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Temporal shift of diet in alternative cannibalistic morphs of the tiger salamander

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Abstract

Evolutionary theory predicts that alternative trophic morphologies are adaptive because they allow a broad use of resources in heterogeneous environments. The development of a cannibal morphology is expected to result in cannibalism and high individual fitness, but conflicting results show that the situation is more complex. The goal of the present study was to increase our understanding of the ultimate benefits of a cannibalistic polyphenism by determining temporal changes in the feeding habits and biomass intake in a population of tiger salamanders (*Ambystoma tigrinum nebulosum*). Cannibals in this species develop a larger head than typicals and have prominent teeth, both useful for consuming large prey. Although cannibalism was only detected in cannibal morphs, large temporal variation in resource partitioning was found between morphs. The two morphs always differed in their foraging habits, but cannibalism mainly occurred immediately after the ontogenetic divergence between morphs. Cannibals shifted their foraging later to a more planktivorous diet (i.e. the primarily prey of the typical morph). Cannibals also obtained more prey biomass than typicals. These results indicate that the cannibalistic morph is advantageous over the typical development, but that these advantages vary ontogenetically. Although the results obtained are consistent with models predicting the maintenance of cannibalism polyphenism in natural populations, they show that the foraging tactics utilized by cannibal morphs, and the fitness consequences accrued by such tactics, are likely to be more complex and dynamic than previous studies have suggested.

Keywords *amphibian; cannibalism; feeding; niche; polymorphism; predation; trophic polyphenism*

INTRODUCTION

Cannibalism is ubiquitous throughout much of the animal kingdom and can provide both nutritional (e.g. energetic) and ecological (reduced intraspecific competition) benefits (Crump, 1992; Elgar & Crespi, 1992; Manica, 2004; Wissinger et al., 2004). Cannibalism is well known in many species of fishes (Manica, 2004) and amphibians (Lannoo, Lowcock & Bogart, 1989; Crump, 1992; Denoël & Andreone, 2003) that prey on eggs and small larvae of their own species, sometimes leading to alternative ontogenetic pathways, such as the elaboration of specialized trophic structures (Polis, 1981). In amphibians, 'cannibal' morphotypes diverge from 'typical' morphs by developing prominent teeth and a larger head (Lannoo & Bachmann, 1984; Pedersen, 1991; Collins, Zerba & Sredl, 1993; Nishihara, 1996; Sheen & Whiteman, 1998). These alternative morphologies are particularly common in salamander larvae such as *Ambystoma tigrinum* (Lannoo & Bachmann, 1984) and Hynobius retardatus (Wakahara, 1995).

The development of alternative phenotypes, including polyphenisms, polymorphisms, and alternative behavioural or physiological traits, are of special interest to evolutionary biologists because they permit the existence of new traits without eliminating established ones (West-Eberhard, 2003). They are considered to be steps towards speciation events (Bush, 1994; Via, 2001), but are also valuable options per se (Roff & Fairbairn, 1991; Denoël, Poncin & Ruwet, 2001). Disruptive selection is particularly expected in heterogeneous environments in which each alternative can be favoured in response to complex trade-offs between costs and benefits (Skulason & Smith, 1995; Schlichting & Pigliucci, 1998; Denoël et al., 2002).

The cannibalism polymorphism in salamanders is an example of phenotypic plasticity because alternative morphs are environmentally induced (Loeb, Collins & Maret, 1994; Maret & Collins, 1994; Hoffman & Pfennig, 1999; Michimae & Wakahara, 2001; Whiteman et al., 2003). The presence of conspecifics is a key-factor in the exhibition of the alternative phenotypes (Loeb et al., 1994; Michimae & Wakahara, 2001), but cannibalism may also have evolved to favour ingestion of large heterospecific prey (Hoffman & Pfennig, 1999; Whiteman et al., 2003). A variety of other factors appear to be involved, including density (Michimae & Wakahara, 2001), tactile contact with prey (Hoffman & Pfennig, 1999), kinship (Pfennig & Collins, 1993; Michimae & Wakahara, 2001), prey availability (Loeb et al., 1994), and population size structure (Maret & Collins, 1994). The benefits of cannibalism rely mainly on fast growth rates (Lannoo & Bachmann, 1984; Wakano, 2004), which allow larvae to metamorphose before pond drying (Lannoo & Bachmann, 1984), acquire a larger size, and thus, perhaps, accrue higher fitness (Semlitsch, 1985; Nishihara, 1996). However, morphological specialization and associated cannibalism is costly because of the risk of eating relatives (Pfennig & Collins, 1993), being infected by pathogens (Pfennig, Loeb & Collins, 1991; Pfennig & Hoffman, 1998), and being more vulnerable to large predators (Wakano, 2004).

