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Changes in food availability mediate the effects of temperature on growth, metamorphosis and survival in endangered yellow spotted mountain newt: implications for captive breeding programs

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Abstract: The effects of temperature and food levels on body size, growth rate, time to metamorphosis and survival were studied in larval and post-metamorphic juvenile endangered yellow spotted mountain newts *Neurergus microspilotus* (Caudata: Salamandridae), which were hatched and reared in a captive breeding facility. We designed a 2 × 3 factorial experiment in which larvae were raised either at high and low temperature (15 ℃ and 18 ℃) of conspecifics and fed either a high, medium and low level of food. The experimental results showed that growth and development rates of *N. microspilotus* were influenced by interaction of temperature and food levels. Larvae raised at the high food level and high temperature exhibited earlier metamorphosis and the greatest snout to vent length (SVL) compared with individuals raised at relatively low food level and low temperature. Over the experimental period, larval growth rate was highest and survival lowest at the high temperature. Our data suggest that in larvae grown at relatively low temperature, the metamorphosis time was significantly longer compared with individuals raised at relatively high temperature. At both low and high temperature, larval growth rates increased with increasing food levels, and the increase was fastest at high food level compared to medium and low food regimes. Larvae exhibited the greatest mean growth rate for SVL (0.41 mm/days) at high food level and high temperature. Information obtained from current experiment could improve the productivity of newts in captive breeding facilities to ensure the release of adequate numbers of individuals for reintroduction programs.

Key words: *Neurergus microspilotus*; temperature; food levels; growth; development; survival

Introduction

Growth and sexual maturation are important life history traits of different organisms and the study of juvenile growth and development in search of basic empirical information on the relationships between growth variables and individual fitness has long been of interest for a range of biological disciplines (Wells 2007). In many species of amphibians, both size and age at metamorphosis are important variables because these factors directly affect survival rate, reproductive output and dispersal ability (Cabrera-Guzmán et al. 2013). The larvae and post-metamorphic juveniles of many species of amphibians cannot change their aquatic environment until metamorphosis is completed. In these amphibians variation in age and size during metamorphosis is a reflection of the interactions between biotic and abiotic factors and is linked to the plasticity in metamorphic events especially in those that develop in ephemeral ponds and streams. As a result, the lower and upper limits to the length of the larval period and body size at metamorphosis are important amphibian life history traits (e.g. Wilbur & Collins 1973; Smith 1987).

Various biotic and abiotic factors have been reported to influence the rates of growth and development including the duration of the larval period and size at metamorphosis of amphibians (Wilbur 1980; Werner 1986; Rose 2005). These include biotic factors such as larval density (Newman 1998; Wildy et al. 2001), presence of predators (Laurila & Kujasalo 1999; Lardner 2000), quantity of available food (Wildy et al. 2001; Warburg 2009; Ogilvy et al. 2012; Dugas et al. 2013; Cothran et al. 2015), and abiotic factors such as type of water level (Maciel & Junca 2009), ultraviolet (UV) radiation (Blaustein et al. 2001) and water temperature (Stahlberg et al. 2001; Browne & Edwards 2003; Hickerson et al. 2005; Sanuy et al. 2008; Smith et al. 2015). Many researchers have shown a strong relationship between growth rate and temperature (Castańeda et al. 2006; Bancroft et al. 2008; Goncalves et al. 2012; Zhang et al. 2014; Bellakhal et al. 2014). Other has shown that growth may depend on quality and quantity of food (Webb & Merritt 1987; Álvarez & Nicieza 2002a; Enriquez-Urzelai et al. 2013; Bellakhal et al. 2014). Temperature is considered as the most important proximal cause of variation in size and age at metamor-

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phosis. While low temperatures retard differentiation, quality and quantity of the food over the larval period have important effects on the time and size at metamorphosis. As a result, interaction between temperature and food availability can cause acceleration or deceleration of the developmental stage at which food levels are changed. However, most often the net outcome of low resource levels is metamorphosis delay (e.g. Crump 1981; Alford & Harris 1988; Newman 1994; Tejedo & Reques 1994, Zhang et al. 2014; Bellakhal et al. 2014; Courtney Jones et al. 2015). In recent years captive breeding and subsequent re-introduction of amphibian species has increased attention to growth and metamorphosis as expanded knowledge of reproduction of endangered species has conservation significance (Fischer & Lindenmayer 2000; Canessa et al. 2014; Sharifi & Vaissi 2014).

