and artificially deepened earthen stock tanks near Portal, Arizona, USA (Pfennig 1990) were studied. In the field, *S. multiplicatus* tadpoles occurred as three forms. One form — termed carnivores (Pomeroy 1981) because their guts contained shrimp and conspecifics — was larger, lighter in coloration, and had a notched keratinized oral beak. Another form — termed omnivores because their guts contained detritus — was smaller, darker in coloration, and had smooth keratinized mouthparts. Finally, a few tadpoles were intermediate in morphology. Before any morphological measurements were taken, each tadpole was categorized as to morphotype according to its keratinized mouthpart morphology and general body shape.

Five morphometric characters that were of taxonomic or functional morphological significance were measured: gut length (GL), m. interhyoideus length (IH, the primary buccal cavity depressor muscle), m. orbitohyoideus width (OH, the primary buccal cavity abductor muscle), snout to mid-eye length (SME), and snout to vent length (SVL). For OH, the width of the OH muscle was measured at its widest point (i.e. perpendicular to the muscle fibres). This distance is directly proportional to the force exerted by the muscle (Alexander 1985). For IH, the straight-line distance between lateral tips of both ceratohyal arms was measured parallel to the muscle fibres. A longer IH correlates with a widening of the ceratohyal, paired cartilages that underlie the floor of the buccal cavity. A long lateral lever ceratohyal arm (Wassersug & Hoff 1979) and a large orbitohyoideus (Satel & Wassersug 1981) enable a tadpole to generate a powerful suction to despatch macroscopic prey quickly. For SME, I measured the straight-line distance from the mid-point of a line bisecting both eyes to the anterior tip of the animal. Finally, for GL, the straight-line distance from the anterior manicotto to the cloaca was measured.

I plotted the frequency distribution of OH/SVL with all three 'morphs' combined to determine if the variation was continuous or discontinuous. I chose this character because variation between trophic morphs should relate to the functional morphology of the feeding apparatus. Finally, it was examined whether morphs shared common larval growth trajectories by comparing static allometric relationships of OH, SME, and GL as a function of SVL for a single cohort of tadpoles.

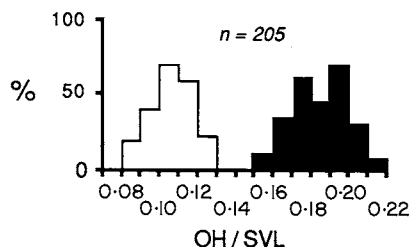


Fig. 1. Ratio of the width of the m. orbitohyoideus (OH) and snout to vent length (SVL) for 8-day-old carnivores (■) and omnivores and intermediates (□) from a single pond. This ratio is the single most diagnostic character of the overall phenotypic variation.

Previous work indicated that morph determination may be reversible (e.g. see Pomeroy 1981; D. Pfennig, submitted for publication). To test this several hundred 4-day-old animals of each morph were collected from a single pond. Forty live tadpoles of each morph were selected at random [Gosner (1960) stages 25–27]. Each animal was placed separately into a 250-ml water-filled cup. Half of the animals of each morph were fed fairy shrimp *ad libitum*. The other half were fed chow *ad libitum*. The animals were fed twice daily and their water replaced every 4 days. The cups were maintained at a constant 29°C and exposed to a natural photoperiod. After 2 weeks each animal was killed and its snout to vent length (SVL) and gut length (GL) were measured. I tested the null hypothesis that an animal could not change morphology.

PROXIMATE BASIS OF THE VARIATION

It was tested whether thyroxine induces morph transformation in *Scaphiopus* by collecting 144 3-day-old omnivores from a pond 13 km south-east of Portal. These animals were placed randomly in groups of 16 in nine different aquaria filled with 10 litres of dechlorinated tap-water and exposed to a 12h light:12h dark photoperiod at 23°C. The nine aquaria were divided into three treatment groups. Animals in three aquaria were fed shrimp from their natal pond *ad libitum*. Animals in three other aquaria were fed 5g of trout chow only. Finally, animals in three aquaria were fed 5g of pulverized trout chow plus 10mg l⁻¹ of dl-thyroxine. Pomeroy (1981) had previously found that older omnivores exposed to much lower levels of thyroxine (0.02–0.08mg l⁻¹) produced a change in jaw musculature in the direction of carnivores. A higher concentration of thyroxine was selected to see if exposure to this hormone would elicit the carnivore morphology completely. Animals were fed once only. The 5g of chow was fed *ad libitum*. I killed all animals in tricaine methanesulphonate at 8 days of age. On this day, 40 8-day-old omnivores and 40 8-day-old carnivores were collected from the pond in which the original animals were captured. Field-caught and laboratory-reared