In most studies on this polyphenism, cannibal morphs primarily ate conspecifics, with other prey items making up a smaller proportion of their diet (Collins & Holomuzki, 1984; Lannoo & Bachmann, 1984; Loeb et al., 1994; Maret & Collins, 1997; Whiteman et al., 2003). Resource partitioning was obvious with the typical morph almost never consuming conspecifics but rather feeding on heterospecific prey that were less used by cannibals (Collins & Holomuzki, 1984; Lannoo & Bachmann, 1984; Loeb et al., 1994; Whiteman et al., 2003). However, cannibal morphs are not always cannibalistic: some individuals appear to specialize on heterospecific prey, such as tadpoles (Loeb et al., 1994; Maret & Collins, 1997). Because the degree of cannibalism can depend on the relative density of conspecific vs. heterospecific prey (Loeb et al., 1994; Maret & Collins, 1997; Michimae & Wakahara, 2001; Whiteman et al., 2003), ontogenetic shifts in foraging behaviour may occur. It is of primary interest to find out whether cannibal morphs are obligatorily cannibalistic or whether they shift their diet with time. In this respect, Whiteman et al. (2003) predicted that, because consuming a conspecific is more beneficial than eating heterospecific prey, cannibals should forage preferentially on conspecifics as long as they are readily available (i.e. at densities high enough to make them profitable). To understand the adaptive benefits of this trophic polyphenism (i.e. cannibalism vs. typical morphology), it is thus important to determine the foraging consequences to each morph in terms of dry mass intake. Although many studies have focused on the diet of the alternative morphs, none have addressed this topic. The aim of the present study was thus to explore the dietary habits of the alternative morphs of a polyphenic salamander over time and to measure the dry mass of ingested prey. It was predicted that cannibals should preferentially consume conspecifics, and thus gain a significantly higher dry mass of prey than typical morphs.

MATERIAL AND METHODS

The study took place at Kettle Pond 6 (‘K6’), a natural glacial kettle located at 2890 m elevation, 2 km south of Gothic (Gunnison County, Colorado, USA; UTM: 0328-4312). The pond is approximately 22 × 46 m, with a maximum depth of 60 cm, and is surrounded by open meadows. K6 is temporary and dries almost every year during summer (H. H. Whiteman, unpubl. data). However, the water level was quite stable during the study period (water decrease of 10 cm). The pond is inhabited by a population of tiger salamander *Ambystoma tigrinum nebulosum* Gehlbach, 1967 (Amphibia, Caudata, Ambystomatidae), which exhibits the cannibalistic polyphenism (Sheen & Whiteman, 1998).

This population was sampled four times at 1-week intervals (29 June to 20 July 2004). Salamander larvae were collected by dip-netting the pond. Twenty typical and 20 cannibal morph larvae were collected during each period. Salamanders were maintained in individual buckets (16 cm in diameter) filled with fresh water to avoid aggression or cannibalism during the handling of larvae. The salamanders were stomach-flushed to collect prey items. The procedure consisted of introducing a plastic catheter into the oesophagus and then injecting water into the stomach, which pushes the prey out of the mouth (Joly, 1987). Each salamander was measured with a digital caliper (snout–vent length; precision of 0.01 mm) and weighed on an electronic scale (precision of 0.01 g).

Prey were identified under a stereoscopic microscope. Each prey item was classed in a different functional category: salamander larvae, plankton, ostracods, chironomid larvae, aquatic hemipterans, other aquatic insect larvae (caddisfly, damselfly, dragonfly, mayfly, and dysticid larvae), aquatic mollusks, and terrestrial invertebrates. The total length of all the prey was measured with a precision of 0.1 mm. After this procedure, the stomach contents of each salamander were weighed on an electronic scale with a precision of 0.1 mg and then dried at 48 °C for 24 h to obtain dry mass.