Knowledge of how interactions between temperature and food availability influence larval growth, metamorphosis and survival may also be of value to amphibian conservation because the ability to generate large numbers of individuals is critical in any captive breeding programs. Captive breeding and reintroductions to the wild have become an important tool in recent species conservation programs (Frankham et al. 2010) because amphibians are declining faster than any other vertebrate group and for threatened species, the recommended recovery action is captive breeding and reintroduction (Stuart et al. 2004; Gascon et al. 2007). With some 32% of amphibian species threatened with extinction, there is an urgent need for various tools to address the global amphibian crisis (Stuart et al. 2004; IUCN 2011). Although captive breeding facilities and their associated reintroduction activities have been established for various endangered amphibian species (Stuart et al. 2004; Gascon et al. 2007), there have been reports of many captive breeding inability to generate large numbers of healthy individuals. Courtney Jones et al. (2015) have indicated three major reasons for this shortcoming: avoiding various demographic and genetic side effects of small population size (Earnhardt et al. 2001), reduction of the cost of captive breeding (Canessa et al. 2014; Tarszisz et al. 2014) and providing larger number of "success predictor" of reintroduction programs (Armstrong & Seddon 2008; Tarszisz et al. 2014).

While the independent and interactive effects of various environmental factors on growth and development in various species of anurans are well established (Sanuy et al. 2008; Inatsuchi et al. 2010), surprising, there remains a very limited understanding of how these factors may influence growth and metamorphosis of caudate species. The main focus of the present study is to investigate the effect temperature, and interactions between food availability and temperature, on growth, survival and development in *N. microspilotus*. We also discuss the significance of our findings in relation to ecological factors in the area.

Material and methods

Species

The yellow spotted mountain newts, *Neurergus microspilotus* (Nesterov, 1916), live in the mid-Zagros range in western Iran and eastern Iraq, where the climate is cold and moist with long winter freezing at high elevation (1250–2000 m a.s.l.) and warm and dry with no winter freezing at lower elevations (500–750 m a.s.l.). This species spawns in mountain streams, and hatchlings appear in early May to mid-June (Sharifi & Assadian 2004). Most larvae metamorphose in small, ephemeral streams into terrestrial juveniles by late autumn of the same year (Sharifi & Assadian 2004). This species is listed as critically endangered by IUCN. There are several threatening processes that may have contributed to the decline of this species. These include habitat loss and alteration, water abstraction, disease and stream drying as results of climate change (Sharifi et al. 2009).

In 2010, a conservation management plan was developed and implemented for the critically endangered yellow-spotted mountain newt by financial assistance of the Mohamed bin Zayed Species Conservation Fund. Part of this plan included the development of a captive breeding facility at Razi University, Kermanshah, Iran. The ultimate goal of this captive breeding program was to provide stock and increase the species' population size across different breeding streams to ensure their long-term survival. This captive breeding program has been successful, with the captive population size increasing each year, including newts from a stream that was previously assumed locally extinct (Sharifi & Assadian 2004; Sharifi & Vaissi 2014) and also a trial release reintroduction demonstrating that post-metamorphic captive-bred *N. microspilotus* released into the wild can survive to the second growing season. This trail reintroduction also provided a choice of life stage for a reintroduction plan (Sharifi & Vaissi 2014).

Experimental design

A 2 × 3 factorial design was employed to examine the effects of temperature and food quantity on larval and post-metamorphic juvenile growth [snout to vent length (SVL)], survival and the time metamorphosis completed. The parent *N. microspilotus* (3 females and 4 males) had been collected from Kavat Stream (35°21′ N, 46°24′ E) in April 2013. We selected approximately 110 eggs and placed them in an aerated aquarium (75 × 25 × 40 cm). We then selected 72 visually similar size larvae at age 2-week in late June 2013. We housed them in 72 single bowls (11 cm in diameter, 492 cm^2 containing 400 ml of water). The larvae were fed by blood worms (*Glycera dibranchiata*) and maintained under a natural light regime. Our experiment began on 3rd July 2013 and involved a 2 × 3 factorial design, crossing two levels of temperatures with three levels of food. Larvae were raised in one of six treatments: (1) high temperature/high food (HT × HF), (2) high temperature/medium food (HT × MF), (3) high temperature/low food (HT × LF), (4) low temperature/high food (LT × HF), (5) low temperature/medium food (LT × MF) and (6) low temperature/low food (LT × LF). In order to prevent cannibalism and inhibit the effect of density on growth, each treatment was replicated twelve times for a total of 72 single bowls.