animals were similar in developmental stage. The OH and SVL were then measured for each animal. The mid-point between the two modes of the OH/SVL frequency distribution for the wild-caught animals was used to distinguish carnivores from omnivores. The number of animals from each laboratory treatment that fell within the carnivore range of OH/SVL values was compared. I also contrasted OH/SVL among laboratory-reared animals from each diet treatment (i.e. chow only, chow+thyroxine, and shrimp only) by performing a one-way analysis of variance. I used Scheffé's *F*-test to compare treatment means. I conducted the ANOVA on angular transformed ratios.

Results

MORPHOLOGY AND ALLOMETRY

The frequency distribution of relative orbitohyoidean muscle width (OH) was discontinuous, with the upper mode comprising carnivores and the lower mode comprising omnivores and intermediates (Fig. 1). The three forms overlapped broadly in body size [as measured by snout to vent length (SVL); Table 1]. Carnivores were significantly larger, however, than omnivores and intermediates ($P < 0.05$, Scheffé's *F*-test for both comparisons). The SVL of intermediates fell entirely within the range of omnivores. Carnivores were the most developmentally advanced (i.e. closer to metamorphosis).

Carnivores and omnivores differed in growth trajectories. Allometric regressions of OH, SME and GL on SVL for both 4- and 14-day-old carnivores, intermediates and omnivores were significantly greater than zero, with the exception of OH on SVL for 14-day-old intermediates (Table 2). Slopes of all regressions for carnivores and omnivores were isometric (slope of one) with two exceptions. The allometric relationship between SVL and SME in 14-day-old carnivores was negative, whereas that between SVL and GL in 14-day-old omnivores was positive. For intermediates, OH displayed negative allometry and GL displayed positive allometry (as in omnivores; Table 2, Fig. 2a). A comparison of slopes and *y*-intercepts of each significant regression revealed that carnivores and omnivores differed significantly in the *y*-intercept for the regression of SME on SVL (Table 2).

Morph determination is not permanent (Fig. 3). Several 4-day-old field-collected omnivores became carnivores when reared on fairy shrimp. Conversely, when 4-day-old field-collected carnivores were reared on trout chow, an apparent regression toward the omnivore morphology occurred. This latter trend appears to represent an actual reversion to omnivory, and probably not a normal ontogenetic process that all carnivores undergo, since both carnivores and

Table 1. Means and standard errors of five morphometric characters in 14-day-old omnivore, intermediate, and carnivore morph *Scaphiopus multiplicatus* tadpoles from a single pond

Variable	Omnivores			Intermediates			Carnivores		
	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE
Gut length (GL)	32	201.72	9.2	18	174.39	12.82	29	101.28	5.17
M. interhyoideus length (IH)	32	7.18	0.18	18	7.63	0.16	29	10.08	0.34
M. orbitohyoideus width (OH)	32	1.73	0.11	18	1.80	0.09	29	3.40	0.20
Snout to mid-eye length (SME)	32	3.40	0.11	18	3.86	0.11	29	5.32	0.15
Snout to vent length (SVL)	32	15.60	0.38	18	15.88	0.28	29	17.46	0.51

omnivores were field collected from the same pond at the end of the experiment.

PROXIMATE BASIS OF THE VARIATION

Whether an animal develops into a carnivore or an omnivore may be hormonally mediated (Table 3, Fig. 4). Using data from wild-caught animals to determine the cut-off between carnivore and omnivore OH/SVL, over half (23 of 44) of the animals exposed to exogenous thyroxine would be classified as carnivores. All of the animals not treated with thyroxine were classified as omnivores ($\chi^2=44.19$, $P<0.0001$). Animals fed chow and thyroxine were morphologically indistinguishable from those fed shrimp (Table 3).

Discussion

In examining polyphenism three questions arise: (1) What is the nature of the variation (e.g. how many morphs are present)? (2) What is the adaptive significance of the variation? (3) What developmental and physiological processes underlie polyphenism? We can examine each question with respect to polyphenism in *Scaphiopus* tadpoles.