A multivariate analysis of variance was used to test for an effect of time, morph, and their interaction on diet, size selective predation, and dry mass. The Bonferonni procedure was used to account for experiment-wise error rate. To determine size-selective predation, the mean length of each prey was calculated for each salamander. All values were transformed appropriately before analysis to reach normality (log10 for continuous data, square root + 0.5 for counts). Alpha was set at 0.05 and all tests were two-tailed (Sokal & Rohlf, 1995; Statsoft-France, 2000). Prey niche overlap between morphs was calculated using Schoener’s (1970) index:

$$C = 1 - 0.5\left(\sum_i |p_{xi} - p_{yi}|\right)$$

where p_{xi} is the proportional utilization of prey type i by morph *x*, and p_{yi} the proportional utilization of prey type *i* by morph *y*. The index ranges from 0 (no prey in common) to 1 (all prey in common).

RESULTS

Diet

There was a significant effect of morph (multivariate analysis of variance: Wilk’s $\lambda = 0.443$, $F_{8,145} = 22.808$, $P < 0.001$), time ($\lambda = 0.227$, $F_{24,421} = 11.754$, $P < 0.001$) and their interaction ($\lambda = 0.567$, $F_{24,421} = 3.787$, $P < 0.001$) on the stomach content of salamanders. The two morphs differed in the consumption of salamanders [analysis of variance (anova); $P < 0.001$], chironomid larvae ($P < 0.001$), mollusks ($P < 0.01$), and terrestrial invertebrates ($P < 0.05$) (Table 1; Fig. 1). The diet of salamanders varied through time for all prey types (ANOVA: all $P < 0.01$), except terrestrial invertebrates ($P = 0.59$) (Table 1).

Only cannibal morphs preyed on conspecifics (a maximum of one or two individuals per stomach), but this difference between morphs was significant only for the two first sampling sessions. During this time, an average of 0.75 salamanders were present in

Table 1 Effect of time, morph, and their interaction on the stomach contents of salamanders (two-way analysis of variance)

Prey	Effect	*F*	*P*
Salamander	Time	9.629	< 0.001
	Morph	70.286	< 0.001
	Time x Morph	8.081	< 0.001
Plankton	Time	56.835	< 0.001
	Morph	2.076	0.15
	Time x Morph	3.362	< 0.05
Ostracods	Time	6.407	< 0.001
	Morph	0.095	0.76
	Time x Morph	0.761	0.52
Chironomid larvae	Time	4.031	<0.01
	Morph	73.480	< 0.001
	Time x Morph	2.165	0.09
Other aquatic insect larvae	Time	14.422	< 0.001
	Morph	2.897	0.09
	Time x Morph	2.479	0.06
Mollusks	Time	29.931	< 0.001
	Morph	5.345	< 0.05
	Time x Morph	7.664	< 0.001
Hemipterans	Time	16.171	< 0.001
	Morph	1.979	0.16
	Time x Morph	2.929	< 0.05
Terrestrial invertebrates	Time	0.644	0.59
	Morph	4.590	< 0.05
	Time x Morph	1.266	0.29

the stomach of cannibals (Bonferonni test, $P < 0.001$; Fig. 1). The cannibalistic diet shifted between the second and third week (Bonferonni test, $P < 0.001$) with cannibals having on average four times fewer salamanders in their stomach than during the first 2 weeks. Cannibal morphs that foraged on conspecifics had similar amounts of heterospecific prey in their stomach compared to cannibals that did not have salamander prey in their stomach (week 1: $F_{1,18} = 1.216$, $P = 0.29$; week 2: $F_{1,18} = 0.074$, $P = 0.79$; week 3: $F_{1,18} = 2.164$, $P = 0.16$; week 4: $F_{1,18} = 1.856$, $P = 0.19$).