As has been reported in Sharifi & Assadian (2004), the yellow spotted mountain newt is distributed in two distinct climatic regimes in highland streams in the Mid-Zagros Range and some streams in steppes of the northern

Table 1. Summary statistics of analysis of effects of temperature and food levels on the length of snout to vent (SVL in mm), growth rate and coefficient of determination (R^2) for SVL of *N. microspilotus* larvae and post-metamorphic juveniles.

Temperature	Food Levels	Mean ± SD (2 weeks)	Mean ± SD (44 weeks)	Growth rates (mm/days)	R^2	P
HT (18 ℃)	HF	14.79 ± 2.73	36.96 ± 2.06	0.41	0.88	0.05
	MF	15.36 ± 2.28	32.08 ± 1.88	0.30	0.83	
	LF	15.12 ± 1.77	30.36 ± 1.13	0.29	0.90	
LT (15 ℃)	HF	14.4 ± 1.42	34.26 ± 1.03	0.39	0.88	0.02
	MF	15.17 ± 1.86	29.07 ± 1.61	0.26	0.81	
	LF	15.18 ± 1.31	26.98 ± 1.44	0.24	0.97	

Explanations: HT – high temperature; LT – low temperature; HF – high food; MF – medium food; LF – low food.

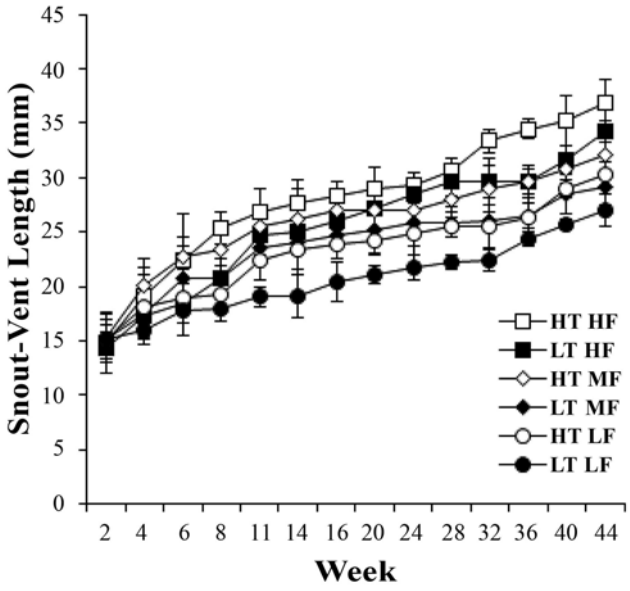

Fig. 1. Average and standard deviation of the snout to vent length (SVL) for larval and post-metamorphic juvenile *N. microspilotus* in high temperature (HT) and low temperature (LT) at high (HF), medium (MF) and low (LF) food levels.

Mesopotamian lowlands. We chose water temperature conditions as reported in these two areas. Temperature regimes consisted of 15 ℃ and 18 ℃ for the low and high temperature, respectively. For the first three months, larvae in the low food treatments were given five blood worms each. In the medium food treatments the larvae were given 15 and in the high food treatments 30 blood worms per larva. As larvae grew, after month three the amount of food increased to eight blood worms in the LF, 20 blood worms in the MF and 40 blood worms in the HF treatments. Larvae were fed every two days and the bowls were cleaned of food leftovers 2.5 h after feeding, and filled with fresh dechlorinated tap water. As test animals reached metamorphosis (i.e., complete gill reabsorption) they were removed from their bowls and metamorphosis time was recorded in days. Growth rate in the larval period was measured by the slope of a linear regression line between time and SVL. The experiment ended after 44 weeks. Measurements were performed at weeks 2, 4, 6, 8, 11, 14, 16, 20, 24, 28, 32, 36, 40, 44.

Photography

Photographs were taken with a digital camera (Sony, DSC-HX9V, 3.6V) on a tripod at a fixed height (30 cm). The newts were put in a petri dish which was located over a latticed paper. Immediately after photography the newts were released into their bowl. All pictures were analyzed using AUTOCAD software 2014 (downloaded free from the Internet: http://getintopc.com/softwares/3d-cad/autocad-2014-free-download-setup/). We measured the snout to vent length (SVL). SVL were calculated by measuring the length of a line drawn down the center of the specimen from the tip of the snout to the point where the hind limbs arise.