Scaphiopus tadpoles occur as two discrete morphs: carnivores and omnivores (Table 1, Fig. 1). Intermediates can be subsumed into the omnivore class (Table 1, Fig. 1). Allometric relationships of cranial musculature suggest that carnivores arise from an omnivore-like form through differential growth of selected features, especially those associated with cranial anatomy. For example, the y-intercept of snout to mid-eye distance (SME) on snout to vent length (SVL) for carnivores was significantly greater than that for omnivores (Table 2). Carnivore orbitohyoidean musculature (OH) initially exhibits strong positive allometry with body size and then exhibits isometry or negative allometry in later developmental stages (compare, e.g., slopes of regressions of OH on SVL for 4- and 14-day-old carnivores; Table 2). Growth disparities may produce a modified

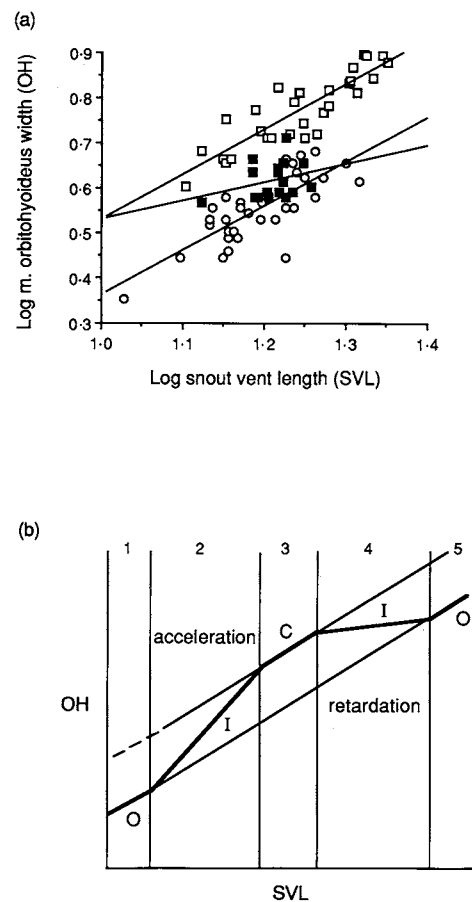


Fig. 2. (a) Allometric relationship of m. orbitohyoideus length (OH) and snout to vent length (SVL) for 14-day-old carnivore (\square), omnivore (\circ), and intermediate (\blacksquare) *Scaphiopus multiplicatus* tadpoles from a single pond. Parameters for the regression equations are given in Table 2. (b) Qualitative model of the developmental trajectories of OH as a function of overall body size (SVL) for carnivores (C), intermediates (I), and omnivores (O). When a young omnivore ingests shrimp (step 1), OH development is accelerated (2) and the animal assumes the carnivore morphology (3). If the intake of shrimp falls below some critical threshold, OH development is retarded (4) and the animal assumes the omnivore morphology (5). Individuals in the process of transforming from the two end morphs are intermediate in morphology (steps 2, 4). The static allometric regressions in Fig. 2a are represented in step 4.

Table 2. Parameters for the regressions of *m. orbitohyoideus* width, snout to eye length, and gut length on snout to vent length for 4- and 14-day-old tadpoles of each morph (data were log-log transformed before analysis). Tadpoles were samples from one cohort in a single pond

Age	$R^2 \pm SE$	Intercept	Slope $\pm SE$	P_1^*	P_2^\dagger
<i>M. orbitohyoideus</i> width					
Carnivores					
4-day-old	0.874 \pm 0.04	-0.586	1.118 \pm 0.085	0.0001	NS
14-day-old	0.765 \pm 0.04	-0.476 ^b	1.000 \pm 0.107 ^g	0.0001	NS
Omnivores					
4-day-old	0.515 \pm 0.08	-0.73	1.09 \pm 0.207	0.0001	NS
14-day-old	0.619 \pm 0.05	-0.67 ^b	1.018 \pm 0.146 ^g	0.0001	NS
Intermediates					
4-day-old	None detected	—	—	—	—
14-day-old	0.184 \pm 0.038	-0.02 ^a	0.518 \pm 0.273 ^h	0.0757	0.0001
<i>Snout to mid-eye length</i>					
Carnivores					
4-day-old	0.689 \pm 0.072	-0.68	1.141 \pm 0.153	0.0001	NS
14-day-old	0.804 \pm 0.029	-0.293 ^c	0.82 \pm 0.078	0.0001	0.0001
Omnivores					
4-day-old	0.754 \pm 0.051	-0.809	1.194 \pm 0.134	0.0001	NS
14-day-old	0.629 \pm 0.051	-0.738 ^d	1.062 \pm 0.15	0.0001	NS
Intermediates					
4-day-old	None detected	—	—	—	—
14-day-old	0.295 \pm 0.044	-0.386 ^e	0.809 \pm 0.313	0.0199	NS
<i>Gut length</i>					
Carnivores					
4-day-old	0.473 \pm 0.084	0.774	0.855 \pm 0.18	0.0001	NS
14-day-old	0.736 \pm 0.087	0.352 ^e	1.323 \pm 0.234 ⁱ	0.0001	NS
Omnivores					
4-day-old	0.49 \pm 0.102	0.624	1.348 \pm 0.269	0.0001	NS
14-day-old	0.64 \pm 0.071	0.445 ^e	1.551 \pm 0.212 ⁱ	0.0001	0.001
Intermediates					
4-day-old	None detected	—	—	—	—
14-day-old	0.375 \pm 0.11	-0.676 ^f	2.416 \pm 0.781 ^j	0.0069	0.001