The two morphs differed significantly in their predation on plankton only during the fourth week (Bonferonni test, $P < 0.05$), when this prey was most abundant in the stomachs of both morphs (Fig. 1). At this time, typical morphs consumed twice as much plankton as the cannibal morphs. Very few planktonic crustaceans were present in stomachs of either morph during the first 2 weeks, but the number of plankton in stomachs increased between the second and third study week, with a larger increase between the third and fourth week. However, this time difference was significant only in the typical morphs (Bonferonni test, $P < 0.05$ for the second–third week transition and $P < 0.001$ for the third–fourth week transition). No significant differences were found between morphs and among time for the predation of ostracods (Bonferonni test, $P > 0.05$). Typical morphs ingested more chironomid larvae than the cannibal morphs in all of the first three study weeks (Bonferonni test, at least $P < 0.01$), but no significant difference between morphs was found during the last week for this prey type. Predation on chironomid larvae did not change with time in typicals, but a significant increase was found in cannibals between the second and third week (Bonferonni test; $P < 0.01$). The two morphs did not differ in foraging on aquatic insect larvae. However, temporal differences in diet were found in cannibals between weeks 2 and 3, and in typicals between weeks 3 and 4. The two morphs preyed differently on mollusks during the fourth week only (Bonferonni test; $P < 0.001$). Typical morphs ingested approximately three-fold more mollusks than cannibal morphs. The temporal increase in this prey was significant only for the typical morphs between the third and fourth study weeks. A large significant temporal increase of foraging on aquatic hemipterans was found in cannibals between the second and third weeks (Bonferonni test; $P < 0.01$), but only a marginal difference was found between morphs on the third week ($P = 0.05$). No significant differences between morphs and across time were found for the terrestrial invertebrates in the diets.

Dietary niche overlap between morphs (in terms of prey number) increased with time from 0.57 in the first week to 0.74 in the second, to 0.91 in the third, and to 0.94 in the fourth week (Table 2). Salamanders constituted between 0.1% and 3.7% of the diet of cannibals, but 0% of that of typicals. Plankton represented the largest part of the diet: from 27% to 86% in typicals and from 13% to 83% in cannibals (Table 2).