Statistical analysis

Univariate analysis of variance (ANOVA) was used to examine the effects of temperature and food level on growth, metamorphosis and survival of the test animals. For each response variable, we calculated bowls means for the animals in each treatment and used these means for all statistical analyses. Post hoc comparisons (Tukey tests) were used to check for differences between means for the six treatments. The statistical program package SPSS (v. 16) was used for all analyses.

Results

Effects of food availability and water temperature on larvae and post-metamorphic juvenile size

Size in larval and post-metamorphic juvenile *N. microspilotus* was influenced by food levels and temperature. Post-metamorphic juveniles, 44 weeks old, exhibited the greatest means of SVL (36.96 ± 2.06 mm) at high food levels and high temperature, followed by the high food/low temperature (34.26 ± 1.03 mm), medium food/high temperature (32.08 ± 1.88 mm), medium food/low temperature (29.07 ± 1.61 mm), low food/high temperature (30.36 ± 1.13 mm) and low food/low temperature treatments (26.98 ± 1.44 mm) (Fig. 1, Table 1). At both low and high temperature, larval growth rates increased with increasing food levels, and the increase was fastest (i.e., the slope was steeper) for high food than medium and low food levels. Larvae and post-metamorphic juveniles exhibited the greatest mean growth rate for SVL (0.41 mm/days, Table 1) at high food levels and high temperature. The results of ANOVA indicated that larvae and post-metamorphic juveniles responded differently with respect to size, depending on the levels of temperature and food at which they were reared. At both high and low temperature, larvae and post-metamorphic juveniles were significantly larger at high food levels than those at the medium and low food levels; individuals reared at low

Table 2. Summary statistics of analysis of variance (ANOVA) for effects of temperature and food levels on snout-vent length, survival and metamorphosis.

Source of variation	F	df	P
Snout-vent length			
Temperature	5.44	1	0.02
Food	6.98	2	0.001
Temperature × food	3.89	5	0.001
Survival			
Temperature	19.98	1	0.01
Food	0.07	2	0.92^{NS}
Temperature × food	56.06	5	0.01
Metamorphosis			
Temperature	3.92	1	0.04
Food	3.96	2	0.02
Temperature × food	2.79	5	0.01

Explanations: NS – non-significant.

Table 3. Numbers of larvae (N) metamorphosed over time in different temperature and food level regimes.

Time (weeks)	HT × HF ($N = 12$)	HT × MF ($N = 12$)	HT × LF ($N = 12$)	LT × HF ($N = 12$)	LT × MF ($N = 12$)	LT × LF ($N = 12$)
12	–	–	–	–	–	–
19	4	2	1	–	–	–
20	3	1	–	–	–	–
23	2	1	–	1	–	1
25	2	1	1	2	–	–
26	–	2	–	1	1	–
31	–	2	–	2	1	–
32	–	–	1	3	1	1
34	–	–	1	1	2	1
35	–	–	1	2	2	1
37	–	–	1	–	1	2
38			1	–	2	2
40	–	–	2	–	2	1
43	–	–	–	–	–	1
44				–	–	1
%Metamorphosed	91.66	75	75	100	100	91.66

Explanations: High temperature/high food (HT× HF), high temperature/medium food (HT× MF), High temperature/low food (HT× LF), low temperature/high food (LT× HF), low temperature/ medium food (LT× MF), low temperature/low food (LT× LT).

food levels were the smallest (Table 1). Food levels experienced during larval life had significant effects on the size (SVL) ($P \leq 0.001$). Different rearing temperatures caused a significant difference ($P \leq 0.02$) in the size (SVL). Combined effect of food level and temperature had strong effect on the size (SVL) ($P \leq 0.001$) (Table 2).

Effects of food availability and water temperature on larval development

Metamorphosis began on week 19 when seven of 72 (9.72%) larvae completed the process. All these larvae belonged to the high temperature treatment. The numbers of larvae metamorphosed over time are shown in Table 3. All larvae in the high food/high temperature treatment finished metamorphosis in 25 weeks. The longest time (44 weeks) of metamorphosis was observed in the low food/low temperature treatment. The results of ANOVA indicated that larvae responded differently with respect to time of metamorphosis, depending on