* Probability value one (P_1) refers to the significance of the regression (Ho: regression slope=0);
 † Probability value two (P_2) refers to the significance of a test for isometry (Ho: regression slope=1).
 Mean values having different superscript letters were significantly different at $P < 0.05$.

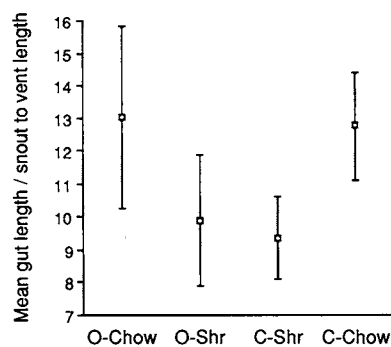


Fig. 3. Effects of diet on the development of the tadpole gut. Abbreviations: O-Chow, omnivore reared on trout chow ('normal' diet); O-Shr, omnivore reared on shrimp ('switched' diet); C-Shr, carnivore reared on shrimp (normal diet); C-Chow, carnivore reared on trout chow (switched diet). Mean gut length/snout to vent length in carnivores reared on shrimp differed significantly from that of carnivores and omnivores reared on trout chow ($P < 0.05$ Games-Howell multiple comparison test). Vertical lines: 95% confidence interval.

Table 3. Summary of a one-way analysis of variance on the effects of diet on orbitohyoidean muscle development (OH/SVL; ratios were arcsine-square root transformed before analysis)

Source of variation	df	MS	F	P
Between group	2	0.041	113.956	0.0001
Within group	129	0.001		
Residual	131			

Treatment	n	OH/SVL
Chow only	44	0.101 (0.002) ^a
Shrimp only	44	0.135 (0.002) ^b
Chow + thyroxine	44	0.140 (0.002) ^b

Means (SEM) of the untransformed data are shown below the ANOVA table. Mean values having different superscript letters were significantly different at $P < 0.05$ (Scheffé's F-test).

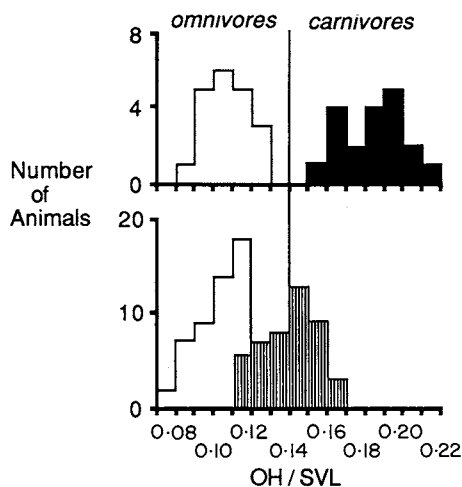


Fig. 4. Effect of thyroxine exposure on morph differentiation. Upper graph=ratio of the width of the m. orbitohyoideus (OH) and snout to vent length (SVL) for 8-day-old carnivores (■) and omnivores and intermediates (□) from a single pond. Lower graph=the same ratio for 8-day-old tadpoles, half of which were exposed to trout chow and exogenous thyroxine (▨) and half of which were exposed to trout chow only (□) for 4 days starting at 4 days old.

cranium in facultatively carnivorous salamanders (Pierce *et al.* 1983) and cichlid fishes (Meyer 1987).

I hypothesize that intermediates are a transient group of individuals transforming from one morph to the other. Unlike omnivores and carnivores, intermediates displayed strong allometry for every character. Morph determination is reversible (Pomeroy 1981; Fig. 3). As illustrated in Fig. 2b, an omnivore undergoing acceleration of OH development eventually would resemble a carnivore; a carnivore undergoing retardation of OH development eventually would resemble an omnivore. Older intermediates probably transformed from carnivore to omnivore, which is consistent with the observation that gut contents of these older intermediates are similar to that of omnivores (Pomeroy 1981). This ability to change morphology and more efficiently utilize different food types (Pomeroy 1981) should enable tadpoles to respond adaptively to an environment in which food types and levels change dramatically (Loring, MacKay & Whitford 1988; Pfennig, Mabry & Orange 1991).