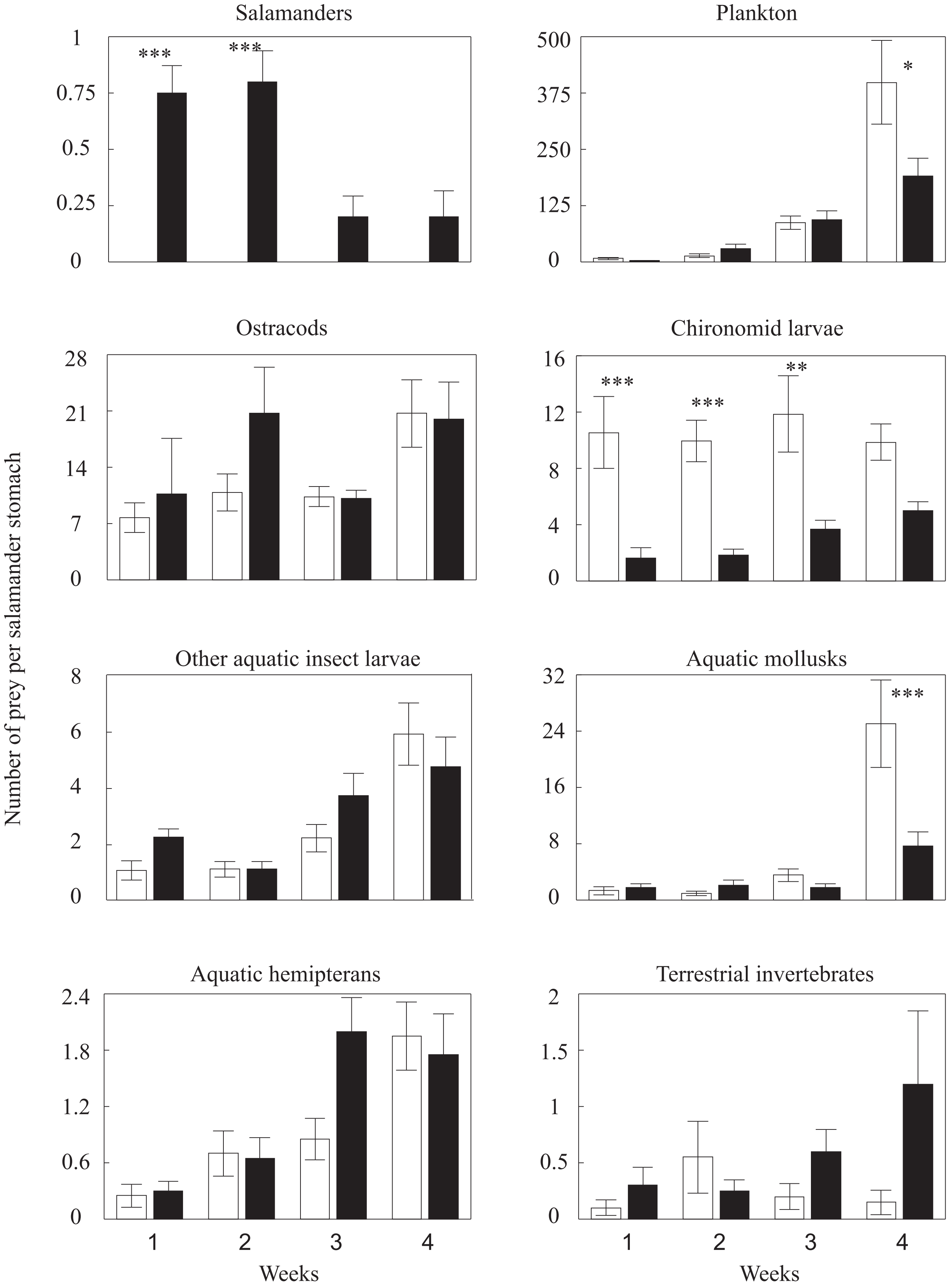
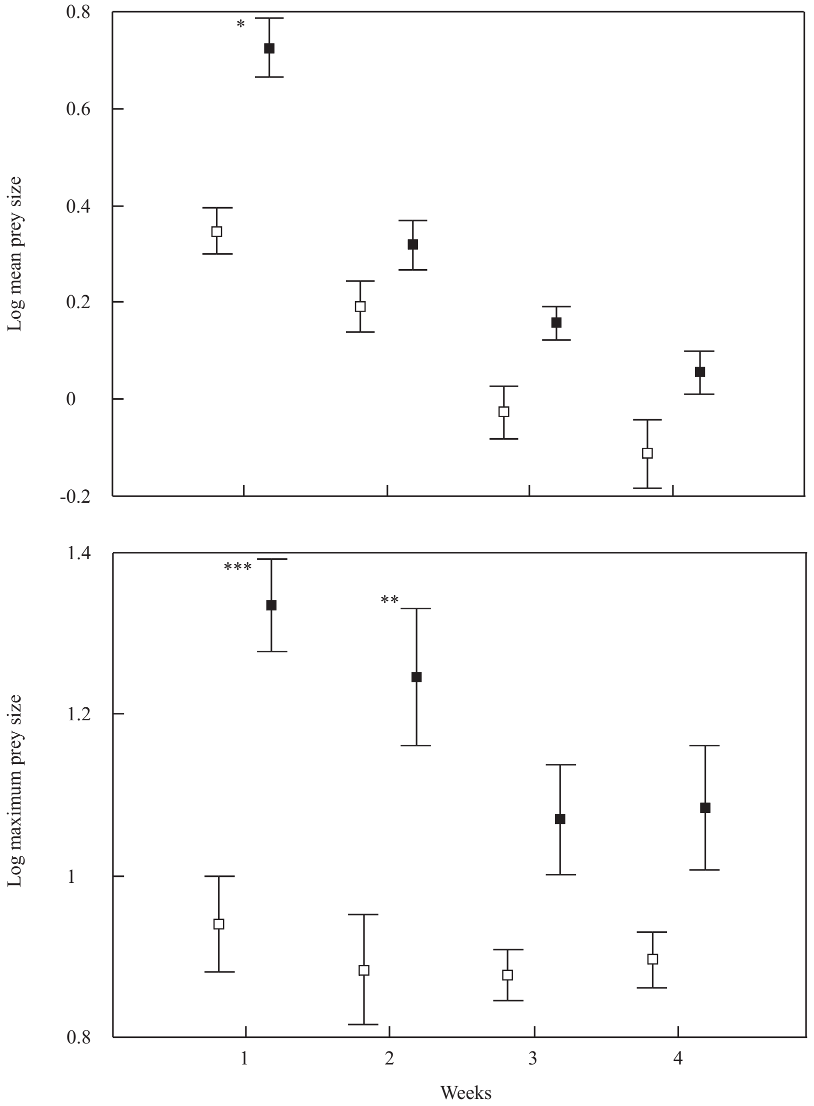


Figure 2 Mean ± SE number of prey per stomach in typical (open bars) and cannibal (full bars) morphs of the tiger salamander. *$P < 0.05$, **$P < 0.01$, *$P < 0.001$ (multivariate analysis of variance: Bonferonni test). More detailed statistical results are provided in Table 1. $N = 20$ in each group.