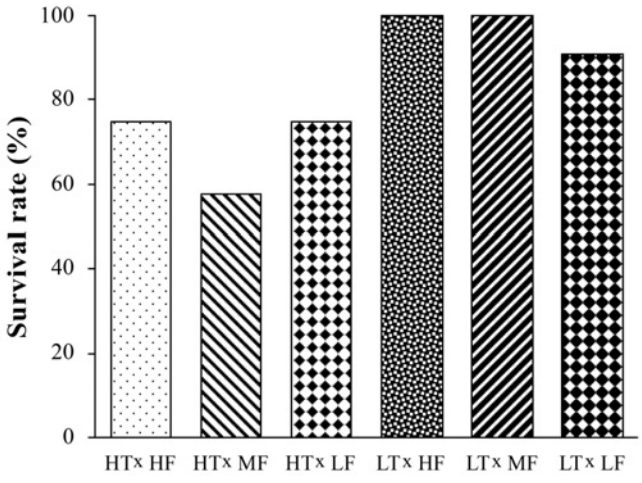

Fig. 2. Survival rate (%) for larval and post-metamorphic juvenile *N. microspilotus* in high temperature (HT) and low temperature (LT) at high (HF), medium (MF) and low (LF) food levels at end experiment.

the levels of temperature and food at which they were reared (Table 2). Food levels experienced during larval life had strong effects on the time of metamorphosis ($P \leq 0.02$). Different rearing temperatures also caused a significant difference ($P \leq 0.04$) in the time of metamorphosis (Table 2). The combined effect of food level and temperature on the time of metamorphosis was significant ($P \leq 0.01$) (Table 2).

Effects of food availability and water temperature on larvae and post-metamorphic juveniles survival

Survival in all treatment groups was high (100%) until week 10. By week 44, survival rate was lowest in the high temperature/medium food (58.33%) and highest in the low temperature/high food (100%) and low temperature/medium food (100%) treatments (Fig. 2). Survival of *N. microspilotus* larvae and post-metamorphic juveniles during the 44 weeks of the experimental period significantly differed at different water temperatures ($P < 0.01$), but not between treatment groups with different food availability ($P = 0.92$). There was significant interaction between food availability and water temperature ($P < 0.01$) (Table 2).

Discussion

The aim of the present study was to investigate effects of food availability and water temperature on larval and post-metamorphic juvenile growth, development and survival in the yellow spotted mountain newts. Variation in temperature was found to impact larval growth, with smaller growth rate at lower temperature and higher growth rate at higher temperature. Furthermore, changes in food availability mediated the effects of increasing water temperature on survival as higher mortality was observed at higher temperature. Specifically, the larval and post-metamorphic juvenile size was smaller in conditions where food availability was low. Since all fertilized eggs used in the present experiment belonged to a clutch of three females and four males, we should expect that intrinsic features resulting from genetic quality of different individuals have bearings on the variables of growth and development in larvae and post-metamorphic juveniles. Such differences in survival and growth among various members of a single cohort may have been under influence of differences in parental genetic quality (Sheldon et al. 2003) as has been reported in anurans (Sheldon et al. 2003; Dziminski & Roberts 2006; Dziminski et al. 2008).

The effects of food levels and the interaction between temperature and food levels are not fully known in urodeles. Growth rate is expected to increase with increasing water temperature, because temperature regulates metabolism, growth and differentiation in ectothermic species (e.g., Takahashi et al. 2012; Peck et al. 2012; McLeod et al. 2013). These results follow a general rule for ectotherms as differentiation rates are more responsive to temperature than growth rates (Smith-Gill & Berven 1979; Álvarez & Nicieza 2002a; Bellakhal et al. 2014). A shift towards a higher food or more energetic food is expected to cause faster growth, therefore allowing for both shorter larval periods and the increase in metamorphic size (Pandian & Marian 1985). Increase in food uptake may also cause an extended larval period to exploit the rapid growth opportunity (Wilbur & Collins 1973). Our data suggest that growth and development rates of *N. microspilotus* are influenced by both temperature and food levels. As expected, *N. microspilotus* metamorphosed at an older age when reared at low temperature. Food levels also influenced growth rates of *N. microspilotus*, and increased growth rates resulted in shorter developmental period.

Present experimental results showed that in larvae and post-metamorphic juveniles grown at the relatively low temperature the time to metamorphosis was significantly prolonged compared with individuals grown at the relatively high temperature. Temperature had significant effect but food level did not influence the survival. However, combined effect of temperature and food level had significant effect on the survival. The impact of water temperature on metamorphic timing and body size at metamorphosis is similar to the temperature effects seen in other amphibian larvae (Álvarez & Nicieza 2002a). For example, the time to metamorphosis was prolonged in larval anurans such as *Discoglossus galganoi* (Capula, Nascetti, Lanza, Bullini & Crespo, 1985), *Bufo calamita* (Laurenti, 1768), *Pelophylax saharicus* (Boulenger in Hartert, 1913) and *Limnodynastes peronii* (Duméril & Bibron, 1841), when grown at low temperatures compared with individuals grown at relatively high temperature (Álvarez & Niciezaa 2002a; Sanuy et al. 2008; Bellakhal et al. 2014; Courtney Jones et al. 2015).