PHYSIOLOGICAL BASIS OF MORPH DETERMINATION

In the Introduction, it was argued that understanding functional significance can clarify proximate causation. Pond longevity differentially selects for carnivores and omnivores: carnivores have higher survivorship than omnivores in highly ephemeral ponds, whereas the opposite is true in longer duration ponds (D.W. Pfennig, submitted for publica-

tion). One therefore might expect pond longevity to affect morph determination. *S. multiplicatus* tadpoles appear to be unable to assess pond longevity directly, however, since pond drying regime does not affect morph expression (Pfennig 1990). There is a cue that correlates with pond longevity that tadpoles apparently can evaluate: the density of shrimp and other tadpoles correlates positively with pond longevity (Pfennig 1990). Carnivores also are more efficient predators on these prey (Pomeroy 1981). Experiments have shown that the ingestion of shrimp or tadpoles, a predictor of the success of the carnivore morph, does indeed trigger the carnivore morphology (Pomeroy 1981; Pfennig 1990).

How might prey ingestion trigger morph differentiation? When fed the diet of the alternative morph, *Scaphiopus* tadpoles assumed the characteristic gut length to snout to vent length ratio of the alternative morph (Fig. 3). Gut length in anurans may be influenced by food particle shape or composition (Yung 1904; Babák 1905). Food particle size does not seem to explain the transition from a carnivore to an omnivore since it is difficult to see how variation in food size alone can explain, e.g., the carnivore's accelerated developmental rate and more concentrated melanophores. Moreover, animals fed large food particles (1000–2000 µm) do not assume a morphology different from those fed smaller food particles (100–500 µm; Pfennig 1989). The larger and more rapidly developing carnivore morph is also unlikely to result simply from ingestion of high quality food. Tadpoles fed trout chow (46% protein) fail to become carnivores, whereas those fed shrimp (~6% protein) can become carnivores (Pomeroy 1981; Pfennig 1990). The transition from an omnivore to a carnivore appears to be a concerted developmental change. Such changes are frequently under hormonal control (Hardie & Lees 1985).

The developmentally accelerated nature of the carnivore suggests that morph determination may occur through the action of the endocrine signal for rapid differentiation, thyroid hormone. Tadpoles may acquire thyroid hormone or its precursors (iodine and tyrosine) through predation on shrimp or tadpoles.

These results indicate that the presence of a thyroid hormone, thyroxine, is sufficient to induce morph differentiation in *Scaphiopus* (Table 3, Fig. 4). Whether thyroxine is necessary to induce this change is unclear. Premature presence of thyroxine may occur through endogenous effects, such as thyroid hyperfunctioning, or through exogenous effects, such as intake of thyroxine or its constituent iodine. Transition to a carnivore morph may occur when a tadpole accumulates sufficient stores of iodides or iodinated tyrosine from the tissues of conspecifics or shrimp. Even minor fluctuations in circulating levels of thyroxine may have profound influences on morph differentiation. In a typical

anuran (*Rana catesbeiana*), plasma thyroxine levels are exceedingly low ($<50\text{ ng }100\text{ ml}^{-1}$) during premetamorphosis (Regard, Taurog & Nakashima 1978), and even during the height of metamorphic climax thyroxine levels do not exceed $0.5\text{ }\mu\text{g }100\text{ ml}^{-1}$ (Regard *et al.* 1978).

The ingestion of shrimp or conspecifics may induce morph transition in at least three ways. First, an influx of iodine may cause hyperfunctioning of the thyroid and, as a consequence, morph transformation. If the appropriate stimulus is present, plasma thyroxine may increase or tissue sensitivities to thyroxine may change. Precocious presence of thyroxine is probably more critical than modification of tissue sensitivities since most larval tissues become reactive to thyroxine before significant amounts of thyroxine are normally available (Dodd & Dodd 1976). Second, exogenous thyroxine may act directly on target tissues, thereby inducing transformation. Third, thyroxine may act as a kairomone by stimulating a neural mechanism (unrelated to the thyroid or its targets), which then triggers morph transformation. Future studies will focus on discriminating among these three mechanisms of morph differentiation. Regardless of the precise mechanism of morph determination, this study links an endocrine cue to the selective factors favouring polyphenism.

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