Table 2 Mean proportions of prey by typical (T) and cannibal (C) larvae and prey niche overlap (Schoener's index) between morphs on each date

Weeks	Morph	Salamanders	Plankton	Ostracods	Chironomid larvae	Other aquatic insect larvae	Mollusks	Aquatic hemipterans	Terrestrial invertebrates	Index
1	T	0	0.275	0.267	0.363	0.036	0.046	0.009	0.003	0.57
	C	0.037	0.132	0.522	0.081	0.110	0.088	0.015	0.015	
2	T	0	0.361	0.288	0.263	0.029	0.025	0.019	0.015	0.74
	C	0.014	0.521	0.361	0.032	0.019	0.037	0.011	0.004	
3	T	0	0.751	0.089	0.102	0.019	0.030	0.007	0.002	0.91
	C	0.002	0.810	0.087	0.032	0.032	0.015	0.017	0.005	
4	T	0	0.862	0.045	0.021	0.013	0.054	0.004	0.000	0.94
	C	0.001	0.825	0.086	0.022	0.021	0.033	0.008	0.005	

Figure 2 Size-selective predation in typical (open squares) and cannibal (full squares) morphs of the tiger salamander across time: mean ± SE of the logarithm of the mean and maximum length of prey (analysis of variance: Bonferonni test). $N = 20$ in each group (except for typical on week 2 for which $N = 19$).



Size -selective predation

Time ($F_{3,151} = 42.408$, $P < 0.001$), morph ($F_{1,151} = 11.604$, $P < 0.001$), and their interaction ($F_{3,151} = 3.309$, $P < 0.05$), had a significant effect on the mean prey size contained in salamander stomachs (Fig. 2). The cannibal morph consumed, on average, larger prey than the typical morphs during the first study week (Bonferonni test; $P < 0.05$), but no significant differences were found at the other dates. After the first week, the mean prey size of cannibals significantly decreased (Bonferonni test; $P < 0.001$).

Time ($F_{3,151} = 2.9$, $P < 0.05$) and morph ($F_{1,151} = 40.8$, $P < 0.001$) had a significant effect on the

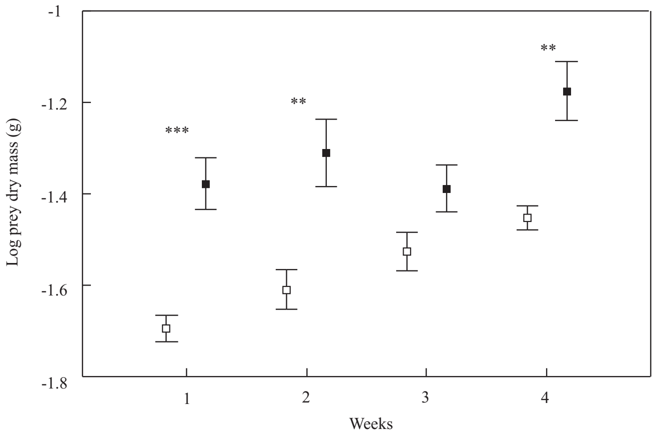


Figure 3. Dry mass of the stomach contents of typical (open squares) and cannibal (full squares) morphs of the tiger salamander. $^{**}P < 0.01$, $^{***}P < 001$ (analysis of variance: Bonferonni test). $N = 20$ in each group.

longest prey present in the stomach of the salamanders. The interaction between these two factors was not significant ($F_{3,151} = 1.5$, $P = 0.21$; Fig. 2). In this analysis, the two morphs significantly differed during the two first weeks, with cannibals preying on larger items than typicals (Bonferonni test; at least $P < 0.01$). Within each morph, no significant differences were found over time (Bonferonni test, $P > 0.05$).