Food availability has been proved to affect larval developmental rates in several anuran and caudate species. In most cases, enhanced growth conditions result in faster development (Leips & Travis 1994; Kohmatsu et al. 2001; Hickerson et al. 2005; Álvarez & Nicieza 2002a; Bellakhal et al. 2014; Courtney Jones et al. 2015). Hickerson et al. (2005) showed that metamorphic timing or the larval period in *Desmognathus quadramaculatus* (Holbrook, 1840) was affected by food. In the same way, high food levels accelerated metamorphosis in *D. ochrophaeus* (Cope, 1859) (Beachy 1995) and in *Hemidactylium scutatum* (Temminck & Schlegel, 1838) (O'laughlin & Harris 2000). In our study, food levels influenced growth rates of *N. microspilotus*, and increased growth rates resulted in shorter developmental period. The results of ANOVA revealed strong interaction between food and temperature on SVL of larvae. In any case, in conjunction with the results presented in another study (Álvarez & Nicieza 2002b), our data suggest that selection of either the thermal habitat or the diet could allow larvae to have some control on their future performance in the terrestrial and aquatic environment.

Mortality in the juvenile life stages of amphibians is typically high (Canessa et al. 2014) and it is difficult to make generalizations about the effects of experimental treatments on growth, development and

survival. Several experimental studies found that survival decreased in the treatments with the highest temperature (Randall et al. 2009; Courtney Jones et al. 2015) and food availability (McLeod et al. 2013). Various mechanism have been put forward for higher mortality at high water temperature including decreased dissolved oxygen availability (O'Connor et al. 2007; Blaustein et al. 2010), higher metabolic rate (Hulbert et al. 2007), the build-up of microbes from decomposing food (McWilliams 2008), nitrogenous waste products (Morey & Reznick 2004) or changes in the intensity of competition (Blaustein et al. 2010; Enriquez-Urzelai et al. 2013; McLeod et al. 2013). In the present study, the long-term food availability treatment reduced the effects of the water temperatures, with higher survival at high food availability and decline in survival at the lowest food availability.

The effects of increasing temperature on larval amphibians may include a reduction in time to metamorphosis, a decrease in size at metamorphosis, or both. Moreover, the effects of temperature on the development may interact with other factors such as food availability (Álvarez & Nicieza 2002a) and hydroperiod (Loman 2002). Exposure to higher temperatures shortens the larval period in many species (Morand et al. 1997). This pattern of accelerated development has been observed in both anurans (Voss 1993; Álvarez & Nicieza 2002a) and urodels (Beachy 1995; Hickerson et al. 2005). Shorter larval periods can increase chances of survival in environments such as ephemeral ponds and streams by increasing the chance of successful emergence from a water body that is drying. For many species, however, a reduction in larval period also results in metamorphosis at a smaller size (Morand et al. 1977; Wilbur & Collins 1973; Werner 1986). This pattern suggests a likely trade-off between rate of development and growth, which might be exacerbated by temperature increases change.

Our finding about changes in food availability mediating the effects of temperature on *N. microspilotus* growth, development and survival has implications for amphibian conservation. The yellow spotted mountain newts as a temperate-zone stream-breeding species, experiences marked fluctuations in temperature and food availability over extended developmental periods. We assume that improving our knowledge of the effects of interactions between environmental factors on growth, development and survival of amphibians might improve the success of management of threatened amphibian species when they are in captive breeding facilities. The present findings suggest that managers of captive breeding facilities might benefit from manipulating both food availability and temperature (Courtney Jones et al. 2015) and avoid breeding such species in constant environmental conditions. Courtney Jones et al. (2015) have suggested that individuals with stochastic food availability at lower temperatures may improve individual survival and the likelihood of generating large numbers of tadpoles in the striped marsh frog, *Limnodynastes peronii* (Duméril & Bibron, 1841). Such ability could help the recovery plans for a target species by improving the sustainability of a captive population (Canessa et al. 2014) and also by ensuring the release of large numbers of individuals for reintroduction programs (Armstrong & Seddon 2008).

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