In both typicals and cannibals, there was a significant effect of salamander snout–vent length on the mean size of the prey in stomachs (Typicals: $R^2 = 0.216$, $F_{1,77} = 21.223$, $P < 0.001$; Cannibals: $R^2 = 0.066$, $F_{1,78} = 5.542$, $P < 0.05$), but not on the maximum length of the prey (Typicals: $R^2 = 0.0002$, $F_{1,77} = 0.001$, $P = 0.97$: Cannibals: $R^2 = 0.00003$, $F_{1,78} = 0.003$, $P = 0.96$). When time was included in the model, both time ($F_{3,75} = 25.109$, $P < 0.001$) and salamander length ($F_{1,75} = 5.619$, $P < 0.05$) had a significant effect on the mean prey length of cannibals. However, in typicals, only time had a significant effect (Salamander length: $F_{1,74} = 1.75$, $P = 0.19$; Time: $F_{3,74} = 11.296$, $P < 0.001$). In every case, mean prey length decreased with time. The mean ± SE snout–vent length of cannibalized salamanders was 26.5 ± 1.4 mm (range 13.7–38.1 mm). Length of salamander prey was not significantly related to the length of the cannibal ($R^2 = 0.111$, $F_{1,18} = 1.988$, $P = 0.18$).

Dry mass of ingested prey

Time ($F_{3,152} = 6.755$, $P < 0.001$) and morph ($F_{1,152} = 51.663$, $P < 0.001$), but not their interaction ($F_{3,152} = 1.277$, $P < 0.28$), had a significant effect on the dry mass of stomach contents (Fig. 3). Cannibals had a higher intake of invertebrates in terms of dry mass than the typicals in three out of the four study weeks (Bonferonni test; at least $P < 0.01$). The only temporal difference in ingestion quantity was between the first and last weeks in typicals ($P < 0.01$).

DISCUSSION

The results of the present study show that the morphological cannibalistic polyphenism in salamanders does not necessarily lead to a cannibalistic diet and that cannibals can be opportunistic feeders on a variety of prey, including small planktonic organisms. This is in contrast with most previous studies that considered that large prey, particularly conspecifics, are the main prey of cannibals, whereas small prey such as plankton are the main food of typicals (Collins & Holomuzki, 1984; Lannoo & Bachmann, 1984; Loeb et al., 1994; Whiteman et al., 2003). Such variation has important implications for our understanding of the causes and consequences of trophic polyphenisms.

Trophic polyphenisms are expected to facilitate resource partitioning and to be favoured in the presence of open niches (Skulason & Smith, 1995). The data on cannibal and typical morphs from the present study are in accordance with these predictions. Only cannibals ingested conspecifics. By contrast, typical morphs ate more aquatic mollusks, plankton, and chironomid larvae. From a general point of view, these results are in accordance with previous field studies (Collins & Holomuzki, 1984; Lannoo & Bachmann, 1984; Whiteman et al., 2003) and show that resource partitioning between trophic morphs is a generalized pattern. Notably, all previous diet analyses stressed the diet specialization of cannibals on conspecifics and that of typicals on small heterospecific prey. Adopting a cannibalistic ontogenetic pathway allows larvae to use an underexploited resource and may then favour coexistence through the shift to a higher trophic level (Skulason & Smith, 1995; Tokeshi, 1999). However, only competition experiments can test the hypothesis that morphological divergence is a response to competition for resources in the presence of an open niche. In support of this hypothesis, Maret & Collins (1997) showed that the advantage of developing the cannibal phenotype is highest when competition among larvae is most intense.

Collins & Holomuzki (1984) and Whiteman et al. (2003) reported that almost all cannibals consumed conspecifics and salamanders constituted a large part of the diet in terms of gut fullness (62–96%). By contrast, Loeb et al. (1994) showed that salamanders constituted a less important part of the diet in terms of gull fullness (5%). The only study that provided values on proportional abundances (i.e. in terms of numbers of prey, not volume) found that salamanders constituted a large part of the diet (11%) (Lannoo & Bachmann, 1984). Although, cannibalistic behaviour was observed in the cannibal morph in the present study, conspecifics represented only 0.1–4% of the diet, and changed temporally. During the first 2 weeks, a large proportion of the cannibals preyed on conspecifics, with an average of 0.8 salamander prey per individual. At that time, typicals foraged more on small prey such as chironomids, but not plankton. Later in the summer, the pattern totally shifted. Most of the cannibals lacked salamander larvae in their stomachs at the time of sampling (on average, 0.2 salamander prey per individual). Instead, they mainly foraged on other prey, especially plankton, which were several orders of magnitude more abundant (> 100 per stomach) compared to other studies (0.2 per stomach, Lannoo & Bachmann, 1984; 0 per stomach, Collins & Holomuzki, 1984; almost 0 per stomach, Whiteman et al., 2003). Although typicals still ate more plankton than cannibals, it is apparent that, in contrast to other studies, cannibals do not necessarily avoid small prey items that are presumably less profitable than large prey. As a consequence, resource overlap was large: from 0.54 to 0.94. Such varied patterns may reflect a lack of temporal sampling in most of the previous studies or be the result of different specializations among populations. It would be interesting to compare the diet of the two morphs across both time and populations. Some preliminary data are provided by Maret & Collins (1997). These authors found shifts in the diet in several populations, but their results are in opposition to those of the present study because the young cannibals that they sampled had a more planktivorous diet than the old ones. Such differences may be a result of the size structure of their population. Maret & Collins (1997) found very small cannibals (2–3 cm snout–vent length) whereas the smallest cannibals in the present study were approximately 4 cm in length. Such a size difference may have reduced cannibalism in their populations because the small mouth opening of young larvae may have precluded the ingestion of conspecifics. Another explanation may come from the advantage of eating conspecifics over heterospecific prey (Whiteman et al., 2003), which increases with prey size. When salamander prey are small, the advantage of eating a conspecific vs. a heterospecific prey may be minimal. But, as salamander prey grow, the advantages become substantial in terms of mass intake (Whiteman et al., 2003).

Size differences between individuals are expected to favour niche segregation through predation on different sized individuals (Hutchinson, 1959). Such a pattern was found in caudate amphibians (Joly & Giacoma, 1992; Denoël & Joly, 2001; Denoël & Andreone, 2003), including tiger salamanders (Leff & Bachmann, 1986), but no cannibals were examined in these studies. The results of the present study partly support the predictions of Hutchinson (1959). Cannibals had a mean prey size and a maximum prey size larger than typicals, but significant differences were only found early in the study period. The low intermorph difference comes from the high consumption of plankton by typicals and the shift from a cannibalistic to heterospecific foraging in cannibals.

The absence of intraspecific predation may be due to a behavioural decision rather than a purely probabilistic situation (Pfennig et al., 1994). Yet it is surprising that individuals do not opt for a high biomass intake if available. Several reasons might explain this pattern (Crump, 1992). First, the benefit of cannibalism can differ with time, specifically with the individual size of salamanders. Slowly growing larvae that do not grow fast enough may be at risk of being too small to undertake metamorphosis when the pond dries (Lannoo & Bachmann, 1984). In addition, small larvae can be preyed upon by those who have reached a larger size (Lannoo & Bachmann, 1984; Maret & Collins, 1997; present study). By adopting a cannibalistic behaviour and morphology, larvae can thus increase their body size and reduce their mortality due to cannibalism or desiccation (Lannoo & Bachmann, 1984). The high cannibalism rate early in the summer is in accordance with this pattern. When cannibals have reached a large body size (> 60 mm snout–vent length), which most did at the third study week, they probably do not face these risks because they have reached a size at which predation is minimal and one that surpasses the minimum size for metamorphosis. At this time, benefits might be exceeded by the costs of cannibalism, especially eating kin (Pfennig & Collins, 1993) and contracting disease (Pfennig et al., 1991).

To understand the maintenance of alternative feeding habits and associated polyphenisms, it is essential to determine their specific benefit (Denoël et al., 2002). One way to estimate such benefits is too compare the dry mass of ingested prey between morphs. Although such analyses have been conducted for other trophic polyphenisms (e.g. facultative paedomorphosis; Denoël et al., 2002), no such data were available for cannibalism in salamanders. Our data revealed that cannibals had higher biomass intake than typicals in three of the four sample periods, supporting the idea that even when consuming plankton, the cannibal morphology provides advantages over the typical morphology.

Alternative ontogenetic pathways are expected to allow individuals to improve their fitness in heterogeneous environments (Skulason & Smith, 1995; West-Eberhard, 2003). Although polyphenisms are potential steps toward speciation through sympatric conditions, the maintenance of intraspecific variation within a species represents a valuable option as long as the benefits are larger than the costs (Denoël et al., 2001; West-Eberhard, 2003). The results obtained in the present study extend previous studies on this polyphenism by showing that foraging behaviour of each morph varies temporally, and that the benefits of the cannibalistic morph go beyond the act of cannibalism per se. More in-depth studies are needed to better understand temporal shifts in cannibalism and its outcome on individual growth and fitness. In particular, laboratory or field experiments could be used to test our hypotheses on the proximate and ultimate mechanisms affecting such temporal shifts.

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